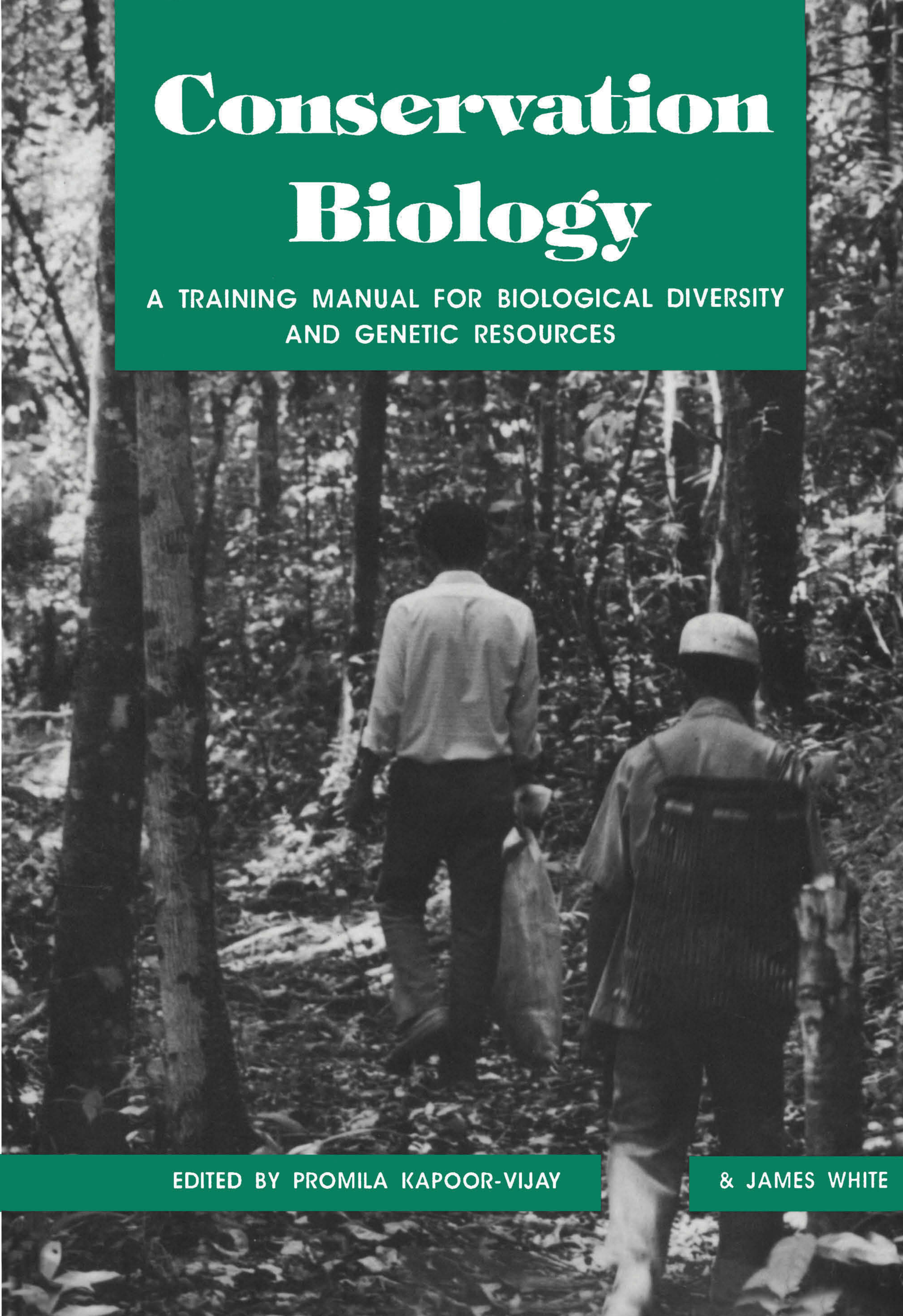
Conservation Biology

A TRAINING MANUAL FOR BIOLOGICAL DIVERSITY AND GENETIC RESOURCES



EDITED BY PROMILA KAPOOR-VIJAY & JAMES WHITE

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A TRAINING MANUAL FOR BIOLOGICAL DIVERSITY AND GENETIC RESOURCES

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FOREWORD

The world is confronted with the need for producing more food both from land and water as well as other agricultural commodities under conditions of shrinking arable land and fresh water resources and expanding biotic and abiotic stresses. Future increases in productivity will also have to be achieved in an ecologically sustainable manner, if further damage to the ecological foundations for sustainable agriculture is to be avoided. In addition, we should start anticipatory research designed to assist in meeting potential changes in climate, sea level and ultraviolet-B radiation. It is in this context that the conservation and sustainable utilisation of biological diversity assume importance. Rapid progress in biotechnology has made it clear that future agricultural progress will be driven by biological findings.

Accelerated research on the development of biological software, such as new crop strains, biofertilizers and biopesticides, is essential for sustainable agriculture. Such a *Biological Software for Sustainable Agriculture* programme should include the following components:

1. Containment of genetic erosion and promotion of genetic conservation through appropriate *in situ* and *ex situ* methods.
2. Evaluation of genetic material and development of specialised gene pools for breeding for tolerance to biotic and abiotic stresses and for potential changes in temperature, precipitation, sea level and ultraviolet-B radiation, and development of computerised information systems.
3. Establishment of genetic enhancement centres where new and novel genetic combinations can be produced and be made available to grassroot-level plant and animal breeders.
4. Linking genetic enhancement centres with genetic conservation centres and 'hot spot' screening locations.
5. Standardisation of procedures for assessing the biosafety and food safety aspects as well as the environmental impact of new biological processes and products.
6. Assessment of the role of intellectual property rights and gene patenting on national research, and international cooperation relating to national and global food security.
7. Capacity-building through training and techno-infrastructure development.
8. Sustained and adequate financial support for genetic conservation, evaluation and utilisation.

To implement the above research and developmental agenda, so very vital for achieving sustainable advances in biological productivity, we need not only funds, but even more importantly 'committed and skilled people', as aptly emphasised by Dr. Promila Kapoor-Vijay in her thought-provoking introduction to this timely and extremely valuable publication.

This publication is comprehensive in its scope, covering both scientific and public policy aspects. It is an invaluable aid to those engaged in imparting training in the conservation and sustainable management of biological diversity. We owe a deep debt of gratitude to the Commonwealth Science Council, editors Dr. Promila Kapoor-Vijay, Dr James White and all the authors of this Training Manual for their important and timely contribution to a topic of supreme importance in achieving the goal of improving the quality of human life within the carrying capacity of supporting ecosystems.

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INTRODUCTION

PROMILA KAPOOR-VIJAY

We are today looking for ways and means of redressing the stress constantly being put on our fragile ecosystem. In our fight to preserve our environment and, therefore, ourselves, conserving biodiversity has come to be recognised as a key strategy for dealing effectively with the environmental decline that stares us in the face. If we can ensure the survival of species, the world can look forward to new and improved foods, new drugs and medicines and new raw materials for industry. Indeed, preservation of genetic variability of the globe will provide us with a vital tool with which to adapt to climatic change and other forms of environmental decline. To implement this strategy, urgent action is needed to conserve our existing biodiversity. Research, training and information management all help expand the human capacity to do so. Our efforts in conservation can succeed only if people understand the distribution and nature of biodiversity, see how it figures in their own lives and aspirations, and know how to manage bioresources to meet human needs without diminishing biodiversity. This capacity is not adequate today: resource managers are not trained in conservation techniques to conserve biodiversity; the number of taxonomists specialising in tropical species needs to be increased ten times; no tropical country has a complete listing of its species; and for most ecosystems little information exists on indicator or key species. Under-investment in biodiversity conservation accounts for these gaps.

Committed and skilled people are the key to the success of the programme on Conservation of Biodiversity and Genetic Resources. Increased funding, international convention, expanded protected-areas systems – all will be ineffective unless the pool of trained human talent for biodiversity conservation is adequately augmented. More and more people need to be trained in techniques needed for biodiversity conservation, and financial and intellectual incentives are required to ensure that they work where necessary, primarily in the field. Biodiversity conservation in the coming years will require a large cadre of 'biodiversity professionals', the people who will manage protected areas, draw biodiversity inventories, develop and safeguard existing collections, and manage such biological resources as forests, fisheries and agricultural lands. The need to train these people is particularly urgent in developing countries. All these professionals will require training in conservation biology.

To optimise biodiversity conservation, far more individuals must be trained *in situ* and *ex situ* conservation and its integration with wider gene pool conservation. Universities in both developed and developing countries, along with gene banks, agriculture, forestry and environment research centres, etc. could help training centres which build personnel capacity for biodiversity conservation. Greatly expanded

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training is also required for both professionals and para-professional conservation biologists.

Training centres therefore need to be established or expanded, curricula updated, and international cooperation and support enhanced. Biodiversity cannot be adequately conserved unless the loss of habitat outside identified areas is slowed down and resources managed with biodiversity conservation as an objective. It has been acknowledged that there is a dearth of experts having knowledge of the simple techniques and methods used for the study of conservation of biological diversity and genetic resources, especially in the tropical environments, both at the trainer and field-extension level. There are no clearly defined courses or educational materials which can be used for the training of trainers and trainees at local level. Subjects like techniques for herbarium development, taxonomy, ethnobotany, conservation biology, tissue culture, biotechnology, basic to the authentication, documentation, maintenance and conservation of species, need urgent and serious attention.

A major impediment to the success of any programme for conserving biodiversity is the virtual absence of any formal training in this field. There are no degree-level programmes providing documented resources available for effective training at research and implementation levels. The transfer of technology for conservation and its rate of diffusion is affected adversely by poor communication between theoreticians and field-oriented scientists. There are several issues to be resolved and addressed at political, social and philosophic levels. Three principal challenges that face us over the short to medium term are:

(a) strengthening of financial and institutional support for training and education in the area of conservation of biodiversity and genetic resources;

(b) strengthening the contacts with related natural resources experts in the academic world and in the field, and at grass-root level;

(c) strengthening contacts with resource allocators.

The Commonwealth Science Council's project on *Biological Diversity and Genetic Resources* has focused, in phase I of the project, on conservation and rational utilisation of indigenous plant resources with promising economic potential in agriculture, forestry, fisheries, wildlife, industry and environment protection (CSC Status Report 1992). It has been accepted that there is an urgent need to develop inexpensive techniques enabling study, use, maintenance and conservation of biodiversity and genetic resources. The International Workshop on Biological Diversity and Genetic Resources of Underexploited Plants by the Commonwealth Science Council at Kew, London in October 1986 recommended that immediate action be taken to provide training both on a short-term and a long-term basis at three levels, because multi-tier action on the training point is necessary for designing effective programmes:

(a) Senior scientists
(b) Junior scientists
(c) Field extension workers

At that Workshop it was also recognised that lack of detailed curriculum, course structure, training materials at each level for subjects like conservation biology, ethnobotany, herbarium development and management, taxonomy, *in situ* and *ex situ* conservation methods, and propagation in field and laboratory using *in-vitro* methods, prevented management of critical key species, their habitats and proper environments. These inadequacies in policies relating to habitat, ecosystem management, and conservation have already caused significant loss of the germplasm wealth in diverse biogeographical regions of the world, necessitating immediate development of effective programmes for conserving biodiversity.

Three workshops organised by the Commonwealth Science Council since 1987 have developed regional training programmes on conservation biology. It was felt at these workshops that the most effective action would be through a comprehensive training manual for different levels of resource persons. This manual has been designed to fulfil this need. It has two purposes: to give a thorough understanding to key persons working in diverse biogeographical regions of the world of the biodiversity conservation programme, and its implications at large, by integrating diverse theoretical concepts; and to provide a guide to the underlying concepts to ensure that formal training programmes developed at different levels attain a uniform degree of high standard.

The collection of relevant chapters on eight topics in this manual is the first attempt to integrate theory and policy relating to the subject matter of conservation biology for its use in developing training programmes and courses for senior scientists. The manual has been structured to meet the demands from research biologists and resource managers: increased collaboration between resource managers and field experts is essential if we are to meet the growing challenge of protecting biological diversity to meet the ever-increasing demands for land and natural resources.

The experts who have contributed to the manual were chosen after careful examination of their contributions to the empirical science of conservation biology. Where possible, their contributions selected have already led to application, and have reached a phase where information can be used for practical purposes on a wider geographical scale, while transcending their application to biodiversity in general. Each topic has been written with a view to cover the latest literature on the subject, and whenever possible detailed references have been given to assist users.

The trainers who will use this manual will be in the best position to advise the editors of improvements to the manual in future editions. It should be noted that tropical countries of our world, where maximum biodiversity is still waiting to be explored, studied, used and conserved, are the countries where senior scientists will be able to give maximum service in the epochal task of training of conservation biologists. It is hoped that these scientists will come forward to give their constructive criticism, comments and advice for continued improvement of this training manual.

SUMMARY OF CHAPTERS

Public policy in relation to biological conservation

Global biodiversity strategy

A global biodiversity strategy has been written jointly by the World Resources

Institute, United Nations Environment Programme and the World Conservation Union; CSC and several other partner organisations have contributed to it. This chapter provides goals and approaches for conserving global biodiversity. The strategy has identified five actions which will be catalysts for other actions. Essential elements of a convention on biodiversity are given.

Harmonising sustainable development with conservation of wildlands

The concept of wildlands is discussed and focuses on harmonising development with the protection of natural environment, especially the importance of wildland management. This chapter discusses the loss of biodiversity and economics, scientific, aesthetic and ethical reasons for preserving it. The importance of wildland management for biological diversity is described, while giving options for preserving genetic diversity.

International legislation supporting conservation of biological diversity

A series of conventions and details of international instruments that promote the conservation of biological diversity are outlined.

Inventory of species

Choice of species

Importance of some of the 'key species' or species groups under threat possess special economic and cultural significance and are essential for the survival of their ecosystem. Importance for the choice of species, need and actions required for the conservation and socioeconomic development of key species is discussed.

Criteria on choice of species for conservation: woody plants

The chapter describes existing strategies of *in situ* and *ex situ* conservation of genetic resources of woody species. International instructions which could decisively and positively influence future action in genetic conservation are given. Sampling and siting reserves, number and management of resources is discussed. The chapter refers to FAO's Tropical Forestry Action Plan as hope for increased and concentrated action in this field.

Criteria for selection of conservation areas for forest genetic resources

A distinction between genetic resources and genetic diversity is given. Most efforts at conserving nature have aimed at saving endangered ecosystems or endangered species. Choice of conservation strategies; *in situ* conservation, principles and practices, species – area relationship and management of the genetic resources is described.

Quantitative aspects of the collection and analysis of inventory data

The chapter concentrates on four areas:

Sampling techniques for biological surveys;

Description of some methods for measuring diversity. Diversity of species within a habitat and diversity of habitats within a landscape;

Simple statistical tests are described to test if there is a difference between two or more sets of data;

Multivariate statistical methods.

It is suggested in this chapter that in the longer term, conservation biology will rely heavily on monitoring programmes and on the identification of appropriate indices or indicators of change.

Sampling plant population for genetic conservation

The success of genetic conservation is heavily dependent upon the effectiveness of sampling techniques. The chapter deals with sampling within and between population. The optimum sampling strategy for collecting genetic conservation within plant species depends on reasons for the collection, on the breeding system in the species and the mode of inheritance of the attribute and the pattern of genetic variation within the species.

Biosystematics

Taxonomy, biosystematics and conservation

In this chapter biodiversity is described on three levels: (i) the ecosystem land, (ii) the taxonomic level (often referred to as the species level) and (iii) the genetic level, which is concerned with diversity in terms of chromosomes, genes and diversity and genetic information. The role and importance of taxonomy in the assessment of biodiversity is discussed in terms of taxonomy and classifications, storage and publication of data, plant biosystematics and taxonomy and genetic resources.

Roles and limits of local herbaria in conservation biology

This chapter deals with the importance of information storage and retrieval related to flora. Knowledge of the flora in tropical countries for the conservation and use of biodiversity is very poorly documented.

The role of botanical documentation provides by herbaria is discussed in detail. The chapter describes herbaria, their tasks and availability, the minimum needs for a national herbarium, and limitations of local herbaria.

Training in herbarium development and management

The chapter suggests that answers to urgent questions on the identification, nomenclature, classification, distribution of plants as well as their ecology can be effectively given if the information available in herbaria is of high quality and complete. Commonwealth Science Council (CSC) has been involved in promoting training in herbarium development and management. An 8-12 week course is held every year at the Royal Botanic Gardens, Kew Herbarium UK, jointly sponsored by CSC and the British Council. The course covers herbarium management; plant collecting; plant morphology, identification and curation of collections; general interest subjects.

Life cycles and population dynamics

Plant population and the management of viable plant populations

This chapter focuses on the importance of population dynamics of plants on plant conservation and habitat conservation. A generalised plant life history is described and then some of the demographic and genetic consideration that characterise plant population biology are discussed. Necessary information for understanding the likely dynamics and status of a given species or population is outlined. Techniques available for active management of plants are given.

Seeds in natural populations: their significance for plant conservation

This chapter highlights the significance of seeds in natural population as they are natural units for studies of plant population dynamics. A review of theory related to the importance of seeds in soil and seed dormancy is given followed by case studies. A strong need for field studies on the genetic significance of seed pools in relation to conservation is urged.

Plant-animal interactions

This chapter deals with practical means of dealing with some key questions about plant-herbivore interactions in the context of conservation in the tropics. Theory of plant-herbivore interaction is described at the ecosystem and at the population level. Some details on manipulative experiments in the field and training methods have been described to understand dynamics of plant and herbivores.

Breeding system of plants

Sexual systems, pollination mechanism and genetic diversity in tropical forest plants

Importance of modes of reproduction in plants for conservation of biological resources is discussed. A review of studies on the patterns of genetic variation in tropical woody species and on modes of reproduction is given. Implications for conservation biology are discussed.

Physiology of plants

Physiological aspects of ex situ seed conservation

This chapter describes the main physiological characteristics of seeds which affect the technology of harvesting, drying, storing, monitoring and regeneration and seed accession for genetic conservation. Attention is drawn to the importance of physiological and genetical principles which influence the practice of seed storage for genetic conservation. A practical methodology for seed conservation is given along with training methods.

Physiological consideration in conservation with special reference to propagation and growth assessment

In this chapter some aspects of propagation – especially vegetative propagation – are discussed in detail. Detailed methodologies required for the assessment of growth responses of plants to water, nutrients and physical factors are discussed. Suggestions are given for simple practical training exercises for propagation, mineral nutrition and growth. The chapter provides some guidelines as to what physiological studies will be required in the establishment of a new 'crop' for preservation of a desirable species not presently cultivated when transferred to a new environment or geographic area.

Biologically active natural products of plant origin

This chapter attempts to describe the diversity of biologically active natural products in plants and their importance in economic development and conservation. Two aspects – plants in medicine and conservation – are discussed in detail. Some examples are given on African plant species and reports of phytochemical and pharmacological studies conducted on them.

Population maintenance and monitoring

The significance of competition in the maintenance and evaluation of plant accessions

The importance of plant competition in genetic conservation, especially in maintaining and evaluation of plant collections is discussed in detail. The relevance of plant competition for maintenance of population *ex situ* and *in situ* is outlined. In crop germplasm conservation evaluation, the role of intraspecies and interspecies competition in breeding programmes is highlighted. The chapter describes how, in the past, much evaluation in plant breeding and in plant introduction has been carried out in artificial conditions of competition. Similarly, plants that would ultimately be grown in single genotype stands have been evaluated in mixed-genotype stands, while those that would be used in mixed species stands have commonly been evaluated in single species stands. The importance of valid methods of assessment is emphasised.

Management of plant populations and problems of erosion in genetic diversity

In this chapter the importance of a management plan for the maintenance of genetic variation is discussed in relation to conservation practices. It is suggested that conservation of genetic resources is essential for two reasons. Firstly, it promotes the long-term survival of the species under management by maintaining both its fitness and natural evolutionary potential. Secondly, it provides genetic variation for genes which can be used in future genetic engineering of plants with beneficial traits. The chapter deals in detail the population size and number of populations in relation to management of genetic diversity. The chapter describes how genetic drift within small population leads to an erosion of genetic diversity by reducing the number of alleles. Relevance of life history characters to genetic differential is discussed besides other species characteristics. Finally, reference is made to the role of migrants in increasing genetic diversity of managed population of animals species. It is suggested that the best approach is to preserve established natural populations.

Biological cropping systems and genetic conservation

This chapter describes the biological exploitation and its relevance to biotic diversity with emphasis on agricultural cropping systems. A review of theory is given which deals with (i) the importance of *in situ* conservation of domesticated germplasm, (ii) *in situ* conservation and wildlife germplasm and (iii) principles and conservation of diversity in ecosystems. Practical methods for crop-based agricultural systems are given as a selection and measures for the conservation of parts of the ecosystem. Based on these methods, some training exercises are suggested.

Documentation

Documentation

This chapter describes documentation as a procedure and discusses the need to design it according to a scientific, accepted biological theory which should also form the basis for international conservation strategy as well as national conservation policy. Criteria for deciding the selection of material that may be relevant for conservation are discussed. Some technical aspects of a computerised documentation system are briefly presented, e.g. databases, codes, etc.

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We are grateful to all the contributors, various experts and scientists working in the field of Conservation Biology who enabled us to prepare this training manual. We are indebted to the CSC members and the Government of Zambia, especially the National Council for Science and Technology for their assistance.

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1. *Conserving the World's Biological Diversity* (1990) by Jeffrey A. McNeely, Kenton R. Muller, Walter V. Reid, Russell A. Mittermeier, Timothy B. Werner, IUCN, Gland, Switzerland; WRI, CI, WWF-US and the World Bank, Washington D.C.

2. *Caring for the Earth: A Strategy for Sustainable Living* (1991), published in partnership by The World Conservation Union, (IUCN), United Nations Environment Programme (UNEP), World Wide Fund for Nature (WWF).
3. C. Palmberg's paper presented at the International Workshop on Research in Protected Areas, held in Galapagos Islands (Ecuador), March 1989.
4. *The Management of Viable Populations: Theory, Applications and Case Studies* (1986). Copyright, Centre for Conservation Biology, Stanford University, USA chapter on *Plant Population Biology and the Management of Viable Plant Populations.*
5. *Global Biodiversity Strategy: Guidelines for Action to Save, Study, and Use Earth's Biotic Wealth Sustainably and Equitably* (1992) by World Resource Institute (WRI), The World Conservation Union (IUCN) and United Nations Environment Programme (UNEP).

PUBLIC POLICY IN RELATION TO BIOLOGICAL CONSERVATION

GLOBAL BIODIVERSITY STRATEGY

World Resources Institute (WRI), The World Conservation Union (IUCN), United Nations Environment Programme (UNEP)

THE GOAL OF BIODIVERSITY CONSERVATION

Successful action to conserve biodiversity must address the full range of causes of its current loss and embrace the opportunities that genes, species and ecosystems provide for sustainable development. Because the goal of biodiversity conservation – supporting sustainable development by protecting and using biological resources in ways that do not diminish the world's variety of genes and species or destroy important habitats and ecosystems – is so broad, any biodiversity conservation strategy must also have a broad scope. But the campaign can be broken down into three basic elements: saving biodiversity, studying it, and using it sustainably and equitably.

Saving biodiversity means taking steps to protect genes, species, habitats and ecosystems. The best way to maintain species is to maintain their habitats. Saving biodiversity therefore often involves efforts to prevent the degradation of key natural ecosystems and to manage and protect them effectively. But because many of the world's habitats have been modified for such human uses as agriculture, the program must include measures to maintain diversity on lands and in waters that have already been disturbed. A third component is restoring lost species to their former habitats and preserving species in genebanks, zoos, botanic gardens and other off-site (*ex situ*) facilities.

Studying biodiversity means documenting its composition, distribution, structure and function; understanding the roles and functions of genes, species and ecosystems; grasping the complex links between modified and natural systems; and using this understanding to support sustainable development. It also means building awareness of the values of biodiversity, providing opportunities for people to appreciate nature's variety, integrating biodiversity issues into educational curricula, and ensuring that the public has access to information on biodiversity, especially on developments that will influence it locally.

Using biodiversity sustainably and equitably means husbanding biological resources so that they last indefinitely, making sure that biodiversity is used improve the human condition, and seeing that these resources are shared equitably. "Use" does not, however, automatically imply consumption. Often, the best economic use of biodiversity may be to maintain it in its natural state for its ecological or cultural values, as in the cases of forested watersheds or sacred groves.

How can biodiversity conservation be addressed within the context of sustainable development, as it must to succeed? There must be new contacts and partnerships

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within communities, bringing biologists and resource managers together with social scientists, political leaders, businessmen, religious leaders, farmers, journalists, artists, planners, teachers and lawyers. There must be dialogue between central and local governments, industry and citizen's groups, including non-governmental environment and development organisations, and women's and indigenous people's organisations. New mechanisms for discussion, negotiation and common action are all essential.

Biodiversity conservation must take place at the individual level, the global level, and in between. Effective conservation efforts begin in the fields, forests, watersheds, grasslands, coastal zones, and settlements where people live and work. But complementary governmental efforts are needed to address the many facets of biodiversity conservation beyond the capacity of local communities, or involving resources that are of national importance. By the same token, international cooperation is essential, given the global nature of the biodiversity crisis and the lack of national resources in many countries.

Immediate action is needed. Irreplaceable genes, species and ecosystems are disappearing at a rate unprecedented in human history, and essential development is at risk as a result. Immediate action is needed to defend these threatened living resources; to reform the policies that invite such losses; to conduct inventory and study of resource use in key ecosystems and countries; to monitor changes and impending threats; to manage threatened protected areas better; to mobilise funding; and to support national and grassroots conservation initiatives.

TEN PRINCIPLES FOR CONSERVING BIODIVERSITY

These ten principles have guided the individuals and institutions involved in development of the Global Biodiversity Strategy.

1. Every form of life is unique, and warrants respect from humanity.
2. Biodiversity conservation is an investment that yield substantial local, national and global benefits.
3. The costs and benefits of biodiversity conservation should be shared more equitably among nations and among people within nations.
4. As part of the larger effort to achieve sustainable development, conserving biodiversity requires fundamental changes in patterns and practices of economic development worldwide.
5. Increased funding for biodiversity conservation will not, by itself, slow biodiversity loss. Policy and institutional reforms are needed to create the conditions under which increased funding can be effective.
6. Priorities for biodiversity conservation differ when viewed from local, national and global perspectives; all are legitimate, and should be taken into account. All countries and communities also have a vested interest in conserving their biodiversity; the focus should not be exclusively on a few species-rich ecosystems or countries.
7. Biodiversity conservation can be sustained only if public awareness and concern

are substantially heightened, and if policy-makers have access to reliable information upon which to base policy choices.

8. Action to conserve biodiversity must be planned and implemented at a scale determined by ecological and social criteria. The focus of activity must be where people live and work, as well as in protected wildland areas.
9. Cultural diversity is closely linked to biodiversity. Humanity's collective knowledge of biodiversity and its use and management resets in cultural diversity; conversely, conserving biodiversity often helps strengthen cultural integrity and values.
10. Increased public participation, respect for basic human rights, improved popular access to education and information and greater institutional accountability are essential elements of biodiversity conservation.

THE APPROACH OF THE STRATEGY

The limited conservation resources available must be focussed strategically on opportunities likely to yield the greatest conservation benefits, and five key strategic objectives offer significant possibilities for effective action.

1. The first objective of a strategy for conserving biodiversity must be the development of national and international policy frameworks that foster the sustainable use of biological resources and the maintenance of biodiversity. The economic policies and legal frameworks established by national governments create the incentives and obstacles that influence decisions about how to utilise and manage biological resources, and these policies – ranging from those covering natural resource exploitation to incentives for technological innovation – need to be revised. To support such changes, better techniques must be developed for determining the value of biological resources and incorporating those values into local and national accounting and cost-benefit analyses.

Nations must also take steps to ensure that benefits from the use of genetic resources are gained nationally and locally. Biotechnology is radically altering the market value of genetic resources. If the right policies are established, countries rich in species and genetic resources stand to benefit substantially from these assets. Aided by the international community, all countries should establish policies that foster the development, acquisition and adaptation of biotechnologies and the development of in-country technical expertise.

2. The second strategic need is to create conditions and incentives for effective conservation by local communities. Action to conserve biodiversity must ultimately be carried out where people live and work. Unless local communities have the incentives, the capacities, and the latitude to manage biodiversity sustainably, national and international actions are unlikely to produce results. Thus, the policy reforms likely to have the greatest short-term impact on biodiversity conservation will be steps taken to create conditions for conservation locally.

Local biodiversity conservation cannot succeed unless communities receive a fair share of the benefits, and assume a greater role in managing their biotic resources –

be they protected areas, coastal fisheries, or forests. In particular, countries should ensure that people who possess local knowledge of genetic resources are rewarded financially when that knowledge is used. Local communities should play a fundamental role in the management of wildlands, as well as in stewardship of their natural resources as a whole.

3. The tools for conserving biodiversity must be strengthened and applied more broadly. The world's protected areas are vital tools for conserving biodiversity. Combined with such off-site facilities as zoos, botanic gardens and seedbanks, they can protect a substantial fraction of the world's biodiversity and help to mobilise its benefits. But these conservation tools cannot serve this role if they remain underfunded and understaffed.

But more funding and personnel are not all that is needed. Biodiversity conservation efforts must be planned and implemented "bioregionally" to reflect both ecological and social realities. The division of government responsibilities among such specialised "sectors" as forestry, agriculture and fisheries reflects neither. Under a bioregional approach, cooperation among sectors, and sometimes across national boundaries, would be built in.

Protected areas would retain their central importance if planning were done bioregionally, although their role would be increasingly complemented by forestry, agricultural, and fisheries-managment techniques that adopt biodiversity conservation among their management objectives. Additionally, national networks of protected areas must be strengthened and expanded to cover all key biomes and ecosystems, and the management objectives of protected areas must be harmonised with those for the surrounding ecosystems and human communities. By employing management techniques ranging from strict protection to extractive reserves and conservation easements on private lands, a nation's network of protected areas can both conserve diversity and meet short-term economic needs.

In many parts of the world, the best means of strengthening protected areas is to better integrate them with local social and economic needs. This *Strategy* emphasises mechanisms for increasing benefits to local communities through ecotourism and sustainable use of non-timber forest products, the establishment of effective buffer zones between protected areas and surrounding communities, compensation to local communities for lost resources, and the use of integrated conservation/development strategies in establishing protected areas.

4. The human capacity for conserving and using biodiversity sustainably must be greatly strengthened, particularly in developing countries. Conservation can succeed only if people understand the distribution and value of biodiversity, see how it influences their own lives and aspirations, and learn to manage areas to meet human needs without diminishing biodiversity. But this capacity is woefully inadequate today: resource managers are not trained to conserve biodiversity; the number of taxonomists specialising in tropical species is grossly inadequate; no country has a complete listing of its species; and for most ecosystems little information exists on indicator and keystone species.

Committed, skilled people are needed in all countries to work on biodiversity conservation. Experts in the biological and social sciences, economics, law, policy analysis, ethics, and community organisations are all required. Needs are most acute in many developing countries, where biodiversity losses are high.

The key to conserving genes, species and ecosystems is increasing our knowledge of biodiversity and its role in human society. Research must be explicitly linked to national and local resource and development needs. Findings, in turn, must be accessible and understandable to decision-makers. The capacities for undertaking research and disseminating data should be developed close to those who need the information – at the national or sub-national level – although the support of international networks is vital. Similarly, the priorities for research and information systems should grow out of consultation with those who need and will use new data and analyses. For many countries, the best option is establishing institutions such as "national biodiversity institutes" to catalogue and explore a nation's biotic wealth, thus helping to mobilise biodiversity to meet national needs.

5. Conservation action must be catalyzed through international cooperation and planning. The international cooperation needed to slow biodiversity loss requires more effective international mechanisms than those we have now. International law and institutions must be able to establish widely accepted international norms of conduct, elicit firm commitments to action from governments, mobilise financial resources, develop accurate and timely information, and invite broad participation from scientific and non-governmental sectors. Existing mechanisms simply cannot perform these functions.

THE STRATEGY: CONTENTS AND CATALYSTS

The *Global Biodiversity Strategy* calls on all nations and peoples to initiate and sustain a Decade of Action to conserve the world's biodiversity for the benefit of present and future generations. During this period, a new and broader policy context must be created – one that addresses the fundamental need for sustainable development and tackles such international issues as world trading patterns and economic policy, debt and technology transfer, and such national issues as population growth, resource consumption and waste, land tenure, education, health care, and poverty. Supported by this policy context, biodiversity must be managed and conserved on the entire landscape, and throughout the full spectrum of human interactions with the environment. Traditional approaches to conservation must be at once strengthened and modified to fit into a more comprehensive approach. At the same time, the human capacity to live sustainably and advance conservation must be expanded through education, information and training

The numerous actions proposed by the *Strategy* support these broad goals and involve a diverse array of individuals and institutions, including international institutions, national governments, non-governmental organisations, scientists, and the private sector. They cannot and should not be undertaken or controlled by a single institution or programme. Nevertheless, the *Strategy* will not work without a mechanism to stimulate the actions proposed here. For this reason, five particular actions have been identified as *catalysts for action* that can be undertaken quickly and at low cost to set off a cascade of subsequent actions by various sectors and institutions.

Action 1. Adopt, in 1992, the International Convention on Biological Diversity.

The Convention on Biological Diversity, currently being negotiated under the auspices of the United Nations Environment Programme (UNEP), should serve as a key coordinating, catalyzing and monitoring mechanism for international biodiversity conservation. It will also be the primary means of establishing accepted international norms for biodiversity conservation (Table 1). Although current international agreements cover some elements of biodiversity conservation, taken together they do not cover all of the world's threatened biodiversity, and they do not adequately address the closely related issues of use, ownership, funding, and technology transfer.

TABLE 1. Essential elements of a convention on biodiversity

- A commitment by governments to survey their natural living resources – both domesticated and wild – and to conserve sites noted for their rich biological diversity, as well as threatened species and domesticated varieties.
- Recognition that both *in situ* conservation and *ex situ* preservation of biodiversity are key tools in any effective biodiversity conservation strategy.
- A commitment by governments to ensure that any use of biodiversity is sustainable and equitable.
- Recognition that conservation of biodiversity is a common concern of all humankind and that states have the sovereign right to use their biological resources.
- Recognition that access to biodiversity is contingent upon prior informed consent of the country concerned and that those who possess traditional knowledge about genetic resources and farmers who have contributed to and maintained diversity in crops and livestock deserve just compensation for the use of their knowledge or their varieties.
- The establishment of a financial mechanism that would provide both technical and financial assistance to developing countries in need of support for surveying, characterising and conserving their biodiversity.
- The establishment of an administrative structure giving equal control to developed and developing countries that are Parties to the Convention in the distribution of

funds under the Convention, and ensuring participation of scientists, governments and non-governmental organisations to advise on funding priorities.

- Arrangements by which the commercial exploiters of biodiversity help finance much of its conservation in the countries that give it refuge.
- Mechanisms to ensure access for developing countries to technologies for conserving and using biodiversity.
- The establishment of a monitoring and early-warning system to alert governments and the public to potential threats to biodiversity.

Equally important, most current agreements are aimed at saving biodiversity, not at using it sustainably and equitably. An international agreement is needed to set guidelines for how genetic resources will be used and to identify who will benefit from their use, particularly as the importance of biotechnology grows.

Another key function for the Convention on Biological Diversity is to establish a mechanism to provide substantial new funding for biodiversity conservation in developing countries.

For developing countries, the attraction of the Convention is that it solidifies commitments of international financial and technical support for conservation, affords these nations greater say than they now have over how that support is allocated, strengthens their technical capacity for benefiting from biodiversity, and recognises their sovereignty over biological resources within their territories. For industrialised countries, the convention will help ensure their continued access to genetic resources – albeit at a higher cost than before. The convention will also help all countries meet their shared commitment to conserve and rationally use biodiversity, and assure equitable sharing of benefits.

Action 2. Adopt, in the General Assembly of the United Nations, a resolution designating 1994-2003 the International Biodiversity Decade.

Declaration by the UN General Assembly of an International Biodiversity Decade would greatly increase awareness about biodiversity and the need to conserve it. A declaration would also signal the intent of governments to act to slow biodiversity loss, and would provide a tool for citizens to use in encouraging their governments to take action. It would help to coordinate and intensify the work of the UN specialised agencies on biodiversity conservation. Finally, a UN Biodiversity Decade would provide impetus for many of the international actions called for in this Strategy, including establishment of the International Panel on Biodiversity Conservation, ratification and implementation of the Convention on Biological Diversity, and the establishment of a Biodiversity Early Warning Network.

Action 3. Establish a mechanism such as an International Panel on Biodiversity Conservation (preferably within the Convention on Biological Diversity), including scientists, non-governmental organisations, and policy-makers to provide guidance on priorities for the protection, understanding and sustainable and equitable use of biodiversity.

Growing international awareness of the threats to biodiversity and increased funding for international conservation alike make it imperative that priorities are set through a process fully representative of local and national interests, and that global cooperation respects national sovereignty. The currently incomplete scientific understanding of biodiversity and lack of agreement on principles for action create a risk that poor choices will be made. Moreover, no framework exists to help guide action to promote and generate knowledge about biodiversity which can in turn guide actions and policies.

To remedy this situation, a mechanism – perhaps temporary – is needed to ensure the participation of all groups with an interest in biodiversity conservation and knowledge to contribute. Accordingly, a mechanism such as an International Panel on Biodiversity Conservation (IPBC) should be established. Members should include representatives of governments inter-governmental agencies, the scientific community, non-governmental organisations and private business, from every part of the globe. The panel would commission studies and contributions by inter-governmental, national and non-governmental technical and scientific centres, to provide background materials, and would publish guidelines and criteria to orient and assist governments, non-governmental groups, business and communities in their conservation activities.

This panel, which might eventually be replaced by a permanent body established under the Convention on Biological Diversity, would address five key needs. First, it would provide an international forum for continuing dialogue and debate among interested parties on the options for action to save, study and use biodiversity sustainably and equitably. This dialogue process, initiated under the auspices of this *Strategy*, the Keystone Centre, FAO, IBPGR, UNEP's multidisciplinary advisory team for Biodiversity, Global Environmental Facility/Scientific and Technical Advisory Panel (GEF/STAP) working group on Biodiversity, and other groups, is currently far from complete. Second, the Panel would summarise knowledge of the current status of biodiversity, rates of loss, and their implications for sustainable development. Third, it would provide advice on priorities for research, funding and action. Fourth, anticipating the needs of the Biodiversity Convention, it would begin to make priority lists of endangered species, sites and ecosystems. Finally, it would develop the terms of reference for an Early Warning Network for Biodiversity.

Action 4. Establish an Early Warning Network, linked to the Convention on Biological Diversity, to monitor potential threats to biodiversity and mobilise action against them.

Much can be done to avert loss of biodiversity in specific regions *if* adequate information on potential threats is available. If a development project is planned for a remote valley, non-governmental organisations or government institutions can arrange to collect traditional varieties of crops or wild relatives before the ecosystem is disturbed, or collaborate with local farmers to conserve their traditional varieties better. The environment ministry and national or international non-governmental organisations can speed up biodiversity assessments to determine if certain areas deserve protected status. And, in some cases, advance notice of project plans may bring to light new data that triggers a change in those plans.

A Biodiversity Early Warning Network should be set up to monitor urgent threats to biodiversity, disseminate information about those threats, and mobilise action against them. Within countries, the network would make use of governmental and non-governmental data sources, channeling information either formally through institutions and data collection networks or informally to the Early Warning Network secretariat. The IPBC could help set criteria for evaluating the urgency of threats, and disseminate information.

An Early-Warning Network should monitor:

- traditional crop or livestock varieties threatened by planned or ongoing development projects or the introductions of new varieties;
- genebank facilities with germplasm at risk due to lack of funding for recurring costs;
- protected areas in urgent need of financial, technical or other support;
- communities that lost access to resources when protected areas were established;
- increasing genetic uniformity of crops;
- climatic threats to biodiversity — including desertification, floods, drought and global warming;
- introductions of exotic species;
- pollutant discharges presenting immediate threats to biodiversity or chronic pollution that might pose longer-term threats;
- rapid habitat loss; and,
- evidence of the over-exploitation of species.

Non-governmental organisations and scientists working in the field are the best sources of early-warning information; the challenge is to make this information widely available to enforcement authorities, advocacy groups, and the general public, so that appropriate actions are swiftly mobilised. A number of existing environmental data reports and evaluations, notably *Global Biodiversity: Status of the Earth's Living Resources* (WCMC), *World Resources* reports (WRI), the *Environmental Data Report* (UNEP), and the UNEP Biodiversity Country Studies can provide valuable baseline information, as well as a vehicle for monitoring longer-term trends. Some of the organisations that produce these reports might also serve as focal points for data collection and dissemination in the Early Warning Network.

Action 5. Integrate biodiversity conservation into national planning processes.

Virtually all countries have various explicit or *de facto* planning processes for setting policy priorities, allocating resources, and dividing authority and responsibility among government agencies, between national and local governments, and between government and the private sector. In most, however, biodiversity concerns are neglected. Until biodiversity conservation becomes a stated national goal, investments will not be targeted to developing the national human, technological and institutional capacity required to save, study and use biodiversity comprehensively. Nor will the appropriate policy environment be established.

Various planning mechanisms can be used to promote and integrate biodiversity conservation in development. Many countries may find national conservation strategies, tropical forest action plans, or environmental action plans useful. Others may be ready for an explicit National Biodiversity Action Plan that integrates disparate initiatives, covers the full range of biodiversity conservation issues, helps set priorities, and catalyzes action. Several countries have established National Biodiversity Units to oversee and co-ordinate the preparation of country studies to develop biodiversity conservation strategies.

HARMONISING SUSTAINABLE DEVELOPMENT WITH CONSERVATION OF WILDLANDS

G. LEDEC AND R. GOODLAND

INTRODUCTION

Wildlands are natural areas that have not been significantly modified by human activities. Until two or three decades ago a large proportion of the world's wildlands were protected by their remoteness, their vastness, and their marginal direct usefulness for agriculture or other economic pursuits. This situation has changed, for the most part, and wildlands are rapidly disappearing in many developing countries. Improved access and the pressures of population growth, landlessness, and economic development are rapidly converting most types of wildlands to other uses. For example, tropical rain forests are being logged or cleared so rapidly that by 2000 as little as one-half of those standing in 1980 may be left. Many other types of wildlands are undergoing similar or even more rapid rates of conversion – that is, they are being significantly modified or completely eliminated. The conversion of wildlands to more intensive uses through land clearing, inundation, the establishment of plantations, or other means can serve important development objectives and is an element of certain projects assisted by the World Bank. But wildlands that are maintained in their natural state can also contribute significantly to economic development. It is therefore important to seek a balance between preservation and conversion.

Our understanding of the complex interactions that have permitted life to arise and survive on this planet – alone in the solar system and perhaps in the universe – is growing continually. Correspondingly, the task of reconciling development with the protection of the natural environment that sustains us has grown more difficult (or, rather, we are increasingly recognising its difficulty). In the past, development projects have emphasised conversion simply because planners did not realise how important wildlands can be for sustainable development and for human well-being, particularly in the long term. Development efforts therefore gave little or no attention to conserving wildlands in their natural state.

Within the past decade there has been growing international recognition of the importance of wildland management as a link in sustainable economic development. Nonetheless, the present worldwide investment in wildland management is not enough to enable wildlands to make their fullest possible contribution to economic and social development now and in the future. Furthermore, the loss of wildlands is continuing, as are the associated extinctions of species and other environmental costs. Governments and development organisations are therefore increasingly seeking ways to prevent or mitigate the environmental degradation that often accompanies

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wildland conversion.

As used here, *wildlands* include the full range of relatively undisturbed ecosystems – forests, woodlands, shrublands, grasslands, natural inland bodies of water, and coastal and marine areas. It should be noted that many wildlands throughout the world have been or are being slightly modified by the traditional activities of indigenous tribal peoples. These activities, which include hunting and gathering, subsistence fishing, nomadic livestock grazing, and low-density shifting agriculture, have been sustained without significantly altering the species composition or other natural features of wildland ecosystems. Their impact on wildlands is therefore fundamentally different from that of the more intensive forms of land and water development practiced by modern societies.

Wildland management is the direct maintenance, protection, or enhancement of virtually unmodified natural ecosystems and their native plant and animal species. Thus, wildland management is a subset of *conservation* – the rational and prudent management of natural resources so that they yield the greatest sustainable benefit to present generations while maintaining their potential for meeting the likely needs and aspirations of future generations. Other conservation activities include the control of soil erosion, the intensified sustainable use of existing agricultural lands, the establishment of timber and fuelwood plantations, land-use planning, and pollution control.

Wildlands, kept in their natural state and properly managed, provide a refuge for plant and animal species that may prove to have direct economic uses and that, more important, form part of the vast and still inadequately understood web of connections among all living things and their environment. Wildlands are also essential for the maintenance of environmental services – water control, soil conservation, and the like – most of them unpriced public goods that are indispensable for meeting human needs and supporting sustainable development.

Because wildlands make significant and even unique long-term contributions to human welfare, prudent development should minimise or mitigate damages from wildland conversion. Indeed, the timely management of strategically important wildlands often prolongs or improves the effectiveness of development projects. Conversely, the unnecessary or short-sighted destruction of wildlands can lead to unanticipated and costly consequences, such as the rapid siltation of reservoirs and waterways, the loss of topsoil and of economically important species, and even the spread of disease. By incorporating wildland management in their projects and other activities, development organisations can improve the prospects for sustainable economic development. The importance of wildlands for sustainable development and improved human well-being now and in the future is discussed here under two headings: biological diversity and environmental services. The essential role of wildlands in maintaining the livelihood of tribal peoples is discussed in Goodland (1982) and Davis (1985).

BIOLOGICAL DIVERSITY

Biological diversity usually refers to three elements: (i) the number of different ecosystems (communities of plants and animals and the environments that sustain them) and their relative frequencies in a country or in the world; (ii) the number of species of animals and plants and their relative frequences; and (iii) the genetic variation within each species.

Genetic variability is greatest among species, but variability among isolated populations of a species or among individuals in a population is also important. A rare species is a genetically vulnerable species. If the number of individuals is small, the probability of advantageous genetic variations occurring is reduced, and inbreeding may perpetuate disadvantageous characteristics. Preserving biological diversity, then, entails preserving not only species but also different populations of species and the largest feasible number of individuals within those populations.

Most of the world's wild plant and animal species depend on wildlands for their existence, as they cannot survive in areas that have been significantly modified by human beings. Moreover, most species depend on specific types of wildland habitats and have limited geographic ranges. The elimination of a unique wildland habitat therefore causes the summary extinction of all the species that are completely dependent on that habitat for their survival. Appropriate wildland management is the only method of preserving large and distinct populations of most species, thereby ensuring species survival and biological diversity. Conservation measures other than wildland management (such as the establishment of plantation forests) preserve some environmental services but cannot by themselves maintain diversity.

Modern loss of biological diversity

Human activities in the last quarter of the 20th century are reducing biological diversity at a rate that may be unprecedented in the history of life on Earth. It is impossible to assess, with our limited knowledge, the consequences of the disappearance of species for the stability of Earth's environment or the economic value lost because of extinctions. The best available estimates indicate that if current trends continue, some 15-20% of the estimated 10 million to 30 million species of plants and animals alive in 1980 may become extinct by 2000 (see Wolf 1987), and many more species could be lost in the early decades of the 21st century. Development activities can be modified to help reduce these disturbing trends. The irreversible large-scale loss of biological diversity is not an unavoidable aspect of modern human survival or of economic development; it is a by-product of conducting human affairs without sufficient regard for long-term human needs or sufficient awareness of the needs of other species.

Human activity is greatly accelerating extinction rates; several hundred species *a day* may become extinct over the next 20-30 years. More species of the Earth's flora and fauna may disappear in the next several decades than were lost in the mass extinction that wiped out whole taxonomic groups of animals, including the dinosaurs, 65 million years ago (Wolf 1987).

The reduction of wildland habitats to less than the critical amount necessary for the survival of a species is by far the greatest cause of modern extinctions. Although many endangered species live in temperate areas, the problem is most severe in tropical regions, where at least two-thirds of the world's species of plants and animals are found. Appropriate, low-cost wildland management can significantly reduce current extinction rates to much lower – perhaps almost "natural" – levels. The approaches discussed here will help ensure that the loss of biological diversity is kept to a minimum in development projects that involve the conversion of wildlands.

Although elimination of wildland habitats accounts for most present-day extinctions, direct overexploitation and the introduction of non-native species that become pests or weeds are also important causes To minimise these extinction risks, development projects must adhere to sustained-yield harvesting of forests and fisheries and must avoid introducing potential pests or weeds in agricultural and fishery projects.

The case for preserving biological diversity

There are compelling economic, scientific, aesthetic and ethical reasons for preserving biological diversity. All of them are grounded in the view that because species extinctions are completely irreversible, preserving biological diversity keeps open important options for the future.

Economic

The economic justification for preserving biological diversity is that many species of wild plants and animals are undeveloped resources – that is, they have significant economic potential that is currently undiscovered, undervalued or underutilised. Biological resources are essential to human existence, and the preservation of biological diversity is important to the maintenance and improvement of agriculture, forestry, ranching, fisheries, medicine, industry and tourism.

The importance of genetic diversity for sustaining and increasing agricultural production is increasingly acknowledged. Without a diverse genetic base for plant breeding, the development of high-yielding crop varieties probably could not be sustained. The disappearance of many domesticated crop varieties and their wild relatives has made many of the world's productive farming areas increasingly susceptible to catastrophic attacks by pests and diseases. Despite efforts to preserve crop germplasm, many domestic varieties and wild relatives of crop plants remain threatened.

An example of the benefits of genetic diversity is a perennial wild maize (*Zea diploperennis*) which has preserved almost accidentally. It may have seemed to be just another weed when it was discovered growing on a few hectares of land in Jalisco, Mexico, but it may become important for higher food production. Perennial maize could be grown in maize orchards that would not have to be ploughed and seeded each year; the advantages for soil and energy conservation are obvious. In addition, cross-breeding with *Zea diploperennis* may significantly improve the resistance of annual varieties of maize to a number of serious diseases and insect pests. Human society is better off because this apparent weed was not eliminated by the conversion of all its wildland habitat to agricultural or other uses.

Besides increased yield, improved quality, and resistance to pests and diseases, wild relatives of crop plants provide numerous other benefits. They may add vigour to crops (as with pineapples, rubber and sugar cane), extend the range of crops (as with grapes and lupins), enable crops to cope with environmental fluctuations (as with cassava and potatoes), and provide genetic bridges that make it possible to cross-breed crops with distantly related species (as with oats, barley, wheat and potatoes).

Wild plant species have even greater potential as completely new crops. Of the world's approximately 250,000 species of plants, only about 3,000 have even been used as food, only 150 have been cultivated on any scale, and a mere 20 account for over 85% of present human consumption (Myers 1979). Population growth, rising per capita consumption, and shortages of arable land may make it important in future years to cultivate new species of crops that can produce calories, protein, specific mineral nutrients, vitamins, or fibres more efficiently than many of the species currently used.

Many otherwise obscure animal species, particularly insects, should also be protected to maintain or enhance agricultural output. For example, the oil palm (*Elaeis guineensis*) is pollinated in the wild in Africa by a weevil, *Elaeidobius kamerunicus*. The oil palm was introduced in what is now Malaysia in 1917 without the weevil and required costly, inefficient, labour-intensive hand pollination. In 1980-81 the pollinator was collected from its native habitat in the forests of Cameroon and brought to Malaysia; it promptly boosted fruiting in oil palm trees by 40-60%. This improvement was worth approximately US$57 million in foreign exchange in the first year alone.

A good example of an economically valuable food plant that depends on a variety of unknown or poorly known species of animals and plants is the Brazil nut (*Bertholletia excelsa*). Almost all commercial Brazil nut production is harvested from the wild rather than grown in plantations. The pollinating insects have not all been identified, but several Euglossine bees visit the flowers. Euglossine males are attractive to females only after they have gathered organic compounds from certain epiphytic orchids, but they depend on other flower species for nectar. Dispersal and germination of Brazil nuts depend on a forest-dwelling rodent, the agouti (*Dasyprocta*), which is able to open the hard fruit case (pyxidium) that encloses the nut. Thus, preserving the Brazil nut industry, which exports more than US$16 million annually to the United States alone, appears to require the conservation of enough natural forest to provide nesting habitats for the Euglossine bees and to support nectar sources, certain orchids and the trees on which they grow, the insects or hummingbirds that pollinate the orchids (and all of their necessities in turn), and agoutis. Smoke from the burning of nearby forests has been suspected of decreasing yields of Brazil nuts by interfering with the pollinators. This illustrates the economic importance of maintaining certain wildlands fully intact so that potentially valuable species are not inadvertently lost.

Wild plants and animals are also fundamentally important for modern medicine and offer even greater future applications. Over 40% of all prescriptions written in the United States contain one or more drugs that originate from wild species (fungi, bacteria, higher plants, and animals); annual sales of such drugs in this one country are over US$8 billion. In many cases it is still impossible to synthesize these compounds, or more costly to synthesise them than to obtain them from living sources; in any case, it would not have been possible to know what compound to synthesise without first having the natural model.

Wild plant and animal species are of great and increasing importance to industry as sources of tannins, resins, gums, oils, dyes, and other commercially useful compounds. Until about 1850 even the rubber tree (*Hevea brasiliensis*) was just another Amazonian tree species of unknown economic value. The potential for new industrial products from currently unknown or poorly known plant and animal species is significant but impossible to quantify. To date there has been little systematic screening of wild plant species for products that can be used by modern society, but some plants naturally manufacture such products in considerable quantities. And other plant compounds may become valuable as new technologies and inventions emerge.

These examples illustrate the range of economic uses of many wild plants and animals. But probably less than 5% of all the world's species have been inventoried and scientifically names, and even fewer have been assessed for possible human use. Moreover, now that genetic engineering techniques increasingly permit the transfer of genes from one species to another, the extinction of any one species means a lost opportunity for transferring potentially useful genes to other species. Biological resources, unlike petroleum and other fossil fuels, are completely renewable, but only if care is taken to keep them alive and able to reproduce. The protection of biological diversity is relatively low in cost and helps to preserve the means available for addressing unpredictable future problems.

Scientific

The scientific reason for species preservation is that we cannot understand the interactions of life forms and their environments unless we can observe how they function in the absence of significant human intervention. It is therefore necessary to conserve comprehensive samples of ecological systems in an undisturbed state. Moreover, each species has unique physiological, biochemical and population characteristics, the study of which can help us to understand basic life processes. In addition to the direct economic applications of research on poorly known species, eventual economic payoffs are likely to emerge from more basic scientific research.

Aesthetic

The aesthetic justification is that many wild species of plants and animals are an irreplaceable source of wonder, inspiration and joy to human beings because of their beauty, intriguing appearance, variety, or fascinating behaviour. The French anthropologist, Claude Levi-Strauss described wild species as "an irreplaceable marvel, equal to the works of art which we religiously preserve in museums." Millions of people who may never actually encounter many wild species derive enrichment and vicarious satisfaction from reading and learning about them; are our descendants to be denied these pleasures?

Ethical

The ethical, or moral, justification, espoused by a significant and growing number of people, is that human beings should not exercise their power to obliterate other species at will – even species not known to have any practical value to humankind. From this perspective nonhuman species have their own intrinsic value independent of any practical or utilitarian value they may have for human beings. This ethical viewpoint has been called the 'Noah principle'. A related, perhaps more traditional, view is that to eradicate other species is to deprive future generations of options and thus to fail in the duty of stewardship. For a couple of generations of human beings to eliminate unnecessarily a sizeable proportion of the diversity of life on Earth can be construed as an act of considerable arrogance.

All of these considerations argue that human beings should exercise great care to avoid inadvertent extinctions. A leading biologist, Edward O. Wilson, has said:

"The worst thing that can happen – will happen – in the 1980s is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes would be for us, they can be repaired within a few generations. The one process ongoing in the 1980s that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us" (Wilson 1985).

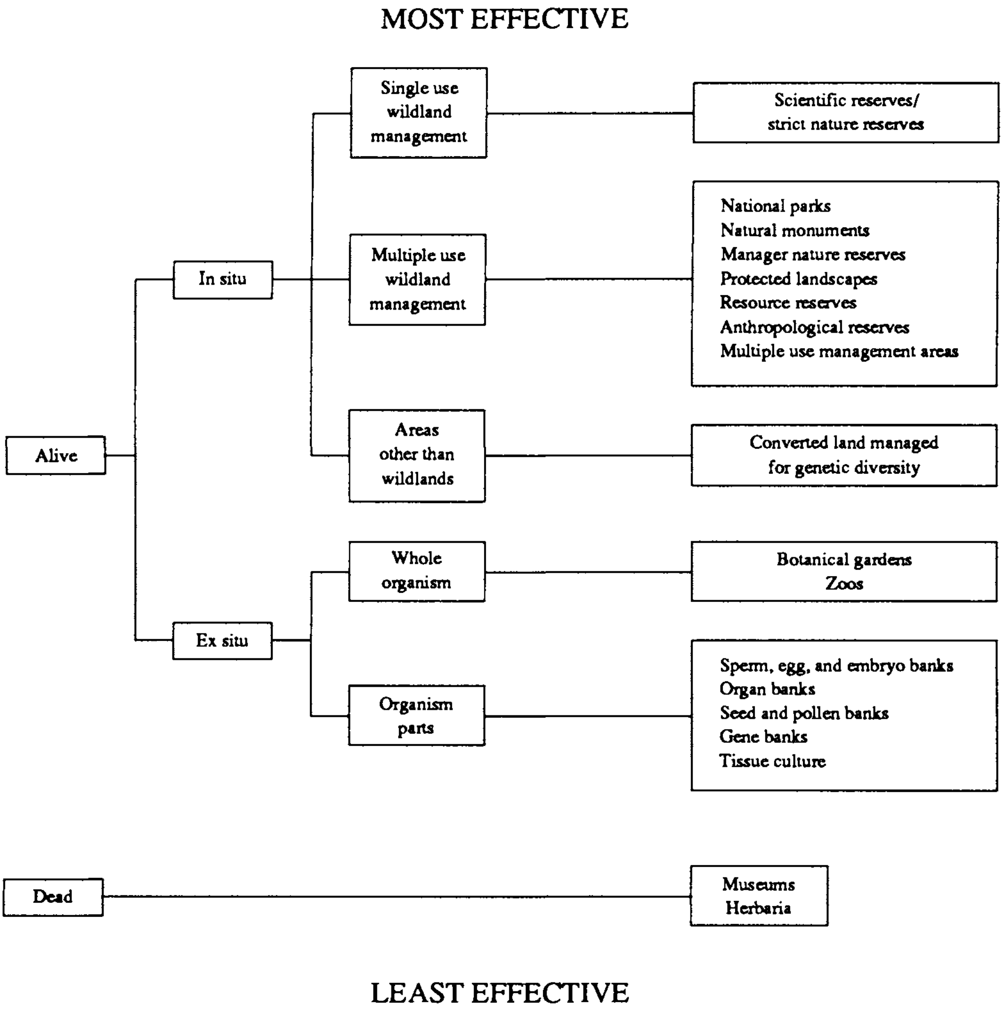
Importance of wildland management for biological diversity

Wildland management is the least costly – and in many cases the only – means available for maintaining biological diversity. For certain groups of plants and animals, off-site (*ex situ*) preservation techniques can be useful supplements to the *in situ* preservation provided by wildlands. But *ex situ* techniques – zoos and other captive-breeding facilities, botanical gardens, arboreta, cryogenic storage of embryos, eggs and sperm, seed and pollen banks, and tissue cultures – cannot be expected to meet most biological conservation needs.

Ex situ preservation is fundamental for conserving for future breeding the wild relatives of crop plants as well as traditional crop varieties that are being displaced by high-yielding varieties. But *ex situ* preservation has limitations: (i) some crop species (including many trees and vegetatively propagated species) are difficult or costly to maintain *ex situ*; (ii) important but rare genotypes are often absent from *ex situ* collections; (iii) collections can be destroyed by mechanical breakdowns or accidents; (iv) coevolution of a crop plant with other organisms, such as pollinators and potential pests and disease, cannot continue *ex situ*; (v) the peculiar characteristics of each crop variety may be more difficult to study *ex situ*; (vi) pollinators, propagule distributors (for example, birds that eat fruit and excrete the seeds), and other species-specific necessities may be difficult or impossible to include in *ex situ* trials. For such reasons, wildlands that contain wild relatives of crops have a high priority as areas to be preserved. It is also advisable to encourage the planting of 'museum strips' of traditional crop varieties alongside new high-yielding varieties.

There are different options for preserving the genetic diversity found in wild species (Fig. 1). It must be stressed that *in situ* preservation is the only feasible way to maintain most species, although ex situ preservation can be a useful supplement. Among the different categories of *in situ* preservation, scientific reserves or strict nature reserves provide the greatest protection. Most of the other categories, however, usually suffice for biological conservation, except that converted lands managed for genetic diversity are typically much less successful in preserving the full range of values of intact wildlands. Maintaining dead specimens in museums and herbaria provides a historical record of their existence and structure but none of the benefits of living species.

FIG. 1. Options for preserving genetic diversity



ENVIRONMENTAL SERVICES

In addition to maintaining biological diversity, and thus the development options available to future generations, wildlands also provide perpetual environmental services that can be vital to successful economic development. These include the creation and protection of soil, the stabilisation of water flow patterns, the amelioration of climate, the breakdown of pollutants, the recycling of wastes, and the provision of nurseries for economically important fisheries and of barriers against weather damage. Despite their economic value and their importance in meeting human needs, environmental services are frequently overlooked or undervalued because they are almost always public goods that are not priced in the marketplace. Wildlands can be regarded as a form of natural capital that provides an unending stream of benefits and services to support and enhance economic development. All development projects support capital formation, and it is equally important that they avoid unnecessarily depreciating the natural capital represented by wildlands. Many costly development failures and much human suffering in recent years are directly attributable to the ill-advised destruction of natural capital.

Forests, and in some cases other wildlands (including woodlands, shrublands and wetlands), support the agricultural sector in important ways. By retaining water, forests prevent or minimise excessive flooding during rainy periods and thus help prevent soil erosion in downstream agricultural areas. Mangrove swamps benefit agriculture by encouraging land accretion in river deltas and by reducing erosion by coastal waves during storms. Wildlands also protect soils on agriculturally marginal lands until economically viable and ecologically sustainable cropping or silvicultural techniques can be introduced. This approach is far less costly than the rehabilitation of marginal lands that have been degraded by inappropriate clearing or subsequent misuse.

Forests and other well-vegetated wildlands help maintain the productivity of irrigated agriculture. As protectors of watersheds they can augment and sustain water flows during the dry season, and they buffer peak flows and reduce inundation of crops during the wet season. Furthermore, by stabilising upstream soils they can greatly reduce sedimentation in irrigation canals and thereby decrease the costs of keeping these systems functional. About 40% of farmers in developing countries live in villages that depend on the watershed functions provided by forests. When forested or other well-vegetated wildlands are eliminated, the damage to agricultural output can be severe. Deforestation and the ensuing sedimentation have reduced the capacity of India's Nizamsagar Reservoir from almost 900 x 10^6 m^3 to less than 340 x 10^6 m^3. As a result, there is now not enough water to irrigate the 1,100 km^2 of rice and sugarcane served by the reservoir, and local sugar factories have considerable underutilized capacity.

Hills (areas with slopes of more than 8 degrees) and highlands (areas well above sea level) cover approximately 50% of the land area of Mexico, Central America, the Andean countries, and the Caribbean. A recent evaluation of the agricultural potential of tropical America (Rockefeller Foundation 1981) recommended that a large proportion of these lands be given protection management because they perform their maximum agricultural service when left in a natural condition. If they were farmed, the combination of steep slopes, high rainfall, and thin soils would mean a high risk of erosion or injurious water runoff. Thus, sometimes the best way to support agriculture is to ensure that certain important wildlands are not converted to agricultural production.

Forests and other wildlands are important for maintaining adequate, high-quality water supplies throughout the year in urban and rural areas. Intact wildlands can thus benefit public health and industries that depend on high-quality water. In some rural areas deforestation causes groundwater sources or springs to dry up, forcing people to drink from polluted streams. In Colombia, deforestation associated with the World Bank-supported Caquetá Land Colonisation project has caused some rivers to run dry part of the year and has produced serious flooding and erosion during the rainy season. The benefits of the water supply services that wildlands provide are often recognised only after the wildlands are gone.

Many or most of the same wildlands that are vital for preserving biological diversity are important in protecting the environmental services necessary to sustain economic development and human well-being. Some, although not all, of these environmental services can be provided by other land-use systems. Most notably, the water retention, soil protection, and climate stabilisation afforded by natural forests can also be provided by plantation forests, although to a lesser degree because the trees are smaller. But even if plantations can adequately protect watersheds, they do not preserve biological diversity. And in any case wildland management is often the easiest and most cost-effective means of protecting important watersheds.

The appendix summarises the environmental services and material goods that can be obtained from different types of wildlands. The most appropriate type of management system (whether strict protection or some form of multiple use) for any particular wildland depends on several factors: biological conservation needs, the environmental services that require protection, regional economic opportunities, the subsistence needs of local people, and adjacent land use patterns.

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APPENDIX 1. Economic benefits of wildland management: some examples adapted from C. Hahn (1982) *The Economic Rationale for Protection and Management of Natural Areas in Developing Countries*. Natural Resources Defense Council, Washington, D.C.

	WILDLAND ECOSYSTEM								
Benefits	Forests	Woodlands and savannas	Brushlands (moist or arid)	Grass-lands	Marshes and similar wetlands	Wooded freshwater swamps	Mangroves	Estuaries and coasal shallows	Coral reefs
Agriculture									
Improved water control for irrigation	x	x	x						
Reduced sedimentation in irrigation works	x	x	x	x					
Control of soil erosion	x	x	x	x	x	x			
Availability of baseline ecological study areas	x	x	x	x	x	x	x		
Support of pollinators and pest control agents	x	x	x	x	x	x	x		
Land accretion in river deltas							x		
Management of marginal lands	x	x	x			x			
Reduction of damage to crops by wildlife	x	x	x	x		x			
Preservation of crop germplasm									
Source of new crops	x	x	x	x		x	x		
Fisheries									
Nursery or feeding grounds for fish, shrimp and the like					x	x	x	x	x

Benefits	WILDLAND ECOSYSTEM								
	Forests	Woodlands and savannas	Brushlands (moist or arid)	Grass-lands	Marshes and similar wetlands	Wooded freshwater swamps	Mangroves	Estuaries and coasal shallows	Coral reefs
Source of new species for harvest or aquaculture					x	x	x	x	x
Livestock									
Sustained-yield harvest of wild game	x	x	x	x	x	x			
Preservation of livestock germplasm	x	x	x	x	x	x			
Source of new species for domestication	x	x	x	x	x	x			
Limited grazing or fodder collection	x	x	x	x	x	x	x		
Forestry									
Preservation of tree germplasm	x	x				x	x		
Source of new forestry species	x	x	x			x	x		
Fruits, nuts, honey, waxes, and other forestry products	x	x	x			x	x		
Limited wood harvest	x	x				x	x		
Energy									
Increased hydroelectric production through reduced sedimentation	x	x	x	x					
Sustained-yield fuelwood harvest	x	x	x						

Source of new biomass energy crops	x	x	x	x	x	x	x	x	x
Industry									
Increased freshwater supplies	x	x	x		x	x	x		
Natural breakdown of pollutants					x	x	x	x	
Source of new species for industrial products	x	x	x	x	x	x	x	x	x
Health									
Increased supply of high-quality water for urban and rural areas	x	x	x		x	x	x		
Source of new and currently used medications	x	x	x	x	x	x	x	x	x
Source of subjects for medical research	x	x	x	x	x	x	x	x	x
Control of yellow fever and other diseases	x x	x							
Transport									
Increased operating efficiency of harbours and navigation canals through reduced sedimentation	x	x	x	x					

	WILDLAND ECOSYSTEM								
Benefits	Forests	Woodlands and savannas	Brushlands (moist or arid)	Grass-lands	Marshes and similar wetlands	Wooded freshwater swamps	Mangroves	Estuaries and coasal shallows	Coral reefs
Reduced erosion, land-slides, and flooding along roads	x	x	x	x					
Tourism									
Preservation of wildlife and other natural attractions	x	x	x	x	x	x	x	x	x
Protection from catastrophes									
Control of inland floods	x	x	x	x	x	x			
Control of coastal floods					x	x	x	x	x
Control of landslides	x	x	x	x					
Control of coastal erosion					x	x	x	x	x
Minimisation of extent of drought	x								

INTERNATIONAL LEGISLATION SUPPORTING CONSERVATION OF BIOLOGICAL DIVERSITY

World Resources Institute (WRI), The World Conservation Union (IUCN), United Nations Environment Programme (UNEP)

INTRODUCTION

International relations often work best within a framework of agreed legal instruments, and considerable effort has been devoted to developing a series of conventions and other international instruments that promote the conservation of biological diversity. This chapter briefly describes the main components of the existing international legal system.

THE SCOPE OF EXISTING CONVENTIONS

At global level, the Ramsar Convention on Wetlands of International Importance especially as Waterfowl Habitat and the Paris Convention on the Protection of the World Cultural and Natural Heritage deal with aspects of habitat conservation. A number of regional measures also touch on or cover this field, notably:

a) the Convention on Nature Protection and Wildlife Preservation in the Western Hemisphere (Washington, 1940);
b) the Antarctic Treaty, with its subordinate Agreed Measures on Conservation of Antarctic Flora and Fauna;
c) the Convention on the Conservation of Nature in the South Pacific (Apia, 1976);
d) the African Convention on the Conservation of Nature and Natural Resources (Algiers, 1968);
e) the Convention on the Conservation of European Wildlife and Natural Habitat (Berne, 1976);
f) certain European Community Directives, notably on the conservation of bird habitats; and
g) the Convention on Biological Diversity (Rio, 1992).

Of these, the World Heritage Convention is of special value in giving added status and some additional supporting resources to outstanding sites that are already protected, but it has so far placed more emphasis on cultural than on natural sites and it is not designed as an instrument for the protection of the world's biological diversity *per se*. The Ramsar Convention has been the means of designation of over 400 sites covering some 30 million hectares, although these, too, are invariably listed after they have gained protection under national legislation. The Convention covers fresh water, estuarine and coastal marine habitats that are important for both the diversity of wild species they support and as the location of relatives of key cultivated

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plants (notably rice). As it has developed, the application of the Ramsar Convention has been broadened and it has become the most important global measure concerned with habitat protection, but it is clearly only able to cover a small part of the world's total biological diversity. In a similar way, while the regional conventions listed above and the designation of Biosphere Reserves under a UNESCO programme provide valuable protection or public recognition of a range of sites, taken collectively they meet only a fraction of the needs we identify in the text.

Various other international measures conserve particular species or groups of species or protect the living resources of designated marine areas. At global level these include the Convention on International Trade in Endangered Species of Wild Flora and Fauna (Washington, 1973) and the Convention on Conservation of Migratory Species of Wild Animals (Bonn, 1979), and on a narrower geographical scale:

a) the Convention on Conservation of Antarctic Marine Living Resources (Canberra, 1982); and
b) various agreements preserving species or classes, etc., e.g.:
   - International Convention for the Regulation of Whaling (Washington, 1946), establishing the International Whaling Commission;
   - agreements protecting birds (International Convention for the Protection of Birds (Paris, 1950); Benelux Convention on the Hunting and Protection of Birds (Brussels, 1970);
   - agreements concerning measures for protection of marine and polar region species (prawns, lobsters and crabs (Oslo, 1952); fur seals (Washington, 1957); Antarctic seals (London, 1972); Convention on Fishing and Conservation of Living Resources in the Baltic Sea and the Belts (Gdansk, 1973); polar bears (Oslo, 1973); salmon (Reykjavik, 1982); and
   - agreements protecting vicuña (Lima, 1979).

Since the biological diversity of the earth is also at risk from pollution, notice also needs to be taken of the substantial number of agreements in this field. At global level these include:

a) the Convention on the Prevention of Marine Pollution by Dumping of Wastes and Other Matters (London, 1972); and
b) the Convention on the Protection of the Ozone Layers (Vienna, 1985), with its Protocol on the regulation of the manufacture and use of chlorofluorocarbons (Montreal, 1987);

and at a regional level a substantial number of measures including the Convention on Long-Range Trans-Boundary Air Pollution in the European region (Geneva, 1979, with protocols), Conventions on the prevention of marine pollution in the waters of the north-east Atlantic (Oslo, 1972), and in the Baltic (Helsinki, 1983), the Regional Seas Conventions of UNEP, and a host of specific measures undertaken especially in Europe and North America.

The Regional Seas Conventions, prepared under UNEP auspices embrace both the protection of particular areas of the marine environment, the safeguarding of marine and coastal species there, and the coordination and strengthening of action against marine pollution in these areas. As such they extend across all three of the categories noted above.

DETAILS OF THE MAJOR INTERNATIONAL INSTRUMENTS FOR CONSERVING BIODIVERSITY

The four major international instruments that make significant contributions to conserving biodiversity are so important that they deserve some expansion. The following high-lights the main elements of these conventions.

1. *The Convention on Wetlands of International Importance especially as Waterfowl Habitat* (*Ramsar*, 1971). Depositary: Director-General, UNESCO. Secretariat: Provided by IUCN, with a branch at International Waterfowl Research Bureau headquarters in the United Kingdom (currently five permanent staff).
   - The only global nature conservation convention designed to cover a particular broad habitat type (inland, coastal and marine wetlands).
   - Broad in scope, as wetlands are defined to encompass a wide variety of areas including rivers, lakes, swamps, coastal areas, tundra, floodplains, and areas of the sea that are less than 6 m deep at low tide. This breadth in scope is both a strength and a weakness of the Convention, as management approaches vary so widely with the habitat type that it is difficult for all relevant agencies to be represented at meetings.
   - Contracting Parties undertake to use wisely all wetland resources under their jurisdiction (the wise-use requirement has been subject to much analysis by a Conference of Parties with guidelines developed for national implementation policies); Contracting Parties also agree to designate for conservation at least one wetland of international importance, under criteria provided by the convention for identifying such wetlands.
   - By January 1989, the 54 Contracting Parties had designated 421 sites (covering almost 30 million hectares) onto the List of Wetlands of International Importance; no site has been removed from the List despite the possibility to do so in "urgent national interest."
   - Requires the establishment of reserve areas for wetlands whether or not included on the List.
   - Monitoring procedure adopted by Standing Committee for secretariat to review status of listed sites and assist Contracting Parties in maintaining ecological character of sites.
   - Requires cross-border cooperation for shared wetland resources and international cooperation along flyways for migratory waterfowl.
   - Financial regime established as from 1 January 1988 based upon mandatory and voluntary contribution from Contracting Parties. Annual budget of SFr 600,000 plus project funding gives annual turnover in the magnitude of SFr 1 million.
2. *The Convention Concerning the Protection of the World Cultural and Natural Heritage* (*Paris*, 1972). Depositary: Director-General, UNESCO. Secretariat: Provided by UNESCO, with specialist assistance provided by IUCN and the

International Council on Monuments and Sites.

- Currently has 109 State Parties, the most of any conservation convention.
- Unique in its use of international NGOs (ICONOS and IUCN) as technical "arbitrators."
- Recognises the obligation of all states to protect unique natural and cultural areas, and recognises the obligation of the international community to help pay for them. The combination of both cultural and natural sites makes the Convention more comprehensive, but also weakens its focus; participation in meetings has tended to be far stronger from the cultural side than the natural side.
- Establishes exceptional World Heritage Sites, of which the natural properties (as opposed to cultural properties, which are far more numerous) protect wild animals and plants and their gene pools in those sites; convention is reinforced by national legislation in some countries, especially those with Federal systems.
- Includes on the list several of the most biologically diverse sites in the world, including Manu National Park (Peru), Queensland Rainforests (Australia), Dja National Park (Cameroon), Serengeti National Park (Tanzania), Great Smokies National Park (USA), Iguaçu (Brazil), and Sinharaja Forest Reserve (Sri Lanka).
- Establishes the World Heritage Fund to ensure that areas are not lost because of a local lack of money or skills (the Fund disperses nearly US$ 2 million per year). Each Party must contribute to the Fund, currently calculated at 1 percent of their contribution to the annual budget of UNESCO.

3. *The Convention on International Trade in Endangered Species of Wild Fauna and Flora* (CITES) (*Washington, 1973*). Depositary: Government of Switzerland. Secretariat: Provided by UNEP; currently located in Lausanne, with eight full-time staff.
    - As of March 1989, some 99 States Parties to the convention.
    - Establishes lists of endangered species for which international trade is to be controlled via permit systems, as a means of combating illegal trade and over-exploitation; revised appendices (listing protected species) now include 406 animals and 146 plants on Appendix I (which prohibits trade), and about 2,500 animals and 25,000 plants on Appendix II (which monitors trade).
    - Encourages international cooperation between governments and organisations to control such trade, particularly through informal consultations at the regular meetings of the Parties.
    - Establishes a network of national Management Authorities (to deal with mechanics of trade), and Scientific Authorities (to deal with biological aspects of trade) which operate in direct communication with each other and the secretariat.
    - Recommends that multilateral and bilateral development agencies assist development countries on request and facilitate exchange of administrative and scientific experience among trading countries.
    - Provides for a Trust Fund (established in 1979 under UN procedures) to finance the Secretariat and meetings of the Conference of the Parties.

- Directed at species rather than habitats, so has neither the goal nor the effect of protecting large areas of the environment from degradation.
- Has sometimes been criticised for being counter-productive in preventing tropical countries from marketing their wildlife products in industrialized countries, even though the species in question are under effective management regimes.
- Supported by technical advice from IUCN's Wildlife Trade Specialist Group, from WWF's TRAFFIC net-work, and from trade data managed by WCMS's Wildlife Trade Monitoring Unit.

4. *The Convention on Conservation of Migratory Species of Wild Animals* (*Bonn, 1979*). Depositary: Government of Germany. Secretariat: Provided by UNEP; currently located in Bonn, with a full-time staff of one.
    - As of August 1988, 24 State Parties had joined.
    - Convention addresses a wider range of threats to migratory species than is to be found in any other global convention. Obligates parties to protect endangered migratory species and to endeavour to conclude international conservation agreements for the conservation of migratory species.
    - Provides a framework for (1) international cooperation between range states for the conservation of certain species of wild animals that regularly migrate across or outside national boundaries, and (2) coordinated research, management, and conservation measures such as habitat protection and hunting regulation under regional and/or species-specific agreements.
    - Provides an important adjunct to wetlands and waterfowl conservation because of the high number of species of waterfowl that are migratory.
    - Provides an important species-by-species complement to a comprehensive scheme for the conservation of biological diversity, as international conventions are the only effective means of protecting animals that cross national boundaries.
    - Limitations include: insufficient Parties, lack of financial support, does not deal with fisheries.
5. *The Convention on Biological Diversity (Rio, 1992).* Depositary: Secretary-General of the United Nations.
    - As of June 1992, 170 countries have signed the Convention.
    - The Convention aims to achieve the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilisation of genetic resources, including the appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and technologies.

INVENTORY OF SPECIES

CHOICE OF SPECIES FOR CONSERVATION

P. KAPOOR-VIJAY

INTRODUCTION

Along with the degradation of ecosystems worldwide, thousands of species and even more genetic variants are being lost. The main causes of this destruction are: rapid growth in human population, unsustainable levels of resource consumption by the relatively affluent, and the impact of the increasing numbers of people struggling of survive. Some of the species (or species groups) under threat possess special economic and cultural significance, and/or are essential for the survival of their ecosystem. They are therefore regarded as "key" species. Conservation and integrated development strategies are needed to halt the biological impoverishment of the planet. Unless human numbers are stabilised and consumption levels are brought into balance with environmental capacities, these strategies will be ineffective.

Conservation efforts to save species and maintain ecosystems have expanded in recent years. Historically these efforts have tended to focus on the rare and the beautiful species. Today, there is increasing concern for species having particular ecological, economic and cultural significance. Although conservation priorities are recognised for species of obvious economic importance, such as rice, *Eucalyptus*, cows or catfish, many other species of key ecological and socioeconomic importance will be lost unless action is taken urgently, i.e. during the next 5 years.

KEY SPECIES

A small, but unknown, fraction of the world's biota of several million species has a disproportionately important role in the ecological processes that maintain life on this planet – including human life and essential biological diversity. These species are called "ecological key species" (or "amplifier species"). Similarly, another unknown fraction of the world's species, used by people and/or part of their culture, makes a disproportionate contribution to people's social and economic well-being. Such species are called "socioeconomic key species" (or "service species"). Both ecological and socioeconomic key species are "life support species". Conservation of these key species will result in the conservation of many other species.

Ecological key species and species groups are 'key' with respect to certain major natural processes, particularly: organic production, nutrient accumulation, habitat structuring, colonisation, herbiviory, pollination, seed dispersal, decomposition, predation, defence against parasites and predators.

Socioeconomic key species and species groups are 'key' with respect to certain

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categories of use, particularly:

commodities – important economic products such as foods, animal feeds, fibres, and medicines;

genetic resources (source of new domesticates and of improvements to established domesticates);

cultural value (significant contribution to the spiritual, emotional, and/or psychological lives of people);

environmental management (use to modify, stabilise or rehabilitate environments).

Certain species and species groups are key both ecologically and socio-economically (and some ecological and socioeconomic key species are important in more than one of the categories listed above. Key species or species groups are usually specific to particular ecological, cultural and economic circumstances. In other words, there are few, if any, universally key species. Likewise, one cannot anticipate which species, or which genetic variants, might become significant in the future. In other words, species not considered important today may become key tomorrow.

Although we know a large number of socioeconomic species, knowledge of key species among them is highly fragmented and often limited to their immediate users. We know much less about ecological key species and can identify only a few. Improving our knowledge of key species is essential; the starting point is in their recognition. As a preliminary step we list in Appendix I examples of key species that have *both* ecological and socioeconomic importance. Because of the rapid loss of species and reduction of genetic variability, direct conservation action is needed now. At the same time international research coordination to identify key species is called for. The sooner the results of research can guide action, the better.

FRAMEWORK FOR ACTION

A strategy for conservation and sustainable use of key species and species groups should include the following points:

- Management and protection of those areas where key species or species groups occur should ensure their long-term survival, at the same time recognising the needs and rights of the local human populations;
- Conservation plans to identify and maintain migratory key species should be developed;

  In human-modified ecosystems, the contribution of agriculture, silviculture and aquaculture to the maintenance and genetic improvement of socioeconomic key species should be encouraged;
- In degraded lands, restoration through use of key species and species groups, particularly nutrient accumulators and colonisers, should be promoted;
- The most efficient and best adapted species – and genetic variants of such species – should be identified;
- Native species and genetic variants of native species should be investigated and tested before using exotic species or variant.

  Particular attention should be paid to:

- species that serve as both ecological and socioeconomic key species;
- threatened ecological and socioeconomic key species;
- key species with known, yet unfulfilled, socioeconomic potential.

Governments should promote the identification of both ecological and socioeconomic key species, and assess their ecological and socioeconomic contribution, within their own countries. They should also support those local socioeconomic systems that are actually, or potentially, compatible with the maintenance of key species, and explore with the local people involved ways of supporting such systems. Governments should determine which key species are adequately maintained in the protected area system of their country, and should make adequate provision for the conservation of those species that are not adequately protected. They should also ensure that the germplasm of key species is properly collected, conserved and made available including, where appropriate, through captive breeding programmes. Regardless of their socioeconomic importance, species should not be translocated to new biogeographic provinces (whether marine or continental) without stringent evaluation of the ecological consequences.

FURTHER INFORMATION

More detailed information is available from the report of the international workshop *Identification of Key Species for Conservation and Socio-economic Development*, organised by the Commonwealth Science Council and the International Union for the Conservation of Nature and Natural Resources, held in Trinidad & Tobago, March 1989.

The following reference may be consulted:

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APPENDIX I. A few examples of key species having *both* ecological and socioeconomic importance (this list is by no means exhaustive, and is merely illustrative)

		ECOLOGICAL FUNCTIONS				SOCIOECONOMIC FUNCTIONS				
PLANT SPECIES (Common name indicated in parentheses)	Region of importance	Primary production	Nutrient accumulation	Habitat structure	Colonisation	Commodity	Genetic resources	Cultural	Environmental management	Reasons for inclusion
Trees										
Azadirachta indica (Neem)	SE Asia	*	*	*		*		*		Outstanding multi-purpose tree
Bertholletia excelsa (Brazilnut)	Brazil	*		*		*		*		Nuts harvested from wild only; now threatened
Dalbergia spp. (Rosewoods)	Worldwide	*	*	*		*				Grossly over-exploited high value timber
Mora excelsa	NS America	*	*	*	*	*			*	High value timber, vigorous; very localised distribution
Parkia roxburgii	SE Asia	*	*		*			*		Edible seed harvested from wild
Shorea spp. (Meranti)	SE Asia	*	*	*		*		*	*	High value timber, some species have edible nuts

Butyrospermum paradoxum (Butter nut)	Africa	*		*		*		*		Provides important source of income for women
Palms										
Bactris spp.	Latin America	*		*	*	*	*			Important for fruit and construction
Borassus spp. (Palmyrahs)	Africa, Asia	*	*	*	*	*	*		*	Many different uses (over 700 reported)
Calamus spp. (Cane palm)	SE Asia	*			*	*	*			Very important for handicraft industries
Jessenia	S America	*		*		*	*			Source of food, beverages and fibres
Mauritia flexuosa	S America	*		*	*	*	*			Source of oil and starch
Raphia excelsa (Raffia)	Africa	*				*	*			Major source of fibres
Bamboos										
Bambusa vulgaris (Common bamboo)	Worldwide	*	*	*	*	*	*			Major source of construction material
Dendrocalamus giganteus (Giant bamboo)	S Asia	*	*	*	*	*	*			Very fast growing, major source of construction material

		ECOLOGICAL FUNCTIONS				SOCIOECONOMIC FUNCTIONS				
PLANT SPECIES (Common name indicated in parentheses)	Region of importance	Primary production	Nutrient accumulation	Habitat structure	Colonisation	Commodity	Genetic resources	Cultural	Environmental management	Reasons for inclusion
Herbaceous Legumes										
Lespedeza spp.	S America/E Asia	*	*			*	*	*	*	Important tropical pasture legumes and in land restoration
Psophocarpus tetragonolobus (Winged bean)	SE Asia New Guinea	*	*			*				Edible tubers, pods and seeds of high protein content
Stylosanthes spp. (Stylo)	S America	*	*			*	*			Important as tropical pasture legumes, not yet fully developed
Grasses										
Cymbopogon spp. (Lemon grass, etc.)	Old World Tropics	*	*		*	*			*	Wild species good colonisers, cultivated species source of essential oil
Saccharum spontaneum (Wild cane)	SE Asia	*	*	*	*	*	*		*	Important for soil stability
Vetiveria zizanioides (Khus-khus)	Asia	*	*	*		*		*	*	Essential oil, roots for insecticide, handicrafts, good soil stabiliser

CRITERIA ON CHOICE OF SPECIES FOR CONSERVATION: WOODY PLANTS

CHRISTEL PALMBERG

SUMMARY

This paper describes existing strategies of conservation of genetic resources of woody species, outlining their respective advantages and underlining the fact that strategies described are complementary. A systematic approach is needed in trying to answer the two basic questions, "What do we conserve?" and "How do we conserve?". In such an approach, both technical/biological and socio-economic questions must be given due attention. The paper further describes some recent international initiatives which could decisively and positively influence future action in genetic conservation.

INTRODUCTION

A serious and often neglected consequence of deforestation and the degradation of ecosystems is the loss of genetic resources of plant and animal species. The tropical forests, which comprise the most complex and species-rich ecosystems in the world, are rapidly being destroyed or altered, causing unprecedented genetic impoverishment. The fragile ecosystems in arid and semi-arid areas are under increasing pressure from man and domestic animals which, coupled with climatic fluctations, lead to desertification and widespread environmental degradation. The influence of atmospheric pollution and fire on the structure and richness of temperate and Mediterranean ecosystems have created a similar threat to the genetic resources of a range of species, especially in Europe and North America. Simultaneously, the domestication and intensive selection and breeding of plants of economic value are homogenising populations, without due attention being paid to conserving the valuable variation that has developed in nature over millennia.

Genetic variation found within and between species serves a number of fundamentally important functions. It constitutes a buffer against changes in the environment (including those brought about by pests and diseases) and climate. It also provides the building blocks for human use in selection and breeding for adaptability to a range of environments and end uses. Genetic conservation is thus a means to achieve well-being, and some cases, essential for the very survival of people, who depend in their daily lives on the many goods and services provided by the woody vegetation. Sustainable development, is, to a large extent, dependent on

Conservation Biology: A Training Manual for Biological Diversity and Genetic Resources
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the conservation and wise utilisation of genetic resources of plants and animals. The need for conservation on a planned, coordinated and scientific basis is now a matter of urgency.

This paper is concerned with the *in situ* conservation of genetic resources of woody species. The term *genetic resources* is defined as the heritable variability of actual or potential value. The concept of value distinguishes genetic resources from the broader term of *genetic diversity*, which includes the totality of the heritable variability of plants, whether of proven or unknown value; and of known harmful organisms such as pests and diseases. Genetic diversity, and hence genetic resources, exists at both the between-species and within-species levels. Most efforts at conserving nature in the past have aimed at saving endangered ecosystems or endangered species. Much more emphasis needs to be placed on conserving valuable, genetically distinct populations or provenances within species; though conservation of genetic resources should not ignore the risks of losing whole species, it should always, and often mainly, be concerned with conserving useful diversity within species.

SAMPLING AND SITING OF RESERVES

The first step in any conservation programme consists of clarifying the objectives and priorities for conservation, including minimum requirements for success. The formulation of conservation objectives will assist in determining the strategy (or strategies) to be used.

Unfortunately, we do not today have information on the genetic variation within the great majority of plant species, which thus can only be inferred from environmental diversity. Ecological zoning of a species is a valuable first step towards identifying intraspecific genetic diversity. Such zoning has been carried out in several countries for some woody species, as a basis for delimiting zones for commercial seed collection, but it is equally applicable for siting reserves or for collection of genetic material for *ex situ* conservation. The simplest systems rely on measures of climate (e.g. rainfall) and contiguity of the populations, but variations in soil and vegetation type are sometimes used in addition.

Both in sampling for collection of genetic materials for *ex situ* conservation and in the establishment of *in situ* reserves, it is generally necessary to sample outlying populations, as well as the main occurrence of the species. Such outlying and sometimes isolated populations have often developed specific physiological and morphological characteristics, in response to diversified natural selection, which will be valuable in selection and breeding.

In the collection of material for *ex situ* conservation, sampling for variation (i.e. random rather than selective sampling within the populations) is essential for conserving the integrity of allele frequencies.

In addition to considering the geographic distribution of *in situ* reserves, based on ecological and/or genetic variation of priority species, the following criteria should be considered:

- Sites should be chosen where management requirements for conserving target populations and intraspecific variation are technically feasible.

- Sites should be chosen where protection would be least disruptive to traditional land use needs and patterns of ownership.
- Sites should be preferred in which conservation can produce other benefits, such as conservation of genetic resources of associated plant and animal species, watershed protection, safeguarding of cultural and heritage values, etc..
- Sites must be accessible for easy procurement of germplasm, and for research.

Number and sizes of reserves

According to Namkoong (Namkoong *et al.* 1980; Namkoong 1986), the maintenance of an array of multiple populations and their development on a number of different sites, using varying selection and management criteria ranging from minimum intervention to intensive selection for different and uses, is the most secure strategy available to ensure conservation of existing genetic resources. Such a strategy will assure maintaining a range of different allelic combination in the various populations, as these separate populations will adapt in response to prevailing environmental pressures and management regimes. This principle holds true both for conservation *in situ* and for conservation stands *ex situ*.

The minimum size of a reserve must reflect the mimimum number of individuals needed to constitute a genetically viable population. Based on experimental results and theoretical considerations, several scientists have put forward the figure of 50 non-related, freely interbreeding individuals as the minimum effective population size required for short-term fitness and survival; and 500 to sustain long-term genetic adaptability to change (see e.g. Roche & Dourojeanni 1984 and Namkoong 1979 for a more detailed treatment of the subject). Thus, it will be desirable to conserve a minimum of 500 representatives of each distinct ecotype (or provenance) of priority species.

Management

In order to maintain the genetic variaton in *in situ* reserves, it is generally necessary to manipulate the habitat. This is especially important in the case of pioneer species or sub-climax species, e.g. tropical pines or acacias, which are dependent on regular fires or other disturbances to regenerate. Because of the dynamic nature of natural forest ecosystems, *in situ* conservation of genetic resources is in fact not possible without management. Management plans, which take into account the factors outlined above, must be prepared to ensure *in situ* conservation of the genetic resources of target species and their subsequent rational and sustained use.

A fundamentally important consideration in the management of *in situ* reserves is that they must assure an uninterrupted supply of genetic material. Very large, old trees are those which arouse the most interest and deserve protection for recreational and touristic reasons; but if they become too overmature to produce seed or viable vegetative material for reproduction, they lose their value as a genetic resource. It is necessary to manage the reserve so as to maintain an array of age classes, so that there is never a lack of reproductive materials for new generations. The same principle governs the management of *ex situ* conservation stands; and also seed banks, which should not depend only on seed storage: part of the resources must be conserved in the form of living trees, preferably of differing age classes, which can produce seed crops with minimum delays, if required.

Generally, it is fully feasible to incorporate aspects of genetic conservation into the management plans of production forests, combining management for goods and services with the conservation of genetic resources; and to make management of protected areas compatible with *in situ* conservation of target species. To differentiate the reserve proper from surrounding areas managed primarily for other purposes, it may be recommendable to demarcate a buffer zone to absorb the effects of practices not compatible with the conservation activities (UNESCO/MAB 1984). Once conservation priorities have been defined, it is important to monitor the situation continually, to ensure that the objectives of conservation are met.

It is important to recognise that the genetic variation present in populations today probably is not in a stable evolutionary state, but that it will fluctuate over time within given, biologically determined limits. Because existing information is so meagre, research on ecosystem dynamics together with genecological, taxonomic and biological studies of target species must form an integral part of any strategy of *in situ* conservation.

DISSEMINATION OF INFORMATION

In all conservation programmes, it is fundamentally important to raise the awareness of the importance of conservation action at local, national and international levels. This action should address the need for informed interest among rural communities as regards their local reserves, among land-use planners concerned with integrating genetic conservation with land management, and among the international community which should facilitate the flow of information, reproductive materials and aid between countries. Information on genetic resources must first be acquired locally and should always be available locally, but plants are no respecters of polictical boundaries, so information needs to be compiled and disseminated also at national, regional and international levels. The case for efficient computerised data storage and retrieval systems of both *in situ* and *ex situ* genetic resources is already strong, and will become stronger as information accumulates.

Management of genetic resources is still a new subject. Training courses, including on-the-job training, which are devoted specifically to genetic resources, will be of prime importance at all levels. In addition, genetic resource management should be injected as an essential component of more general training courses, both for scientists (agronomists, foresters) and for administrators (land-use planners, economists, etc.).

NATIONAL AND INTERNATIONAL ACTION

Conservation of ecosystems and the conservation of genetic resources must be integrated with each other, and both treated as an integral part of development and overall land-use policies and land husbandry.

Conservation of nature, often with emphasis on fauna, has long been practised in national parks. Managed forests reserves, in contrast, combine production of wood with the regeneration and conservation of tree species which produce it, as well as protection of soil and water resources. Both national parks and forest reserves protect plants (and the genes packaged in plants), but we need reassurance on two main questions: (i) What is being conserved? What percentage of the total genetic variation and/or of existing genetic resources is included in the protected areas? Do the siting and size of such reserves respond to the objective of conserving the intra-specific variation of target species? (ii) How well is it being conserved? Does conservation combine effective protection against destruction or adulteration of the genetic resource with the opportunity for its wise use and provision of information and genetic materials to scientists, geneticists and *ex situ* gene banks?

What to conserve

According to an FAO/UNEP assessment on tropical forest resources (Lanly 1982), which included 76 tropical countries and 97% of the total area of the tropical forest, national parks and equivalent reserves contain 41 million hectares of closed forests (mostly moist and wet types of the humid tropics), which is less than 3.5% of the total area of these forest types; and 45 million hectares of open forests (mostly mixed forest-grassland formations of the dry tropics, such as African savanna woodlands, or the Chaco or Cerrado of South America), or about 6% of the total areas of these woody vegetation types; i.e. a total of 86 million hectares, or less than 4.5% of the total area of tropical forest formations. Annual deforestation is estimated at a total of 11.3 million hectares (0.58%).

Even though it is difficult to relate loss of species to rates of deforestation, complementary information on endangered species and ecosystems is, at least partially, available from other sources. Maps have been prepared in many countries which show the distribution of (i) protected areas, (ii) vegetation types, and (iii) the presently most important species. International action in the mapping and description of protected areas has been taken, among others, by IUCN (Commission for National Parks and Protected Areas; Conservation Monitoring Centre; Plants Programme) and UNESCO (Biosphere Reserve Programme). It is important to underline that where plant inventories are carried out, not only occurrence, but also relative abundance of a species in a given area must be indicated. Based on such information, it should be possible to estimate how well ecosystems and socio-economically important species are represented in already-existing protected areas.

There are thousands of woody species in the tropics. It is estimated that the forests of the Malay Peninsula alone contain approximately 2,500 species of trees; and one hectare of Amazon forest may contain more than 500 woody species. However, not all woody species of the tropics are utilised. Nevertheless, if all of those presently used for wood, food, fodder and a great diversity of medicinal and other products by local people are taken into account, they will number several thousands.

It is thus obvious that priorities for action must be set in conservation programmes; some guidance to setting of priorities is contained e.g. in the lists of Forest Genetic Resources Priorities (by region, species and operation), published in the reports of the FAO Panel of Experts on Forest Gene Resources. The most recent list (FAO 1984) includes over 140 tropical species rated as 'priority 1' for some form of conservation, of which 81 are endangered (see Appendix). These are largely species important for wood production, but many also have leaves, flowers, fruits or roots which are used for food, fodder or medicinal purposes, for the extraction of gums and resins, etc. As this list contains species which are mainly of international or regional importance, it is essential to complement it with national and local lists.

The selection of populations within a species is more difficult, because few tropical species have been subjected to systematic genecological investigation. Even species producing a major commercial product, – for example, *Acacia senegal* which produces gum arabic in dry-zone Africa – have not until recently been subjected to such investigations, and their genetic potential remains largely unknown (Palmberg 1981). However, it is known that almost every temperate and tropical tree species that has been subjected to genecological investigation shows a remarkable degree of intraspecific genetic variation, nearly always related to variation of habitats. Furthermore, the characteristics of the species exhibting this variation are often of major economic importance. When genetic resources are in danger, there are no excuses to delay action in conservation until results are available from studies on intraspecific variation. However, genecological studies must proceed hand in hand with conservation programmes. In this context, it is important to realize that field trials established to clarify variation patterns and intraspecific variation of species, if correctly laid out with this in mind, can also as such contribute significantly to conservation efforts.

Recent international initiatives

Although some 40 countries have prepared National Conservation Strategies, which include the conservation of plant genetic resources, it remains extremely difficult to identify projects where *in situ* conservation is actually one of the stated objectives and is being practised; also systematic efforts in *ex situ* conservation are relatively few and scattered, and have been concentrated on a few industrially valuable species.

In Canada and in the Nordic countries, efforts have been going on for some time to conserve *in situ* gene pools of native, temperate species *(Pinus, Picea, Betula)* (FAO 1975). In the tropics, FAO/UNEP in collaboration with the Government of Zambia, has demarcated two reserves for the *in situ* conservation of the forest tree species *Balikaea plurijuga* (Zambesi redwood or Zambian teak), and lists of associated tree, shrub and climber species growing in the reserves have been compiled (FAO 1985d). There are also proposals to conserve *in situ* important populations of the drought-resistant shrub species *Prosopis cineraria* in the Balhaf area of the People's Democratic Republic of Yemen, with the technical and financial assistance of FAO.

Pilot areas are, furthermore, being developed within the framework of a FAO/UNEP project in Cameroon, Malaysia and Peru, for the *in situ* conservation of a number of important woody species, which provide a range of goods and services (FAO 1985, 1985a, 1987, 1972-85 (esp. no.13/1985); Roche & Dourojeanni 1984).

As regards fruit trees, the first gene sanctuary – for *Citrus* – has been designated in the Garo Hills, Meghalaya, India; and it is expected that Biosphere Reserves such as the one proposed for the Nilgiri Hills in the Western Ghats (rich in wild forms of arecanut, ginger, tumeric, cardamom, black pepper, mango, jackfruit, plantain, rice and millets) will have gene-pool conservation as a major objective. IBPGR has recently contracted IUCN to study the possibilties of establishing an *in situ* gene bank for wild species of mango (*Mangifera*) in Indonesia. The first step in this project has been the exploration of the existing resources and their ecological variation in the natural distribution area of the genus.

Ex situ conservation activities include the establishment of more than 400 hectares of *ex situ* conservation stands in six tropical countries in the 1970s, within the framework of an FAO/UNEP project. These stands were established using a total of eleven provenances of pines and eucalypts, which had earlier been studied and evaluated in international provenance trials (FAO 1985d; see also FAO 1977 and FAO 1972-85 (no.10/1981)). Several of the countries which participated in the FAO/UNEP project have later established additional national conservation stands, using the same methodology of the project; and this methodology has recently been adapted also to other genera of woody species (see e.g. Palmberg 1981).

This brief review of efforts in the field of conservation of plant genetic resouces indicates that measures are very recent and cover only a small fraction of the needs. However, two events may give a major push to conservation programmes; the establishment of an Inter-Governmental Commission, the FAO Commission on Plant Genetic Resources in 1983 (FAO 1972-85 (esp. no.13/1983)); and the elaboration of FAO's Tropical Forestry Action Plan, published in 1985 in response to the recommendations of FAO's Committee on Forest Development in the Tropics (CFDT) (FAO 1985b, 1986). At its First Session in March 1985, the FAO Commission on Plant Genetic Resources paid particular attention to four aspects of plant genetic resources: (i) base collections of plant genetic resources; (ii) status of *in situ* conservation of plant genetic resources; (iii) international information system on plant genetic resources; and (iv) training activities and training requirements in the fields of plant genetic resources, plant breeding and seed production. The Commission, to which 67 member Governments of FAO adhered at the time of its First Session, recommended that necessary action be taken to ensure global coverage of the International Undertaking on Plant Genetic Resoruces (adopted by the 22nd Conference of FAO in November 1983). The Undertaking aims to ensure that "plant genetic resources of economic and/or social interest, particularly for agriculture, will be explored, preserved, evaluated and made available for plant breeding and scientific purposes". The Undertaking is open to all countries, and is based on the universally accepted principle that plant genetic resources are a heritage of mankind and consequently should be available without restriction. The Undertaking will seek to facilitate the exchange of genetic material, to promote international cooperation in the conservation, evaluation and documentation of plant genetic resources, and establish an internationally coordinated network of national, regional and international centres, including a network of base collections of gene banks under the auspecies or jurisdiction of FAO. Further, the Commission underlined the need for urgent and increased, globally-coordinated action in all the fields examined (FAO 1985C).

The Tropical Forestry Action Plan is a conceptual framework for the harmonization of international action programmes in developing countries; it has been recognized at various international fora, by a large number of countries, international organizations and donors (CEDT and the Council of FAO; the 9th World Forestry Congress in Mexico in 1985; the Silva Conference in France in 1986, etc.). Considering the collective needs of tropical needs of tropical countries, five priority areas have been selected: (i) forestry in land use, (ii) forest-based industrial development, (iii) fuelwood and energy, (iv) conservation of tropical forest ecosystems, and (v) institutions. The programme on conservation of forest ecosystems contains proposals on the development of national networks of protected areas; assistance in the planning, management and development of individual protected areas and *in situ* reserves; conservation *in situ* of genetic resources of woody species; and the active promotion of research into management of tropical forests for sustainable production.

Funding requirements to support the programme components of tropical forest ecosystem conservation over 10 years, have been estimated to amount to US$ 661 million, with the share of international development assistance being approximately 50% of this total cost; plus foreign investment amounting to 80-100% of the national contribution towards the programme. Action within the framework of the TFAP has been started at national level, through multi-sectorial and multi-donor missions to countries which have expressed their interest in the elaboration of a national programme; and national round-tables, as a first step in the elaboration of such programmes, with or without the participation of international agencies. The focus point for the TFAP is the Forestry Department of FAO.

CONCLUSIONS

The concerns for conservation of genetic resources have steadily increased over the past 20 years. However, efforts have been minimal when compared to global needs, and most of the strong recommendations of national and international meetings in this field have been left unheeded. Two recent events, the establishment of the FAO Commission on Plant Genetic Resources and the launching of FAO's Tropical Forestry Action Plan, give some hope for increased and concentrated action in this field in the future, at international, regional, sub-regional and national levels.

Genetic resources are a common heritage of mankind; they should be made available to promote development in present generations while, at the same time, their availability for the benefit of future generations must be assured. The management and sustained utilisation of these resources must therefore be given the highest priority. Degraded lands and watersheds may be rehabilitated, and denuded hillside reforested; but when a plant or animal species becomes extinct, or genetic variation is depleted, the loss is permanent. If human beings cause massive disturbance to natural environments, as is at present the case, they can no longer leave the conservation of genetic diversity to nature; they must take active steps to conserve it themselves. The remaining years of this century are critical for genetic resource conservation, especially in the tropics: time is running out and it is essential that we vigorously confront the challenge facing us.

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ACRONYMS

FAO Food and Agriculture Organization of the United Nations
IBPGR International Board for Plant Genetic Resources
IUCN International Union for the Conservation of Nature and Natural Resources
UNEP United Nations Environment Programme
UNESCO United Nations Educational, Scientific and Cultural Organization

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APPENDIX

Forest Tree Species: Conservation Priorities by Regions

At its 5th Session in December 1981, the *FAO Panel of Experts on Forest Gene Resources* drew up a list of woody species and genera which are considered to be need of attention in any one of the field operations (exploration, collection, evaluation, conservation, utilisation). These priority species, arranged by regions, are based not only on the information of the Panel Member and his/her alternate, but also on information gained through consultation with institutes, organisations and professionals in the regions and individual countries, identified for their knowledge in the genetic resources field.

The full list of species, with priority ratings from 1 (urgent attention needed) through 3 (medium priority) to 4 (action already started and activity adequately covered by existing schemes), can be found in Appendix 8 of the Report of the Panel (FAO 1984).

The table below summarises some of the information contained in the list, showing number of priority species by region and the number of species rated priority 1 in conservation; 81 of these species are considered endangered with extinction in all, or part of, their natural ranges. It should be recognised that any list will reflect present-day knowledge: exact information on the status and on the potential value of a species will become available only in the course of exploration and evaluation.

Country/Region	No. of species rated Priority 1 for conservation activities*	Total number of species identified**
Africa	36	55
South/SE Asia	30	45
Mexico	31	54
Brazil	30	56
Caribbean, Central/South America (excl Brazil)	28	44
South Europe, Mediterranean, Near East	16	33
North/NE/Central Asia	13	192
Australia	5	159
U.S.A. and Canada	2	65
North/Central Europe	–	15
Totals	191	718

* Conservation *in situ*; collection for conservation; conservation *ex situ* in (i) live collections / *ex situ* conservation stands and (ii) as seed.

** Priorities 1-3 in exploration, collection, evaluation, conservation and utilisation.

CRITERIA FOR SELECTION OF CONSERVATION AREAS FOR FOREST GENETIC RESOURCES

L. ROCHE and M.J. DOUROJEANNI

INTRODUCTION

Tropical forests, which provide habitats for an extraordinarily diverse flora and fauna, constitute the last great natural plant and animal communities on the face of the earth. We are very ignorant about these communities. Species are often known taxonomically, and many have yet to be discovered and named. Furthermore, we frequently do not possess the knowledge that local people have concerning the everyday use of forest products. With the disruption and destruction of these forests, nations may forego use of tropical forest genetic resources before they are even known.

Concern for the conservation of genetic resources in general, and of forest genetic resources in particular, has been building up steadily over the past twenty years. The establishment of UNEP stimulated action on conservation and gave rise first to a report on the methodology of conservation of forest genetic resources (FAO 1975) and then to field projects in a number of African and Asian countries. The latter produced positive results in seed collection for conservation purposes and in the establishment of a number of *ex situ* conservation stands. It proved much more difficult to identify and carry out field projects for *in situ* conservation, but the project assisted in setting up the Malvwe Botanical Reserves in Zambia for the *in situ* conservation of genetic resources of *Balikiaea plurijuga.* The comparative lack of success in generating field activities for *in situ* conservation led to the FAO/UNEP Expert Consultation on *in situ* Conservation of Forest Genetic Resources, which advised on guidelines for the selection and management of *in situ* genetic conservation areas and identified a number of needs for international action (FAO 1981). Among them was the preparation of a guide on *in situ* conservation of forest genetic resources, with special reference to the integration of the management of genetic resources with forest and land management (Roche & Dourojeanni 1984).

There have been references to the *need* to conserve forest genetic resources in the tropics (e.g. Burley & Styles 1976; IUCN 1980), as well as proposals for conserving genetic diversity in temperate countries but no detailed prescriptions on *how* to go about *in situ* conservation of genetic resources, still less examples of projects where conservation measures are already being implemented. This confirms that there is still a need to be filled. *Resources* are defined as "a means of supplying some want of deficiency" (Shorter Oxford Dictionary); therefore, they should be of *value* for

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one or more purposes. Because future needs cannot be forecast precisely in the present state of knowledge, the value may be *actual* and immediate or *potential* for the future. A second definition given for resources by the Shorter Oxford Dictionary "a stock or reserve upon which one can draw when necessary", is a salutary reminder of the need to emphasise the importance of the genetic resources of a potential value, which have often been neglected in the past. Those of immediate value, such as advanced cultivars of crop plants or forest trees widely used for afforestation, run little risk of being lost; it is the wild relatives of crop plants and wild forest trees which have promise but are still unproven, that merit high priority, especially for *in situ* conservation.

The concept of value distinguishes *genetic resources* from the broader term of *genetic diversity*, which includes the totality of plant and animal heritable variability throughout the world, whether of proven value, or of known (or unknown) harmful organisms, such as pests and diseases. Genetic diversity, and hence genetic resources, exist at both the between-species and within-species levels. Most efforts at conserving nature in the past have aimed at saving endangered ecosystems or endangered species. Much more emphasis needs to be placed on conserving valuable populations or provenances *within species*, because there is increasing evidence of the wide variation which can occur. Though conservation of genetic resources should not ignore the risks of losing whole species, it should always, and often mainly, be concerned with conserving useful diversity within species.

The main emphasis of this chapter is directed towards the conservation of woody species. The term 'forest genetic resources' has often been used in the past, but is sometimes interpreted as applying mainly or exclusively to closed forests. Although the tropical moist forests contain the greatest wealth of genetic diversity and have received most attention in recent literature, the woody species of the more arid areas are also very important and are still more critically threatened. Arid and semi-arid zone vegetation cannot be called forest, but small, scattered trees and shrubs in these zones have great value for fuelwood, soil stabilisation, etc.

It is not possible to provide detailed guidelines on *in situ* conservation of forest genetic resources appropriate for every contingency. The ecological and socio-economic differences within and between nations and the diversity of conservation problems are too great to allow such an attempt. In addition, there is a lack of descriptive information on almost every aspect of the general problem, and even uncertainty in regard to basic scientific criteria, e.g. given the conservation objectives, what number of individuals constitutes a breeding population of a given tropical hardwood? What is the minimum critical size of a strict natural reserve when buffered by a managed, utilised forest? What is the minimum size of a reserve when not buffered by a managed forest? What should be the size of a buffer zone and how should it be managed?

The remaining years of this century are critical in terms of conservation of forest genetic resources in the tropics. There is not much time left. Therefore, despite the lack of information, and general uncertainty in regard to scientific criteria for *in situ* conservation, it is necessary to act now and to provide guidelines, however broad, for practical field programmes of *in situ* conservation of woody genetic resources.

CHOICE OF CONSERVATION STRATEGIES

In the past, conservation of genetic diversity by man was unconscious, and related to use. Material was conserved because it was immediately useful, not because it was diverse. As long as agriculture was practised on a multiplicity of different site types and exchange of seeds was limited to short distances, the conservation of many locally useful cultivars incidentally conserved a great amount of overall genetic diversity.

The 20th century movement for the establishment of national parks, forest reserves, wildlife reserves, etc. has also been beneficial in conserving genetic diversity of woody species, but again this has been incidental rather than deliberate. National parks have been designed to protect ecosystems or individual species but emphasis has often been concentrated exclusively on the larger mammals or birds and the need to conserve within-species genetic diversity of plants has not been considered. Because of the increased scale of man-made disruption of tropical ecosystems, previous *laissez-faire* methods of genetic conservation must now give place to more deliberate planning, and more positive management of genetic resources. The two critical questions to decide are (i) what to conserve? and (ii) how to conserve it?

The broadleaved tree species of the tropics occur in their thousands. It is estimated that the forests of the Malay Peninsula alone contain approximately 2500 species of trees. Not all woody species of the tropics are utilised. Nevertheless, if all those presently used for wood, food, fodder and a great diversity of medicinal and other products by local people are taken into account, then the number of useful species is, at least, hundreds.

Some guide to selection of species is contained in the lists of Forest Genetic Resources Priorities (by region, species and operation) published in the reports by the FAO Panel on Forest Gene Resources: these include over 140 tropical species rated as priority 1 for some form of conservation, of which 60 are endangered. These are primarily for wood production, but many other species have leaves, flowers, fruits or roots which are used for food, fodder or medicinal purposes. In Nigeria, for example, field assessment has shown that there are 150 species of woody plants covering 103 genera and 48 families used by local people for a variety of nutritional purposes (Okafor 1977, 1980).

The selection of populations within a species is more difficult, because few tropical species have been subjected to systematic genecological investigation. Even species producing a major commercial product, for example, gum arabic from *Acacia senegal* in the Sudan, have not until recently been subjected to such investigations and their genetic potential remains largely unknown (Palmberg 1981).

Almost every temperate tree species that has been subjected to genecological investigation has shown a quite remarkable degree of genetic variation, nearly always related to variation of habitat. Furthermore, the characteristics of the species exhibiting this variation are often of major sub-tropical species; e.g. *Eucalyptus* *camaldulensis* (Lacaze 1978), and *Pinus caribaea* (Gibson 1982) have shown that genetic variation in these is at least as great and economically important as in temperate species. The number of tropical species which are not currently utilised far exceeds those that are exploited in the natural forests, still more those that are planted. Specific action to conserve each of these unproven, and largely unknown species is impracticable, but many of them may be conserved incidentally wherever *in situ* conservation of associated valuable species and their ecosystems is practised.

The choice of conservation strategy for any plant species or population – how to conserve the genetic resource – will be determined by the biology of the species and the degree to which it is known and used by man. The strategy may be *ex situ* or *in situ*; very often it will be a combination of both. Just as lack of knowledge complicates the choice of what to conserve, so it renders difficult the choice of how to conserve. Where genetic resources are endangered, there is no justification in delaying the development of conservation strategies for particular species until the results of studies of intraspecific variation of these species are known. Genecological investigation, however, should proceed hand in hand with conservation programmes. In this regard it is important to note that the comparative field trials of genecological research can themselves, when appropriately designed, make a significant contribution to *ex situ* conservation of arboreal genetic resources (FAO 1975; Roche 1971).

Genecological research involves the phases of exploration, collection of reproductive material and evaluation of the material through comparative provenance trials. The sort of questions which need to be answered for the tropical example of a woody species traditionally exploited for wood but known only taxonomically are:

- What is its actual distribution and regeneration capacity?
- Does it occur in parks or protected areas, nationally and in neighbouring countries?
- Does it grow in different edaphic and climatic zones in different parts of its range?
- What are its breeding system, modes of pollination and of seed dispersal?
- What are the principle factors influencing its reproductive and vegetative phases?
- What are the largest and smallest values of a given character, physiological or morphological, for the species as a whole?
- Do values for different localities of origin depart significantly from the mean of the species?
- Over what part of its range is it the most variable, over what part the least?
- Are there distinct forms, and if so what is their comparative frequency in different localities?
- Can the species be propagated vegetatively?
- Can seed and/or pollen be stored and if so how long will they remain viable?
- Can the species be grown as a monoculture?

IN SITU CONSERVATION: PRINCIPLES AND PRACTICES

Now and in the immediate future, as in the past, areas will be set aside with the objective of conserving the habitats of particular mammals and plants which are considered to be endangered. The impetus for such action will often arise from national and international publicity and pressure for conservation, and the size and shape of the area set aside will often be determined pragmatically on the basis of local constraints and opportunities, social and legal considerations, and very general ecological data, rather than on the results of scientific investigation of the problem. In the absence of more detailed scientific criteria such an approach is inevitable. In recent years, however, with the development of conservation biology as an applied science, there is an increasing awareness of the need for a firmer data base for national conservation action, particularly in regard to *in situ* conservation.

Since the publication in the 1960s of the theory of island biogeography, there have been many papers which deal with the implications of the theory in conservation practice. The theory has been developed primarily on the basis of studies of bird populations on islands, and its basic tenet is that there is a close and predictable relationship between the size of a conserved habitat and the number of species present in the habitat. Species composition may change but not the total number which is an equilibrium established by immigration and extinction rates. Immigration rates are inversely related to isolation from a potential source of colonisation, while extinction rates are inversely related to population size and proportional to isolation. Thus, on this basis, large reserves are better than small. If the reserved area is reduced in size, the number of species present will come to a new equilibrium at a lower level characteristic of the size and position of the site (see e.g. Terborgh 1975; Wilcox 1980; Lovejoy *et al.* 1983). The theory has been extended to all species and to mainland reserves which are surrounded by large areas of land massively changed by man's activities, e.g. agriculture and urban development, and which can therefore be expected to have the same species – area relationships as islands.

Here, we extract and highlight those elements of the theory which provide additional criteria in guiding research, in planning *in situ* conservation programmes of forest genetic resources, and in the management of these resources in protected areas. This can be appropriately done under the following headings: (i) species – area relationships, (ii) mininum population size, (iii) minimum area requirements and (iv) ecosystem dynamics.

But first a word on what Wilcox (1982) has called the *focus* of *in situ* conservation. The establishment of a protected area may focus on either conserving some specific type of community, e.g., the Peat Swamp Forests or Heath Forests of Malaysia, or a particular and important tree species of one of those communities such as *Gonystylus bancanus* found in Peat Swamp Forests. A protected area may also be established to conserve genetically distinct populations of *Gonstylus bancanus* if such have been identified. Therefore, three different foci of *in situ* conservation can be distinguished, that is, community conservation, species conservation, and gene conservation. Wilcox goes on to point out:

> "It is important to realise that preserving communities is not the same as preserving genes. Since communities are classified according to vegetation structure, and dominant plant and animal species, it is quite possible to preserve a community-type and still lose many species. It is also possible to preserve a species and lose genetically distinct populations, although this loss may contribute

in the long-term to its extinction. Although *in situ* conservation requires that biological diversity be considered as a whole, that is, in the form of intact communities, the type of conservation strategies employed and their outcomes may differ somewhat depending on the focus."

SPECIES – AREA RELATIONSHIP

There are many examples which illustrate the relationship between the size of a sampled area and the number of species encountered, both for tree species and animal populations. Nearly all species – area curves are similar in so far as the addition of equal amounts of area result in fewer species being added. Areas set aside to ensure the conservation of particular plants and/or animals are often initially samples of large intact ecosystems. Thus, the Serengeti National Park in Tanzania and Manu National Park in Peru are samples of African savanna and Amazon rainforest, respectively. They contain fewer species, fewer individuals within species, and more species represented by only a few individuals than would similar but larger reserves (Wilcox 1980). On average, a reserve of this type will initially exclude approximately 30% of the species of the original large community for every ten-fold decrease in area. For example, a reserve of 10 km^2 will contain only 7 out of every 10 species found in 100 km^2 of surrounding habitat and only 4 out of 10 species found in 1000 km^2. This initial exclusion of species has been referred to as the 'sample effect' (Wilcox 1980). 'Insularisation' results when the habitat surrounding a reserve is destroyed. The reserve then becomes an ecological island with limited opportunities for recruitment of species. The rate and extent of species reduction in such a reserve are dependent on the initial number of species present as well as the size of the reserve.

As already indicated, these general conclusions are made primarily in relation to studies of animal populations. It has yet to be determined to what extent they have equal validity for tree species of either tropical moist forest or savanna woodlands, and their distribution in protected areas, particularly if the protected area is surrounded by managed forest, such as the Virgin Jungle Reserves of Malaysia. In one of the few published studies of woodlots as biogeographic islands no species – area relationship was demonstrated and the author of this excellent study (Levenson 1981), which provides guidelines for future research, concluded that, attractive as the ability to predict plant species richness by island size appears, additional variables, such as heterogeneity of site, must be taken into consideration. Adding more of the same habitat does not necessarily increase the number of species in the reserved area. Confirmatory evidence is available from the United Kingdom, where a species of small reserves in ancient woods yielded more species than a single large one (Game 1980). There is, of course, ample evidence of species – area relationships for tropical tree species in continuous relatively undisturbed habitats. However, the study referred to here relates to broadleaved woodlots of varying size surrounded by agro-urban environments. The relevance of island biogeography theories to plants has still to be demonstrated. As for populations, so for species, it seems unlikely that area *per* *se* is much less important than the number of breeding individuals required for long-term genetic adaptability and the area of habitat which they need to sustain them.

Minimum population size

A basic rule of conservation genetics is that, for normally outbreeding organisms, the amount of inbreeding should be kept a minimum. Soulé (1980) recommends no more than 1% inbreeding per generation. Although the evidence is scanty, it is safe to assume that most tropical woody species are to varying degrees heterozygous outbreeding organisms (see chapter by Bawa in this volume). The smaller the population of an outbreeding species, the greater the degree of inbreeding that is likely to occur, leading to loss of fitness and increased mortality.

Inbreeding depression is, of course, not the only factor resulting in increased mortality in a conserved population. Dramatic losses can occur in relatively large populations in even one generation, for example, as a result of insect attack. However, in such instances the long-term loss of heterozygosity is generally not severe; variation that is lost following a sudden decline in population numbers in one generation may be recovered in subsequent generations, depending on how fast the population increases in numbers to several hundred or more. On the other hand, chronically small populations, such as those isolated in small protected areas, produce random gene frequency changes which may lead eventually to fixation of some alleles and loss of others. Such random fluctuations are referred to as genetic drift. A few generations of genetic drift is much more erosive of genetic variation in a population than a dramatic reduction in numbers followed by a rapid recovery.

Therefore, in seeking to ensure *in situ* conservation of the genetic resources of a particular species, the forester is faced with the fundamental question as to what constitutes a *minimum viable population.* In other words, what is the minimum number of individuals which must be maintained in a protected area or areas to conserve all or a particular part of the spectrum of genetic variation within the species? At the present time, the forester cannot draw on studies of tropical species in determining this figure. Appropriate data are simply not available. Nor is the situation much better for temperate species.

Based on experimental work with animal populations and on theoretical considerations, several workers have put forward the figure of 50 as the minimum effective population size required for short-term fitness and survival and 500 to sustain long-term genetic adaptability to change (Franklin 1980, Frankel & Soulé 1981). Independently estimates by other authors are also of the same order (Marshall & Brown 1975). These rule-of-thumb estimates are the best available at the present time, and the higher figure provides guidelines for the forester in decisions concerning size and shape of a protected area. Thus, in theory, once a target species is identified, and on the assumption that inventory data are available, it is possible to determine the area that is required to contain a minimum of 500 individuals of the species. A figure higher or lower than 500 would require the monitoring of genetic variation in the target species, and the adjustment of effective population size in accordance with the observed rate of change in the level of variation. As Frankel & Soulé pointed out, for most species this suggestion is impractical at least for the immediate future.

In regard to the conservation of wild woody genetic resources, 500 trees would form a particular population which might include a portion of the clinal pattern of genetic variability within the species or, in the case of isolated populations, could represent an endangered and unique ecotype. If the species itself is endangered throughout its range rather than part of it, then it would be desirable to conserve up to 500 representatives of the species for each endangered and distinct ecotype.

Ecosystem dynamics

To varying degrees, most tree species of tropical moist forests are integrated with and dependant on the ecosystem in which they occur. The ecological niche which each species occupies is provided by the presence of other components of the ecosystem, both plant and animal, as well as by the abiotic environment. Knowledge of the biology, variation and management of most tropical species is almost entirely lacking. Repeatedly in the future the forester will be concerned with *in situ* conservation of forest genetic resources of just such species. The only information at his disposal is likely to be forest inventory data which indicate increasing scarcity of the species as a result of exploitation and the conversion of forest land to other uses. It is not possible to ensure *in situ* conservation of the genetic resources of such species, nor indeed species for which more information is available, without an understanding of some basic ecological principles concerning ecosystem dynamics. If the genetic resources of these species are to be conserved, it will be necessary to ensure the integrity and conservation of the ecosystems in which they occur.

Co-evolution has ensured the interdependence of plant and animals. In tropical forests a diversity of animals depend on tree species for food, and in turn ensure the perpetuation of the tree species either by acting as pollen vectors or by the dispersal of seed. It has been shown that, of some 40 species of *Ficus* studied in Central America, only one had two species of pollen vector; each of the others relied on a single vector. Of the two broad taxa of *Ficus* studied, each possessed its own pollinator, a species of wasp (Agaonidae). Introduced species of *Ficus* did not produce seed if the right pollinator was missing (Ramirez 1970). This interdependence of vector and tree species indicates that, if the ecosystem were so disrupted that the vector were no longer present in sufficient numbers to ensure pollination, seed set would be reduced, and the *Ficus* species eventually eliminated if no change in the breeding system occurred. The genus *Ficus* is often a major source of food supply for animal species, hence its elimination from an ecosystem would trigger other effects leading to ecosystem impoverishment.

Animals that are significant factors in the persistence of plant species have been termed 'mobile links', and organisms, typically plants, which provide critical support to large numbers of mobile links have been termed 'keystone mutualists' (Gilbert 1980). A single large fruit-bearing tree species may depend on only one mobile link, for example a bat or a small mammal, for effective seed dispersal. Yet such trees can provide critical support for several other fruit-eating animals. The loss of a single key species from a conserved ecosystem could result in the disappearance of many other species, including tree species conserved because of utility and scarcity. In addition to taking into account the role of such ecologically important species and their linkages, the conservation manager should also have information about ecological heterogeneity due to disturbance, succession or variation in the physical environment. Ecological heterogeneity results in resources for organisms which are patchily distributed. As already indicated, simply adding more of the same habitat to a reserve does not necessarily increase the probability of survival of the conserved species. For a fuller treatment of heterogeneity and disturbance in tropical vegetation see Foster (1980).

For all of these reasons, the conservation of a particular tree species, or part of the genetic resources of that species, is not necessarily guaranteed by ensuring that 500 representatives of the species are conserved in a particular reserve. As much information as possible must be obtained concerning ecosystem dynamics before the size and shape of a new reserve is decided upon. Such information is also requisite in judging the effectiveness of the existing protected area in conserving particular genetic resources. Because existing information is so meagre, research on ecosystem dynamics together with genecological studies of target species must form an integral part of an strategy of *in situ* conservation of woody genetic resources.

MANAGEMENT

It must be now apparent that *in situ* conservation of genetic resources is not, because of the dynamic nature of natural forest ecosystems, a practical possibility without management. Management plans, which take into account the factors outlined in the previous section, must be prepared to ensure *in situ* conservation of the genetic resources of the target species and the subsequent use of these resources. A final but most important point must be made. The principles and practices of *in situ* conservation, outlined in this chapter, are as valid for degraded secondary forests as they are for primary forests which have not been subjected to exploitation. There is ample evidence that, with protection, secondary forests can recover rapidly and in time advance ecologically to the species mix of a primary forest. There is also ample evidence that the development of conservation and management programmes in secondary forest ecosystems will be necessary in many nations presently without adequate representation of primary forest ecosystems in protected areas, and without scope for alternative remedial action because of the inadequacies of past policies. These remarks refer to all the species of secondary forests, both plants and animals, and not just to tree species. In time, research and development programmes on *in situ* conservation in many tropical countries will relate as much to secondary forest ecosystems surrounded by agro-urban environments as they do at the present time in the industralized countries of the world. For this reason much of the information in recent basic texts, such as Soulé & Wilcox (1980), and Frankel & Soulé (1981), will be found relevant.

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QUANTITATIVE ASPECTS OF THE COLLECTION AND ANALYSIS OF INVENTORY DATA

MICHAEL B. USHER

INTRODUCTION

Many aspects of sampling theory, experimental design, statistical analysis and multivariate statistics are relevant to the collection, analysis and interpretation of data obtained in biological surveys and inventories. The important initial question to answer is: what is the aim of the survey? When this is answered, appropriate sampling methods can be selected and the methods of analysis can be chosen a priori. The formulation of an appropriate hypothesis before data collection begins ensures that the correct kinds of data are collected; all too frequently data are collected before the methods of statistical treatment are considered, by which time these data are found to be only partly appropriate for the task for which they are required.

This chapter concentrates on only a few tropics. First, there is a brief consideration of sampling techniques. Second, there is a description of some methods for measuring diversity, the criterion which is most frequently used in conservation evaluation (Usher 1986). Diversity, however, is used by conservationists in two completely separate ways: diversity of species within a habitat and diversity of habitats within a landscape. Third, two simple statistical tests are described; both of these tests aims to answer the question: is there a difference between two or more sets of data? Finally, there is a brief introduction to multivariate statistical methods, a very valuable branch of statistical analysis for probing both the criterion of representativeness in conservation evaluation studies and concepts of biogeography.

CONCEPTS OF SAMPLING

The majority of ecological studies make claims such as "sampling was at random" or "random samples were taken". Genuinely random sampling is difficult to achieve and in many instances may not be particularly desirable. The aim of this section is to investigate how a random sampling scheme may be carried out and then to explore one method of improving on randomness. The majority of simple introductory textbooks on biological statistics (e.g. Bailey 1981, Sokal & Rohlf 1987) contain at least a brief introduction on this subject.

There is essentially only one satisfactory method of selecting samples randomly: the use of a series of random numbers, either derived from a table or by a computer program. For field survey work a grid can be placed over a map of the area to be surveyed. Grid cells can be selected by the choice of two random numbers, one to represent rows of the grid and the other to represent columns of the grid. The process

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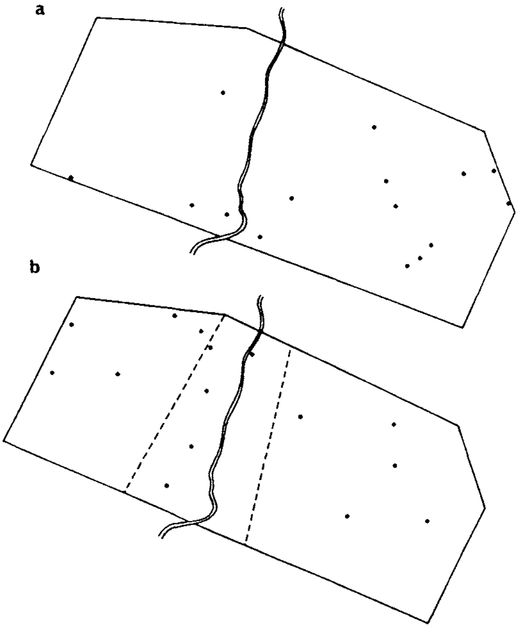
is explained in Example 1 (see page 80). On the ground there is then the problems of locating the grid cell; generally this can be achieved by using a compass bearing and measuring distances (accurately with a tape, etc. or approximately by pacing). Note that procedures such as 'throwing a quadrat over your shoulder' can easily lead to biases, either in terms of an element of subjective assessment as to where the quadrat should fall or to relatively equal spacing between the quadrats.

A hypothetical forest that is to be surveyed is shown in Fig. 1. A maximum of 15 sample plots are to be enumerated. Larger numbers of samples generally yield more accurate estimates of the statistics in which surveyors are interested, but sampling takes time and costs money; hence any sampling programme is a compromise between the requirements for accuracy and the availability of resources. In Fig. 1a a completely random sample is indicated. The grid that was used to construct this sample contained 148 rows and 236 columns, and random numbers (in groups of three digits) were taken from the table in Sokal & Rohlf (1987). One undesirable feature of random sampling that sometimes arises, and is obvious here, is that the particular selection of random grid cells has the majority of the samples close together; towards the right of the illustration, with only one sample towards the left. Data for the numbers of trees in each of the 15 plots, selected from a table of random numbers, together with the calculation of the mean with standard deviation, are given in Example 2 (see page 80).

FIG. 1. (a) A plan of a forest area, over which a square grid has been placed (only every 20th grid line is shown), with a set of 15 completely random samples. (b) The forest area has been divided into three strata, termed left, centre and right. The same grid has been used to locate five completely random samples in each of the three strata.



Examining the land to be surveyed, it can be seen in this hypothetical example that there is a stream running down the centre with land sloping up from the stream to both the left and the right. A hypothesis would be that the land in the centre, which is lower lying, is wetter than the land on the two slopes, which face in opposite directions. In Fig. 1b the area has been divided into three strata to represent these likely environmental differences. A system of stratified random sampling (five completely random samples in each of the three strata) has been used; Example 3 (see page 81) indicates how a mean number of trees per sample plot for the whole area can be calculated. The method of assessing whether the strata are similar or different is described later.

Ecological and conservational survey work should be based on random methods of sampling. The use of non-random sampling methods for data collection will often lead to the data being valueless for ecological and conservational use; both time and resources will have been wasted.

It is, therefore, essential to spend some time in the planning stage of an inventory considering how the sampling will be carried out and how any foreseeable biases can be eliminated.

HOW IS DIVERSITY MEASURED?

Diversity can relate either to the diversity of species within a habitat or to the diversity of habitats within a landscape. For species diversity the simplest measure is a count of the number of species present in area of land; this is the species richness, *S*. Sites can be compared in a qualitative way on the basis of this stastistic. For example, it can be said that Afram Headwaters Forest Reserve, Ghana, which has 262 species of trees larger than 10cm in diameter, is more species rich than Worobong South Forest Reserve, which has only 200 species (both of these forest reserves are located in the same tropical forest association, as defined by Taylor (1960)).

Species richness as a statistic has one great advantage; it is very simple to estimate. It does, however, have two great disadvantages. First, the number of species tends to increase with the area of the site being investigated. This is a well-known fact in island biogeography (MacArthur & Wilson 1967) and one that has implications in conservation survey work (Usher 1985). In the example above, since Afram Headwaters F.R. is three to four times as large as Worobong South F.R., then the discrepancy in the numbers of species might be considered to be an area effect. Secondly, a count of the number of species does not take any account of the comparative commoness and rarity of the individual species. Take as an example forests of six species of trees. Suppose that in one forest the number of these trees were approximately equal, say, for a sample of 1000,

170 170 170 170 160 160

and that in another forest the counts of the six species were

995 1 1 1 1 1

Intuitively the first forest is more diverse than the second forest (which is virtually a monoculture because one species is dominant with 99.5% of all individuals). Both forests are, however, equally species rich.

Because of these defects in S as a measure of diversity, various indices have been proposed to combine features of both species richness and the equality of the distribution of individuals among the species. The most frequently used are the Shannon index,

$$H' = \sum_{i=1}^{s} = p_i \ln p_i$$

which is based on concepts of information theory and the Simpson index,

$$D = \sum_{i=1}^{s} p_i^2$$

where p_i is the proportion of the ith species in the sample, i.e. n_i/N (where there are n_i individuals of the ith species in a sample of N individuals) or b_i/N (where b_i is the biomass of the i th species in a sample of total biomass B), etc. The formulae for both H' and D given above are approximations, but they are reasonably satisfactory for large sample sizes, especially if indices are to be calculated without the use of computer.

H' has a minimum value of 0 in a monoculture, and increases to a maximum of S in a community where all individuals are in different species. It, has therefore a characteristic of becoming larger as a community becomes more diverse.

D has a maximum value of 1 in a monoculture, and becomes smaller as the community becomes more diverse. In order to have an index that increases with diversity, modified Simpson's indices are sometimes given as

$D' = 1 - D$, or $d = 1/D$

Simpson's index has an intuitive meaning: D is approximately the probability that two individuals, picked at random, will be in same species (alternatively, D' is the probability that two randomly selected individuals will be in different species). Morris & Lakhani (1979) consider that D (or D') is a suitable index if statistical tests are to be used on series of diversity measurements.

Example 4 (see page 81) shows how diversity indices are calculated. A wider range of examples is given by Usher (1983); a modern textbook on the subject is that of Magurran (1988).

Although species diversity is relatively simple to deal with, habitat diversity is a more difficult concept. First, one needs a working definition of habitats. This may be broadly related to botanical composition (essentially phytosociology), or to geological or soil types, or to much smaller structural divisions such as the presence of dead wood, mammal dung, etc., as discussed by Elton (1966). It is possible to use some kind of an analogue of S to give a habitat richness by counting the numbers of habitats present, or to use analogues of D or H to give habitat diversity indices if the area of each habitat type can be measured. In this context, D has an intuitive meaning, being the probability that two random points will fall in the same habitat type. The procedure is demonstrated using a soil survey map (as a physical definition of habitats) in Example 5 (see page 82).

COMPARISONS

Comparing two sets of samples

An appropriate statistical method for comparing two series of samples is a Student's t test. The use of the t statistic for comparing the means of two small samples is described in the basic statistics textbooks (e.g. Bailey 1981, Sokal & Rohlf 1987). If the subscripts 1 and 2 denote the two samples, then sample means are given by m_1 and m_2 respectively, with the corresponding sample sizes n_1 and n_2 and variances s_1^2 and s_2^2.

A pooled variance for the two samples, weighted according to the sizes of the samples, is given by

$$s^2 = \frac{s_1^2(n_1 - 1) + s_2^2(n_2 - 1)}{n_1 + n_2 - 2}$$

The standard error for the difference between the means is given by

$$\mathrm{SE} = \sqrt{s^2\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}$$

The t test is then simply the ratio of the positive difference between the means to this standard error, i.e.

$$t = \frac{|m_1 - m_2|}{\mathrm{SE}}$$

There are three points to note in using this test. First, the null hypothesis is that the two population means are equal (thus $\mu_1 = \mu_2$); if t is larger than the value in tables the null hypothesis is rejected. Second, t has $(n_1 + n_2 - 2)$ degrees of freedom; usually in conservation studies no a priori difference can be expected and hence a 2-tailed test should be used when looking up t with its appropriate degrees of freedom. Third, it is assumed that the two samples are drawn from populations with identical variances, i.e. that $\sigma_1^2 = \sigma_2^2$; this assumption should be tested with an F test.

Example 6 (see page 83) shows how this test can be used to compare diversity indices for forest reserves in two climatic zones in Ghana, West Africa.

Comparing multiple sets of samples

Above only two series of samples were compared. More generally, there may be a larger number of series to compare, in which case an analysis of variance would be an appropriate statistical method to use. The simplest of these analysis is described as the 'completely randomised design' by Bailey (1981) and as a 'single-classification analysis of variance' by Sokal & Rohlf (1987). In order to understand the methods for comparing samples, it is useful to refer to an example. Example 7 (see page 85) re-uses the data of Section 2, where a stratified random sampling scheme was used. As indicated by that analysis, when the null hypothesis (that the mean densities of the trees in the three strata are identical) is accepted, it is appropriate to calculate a weighted average density for the whole woodland.

INVESTIGATION OF MULTIVARIATE DATA

In much inventory work, the data are collected into a large table of species (usually the rows in the table). An example of a typical table of this nature, the carabid beetles (family Carabidae) collected from species-poor heathland habitats on the North York Moors, UK is shown in Table 1. Two questions will immediately become apparent. First, are there groups of beetles that tend to occur together? If such groups can be detected, it is usually assumed that they have similar ecological characteristics and hence that they might be characteristic of some kind of habitat. Second, can the sample sites be classified into groups whose members are internally similar to each other but relatively more dissimilar from the members of other groups? The groups formed may then be taken as a basis for assigning sampling sites to habitat types or, on a larger geographical scale, possibly for erecting hypotheses about biogeographical differences.

TABLE 1. An example of a survey dataset of ground beetles (family Carabidae) recorded in the species-poor heathland communities of the North York Moors National Park, UK. Note that only a portion of the complete data table (31 species, represented in a collection of 1434 individuals by 25 sites) is shown. The data are taken from Fishpool & Usher (in press).

	Sample sites				
Species	1	2	3	4 ...	Total
Agonum ericeti	0	0	0	0 ...	14
Amara apricaria	0	0	0	1 ...	2
Amara equestris	0	0	0	0 ...	1
Bradycellus harpalinus	0	0	0	0 ...	1
Bradycellus ruficollis	2	0	2	2 ...	122
Calathus erratus	0	0	0	18 ...	52
Calathus melanocephalus	0	1	0	2 ...	46
Carabus nemoralis	0	0	3	2 ...	5
Carabus nitens	0	0	0	0 ...	16
Carabus problematicus	5	34	51	22 ...	304
Carabus violaceus	2	13	13	0 ...	38
Cymindis vaporariorum	0	0	0	1 ...	1
Dyschirius sp.	0	0	0	0 ...	2
Leistus rufescens	1	5	0	0 ...	9
Loricera pilicornis	0	0	1	0 ...	1
Total	12	55	74	126	1434

The methods of analysing such data, in order to answer these questions, fall into two groups, termed classification (or clustering) and ordination (a pictorial representation of the sampling units, usually in 2-dimensional space). The mathematical methods required for the analyses are generally complex and beyond the scope of an introduction such as this. A simple introduction to the methods is given by Manly (1986); more extensive treatments specifically aimed at ecological analyses are by Gauch (1982) and by Digby & Kempton (1987). All of the analyses use computers and many computer packages (some mentioned in the references above) are available for both mainframe and micro-computers. However, one package that is being

TABLE 2. A TWINSPAN analysis of the dataset shown in Table 2. The analysis indicates how sites can be classified into groups, and how species with similar ecological characteristics can be used to characterise each of these groups of sites (from Fishpool & Usher, in press).

	Species and species groups	Sites and site groups		
		III	II	I
		11212221	22	111111
		2189071236	474556389	201354
B	*Miscodera arctica*	----------	x--xx----	------
	Amara apricaria	----------	x--x-----	------
	Amara equestris	----------	-x-------	------
	Bradycellus harpalinus	----------	-x-------	------
	Cymindis vaporariorum	----------	x--------	------
	Carabus nemoralis	----------	x------x-	------
	Loricera pilicornis	----------	-------x-	------
	Pterostichus adstrictus	----x-----	xxxx---xx	------
	Calathus erratus	-----x-x--	xxxxxx-xx	------
	Trechus secalis	x---------	------x-x	------
C	*Bradycellus ruficollis*	-xxxxxxxxx	xxxxxxxxx	------
	Notiophilus biguttatus	---------x	x--------	------
	Pterostichus madidus	--------xx	--x-x----	------
	Trechus quadristriatus	-xxx-xx-x-	xxxxxx---	------
	Trechus obtusus	x-xxxxxxxx	x-xx-xxx-	------
	Calathus melanocephalus	x-x-xxxxxx	x--x-----	------
	Notiophilus germinyi	------xx--	---x----x	------
	Trichocellus cognatus	--x-x-xx-x	--xx-----	------
W	*Carabus violaceus*	xxx-x----x	--x---x-x	x-----
	Leistus rufescens	xx-x--xx--	---------	------
	Olisthopus rotundatus	--xxxxxxxx	xxxx-x-xx	x-x-x-
	Carabus problematicus	xxxxxxxxxx	xxxxxxxxx	xx--x-
	Notiophilus aquaticus	------xxx-	-x-x-----	xx--x-
D	*Nebria brevicollis*	----------	----x----	----x-
	Nebria salina	-------xxx	xxxxxxxxx	xxxxxx
	Patrobus assimilis	----------	xx---xxxx	xxxxx-
A	*Dyschirius* spp.	----------	---------	x-----
	Pterostichus nigrita	----------	----xx---	x-x-xx
	Agonum ericeti	----------	-----x-—	x-xxx
	Carabus nitens	--x-------	-------x-	xxxxxx
	Pterostichus diligens	----------	-----x--x	xxxxxx

increasingly used is TWINSPAN (Hill 1979); this incorporates elements of both a classification and an ordination.

An example of the use of multivariate approaches in the recognition of biogeographic regions is discussed by Austin & Margules (1986) for assessing the criterion of representativeness in Australia. However, multivariate analyses have been used more frequently at a local scale, exploring the relationships between species and habitats. A TWINSPAN analysis of the data in Table 1 is shown in Table 2. The output from the programme is an ordered table; thus sites most similar to each other are in adjacent rows. The number of groups selected in arbitrary. Thus, the first division in Table 2 divided the 25 sites into two groups, one with 6 sites generally near freshwater flushes and one with 19 sites; this latter was divided again so as to yield the three groups of sites shown in Table 2. Similarly, the number of groups of beetles is arbitrary, but the five groups shown in Table 2 are a compromise between too many groups, when interpretation of the results could be difficult, and too few groups, when major ecological differences could be obscured. Only experience with multivariate analyses can indicate the appropriate compromise between too many and too few groups, when major ecological differences could be obscured. Only experience with multivariate analyses can indicate the appropriate compromise between too many and too few groups.

CONCLUSIONS

This brief review incorporates only a few of the statistical and numerical techniques available to a conservationist. Broadly speaking, inventory work will require three types of technique:

(i) statistics that summarise a lot of data,
(ii) statistics that aid in answering the question "is there a difference?",
(iii) statistical analyses that can be used to generate hypotheses.

The estimation of means, variances, diversity indices, etc. are all based on sampling biological communities. The methods of sampling are, therefore, important, although it should be remembered that there is no multi-purpose sampling scheme. Different sampling methods will be required for inventories of plants, birds, spiders, butterflies, soil mites, etc. Hence, although a method of sampling may be well suited to gaining data on one particular group of organisms, it may be inappropriate for determining the other groups of organisms related in a food web to the target group.

The investigation of differences is frequently important. There is a range of analyses of variance, *t* – tests and chi-squared tests (the latter for frequency data) that can be used. However, conservation studies, after the initial survey phase, are often concerned with answering the question "is there a relationship?". The appropriate statistics for exploring this question– correlation coefficients, regression analysis and chi-squared-tests for frequency data– have not been discussed in the context of collecting inventory data.

The generation of hypotheses is an area that has not been stressed in the conservation literature, though it is potentially important. The majority of multivariate statistical methods are essentially hypothesis generating. The starting data for the analyses are multivariate, usually without clear patterns in the data. The analyses aim to simplify the data, demonstrating axes that are associated with the greatest amount of variation or demonstrating species or sites that are similar (clusters). Usually no tests of significance are involved, and hence interpretation of the output from the computer programs, which have been used to undertake the multivariate analyses, can involve the generation of hypotheses about the original data. Such hypotheses are all too rarely tested subseqeuntly either by directed sampling programmes or by experimental approaches.

This review has concentrated on the planning of one-off inventories and the analysis of such data. In the longer term, conservation biology will rely more heavily on monitoring programmes and on the identification of appropriate indices or indicators of change. For such analyses, different sets of statistical techniques will be required; moving averages and time-series analysis are likely to be suitable. However, a consideration of such techniques is also beyond the scope of this review. Quantification supports much of conservation biology. Textbooks in the reference list will need to be consulted at all stages; planning, data collection, data handling, data interpretation, and the drawing of inferences. Successful conservation relies on suitable data being collected and on the correct inferences being drawn from those data.

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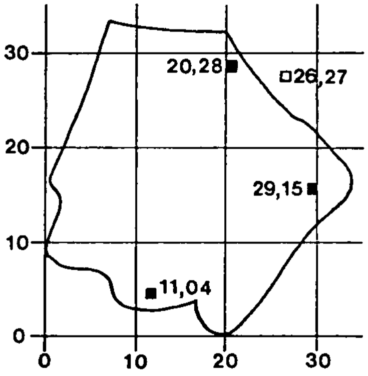
EXAMPLE 1. Selecting random samples for ecological survey



The land area to be surveyed is shown above. Superimposed on this is an arbitrary grid of squares (note that for clarity only every tenth line in the grid of squares is shown). If pairs of random digits from the table of random numbers are
48 20 69 59 28 29 15 26 84 99 27 97 37 11 96 04 06 ...

The first pair of numbers (48) is out of range (the maximum extent of the area in either a vertical or horizontal direction is about 32). 20 is then potentially useful, with 28 as the next useful pair. The location of (20, 28), based on vertical lines followed by horizontal lines, is shown on the plan above. The next pair of random numbers (29,15) is also shown. The next potential pair of numbers is (26,27), but as shown this falls outside the boundary and hence is useless. (11,04) forms the next pair, and this is shown. The process of selecting random grid squares continues until a sufficiently large sample size has been obtained.

Note that it is often useful to have chosen a few 'extra' samples. It sometimes happens that field conditions (e.g. a fire, flood, illegal clearance, etc.) mean that one or two of the randomly selected sample units are unusable.

EXAMPLE 2. A fully randomised sample of the forest area shown in Figure 1a

The data below show the number of trees per sample plot (note that the order is arbitrary, being the sequence in which the plots were measured) for the 15 (*n*) sample plots:

12	24	36	48	60
19	13	10	17	17
24	14	12	24	20
10	20	23	28	21

The total number of trees (Σx) is 278, giving a mean (m) of 18.5 trees per plot. The standard deviation (s) is 5.6712, giving a standard error of the mean ($SE = s/\sqrt{n}$) of 1.4504; 95% confidence limits, based on Student's t with 14 degrees of freedom and two-tailed tabulation with $P = 0.05$, are ±1.4504% x 2.145% = ±3.1 (i.e. there is a 95% probability that the true mean density of trees lies in the range of 18.5% ±3.1% trees per plot, or between 15.4 and 21.6 trees per plot).

EXAMPLE 3. A stratified random sample of the forest area shown in Figure 1b

The stratum to the left has an area of 60 units. The 5 sample plots located in it gave the following data:

27 10 23 15 25

Thus, the mean number of trees per plot in the left stratum is 20, with a standard deviation of 7.2111. In the centre plot, the data are:

16 21 14 11 8

In this plot the mean number of trees is 14 sample plot, with a standard deviation of 4.9497. The area of this central stratum is 45 units. The right hand stratum is the largest, with an area of 95 units. The data from the 5 sample plots are

15 24 2 114 21

In this stratum the mean is 19 trees per plot, with a standard deviation of 4.3012.

Each stratum has a slightly different mean, and the problem now becomes one of combining these data to get an overall estimate of the mean for the whole forest. Whether or not these data should be combined is discussed in the text. However, assuming that they can be combined, a weighted mean is required. This is undertaken by weighting each of the three separate means according to the area of the plot that it represents. Thus the weighted mean is given by

$$M = \frac{20 \times 60 + 13.6 \times 45 + 19 \times 95}{200}$$

$$= 18.1 \text{ trees per sample plot.}$$

As can be seen from the above formula, each of the separate means was multipled by its area and their sum was then divided by the area of the total forest (200 units). Suppose that an inventory of a forest nature reserve yields information on 240 trees in 12 species. In the table below the 12 species are named 'A' to 'L' inclusive and the numbers belonging to each species are shown in the n_i column.

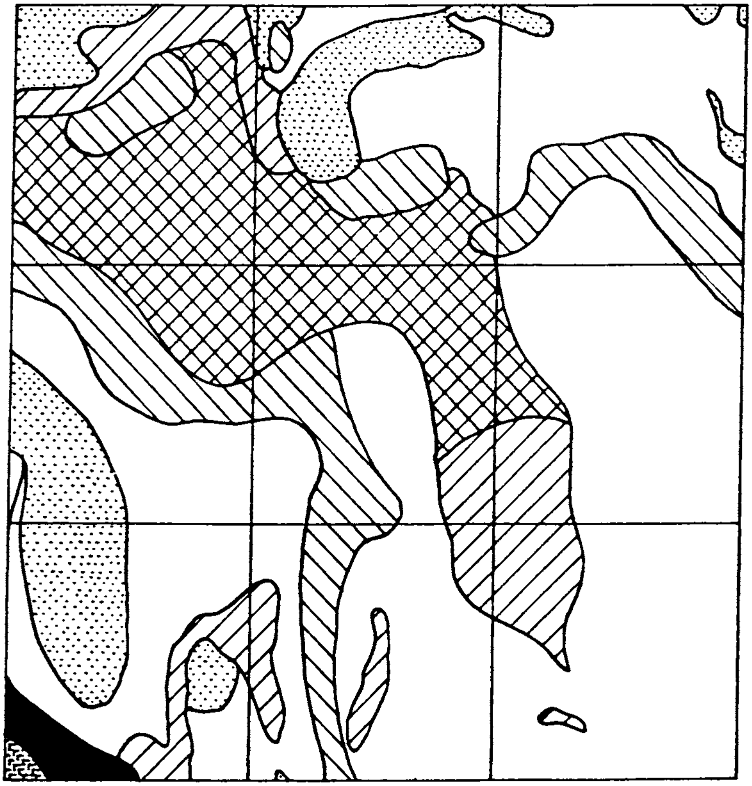
EXAMPLE 4. Calculating diversity indices

Species name	No. of individuals	Proportions	Shannon index	Simpson index
(i)	(n_i)	(p_i)	$(-p_i \ln p_i)$	(p_i^2)
A	72	0.3000	0.3612	0.0900
B	54	0.2250	0.3356	0.0506
C	36	0.1500	0.2846	0.0225
D	24	0.1000	0.2303	0.0100
E	18	0.0750	0.1943	0.0056
F	12	0.5000	0.1498	0.0025
G	6	0.0250	0.0922	0.0006
H	6	0.0250	0.0922	0.0006
I	3	0.0125	0.0548	0.0002
J	3	0.0125	0.0548	0.0002
K	3	0.0125	0.0548	0.0002
L	3	0.0125	0.0548	0.0002
Total	240	1.0000	1.9594	0.1832

Proportions of each of the species (p_i) are calculated by dividing the number of species by the total number of individuals; thus, for species A the proportion is 72/240 = 0.3000. These are shown in the third column in the table below. Steps in calculating the Shannon Index are also shown. Thus, the contribution made to the index by species A is -0.3000 ln 0.3000 = 0.3612. Summation of the individual components gives the appropriate H' = 1.959 (to three decimal places). Magurran (1988) gives a formula for an exact value of H', which for the example in the table is 1.913.

Steps in calculating the Simpson Index are shown in the final column of the table above. The contribution made by species A is 0.3000 x 0.3000 = 0.0900. Again, summation of the individual components gives the appropriate D = 0.183 (to three decimal places). Magurran (1988) also gives a formula for an exact value of D, which for this example is 0.180.

EXAMPLE 5. Use of Simpson's Index to explore habitat diversity



The soil map above shows an area of 900 ha of the North York Moors, UK; the vertical and horizontal lines are 1 km apart on the ground. There are a total of seven different soil types mapped; the area of each is shown in the table below. One soil group, coded On$_2$ (unshaded on the plan), is dominant, occupying just over half of the area. Two of the soil group (coded Da and Fv$_1$) are uncommon, being confined to the south west corner of the mapped area (both shaded dark). The other four soil types (shown in stippled, hatched in two directions, and cross hatched) each occupy between 8 and 17% of the mapped area. The Simpson's Index (*D*) can be calculated as previously. It is given by

$$D = 0.51312 + 0.1682^2 + \ldots\ldots 0.0027^2$$
$$= 0.324$$

There is thus a probability of 0.324 (approximately one third) that two random points will fall in areas with the same soil type (note that in this example soil type is equated to habitat). One might wish to use the alternative version of the Simpson Index,

$$D' = 1 - D = 0.676$$

to give the probability that two random points will be in different soil types. The larger the value of *D'* the more diverse the habitats in the area of land being considered.

Soil type	Area (ha)	Percentage of 900 ha	p_i
On$_2$	461.8	51.3	0.5131
WH	151.4	16.8	0.1682
rV	112.2	12.5	0.1247
MA	94.5	10.5	0.1050
HJ	68.8	7.6	0.0764
Da	8.9	1.0	0.0099
Fv$_1$	2.4	0.3	0.0027
Total	900.0	100.1	1.0000

EXAMPLE 6. Comparison of diversity indices derived from forest reserves in two forest zones in Ghana

The semi-decidous forest zone of Ghana was divided into two associations by Taylor (1960); these are termed the *Antiaris-Chlorophora* Association (to the north) and the *Celtis-Triplochiton* Association (to the south). These two associations approximately correspond to the dry and moist semi-deciduous forest regions of Hall & Swaine (1981).

Forest enumeration data were available for ten forest reserves in the *Antiaris-Chlorophora* association and for sixteen forest reserves in the *Celtis-Triplochiton* association. The Simpson diversity indices are shown in the table below.

The order of the indices is of no importance, being alphabetical by forest reserves (i.e. Afram Headwaters F.R. has an index value of 0.0366 and Worobong South F.R. of 0.0402).

The question to be explored is: "is the diversity of forest trees different in two associations?" The null hypothesis to test is that there is no difference, i.e. μ_1 (the

Association	Simpsons diversity indices (D)				
Antiaris-Chlorophora	0.0366	0.0502	0.0412	0.0293	0.0660
	0.0319	0.0471	0.0439	0.0668	0.0402
Celtis-Triplochiton	0.0285	0.0265	0.0317	0.0313	0.0271
	0.0261	0.0485	0.0339	0.0491	0.0361
	0.0443	0.0351	0.0412	0.0246	0.0285
	0.0497				

population mean of the *Antiaris-Chlorophora* association) equals μ_2 (the population mean of the *Celtis-Triplochiton* association). Steps in the use of a t-test to compare the two sample means are shown in the table below.

Statistic	*Antiaris-Chlorophora* association	*Celtis-Triplochiton* association
Sample size (n)	10	16
Mean (m)	0.0453	0.0351
Variance (s^2)	1.6378×10^{-4}	7.7071×10^{-5}

The first step is to test for homogenity of the two variances (i.e. can they be assumed to be equal?). An F-test is appropriate, dividing the larger by the smaller variance, thus

$$F = \frac{s_1^2}{s_2^2} = 2.13$$

This is less than the tabulated value with (9,15) degrees of freedom and $P = 0.05$ for a 2-tailed test (note that F tables are generally 1-tailed, and hence one enters with $P = 0.025$ in such tables for the 2-tailed test). Because 2.13 is less than the tabulated value of 3.12, homogeneity of variance can be assumed.

The two variances can therefore be pooled, weighting each by its degrees of freedom, thus

$$s^2 = \frac{\left(n_1 - 1\right) s_1^2 + \left(n_2 - 1\right) s_2^2}{n_1 + n_2 - 2}$$

$$= \frac{9 \times 1.6378 \times 10^{-4} + 15 \times 7.7071 \times 10^{-5}}{24} \qquad = 1.0959 \times 10^{-4}$$

and the pooled standard deviation is
$s = 0.010468$.

The means are compared by Student's t, which is calculated as

$$t = \frac{|m_1 - m_2|}{s\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}$$

where the vertical lines indicate the positive difference between the means. In this example,

$$t = \frac{|0.0453 - 0.0351|}{0.010468\sqrt{\frac{1}{10}+\frac{1}{16}}}$$

$$= 2.417$$

t has 24 degrees of freedom ($n_1 + n_2 - 2$), and, as no a priori difference in the mean diversities was specified, a 2-tailed test is appropriate. The tabulated value with $P = 0.05$ is 2.064, so the null hypothesis can be rejected with a probability of between 0.05 and 0.01. The mean diversity index of the forest reserves in the *Celtis-Triplochiton* association (0.0351) can be inferred to be less than that of the *Antiaris-Chlorophora* association. Note that this implies that the *Celtis-Triplochiton* association forest reserves are more diverse than those of the *Antiaris-Chlorophora* association because the Simpson Index measures the probability that two trees, picked at random, will be of the same species.

EXAMPLE 7. Comparing three series of data

The table below sets out the counts in the three strata shown in Fig. 1b.

Stratum	Counts (x_i)	Totals (x_i)	Means	Total of counts squared (x_i^2)
Left	27, 10, 23, 15, 25	100	20	2208
Centre	16, 21, 14, 11, 8	70	14	1078
Right	15, 24, 21, 14, 21	21	95	1879
Total		265	–	5165

The total sum of squares (S.S.), ignoring the three strata, is given by the formula

$$\sum x_i^2 - \frac{(\Sigma x_i)^2}{n}$$

where n is the total number of samples. In the example above this is
$5165 - 265^2/15 = 483.3333$.

The sum of squares within the left stratum is similarly calculated, being
$2208 - 100^2/5 = 208.000$
and in the centre and the right strata as
$1078 - 70^2/5 = 98.000$, and
$1879 - 9^2/5 = 74.0000$,
respectively. This gives a combined within-strata S.S. of 380.0000, which, by difference with the total S.S., gives a between-strata S.S. of 103.3333. An independent way of calculating the between-strata S.S., using the totals in the table above, is
$100^2/5 + 70^2/5 + 95^2/5 - 265^2/15 = 103.3333$.

The variability between strata is then compared with the variability within strata by an analysis of variance, thus

Source of variation	S.S.	Degrees of freedom	Variance (M.S.)	Variance ratio (*F*)
Between strata	103.3333	2	51.6667	1.632
Within strata	380.0000	12	31.6667	
Total	483.333	14		

Note that the number of degrees of freedom for the between-strata variability is one less than the number of strata (3), and the total degrees of freedom is one less than the number of samples taken (15). The variance or mean square (M.S) is calculated as the S.S. divided by its degree of freedom. The variance ratio is a comparison of the between-strata variance to the within-strata variance; in this example, it is not significant. This means that the null hypothesis, that the population means of the three strata are identical, can be accepted.

Statistical textbooks should be consulted to verify that all assumptions that have to be made are justified by the data being analysed.

SAMPLING PLANT POPULATIONS FOR GENETIC CONSERVATION

R.W. SNAYDON

INTRODUCTION

The success of any programme of genetic conservation is heavily dependent upon the effectiveness of the sampling techniques used during the original collections. The principles of sampling for genetic conservation are similar to those for plant introduction, and for studies of the ecological genetics of species. However, it is surprising how little attention has been given to sampling techniques in any of these contexts. Some attention was given to sampling techniques at an earlier stage in ecological genetics (e.g. Harberd 1957; Wilkins 1959; Clausen 1960), while several attempts have been made since then to define sampling requirements for genetic conservation (Allard 1970; Marshall & Brown 1975). These various approaches, part theoretical and part empirical, constitute a reasonable basis for assessing sampling procedures.

It is important to recognise from the outset that the optimum sampling strategy depends on the reasons for which the collection is being made. Collections may be made (a) to conserve, as accurately as possible, a particular population perhaps in danger of extinction; (b) to conserve, as accurately as possible, the overall pattern of genetic variation in a particular species, perhaps again in danger of extinction; (c) to conserve, or perhaps only to maintain temporarily, a wide range of useful variation for a breeding programme; (d) to conserve, or maintain temporarily, variation in some specific attribute (e.g. cold tolerance or disease resistance) for a breeding programme. If the main objective is simply to conserve a specific populations, then adequate sampling of the genotypes within populations is clearly most important. If the objective is to conserve intact the overall pattern of variation in a species, then adequate sampling of the range of populations is also important. If the objective is to provide a gene pool for breeding purposes, it is more important to conserve intact the actual pattern of variation for particular attributes than to conserve intact the actual pattern of variation within the species; however, since the range of variability for the specific attribute is usually not known beforehand, the optimum sampling strategy may often be similar to that used for conserving the overall pattern of variation within a species.

SAMPLING WITHIN POPULATIONS

It is easiest first to consider individual characters or attributes when investigating

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the pattern of variation within populations and how it is to be conserved. The pattern of genetic variation of a given attribute within a population is best described by its frequency distribution; the most common pattern is the normal distribution, although other patterns can exist. For example, if the attribute is determined by a single dominant gene, the frequency distribution will be bimodal, one group being individuals bearing the dominant gene and the other group being individuals homozygous for the recessive; although incomplete dominance will produce a trimodal distribution, this may appear much like a normal distribution.

Most of the attributes that are important in plant breeding (e.g. yield) and ecological genetics (e.g. adaptations to specific environmental conditions) are polygenically inherited. The most common frequency distribution for such characters is a normal distribution, although the distribution may be skewed by directional selection, and may even become bimodal under disruptive selection (Mather 1973).

If a population with a normal distribution is randomly sampled, there is a low probability of obtaining the genetically most extreme individuals, although the probability can be increased by increasing the sample size, and it is fairly easy to calculate the sample size required to include any given proportion of the total genetic variation. In fact, it is rarely necessary to include the complete range of genetic variation because, if the genetic linkage between polygenes is not tight, there will be recombination of the polygenes during sexual reproduction which will regenerate the complete range of variation, as shown theoretically by Falconer (1981) and experimentally by Cooper (1959) and others. If there is tight linkage, the polygenes will act more like major genes and sampling of the complete range of variation is necessary. The amount of variation regenerated by recombination will also depend on the extent of heterozygosity within individuals, because this represents cryptic variation that can be uncovered by crossing. To some extent, the amount of heterozygosity is determined by the breeding system of the population, with inbreeders showing less heterozygosity, although only a small amount of outcrossing is necessary to generate heterozygosity (Allard *et al.* 1968; Loveless & Hamrick 1984).

The theory so far has been simplified by the fact that only *genetic* variation within populations has been considered, while the variation that is measured is *phenotypic*, i.e. the result of both genetic variation and environmental variation, where much of the environmentally induced variation is caused by competition within and between species. The relative importance of genetic and environmental variation can differ widely. For example, if environmental variation can be eliminated entirely, i.e. by growing accessions in a uniform environment, then only genetic variation is expressed; on the other hand, if sampling or selection is carried out in the wild, much of the observed variation is likely to be environmentally induced rather than genetic.

In cases where the population is sampled at random, environmentally induced phenotypic variation will not affect the outcome of sampling. However, it is sometimes advantageous to sample selectively and, in such cases, environmental variation can influence the effectiveness of sampling. For example, if it is important to obtain the complete range of genetic variation, but not necessarily to maintain the natural frequency distribution of the population, as might be the case for gene pools used in breeding programmes, it will usually be more effective to select extreme types, rather than to sample at random. However, if environmentally induced variation partially conceals genetic variation, as commonly happens in the field, selection of the extreme types will be less efficient.

The considerations so far have been simplified by the fact that only single attributes have been examined. Such a simplified approach is only justified when there is collection for a specific attribute (e.g. cold tolerance) but, in most cases, collections are undertaken to conserve the complete pattern of genetic variation, i.e. the pattern of variation is multidimensional, rather than unidimensional. Under these conditions, the sampling requirements become more demanding. If the complete range of variation for all the attributes is to be encompassed, then a much larger number of individuals must be sampled. As in the case of single attributes, however, as long as there is not tight genetic linkage between the various attributes, recombination during sexual reproduction will regenerate the complete range of variation from a quite limited sample.

It is already clear that the optimum sampling strategy for populations will depend on a number of factors: (i) the purpose for which the collection is made, e.g. as an accurate representation of the genetic structure of the natural population or as a wide gene pool for breeding programmes; (ii) the proposed content of the collection, i.e. whether representing a single attribute or all attributes; (iii) the breeding system of the population, i.e. degree of inbreeding; (iv) the mode of inheritance of the attribute(s) considered, i.e. the number of genes involved and the degree of linkage between them; finally, if some form of selective sampling is to be used, a further factor is important: (v) the relative importance of genotype and environment in determining the phenotype, i.e. broad-sense heritability. Since there is usually little information on factors (iii) – (v), most recommendations on sampling methods have been general and empirical, rather than specific and based on theory. All too often, even the purpose of the collection (i, ii) has not been considered.

The usual recommendations (e.g. Whyte 1958; Allard 1970; Marshall & Brown (1975) is that seed should be collected from between 50 and 200 plants per population, although Marshall & Brown (1975) accept that even fewer plants might be sampled " in many circumstances". In cases where there is a substantial amount of out-crossing, the number of plants sampled can be substantially reduced, because of the large amount of cryptic variation present in each seed. However, the number of plants that should be sampled must also depend on the number seeds collected per plant. In the case of totally inbreeding species, where individuals are homozygous, only one seed should be collected per plant, because all the offspring of a single plant are genetically identical, but seed should be collected from a large number of plants in the population; in this case, one seed from each of 200 plants seems reasonable. In the case of predominantly out-crossing populations, 5 seeds from each of 10 individuals would probably be adequate, although it would also be possible to collect 1 seed from each of 50 individuals. To some extent, the number of seeds required will also depend on the efficiency of the seed storage facility; more seeds are required if storage facilities are poor, because considerable losses will be sustained before further multiplication occurs. It should be recognized, however, that such losses may also cause important shifts in the genetic structure of the population, and should therefore be prevented if possible.

SAMPLING BETWEEN POPULATIONS

It is even more difficult to determine optimum strategies for sampling populations within species than it is to determine strategies for sampling within populations. The main reason for this is that usually even less is known about the pattern of variation between populations within species than is known about the variations within populations. Even in species where extensive studies of ecological genetics or taxonomy have been undertaken, evidence on the overall pattern of genetic variation is suprisingly incomplete. On the one hand, sampling for taxonomic purposes is often quite widespread, but the nature of sampling is usually suspect (Snaydon 1984); the data from most taxonomic studies are also of little use for genetic purposes, because they are obtained from plants collected directly from the field, and so have a large component of environmentally induced vegetation. On the other hand, many of the data from studies of the ecological genetics of species are obtained from studies in uniform conditions, where genetic differences are more clearly expressed, but most studies have been designed to investigate genetic differences between populations in response to specific environmental factors, such as heavy metals or low temperatures, rather than to investigate the overall pattern of genetic variation. In addition, there is usually a tendency to sample only the extreme habitats, rather than explore the full range of conditions for that particular factor. As a result, even in the most intensively studied species, surprisingly little is known about the overall pattern of genetic variation. Most of the species that are likely to be collected for genetic conservation will not have been studied, so almost nothing will be known about the pattern of genetic variation in these species, and sampling strategies must be based upon other considerations.

If the main objective of the collection is to simulate the existing pattern of genetic variation within the species, then random sampling, both within and between populations, would seem to be the only valid method of sampling. On the other hand, if the main objective is to provide a wide genetic base, e.g. for a breeding programme, then it would more efficient and effective to collect the more extreme populations; this would ensure that the extreme genotypes are included, and would probably allow the intermediate genotypes to be regenerated by crossing, even if they did not already exist within the sample populations. The main difficulty here is that, since the pattern of genetic variation within the species is probably unknown, the extreme populations will not have been identified. In the absence of the necessary genetic information, the best strategy would be to assume that the important differences between populations probably follows habitat differences, and so to collect from a wide diversity of ecological and, if necessary, agronomic habitats. The collection should also be over as wide a geographical range as posssible, both to encompass a wide range of climatic conditions and to ensure that any population differentiation caused by geographical spread is included.

The amount of genetic variation present within plant populations is associated with, and may often be the result of, various other factors. Knowledge of these factors may help in designing a more efficient sampling system, i.e. increasing the amount of genetic variation collected per unit of effort. For example, there is evidence that genetic variation is greatest within large and stable populations (Loveless & Hamrick 1984), and in environmentally heterogeneous areas (Hedrick *et al.* 1976; Hedrick 1986), so collection in such areas should increase the efficiency of sampling. There is also evidence that areas of greater genetic variation, often termed centres of genetic diversity, occur in many crop species (Zohary 1970) and may be associated with centres of origin in many cases; similarly, in wild species, there is some indication (e.g. Baker 1953) that genetic variation may be greater at the centre of distribution of species. Once again, this information may be used to increase the efficiency of sampling.

CONCLUSIONS

The optimum sampling strategy for collecting genetic variation within plant species will depend on the reasons for the collection, on the breeding system in the species and the mode of inheritance of the attribute, and the pattern of genetic variation within the species.

If the objective of sampling is to simulate the original genetic structure of a population as accurately as possible, then individuals within the population should be randomly sampled. Similarly, if the pattern of variation between populations is to be simulated, populations within the species should be randomly sampled. However, if the objective is to collect the maximum amount of variation as efficiently as possible, then it is better to collect seeds from large, stable populations growing in the most diverse environments, in environmentally heterogeneous environments, and in centres of genetic variation, if these are known.

In predominantly outbreeding species, where there is usually a high degree of heterozygosity, only a small number of individuals per population is required to capture the full range of variation, because additional variation is released by recombination. It is probably worthwhile to collect seeds from the most extreme plants in the population, although much of the observed phenotypic variation in the field will probably be environmentally induced. The necessary sample is probably 5 seeds from each of 10 plants per population, although one seed from each of 50 plants is also possible. More seeds should be collected if large losses of seeds are expected, because of poor storage conditions or an inherently large mortality rate.

In highly inbreeding species, where individuals are predominantly homozygous and the offspring of an individual identical, there is no point in collecting more than one seed per plant, but more individuals per population should be sampled. The necessary sample is probably one seed from each of 200 individuals per population. In populations with an appreciable amount of outcrossing, a strategy intermediate between that suggested for fully outbreeding and fully inbreeding species can be used. Once again, more seeds should be collected if large seed losses are expected.

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BIOSYSTEMATICS

TAXONOMY, BIOSYSTEMATICS AND CONSERVATION

VERNON H. HEYWOOD

THE THREE LEVELS OF BIODIVERSITY

It is customary to consider biodiversity as occurring at three levels:

(i) The ecosystem or landscape level, which is concerned with the enormous range of ecosystems, landscapes and habitats that exist today, and with the relationships and processes that occur within them. Although the general structure and composition of most ecosystems is reasonably well known at a general level, their detailed functioning is poorly understood, nor do we know much about questions such as redundancy in ecosystems, keystone species, etc.

(ii) The taxonomic level, often referred to as the species level, but which, in fact, covers biodiversity at all taxonomic levels, although with a focus especially on families, genera and species. One of the commonest assessments of biological diversity is in terms of species (which of necessity involves a knowledge of the genera concerned), such as floristic or faunistic richness, numbers of endemic species, etc. However, in some parts of the tropics classification at the species level is so tentative and unsatisfactory that the number of genera is sometimes advocated as a measure of floristic or faunistic richness. The inventory of the world's flora and fauna is very uneven and for many groups highly incomplete. It is reckoned that about 1.5 million species of organisms have been described of which about half are insects. In global terms the flowering plants and ferns and the vertebrates are reasonably well known, although many species remain to be discovered in the tropics and many of those that have been described are known only superficially. On the other hand, there are several groups such as soil fungi, insects and nematodes where it is believed that tens or hundreds of thousands of species (or in the case of insects, millions) remain undiscovered and unknown to science. It is widely believed that the total number of species on our planet today is of the order of ten million, although up to thirty to fifty million (most of them insects) has been suggested by some specialists. It is quite clear that a considerable proportion of these will become extinct before they are even described. The task of describing scientifically plants and animals, giving them names and arranging them in groups such as genera, families and orders, falls to scientists known as taxonomists. Unfortunately, although scientific classification of plants, animals and microorganisms has been carried out for over two centuries, a vast number of species remain to be described and the numbers of taxonomists available in herbaria, museums and universities are quite inadequate to meet the challenge of describing the diversity that we know exists. This is especially true in the tropics

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where the resources do not exist although the biological diversity is greatest. Not only are there not enough taxonomists available to undertake the necessary work, but support for taxonomic activity is on the decline in most countries. This is partly due to a failure on the part of governments and administrations to recognise the importance of taxonomic classification as the basis of biological knowledge, partly caused by the attitudes of some taxonomists who adopt a too-academic approach to their subject, and partly due to the short-sighted and disparaging attitude of other biological scientists who in their ignorance regard taxonomy as outmoded. The training of taxonomists is an urgent necessity so that work on the inventory of the world's biological resources can not only continue but accelerate.

(iii) The genetic level, which is concerned with the diversity found within populations of species in terms of chromosomes, genes and genetic information. This is perhaps the most neglected and least understood area of biological diversity and one that conservation biologists have only begun to address.

TAXONOMY AND CLASSIFICATION

A major function of taxonomy is the production of a classification so as to allow the diversity of nature to be broken down into smaller manageable units that can be recognised, named and communicated. The need for a system of classification is absolute, for it is only through describing and naming organisms and then grouping them into a classification that we can begin to comprehend and handle the diversity of nature. Taxonomy, the procedures and methodologies for the scientific classification of plants, is therefore essential as a means of communication: the name of a plant or animal is the key to the literature about it.

Classification is both the process of grouping species into classes and the resultant arrangement. The units of classification, i.e. the taxonomic groups are known as taxa (singular: taxon) and these are arranged in a nested hierarchy:

The basic unit is the species, composed of populations of individuals which more closely resemble each other than they do the members of other such assemblages. For practical purposes species are normally recognisable morphologically. They do not necessarily correspond with genetically defined breeding groups but it is probable that most of the members of a species are able, at least in theory, to breed with each other, although there are many exceptions to this simple proposition. Species are grouped into more inclusive groups called genera (singular genus) and these in turn are grouped into yet more inclusive groups called families (in the case of plants). These three taxa or taxonomic groups – species, genus and family – are the ones most frequently used by general biologists, conservationists, ecologists and others.

The different arrangement of the families are known as systems of classification. These may purport to indicate the assumed evolutionary or phylogenetic relationships and derivations between the component families and higher groupings, and may be presented in the form of a diagram or tree (phylogram or cladogram); or the arrangement may be based on assessments of overall similarities without any necessary evolutionary or phylogenetic implications. They, too, may be arranged in a tree-like diagram, known as a phenogram. These different systems of classification do not affect the basic classification of the component groups into species, genera and families and for most practical purposes need not concern the users of taxonomy. Moreover, on the printed pages of a Flora or Handbook only simple linear system can be followed. The arrangement of the herbarium cannot reflect closely any complex system and quite a number of herbaria follow an alphabetical arrangement by families.

Identification or determination is the term applied to the process of ascertaining to which family, genus and species a sample of an organism belongs. This is usually undertaken by the use of identification keys, handbooks, comparison with herbarium or museum specimens or illustrations. Skilled taxonomists normally can recognise several thousand species by sight after years of experience.

Floristic taxonomy is concerned with making inventories of the plants occurring in an area. The total number of flowering plant species is estimated at 250,000 of which about 170,000 are tropical or subtropical in their distribution. Over 95,000 species occur in tropical America with an estimated 50,000 in Brazil and 45,000 in Colombia. Tropical and subtropical Asia contain some 50,000 plant species, with 20,000 in Indonesia alone. Tropical Africa, on the other hand, is relatively poor floristically with an estimated 35,000 species, including 10,000 in Madagascar, while Southern Africa has 20,000 species. In contrast the whole of Europe has 11,500 species in an area about four times the size of the three northern Andean countries of Colombia, Ecuador and Peru combined, which together house over 60,000 species of plants.

For historical reasons, the floras of temperate countries have been very much better and more intensively studied than those of tropical regions and today there is a great need for much more floristic and taxonomic work to be undertaken in the tropics. The basic floristic inventory needs to be completed as a matter of urgency but it has to be recognised that there is an imbalance between tropical and temperate countries in terms of trained taxonomists and institutional resources such as herbaria, libraries and botanic gardens: the general rule is that the greater the biological diversity, the fewer the taxonomic resources. In addition there is an overall shortage of trained plant taxonomists. In many temperate countries the standing of taxonomy has seriously declined and consequently support for both training and research has decreased considerably.

STORAGE AND PUBLICATIONS OF DATA

Taxonomic data consist of (i) label data, i.e. details of the material or specimens collected in the field such as locality, habitat, date, reported uses, collector, reference number, etc; and (ii) information extracted from the specimens by a wide variety of techniques (morphology, anatomy, cytology, embryology, etc.). In the last few decades there has been an increasing use of an over-expanding range of characters as a result of the application of chemical, physical and electronic techniques of analysis, including light and electron microscopy, chromatography, electrophoresis, isozyme analysis, etc. The data are presented in indirect form as spots on chromatography paper, bands on electrophoretograms, graphs, print-outs, etc. These more sophisticated approaches are, however, only applied to a limited number of groups and the bulk of taxonomic work is still undertaken using basic floristic techniques in the field and herbarium, relying on easily visible morphological characters for recognition, description and identification.

The vehicles for the publication of taxonomic data are many and varied. They include *Index Kewensis* (1895 to date) which lists all binomials (species and generic names) of angiosperms and gymnosperms published, and, as from the 16th quinquennial supplement, also infraspecific taxa. Recently, annual supplements have been issued and the whole *Index* computerised. Generic names are listed in *Index Nominum Genericorum* published originally as a card index and later (1979) as three volumes of *Regnum Vegetabile*, giving details of place of publication, nomenclatural information and indication of type-species.

A very widely used compilation is Willis's *A Dictionary of Flowering Plants and Ferns*, 8th edition by H.K.A. Shaw (1973), which lists all family and generic names and attempts to indicate which are nomenclaturally correct and which are synonyms. A useful complement to Willis is *The Plant Book – A Portable Dictionary of the Higher Plants* by D.J. Mabberley (1987) which gives the families and genera of the flowering plants, conifers, ferns and their allies together with their common names and uses.

Indexes to taxonomic literature as opposed to the names of plants are common, and produced by many countries. A more comprehensive one is the *Kew Record of Taxonomic Literature* which subsumed several previous abstracting journals or indexes and attempts a world coverage of the literature of plant taxonomy.

The traditional form of publication of taxonomic data is in the form of Floras, monographs and checklists or catalogues. The primary function of a Flora is, in the words of Bentham, "to afford the means of determining any plant growing in the area concerned." It attempts to establish how many groups there are in the area concerned that merit the rank of genus, species, subspecies, etc.; it indicates how they may be recognised by means of keys, descriptions, illustrations, and where they may be found and in what habitats.

There is an enormous diversity of Floras in terms of size, content, scope and ease of use. They vary from multi-volumed, detailed works which are almost monographic in scope, published over a period of years to pocket-sized single-volume excursion Floras. Yet others are little more than floristic lists containing only lists of species but with no keys or descriptions. No comprehensive listing of the world's Floras is available but Frodin's *Guide to Standard Floras of the World* (1984) is extremely useful as an annotated, geographically arranged systematic bibliography of the principal floras, enumerations, checklists, and chorological atlases of different areas. Some Floras include lists of specimens in herbaria that have been consulted during the preparation of the work. Users without access to a sizeable herbarium can practically ignore these citations.

Many Floras include synonyms after the names of the species or infraspecific taxa included. The non-specialist user of taxonomic publications has to appreciate that, although every taxonomic group has only one correct name, different names have frequently been applied to the same species through their having been described independently more than once, or due to technical reasons concerning the application of the International Code of Botanical Nomenclature which governs the naming of wild plants. Cultivated plants are covered by a separate code – International Code of Nomenclature of Cultivated Plants. A useful guide to the Codes and other aspects of biological nomenclature is given in Jeffrey's *Biological Nomenclature* (1989).

Monographs are detailed studies of a single genus, group of species or occasionally a whole family. They not only involve a detailed taxonomic revision of the group concerned but a synthesis of all relevant data such as anatomy, cytology, palynology, chemistry, crossing experiments, phytogeography, plus a discussion of the evolution and phylogeny of the group. They are normally of use to trained taxonomists only because of the specialist nature of the information they contain.

The other data of systematic botany are to some extent brought together into handbooks such as Metcalfe & Chalk's *Anatomy of the Dicotyledons*, 2nd edition (1979–83) and the series *Anatomy of the Monocotyledons* edited by Metcalfe; Corner's *The Seeds of the Dicotyledons* (1976), and various chromosome atlases. References to such compilations will be found in A.C. Stace *Plant Taxonomy and Biosystematics*, 2nd edition (1989) and in T.F. Stuessy *Plant Taxonomy* (1990).

PLANT BIOSYSTEMATICS

Conventional taxonomy as practised largely in the herbarium and laboratory is often distinguished from biosystematics, which has been defined as the taxonomic application of the discipline known as genecology – the study of the genotypic and phenotypic variation within species in relation to the factors of the habitats in which they occur. Biosystematics focuses, therefore, on variation within and between populations, on the evolutionary processes that occur within them, and relies heavily on cytological, genetical and ecological data. The term experimental taxonomy is sometimes used for this approach. With its focus on infraspecific variation and on processes and patterns within populations, the results cannot often be fitted into the straightjacket of the conventional taxonomic hierarchy of family, genus, species, subspecies, variety. Consequently special categories have been devised to cater for the kinds of situations covered by biosystematics. Examples are the genecological hierarchy of ecotype, ecospecies, coenospecies and comparium, referring to decreasing degrees of crossability between members of the different groups, and the -deme terminology (e.g. cytodeme, gamodeme, ecodeme), aimed at covering in an informal manner virtually any microevolutionary situation. The trouble with such special classification is that there is no formal system for the recompilation, storage and retrieval of the units, and no consistent mechanism for their description; so they are difficult to handle and refer to.

The conventional taxonomic units, especially the species, subspecies and variety, have been regarded by some users of taxonomy as unsatisfactory on the grounds that they lack precision, are based on inadequate population sampling, or are not defined in terms of crossability. Plant breeders, in particular, prefer to use their own system of primary, secondary and tertiary genepools (analogous to the genecological hierarchy) and then to relate taxonomic species to these. It has, however, to be recognised that taxonomic species are seldom defined in terms of the ability of their constituent members to exchange genes and their inability to do so with members of other species as the so-called 'biological species concept' would require, but on estimates of their distinctiveness as based on morphological features supported by whatever field or laboratory information may be available. Indeed thousands of the 250,000 species of higher plants accepted today have been based on one or a few specimens, and it has to be assumed that they represent no more than samples of populations bearing similar characteristics that will be found in the field. Moreover, there is an increasing likelihood that as habitat loss continues at its present scale worldwide, many of such species will remain known from a handful of specimens and become rare and endangered even before they are well known. It should also be noted that for the majority of species little is known about them apart from a few morphological or anatomical characteristics. The sophisticated tools of modern taxonomy have been applied to a small minority of species to date, most of them from temperate regions.

TAXONOMY AND GENETIC RESOURCES

In the assessment of biological diversity, sound taxonomy is the necessary underpinning. As has been frequently pointed out, we do not even know to an order of magnitude how many species of all kinds exist on earth today. While our estimates of the number of flowering plants and ferns are fairly accurate and only perhaps about 5% remain to be discovered, for other groups like tropical soil fungi we can only hazard a guess based on extrapolations from inadequate samples. Many tropical plant species are very poorly known as regards their population distribution and variation, and consequently it is virtually impossible to assess their conservation status with any degree of confidence.

At the level of genetic variation within populations, biodiversity is poorly studied or understood. There is increasing concern with the conservation not only of species but of genetic resources of wild species. By genetic resource is meant the heritable characteristics of a plant (or animal) or real or potential benefit to people. Most of the work on genetic resources has been concentrated on a relatively small number of crop plants, pasture and forage species, and important tree species, together with some of their wild relatives. There is an urgent need to extend and broaden the basis of genetic resource conservation of wild species so as to cover a greater range of crops, especially those used in local socio-economic systems in developing countries, including root crops, fruits, fibres, fuelwood and oil plants, and the tens of thousands of species which are used in local medicines. Additionally, germplasm of wild species will become increasingly needed for habitat restoration and rehabilitation during the coming decades.

The conservation of germplasm of wild species and of wild relatives of crop plants (see Hoyt (1988) *Conserving the Wild Relatives of Crops*) has been advocated by IUCN, WWF and by IBPGR, and it is one of the main objectives of the Botanic Gardens Conservation Secretariat as outlined in the recently published *Botanic Gardens Conservation Strategy* (WWF/IUCN/BGCS 1989). An essential basis for such work is sound taxonomic knowledge for the sampling, identification and handling of the material. Taxonomists, conservationists and geneticists have to work in close collaboration if we are to achieve the maximum conservation of biological diversity.

ROLES AND LIMITS OF LOCAL HERBARIA IN CONSERVATION BIOLOGY

INGA AND OLOV HEDBERG

INTRODUCTION

The accelerating conversion of tropical moist forests (cf. Myers 1980) and of other ecosystems as well as the catastrophical gene erosion following in the wake of the green revolution some 25 years ago has alerted the world to the necessity of conserving as much as possible of the biological resources on which our future depends (World Conservation Strategy 1980). Many insufficiently known and under-utilised plants may prove very useful for mankind – if they survive long enough (Anonymous 1957). 'Biodiversity' has become a word in vogue in the international debate – although one fears that many of those using it know very little of its meaning and importance. An elegant and comprehensive presentation has been provided by Wilson (1988). According to a draft 'Biodiversity Convention' prepared by UNEP for the Brazil conference in 1992 all countries should attempt "to conserve the maximum possible biodiversity for the benefit of present and future generations and for its intrinsic value".

A first step towards conservation of botanical biodiversity was the establishment of gene banks, first in the developed countries and now also in the underdeveloped countries (Anonymous 1989). These are intended to safeguard future availability of plant genetic resources of species of current or potential interest, not only as cereals and tubers but also fodder and forage plants, oil seed crops, cultivated, weedy or wild vegetables, wild fruits and nuts, ornamentals, medicinal plants and forest trees. Preservation is effected or envisaged not only through storage of frozen seeds but also through cultivation in botanic gardens and field gene banks, as well as through *in situ* conservation in national parks and reserves of various kinds.

An indispensable prerequisite for rational conservation is to know which species need protection and where these occur. In many northern countries the flora is comparatively poor in species and well known, and much attention has been paid to endangered plant species and ecosystems. In contrast, most tropical countries have a much richer flora and far less exploration has been done, which means that many new species await discovery. The reckless exploitation of tropical forest by timber and pulp companies in the developed world and the accelerating conversion of tropical ecosystems to farmland, pasture and forest plantations caused by rapid population growth makes it very urgent to record and document their flora as well as

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the local uses of wild plants for food, medicine and technical products so that efficient conservation measures can be taken.

On a global scale IUCN is keeping computerised indexes of threatened species and ecosystems as well as of national parks and other protected areas and publishes Red Data Books (e.g. Lucas & Synge 1978). This work is greatly facilitated in northern countries due to the wealth of information available, whereas it is considerably hampered in tropical countries by the lack of knowledge about species and ecosystems.

Fundamental for all conservation efforts is the possibility for information storage and retrieval – be it in card indexes or computer systems. Probably not many botanists today realise that it was Linnaeus who through his binominal nomenclature and his sexual system made this possible for plants. All information published about new species or facts about plants must be documented with a Latin name. When, for example, an agriculturally very interesting new species of perennial maize was recently discovered in Mexico available information about it was given under the name *Zea diploperennis* (Iltis *et al.* 1979), and this documentation was fundamental to achieve safe conservation of the only known wild population of it for the future (Iltis, in Wilson 1988, pp. 98-105).

Documentation of botanical information always uses international names in Latin. This may appear cumbersome to some users, but it is indispensable for international communication – Latin names are sometimes the only intelligible words for many of us in Floras from foreign countries. Finding the correct Latin name for a species is not always easy, but guidance for naming is given in the *International Code of Botanical Nomenclature* (1988). According to this Code each new taxon must have a diagnosis in Latin, and many old publications are published in Latin. Assistance in interpreting such description is given by Stearn (1966).

Information about plant species and genera is usually summarised in published works such as Floras and monographs. The importance of a Flora (handbook) to a developing country can hardly be overestimated – it provides essential assistance towards rational use of biological resources (Brenan 1963). It is therefore natural that during colonial times large resources were invested in elaborating Floras for the colonies, and that these efforts have continued after decolonising. But for many purposes literature is not enough – in order to study additional details or check the identity of a record or notes on a label, etc. it is essential to resort to the botanical documentation provided by herbaria.

HERBARIA

A herbarium is a collection of reference specimens of plants, which have been flattened and dried, so that they take as little space as possible but still retain most of their original appearances. Each collection, which may consist of one or more specimens, or of branches of taller plants like trees and shrubs, is mounted on a sheet of stiff paper of standard format (about 28cm x 45cm) and provided with a label giving information on the scientific (and – if available – vernacular) name of the species, the detailed locality (preferably giving latitude and longitude as well as the name), a short site description, date of collecting and the collector's name and collection number. It may also provide information about colour of flowers and other parts, on other characters and on local uses of the plant. In the herbarium the collections are sorted into genera and families, which are nowadays (in most herbaria) kept in alphabetical order (under the main divisions Monocotyledons, Dicotyledons and Cryptogams). To prepare good herbarium specimens, mount them and protect them against insect attack requires considerable skill, and special training of both botanists and technicians in this area is essential. To be secured against insect attacks a herbarium needs constant attention by competent staff.

Main tasks of herbaria

A basic task for a national herbarium is to name plant specimens delivered to it by government officials, forest officers, farmers, or the general public – and to provide information about the plants in question, be it an accessory food plant, a weed, a medicinal plant, or a poisonous plant used in a murder case. It is also desirable that the staff of a herbarium provides information to relevant authorities and the general public on points of interest such as increase of obnoxious water weeds, scarcity of important medicinal plants, or threats to important vegetation types. Another main function of a herbarium is to serve as a repository or archive for reference specimens of plant material, e.g. vouchers for a gene-bank acquisition of a wild plant, a reference sheet for published information on chromosome number, chemical contents, or medicinal use, etc. Every piece of new scientific information about a plant species *must* refer to a voucher specimen in a public herbarium so that the determination can be checked if desirable. This need of documentation is augmented by the fact that the flora of most tropical countries is yet so insufficiently known that the naming of plants may be changed. Another important function, especially of a national herbarium, is to keep a representative and adequately named collection of the country's flora to assist in the naming of new plant material for government departments of agriculture, forestry, land use planning, health, etc., as well as to the general public. A third function, important not least for conservation purposes, is to provide – through herbarium specimens and inventories of national parks and reserves, etc. – a survey of all known information about the distribution of every plant species of the country. The latter function is nowadays increasingly served through a computerised index. Considering the rapid changes in land use at present occurring in most tropical countries, such an index is urgently needed to improve the knowledge of the flora, especially of actually or potentially useful plants, through inventories of insufficiently know areas, particularly when these are threatened by exploitation.

Availability of herbaria

Herbaria have long existed in most developed countries and have served as invaluable centres of documentation for rational utilisation of plant products throughout the world, but both herbaria and systematic botanists are threatened by the unbalance caused by the tendency by research councils and financing agencies to give priority to the newest developments in science – and disregard the fundamental importance of taxonomy for conservation. A recent evaluation by the US National Academy of Sciences therefore urged that increased attention must be given to the training of more taxonomists and of more taxonomic work in the tropics (Anonymous 1980).

The largest herbaria, e.g. in Berlin, Brussels, Leningrad, London, Missouri, New York, Paris, Stockholm, etc. have millions of herbarium specimens and large botanical libraries at their disposal. In the tropics, conditions are quite different, however. There are fairly large herbaria in a few tropical centres like Bogota, Nairobi and Singapore, but their collections are much younger and much smaller – although the floras of the countries they serve are so rich. Most tropical developing countries have small and insufficiently funded herbaria – if any.

During colonial times botanical matters concerning agriculture, plant breeding and conservation of vegetation were in the main dealt with by the colonial powers, which had both herbaria and botanists available in their home countries, but after decolonisation circumstances changed dramatically. Even if there are still some possibilities for collaboration, neither resources nor interest in the ex-colonial powers suffice for the need. To obtain rational conservation of genetic diversity in useful plants as well as for conservation of threatened species and ecosystems, a considerable increase in number and quality of local herbaria will therefore be required.

Minimum needs for a National Herbarium

Existing national herbaria in tropical underdeveloped countries vary very much in size, staffing and equipment and their needs differ of course according to the size of the country concerned. There are certain minimum needs for satisfactory functioning herbaria, such as, for example, adequate localities, adequate cupboards close enough to keep insects out, and a freezer for elimination of insect attacks. Also adequate staffing and working equipment are essential.

Very important for smooth functioning of a herbarium is also contact with other herbaria in the region, for information exchange, joint technician courses, etc. It is also essential to affiliate to the International Association of Plant Taxonomists (IAPT), whose journal *Taxon* contains much useful information. Contacts with other herbaria is facilitated through *Index Herbariorum*, published by IAPT, which also lists the botanists attached to each herbarium. There is also a *Manual for Tropical Herbaria* (Fosberg & Sachet 1965).

One of the most important roles for a herbarium, not least in a tropical developing country, should be to work for conservation of biodiversity and of the biological environment in general. Few other biologists have such good opportunities as experienced herbarium taxonomists – also doing field inventories – to find out when species and ecosystems are becoming threatened, so that urgent conservation measures are required. Given the rapid population growth and the scarcity of money for conservation purposes in most developing countries, it is imperative to monitor any depletion in biological diversity or natural vegetation so that international support for conservation can be secured in time when needed.

For rational conservation planning it is essential to survey the distribution of each relevant species. For that purpose it is desirable to enter both herbarium records and published information into a computerised index. If similar inventories are made in adjacent countries the prospects for successful monitoring and conservation of threatened species are much improved.

Limitations of local herbaria

While herbaria are indispensable for documentation and classification of plant species they also have obvious limitations. A local herbarium may only register the variation of a species within the country concerned. To catch its full range of variation, one often has to consult material from other herbaria. For definite taxonomic revisions a taxonomist will often depend on loans from other regional herbaria, information about which are conveniently found in *Index Herbariorum*. For reliable naming of a taxon one must often compare the relevant material to a type specimen for the name in question, and because the types of most tropical species are in European or North American herbaria this, in many cases, requires sending a duplicate collection abroad for comparison. For taxonomic revisions of a particular group it is often necessary to scrutinise material from the large northern herbaria – here, also, collaboration between herbaria is essential.

In spite of their usefulness in conservation work, herbaria alone are not sufficient – often living material in nature or botanic gardens must also be consulted. Data on pollination, seed dispersal and germination, and hybridisation with other species, etc. may be very helpful for efficient conservation.

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TRAINING IN HERBARIUM DEVELOPMENT AND MANAGEMENT

P. KAPOOR-VIJAY and G. LUCAS

The drastic degradation of the environment which is apparent throughout the world today has demonstrated how little we know about the plant diversity which is so fundamental to successful human existence. To a large extent plants are our environment. Knowledge of plant diversity is essential in the quest to breed pest resistance into our crops, and to find new sources of energy, food, medicine and useful materials. A taxonomist is hence being asked urgent questions on the identification, nomenclature, classification and distribution of plants, as well as their ecology and use. These questions can be answered effectively if the information available in herbaria is of high quality and complete. In short, there can be no taxonomy without herbaria. With this essential case in mind, this keystone training course was initiated in Kew in the hope that it would become an example to be followed around the world.

The Commonwealth Science Council (CSC) has been involved in promoting the techniques and methods in the study, use and conservation of biodiversity of plant genetic resources since 1986 and has been closely involved with the training in 'Herbarium Development and Management'.

At present, an 8-12 week course is held every year (co-sponsored by the CSC and the British Council) at the Kew Herbarium. The course has the following aims:

- give each student the knowledge and skills to become a proficient herbarium technician
- give each student the insight to select methods most appropriate to the needs of his/her own institute
- enable students to understand the principles of herbarium management
- enable students to appreciate the value of information available in a herbarium and make it accessible to a wider audience
- enable students to gain a wider understanding of conservation and development policy in other countries

The course is divided into two component, formal and optional. The formal and major part of the course is concentrated in the first 6 weeks with practical assignments and options occurring in the last fortnight.

FORMAL COMPONENT

The formal component includes the following lectures and demonstrations:

Herbarium management, routine and materials
Plant collecting, preservation and related subjects

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Edited by P. Kapoor-Vijay and J. White.

Plant morphology, identification and curation of collections
General interest subjects

These components are covered under the following headings:

The development, purpose and types of herbaria
The role of taxonomy
Arrangement of herbarium collections
The herbarium building and specimen storage
Pests and treatments
Materials
Ancillary collections (i) spirit, carpological and wood
Ancillary collections (ii) illustrations and photographic records
Centralised accessioning, recording and dispatch procedures (GSU introduction)
Duplicate distribution
Loans to other institutions
Preparation for mounting
Mounting
Good and bad practice
Special curation (succulents, *Palmae* and *Pandanaceae*)
Curation of fungi
Plant names
Palynology (lecture and tour of laboratory)
Incorporation of mounted specimens (laying-in)
Essential herbarium literature (including tour of library)
Removal of samples from herbarium sheets
Arrangement of herbarium collections according to new publications (curation)
Label design and production (including demonstration of printing press)
Photographic copying of herbarium sheets (including tour of studios)
Illustration
Plant identification and family recognition
Ecology and taxonomy
Introduction to computers
Collecting and preserving specimens
Notes on the collection and preservation of fungi
Collecting materials for ancillary disciplines (anatomy, cytology, palynology and phytochemistry)
The collection and curation of pteridophytes
Collecting living material
Accessioning living material and phytosanitary regulations
Photography and fieldwork
Keys – punched-card and computerised
Check-lists
Collectors, itineraries, maps and gazetteer (including a tour of the map room)
Role of botanic gardens

Seed bank (lecture and tour)
Conservation and the herbarium
Economic botany (lecture and museum tour)

Practical sessions are dealt either in the form of one-to-one instruction session with staff members or are organised to a 'workshop' format. A 'work sheet' is provided to help guide the students through most of the one-to-one sessions where Kew in-house procedures must be strictly followed. Two unaided practical assignments for assessment are also included (see note below).

List of practical sessions

- General Services Unit (GSU) – practical work relating to accessioning, recording and dispatch procedures
- Preparation for mounting
- Mounting one-to-one with a staff member (from the mounting team)
- Laying-in one-to-one with ASO/SO staff member. Work sheet provided
- Collecting
- Pressing, and preparation of data labels
- Preparation for mounting, and mounting
- Vegetative morphology
- Floral morphology, dissecting fresh material
- Floral morphology, dissecting and preserving dried material
- Curation (i.e. the use of a revision to up date specimen names)
- Keys – practice with dichotomous and multiaccess keys

Family recognition

Family sort of east African specimens
Family sort for Malesian specimens
Compositae workshop
Graminae workshop
Rubiaceae workshop
Leguminosae workshop
Ferns and fern allies workshop

OPTIONAL COMPONENT

This aspect of the course aims to provide the students with an introduction to a supplementary skill which would be of benefit both to the individual to his/her home institution. The students are offered a choice of five options form which they are asked to indicate their first and second preferences.

Option 1 – Additional herbarium curation

This option gives the opportunity to help rearrange the collections in accordance with a newly published work and extract loans as requested by other institutions.

Option 2 – Practical plant identification

Plant identification is a skill frequently required of herbarium technicians. Specimens from certain geographical areas and families can be selected to give students practical experience in identification.

Option 3 – Checklist compilation

This option is suitable for trainees with some previous experience of herbarium routines and plant identification.

Option 4 – Illustration

Local or specialised herbaria often do not have the services of a professional illustrator. Students are encouraged to develop their skill in drawing plants, maps and diagrams.

Option 5 – An introduction to library management

In a local or specialised herbarium the duties of a herbarium technician often include routine library maintenance. This option introduces the student to acquisition, cataloguing storage (with special reference to tropical conditions).

PROJECTS

These are additional to the course and only available to those students who are granted 12-week subsistence by their sponsor. The students are provided with facilities and given help and guidance as necessary. The projects are not assessed by Kew staff.

Both projects and options should reflect the personal needs of the candidate and the needs of their home institution and are chosen with the approval of the candidate's Head of Department or Director.

LIFE CYCLES AND POPULATION DYNAMICS

PLANT POPULATION BIOLOGY AND THE MANAGEMENT OF VIABLE PLANT POPULATIONS

L.F. HUENNEKE, K. HOLSINGER & M.E. PALMER

INTRODUCTION

Wildlife conservation has focused on population dynamics as the key to managing animal populations. The most familiar examples, and the species that have been easiest to study, are vertebrates – mammals, birds, herps and fish. In studying such populations, it is natural to focus on the number, age and sex of individuals, demographic rates, social behaviour, breeding behaviour, and feeding or other resource use. In managing for viable populations, scientists have concentrated on understanding how these features of species or of particular populations affect short- and long-term changes in population size and chances of extinction. Observation of population dynamics and modelling the effects of changes in life histories allow the analysis of possible interventions at various stages of the life history, e.g. the minimisation of mortality risks at some critical point of the life cycle.

The traditional approach to plant conservation, in contrast, has emphasised little direct action beyond the protection of habitats supporting an extant population of the desired species. Recently some efforts have been made to achieve the same understanding of population dynamics and the factors affecting a population's demographic behaviour for certain plant species that we have reached for vertebrates (Harper & White 1974; Harper 1977). However, plants are not animals – certainly not like the familiar terrestrial vertebrates, with their discrete and mobile individuals, determinate growth pattern, and two separate sexes. In this chapter we begin by describing a generalised plant life history, and discuss some of the demographic and genetic considerations that characterise plant population biology. We outline the information necessary for understanding the likely dynamics and status of a given species or population, describe those types of plants we feel might be managed as populations of individuals (in ways similar to those being used in the management of vertebrate populations), and list a few of the techniques available for active management of plants. For most plant taxa, habitat preservation will continue to be the method of choice, but many of the demographic and genetic factors described below must still be considered in developing a sound management plan.

PLANT POPULATION BIOLOGY

A general plant life history

Plants show a greater range of life histories and demographic patterns than do the

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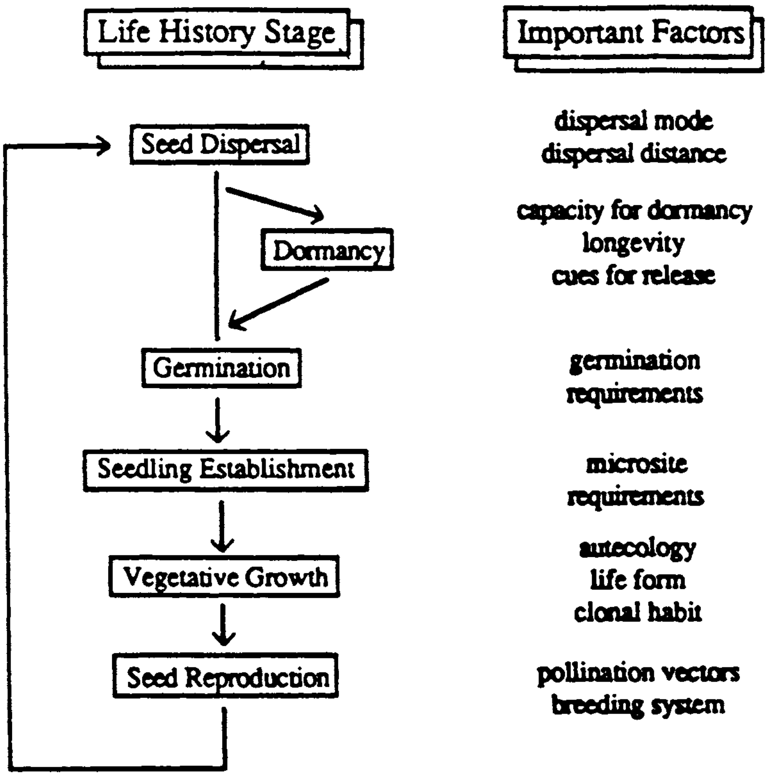
familiar vertebrates, but most share at least some features that distinguish them from animals (Bradshaw 1972). We present here a pattern typical of most spermatophytes or seed plans (Fig. 1). Individuals begin life as a seed, following the fusion of male gametes (in pollen) with female eggs (in ovules). The seed stage is virtually the only stage of the life history with mobility – any movement to another location, whether centimetres or kilometres away from the parent plant, occurs now. Seed dispersal is a passive motion, unlike that of most vertebrates; some dispersal vector, whether wind, gravity or animal, is responsible for the seed's arrival in a new location.

FIG. 1. A generalised plant life history

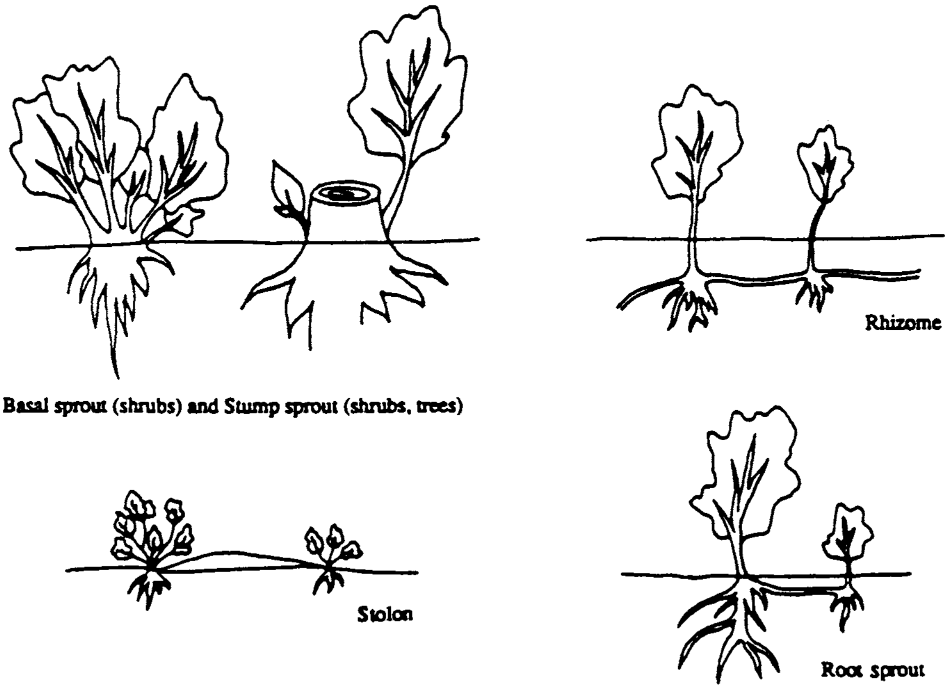


When the seed arrives in a site it may either die, germinate during the next favourable season, or become dormant. Seeds of many species possess dormancy, often these dormant seeds become incorporated into the soil and remain in the site for long periods, germinating only after some disturbance or environmental change creates favourable growth conditions. Germination, the initiation of active growth, may require highly specific conditions or environmental cues or triggers. Many species germinate only in the presence of certain temperatures, moisture conditions, or light quality. Other seeds germinate only after passage through the gut of a seed-eating animal (which also provides dispersal).

Seedling establishment is the next crucial step of the life history. Only if the seed has arrived in a favourable location will the seedling take root and begin to photosynthesize, becoming independent of the seed reserves which allowed it to begin growth. Microsite requirements may be as specific, or more so, than germination requirements, and the availability of suitable microsites in an area often constrains the rate and success of reproduction.

After the seedling is well established, the period of vegetative growth continues. Unlike most vertebrates, most plants show indeterminate growth – the individual may grow continuously by repeating the modules of which it is constructed. In simple plants the modules are merely units of stem with associated leaves; the plant's axis grows by the addition of modules. In multiple-stemmed plants the axis itself is repeated. In many species these replicated modules are merely units of independent physiological life – each ramet can live and behave as an individual. These are clonal plants, which form genetically identical copies of themselves. The genet, or genetic individual comprising the daughter ramets, may create the ramets in any of several ways (Fig. 2). Some species are rhizomatous – underground 'stems' or rhizomes connect the ramets, at least temporarily. Daughter plants may form at the ends of stolons or above-ground runners in plants such as strawberries. Others form sprouts from roots or from the base of existing ramets. The unifying characteristic of these plants is that each ramet behaves as an individual with respect to ecological processes, although they represent only parts of a single genetic individual.

FIG. 2. Modes of clonal behaviour



The vegetative growth phase may last for varying periods of time. In annual plants it continues for only one growing season; during or at the end of that season the plant flowers, sets seed, and dies. A perennial survives to grow in the following seasons, either by becoming woody (as in trees and shrubs) or by surviving the unfavourable season below ground and regrowing the above-ground portions of the plant each season (herbaceous perennial).

Seed reproduction can be considered the final phase of the life cycle. Male and female gametes unite to form the zygote, or new individual, but the gametes do not necessarily come from different individuals, and a single individual may provide either or both. In breeding systems, then, plants display far greater variation than do vertebrates. Pollination, the equivalent of an animal's breeding behaviour, is largely a passive process (just as seed dispersal is). In most cases, pollen is moved between flowers by air currents and wind, or by animals. Annual plants reproduce by seed only once, at the end of their single growing season. Perennials may flower and reproduce only once (monocarpic species), senescing after reproduction, but more commonly perennials are capable of flowering repeatedly (polycarpic). In the latter plants, seed reproduction is uncoupled from senescence or the cessation of vegetative growth.

Demographic considerations

Immobility and the importance of spatial variability

Because plants are sessile through most of their life histories, they are greatly affected by local conditions. Variation in abiotic environmental factors or in the composition and vigour of neighbours (competitors) may thus greatly affect an individual plant's growth rate, chance of survival, and reproductive success. A complete description of a plant population, then, should include information on: i) the distribution of individuals among habitat types or microsites, and ii) the demographic rates of individuals in each habitat type. For example, many understorey plants may survive in a vegetative (non-flowering) state beneath a closed forest canopy, but individuals become vigorous enough to flower only when a canopy tree overhead dies (forming a light gap) and the light environment improves.

Lack of mobility eliminates the possibility of behavioural responses to many selective pressures. For example, plants have no active way to escape herbivores or grazers; only those plants occurring by chance in inconspicuous or inaccessible locations may escape persistent grazers. On the island of Hawaii, a native silversword has been nearly eliminated by exotic mouflon sheep. The sheep, excellent climbers, have eaten all but a handful of the silverswords on the most inaccessible cliff faces (Powell 1985). Similarly, seeds and seedlings have no way of moving themselves to a more favourable site if conditions are poor locally. A high percentage of the mortality of most plant populations occurs when seedlings germinate in unfavourable microsites.

Because plants are sessile, they are also affected by their relative positions in space. All plants rely on the same basic resources (light, water, soil, nutrients), and the success of an individual is often influenced by the numbers and sizes of its neighbouring plants. Competition for resources, from conspecifics or from individuals of other species, may limit the growth and reproductive success of individual plants. Conversely, the success of seed reproduction may depend upon the proximity of conspecifics. If a taxon is primarily outcrossing (relies on pollen from other individuals for successful seed set), its chances of reproductive success may depend greatly on the number and genetic identity of conspecifics located nearby. We are only now beginning to appreciate the importance of population structure on this fine scale. Clearly, though, in some cases the manager may need information on the spatial distribution of individuals.

Importance of size rather than age

For most plants, size rather than age is the most important determinant of demographic fate (survivorship, likelihoods of sexual or vegetative reproduction). Well-studied vertebrate populations often display differences in mortality and reproductive success of individuals of different ages or experience; in plants the equivalent relationship is between size and demography. Larger seed size, and the resultant larger initial size of the seedling, often confer a relative advantage over other seedlings. Earlier germination, and the 'head start' on growth, often gives the same advantage when later seedlings become established and begin to compete for resources. The largest individuals (larger because of genetic differences, earlier germination, more favourable microsite) usually contribute disproportionally greater percentages of seed output.

Size may even influence the plant's gender in some cases. In *Arisaema triphyllum* (the woodland jack-in-the-pulpit), for example, the largest indviduals function as females; smaller individuals produce only male flowers, and the smallest plants do not flower at all (Bierzychudek 1982). An individual that is large (and female) in one year might easily become smaller (and male or non-reproductive) the next year, if fruit production or herbivory or unfavourable growing conditions diminish the plant's underground energy reserves.

Vegetative or clonal growth

For vertebrates, the number of individuals is a simple discrete concept (although it may not be so easy to observe and count them in the field directly). For many plants, though, population number is a more complex issue. First, in many ecological considerations the number of individual plants is not a very meaningful statistic – plants are extremely plastic in size (there is no standard size for an adult, as in vertebrates), and it may be far more important to consider the total biomass of a species present in a site, or to weight individuals according to size, recognizing that the larger individuals have a greater impact on population dynamics (and on ecosystem resources).

Even if one decides to count individuals, the task is not so easy. Does one count the number of stems or the number of clumps of a shrub? The number of clumps or the individual tillers of a bunchgrass? For those plants capable of clonal behaviour, should one count ramets or genets? In most vertebrates, of course, the number of 'bodies' equals the number of genetic individuals; in clonal plants the number of ramets may be many times the number of genets. In a clonal plant population it may be very difficult to determine the number of genets; tracing underground connections such as rhizomes may destroy the population, and such connections often rot away, making it impossible to determine any physical relationship among ramets. However, electrophoresis and other types of genetic analysis have recently provided methods of identifying the daughter ramets of a single genet, and have been used with great success in tree, shrub and herb taxa.

For purposes of tracking the persistence of a population, it is naturally easiest simply to count or monitor ramets; successful clonal reproduction may ensure local persistence for a long period. For long-term considerations, however, it is probably necessary to understand the underlying genetic structure and the dynamics of genets (rates of new seedling establishment and of genet death) as well as ramets (see discussion of genetic considerations, below).

Seed bank of other dormant stages

One would hope that, in studying sessile organisms like plants, one has the advantage of being able to census and relocate individuals easily, with no need to rely on trapping, mark/recapture, etc. This ease of observation is true of some species, but many plant populations have an 'invisible' component – the seed bank on or in the soil. If seeds remain viable but dormant in the soil or litter layer, the individuals growing above ground may represent only a portion of the entire population. They may not even be truly representative of the gene pool (see later section on genetic considerations). In some species there may also be underground dormant individuals (corms or bulbs, root systems) – e.g. some woodland orchids, which spend one to several years in dormancy between episodes of flowering and growth.

These unseen individuals may be very important in moderating the influences of environmental or demographic stochasticity – even if reproduction fails entirely in an annual population (an extreme case), the seed bank may provide recruits for the coming year. Such dormancy has allowed the re-establishment of the rare vernal-pool annual grass, *Orcutia tenuis*, after years of total reproductive failure (Griggs & Jain 1983). Thus, it is crucial to determine whether or not seeds do remain viable for more than one year in the soil. Seed dormancy may account for the reappearance of taxa presumed absent or locally extinct as occurred after the cessation of grazing in the Hawaiian grassland (Loope & Scrowcroft 1985).

Plasticity of reproductive allocation

Plants show a greater range of life histories than do vertebrates. Many taxa are monocarpic, with the potential to reproduce only once. These plants may be annual, biennial (in which case they reproduce during their second growing season and then die), or monocarpic perennials, which live for several years before flowering and senescing. These monocarpic taxa are particularly vulnerable to stochastic effects, particularly environmental stochasticity. If the individual initiates flowering in an unfavourable year, it may die without leaving any viable progeny (no seed set). The timing of reproduction in monocarpic perennials may be especially tricky; in some small populations (e.g. the Hawaiian silversword, Powell 1985; bat-pollinated agaves of the southwest U.S., Howell & Roth 1981), an individual may flower in a year when few or no other individuals flower and no pollen is available for the outcrossing that produces viable seeds. In this case also the individual fails to leave any offspring.

Even if reproduction is successful, the monocarpic plant is somewhat constrained in its total reproductive effort, because it reproduces only once. Many monocarpic taxa, as compensation, produce large numbers of flowers and (potentially) seeds in comparison with closely-related polycarpic taxa.

Polycarpic plants, in contrast, have indeterminate lifespans and may display great plasticity in reproductive effort from year to year. Abundant seed production in a good year can compensate for poor or no seed set in bad years. Thus the polycarpic habit minimizes the importance of stochastic factors in the persistence of the population.

IMPORTANCE OF MUTUALISTIC RELATIONSHIPS

Plants are often involved in mutualistic relationships with other organisms, particularly animals. The dynamics of the mutualist may influence the dynamics of the plant population of interest. Pollination biology provides the classic examples of such relationships. A wide range of vectors serve to transport pollen from one plant to another (Table 1): these vectors differ in their selectivity and faithfulness to particular plant species, in the average distance pollen is transported, and in their vulnerability to environmental change.

Insect pollinators may be highly specific or generalised in their behaviour (Real 1983). We may assume that the more diverse the insect pollinators of a plant species, the less vulnerable that species is to fluctuations in the abundance of a given insect. (Wind-pollinated plants, the extreme case, require no mutualist for pollination and are thus buffered from such indirect effects.) Accurate assessment of the pollination biology of a plant often requires intensive field effort, however. It is particularly difficult, for example, to reconstruct now the original dynamics and population biology of those North American wildflowers whose native pollinators have been reduced or displaced by the European honeybee.

Vertebrate pollinators seem especially sensitive to habitat fragmentation and other disturbance. For example, declines in the abundance of bats have apparently affected the reproductive success of the southwestern agaves (Howell & Roth 1981). The manager must, therefore, be alert to the plant population's requirements for a specific pollen vector and to the status of that animal vector.

Seed dispersal is another portion of the plant life cycle that can be influenced by mutualists (van der Pijl 1982). Seeds display a variety of morphological structures

TABLE 1. Pollination vectors and associated plant adaptations.

Vector	Flower colour	Odour	Shape
wind	dull	none	small
beetles	dull	fruity	round, flat
carrion flies	brown, green	rotting	variable
syrphids, bee flies	variable	variable	round
bees	white, yellow	sweet	round or 2-lipped
hawkmoths	white, pale green	sweet	tubular/spurred
butterflies	red, yellow, blue	sweet	tubular/spurred
birds	bright red	none	tubular/spurred
bats	white, green	fermented	bowl

(modified from Wyatt in L.Real (Ed) (1983), *Pollination Biology*)

that can be considered adaptations to particular modes of dispersal (Table 2). As in pollination relationships, the more specifically a plant is tied to a single mutualist species, the more vulnerable it is to declines in the abundance of that mutualist. Dispersers may move seeds to specific habitats, increasing the chances of a seed arriving in a favourable microsite. For example, birds that eat the fruits of shrubs growing in light gaps in the forest usually move to other open areas or gaps, excreting the seeds in favourable locations for shrub growth. A dispersal vector may do more than simply move seeds around, of course: often handling by the animal, or passage through the disperser's gut, increase the germinability of the seeds.

TABLE 2. Seed dispersal vectors and associated seed characters.

Vector	Transport mode	Seed shape	Reward to disperser
vertebrates	external (as in fur)	hooks or barbs	none
birds,	in gut	small hard seeds in sweet colourful fruit	fruit
ants	carried	small, with attached starch body (elaisome)	starch
wind	passive	small, winged or plumed	none

Interestingly, many of these mutualistic relationships are density-dependent (affected by plant population size). For example, a hummingbird-pollinated plant might occur in such a small population that not even a single hummingbird could support itself on the population's nectar while defending the territory. Plants in small populations thus suffer the risk of being unable to attract pollinators, and reproductive failure may follow. Awareness of this kind of threshold effect would be necessary in deciding the proper use of intervention, such as hand-pollination in years of isufficient natural pollination.

Adaptation to natural disturbance regimes

In managing natural areas, preserves or populations we usually attempt to minimise disturbances to the area. Many plant species, however, are adapted to certain natural disturbances. A forest tree may require the high-light environment of treefall gaps for successful seedling establishment; seeds of a riparian shrub may germinate only on recently-flooded gravel flats; many plants become established only on newly-burned areas. It is critical, then, to understand the types, intensities and frequencies of disturbances to which plants are adapted (Pickett & White 1985). For example, the underground portion of plants in a perennial grassland may survive periodic light fires, but extremely hot or unusually frequent fires will kill individuals and alter species composition. Very small soil disturbances may have little or no effect on those prairie plants, while badger mounds provide favourable microsites for seedling establishment, and larger disturbances (e.g. bulldozer tracks) destroy or inhibit the recovery of the prairie. In considering the effects of disturbance, then, one should consider the separate responses of ramets and genets.

GENETIC CONSIDERATIONS

It is important for a manager of endangered plant taxa to consider the possible genetic consequences of management alternatives before making a management decision. Making a decision to manage for a viable population simply by preserving the habitat is equivalent to making a decision that maintenance of the existing population structure is sufficient to ensure the long-term survival of the taxon. Any management decision has consequences for the genetics of the taxon, so some understanding of the genetic aspects of plant populations is necessary for successful management of endangered plant taxa.

In many ways, genetic processes in plant populations are similar to those in vertebrates. Loss of genetic variability as a result of drift diminishes the ability of a population to respond adaptively to changing environmental conditions and can lead to inbreeding depression in normally outcrossing plants. In either case, the long-term survival of individual populations, and perhaps of the taxon as a whole, is jeopardised. In spite of these similarities, there are significant biological differences between plant and vertebrates that require a different strategy for management in plants. In particular, plants reproduce in many more ways than vertebrates; and they have a much greater diversity of life histories than vertebrates. As a result, there is a much greater diversity of genetic structures among plant taxa than among vertebrates (Table 3). Different management strategies are required for different combinations of life history and mode of reproduction.

Diversity of breeding systems and genetic processes

Plants show a bewildering variety of breeding systems. These range from the plants with cleistogamous or closed flowers, within which only self-pollination occurs, to the obligate outcrossers (those producing viable seeds only after receiving pollen from another genetic individual), with every conceivable intermediate case found in one plant or another. Obligate outcrossers may have any of serveral features which ensure pollination by other genets. The plant may be self-incompatible, with self-pollen unable to fertilize the ovules and produce viable seed. The two sexual functions of a flower may be separated temporally, so that pollen is shed by the stamens only at a time when the pistil of that flower is not receptive. In the extreme case, dioecious taxa are those in which the sexes occur on separate plants, with individuals being either staminate or pistillate (the closest parallel to vertebrates).

Many plant taxa are intermediate in breeding pattern, i.e. they are facultative selfers. The spatial arrangement of stamens and pistils may encourage the reception of pollen from other individuals (e.g. that carried by insect vectors) but not preclude the possibility of self-pollination. Some plants hedge their bets by producing both cleistogamous flowers, which produce self-pollinated seed, and chasmogamous or open flowers that produce outcrossed progeny.

Understanding the breeding system is crucial to many management questions. For example, the effective population size, N_e, is often calculated for vertebrate populations to give some estimate of the population's vulnerability to genetic drift or inbreeding. A skewed sex ratio, or unequal reproductive contributions by various individuals, is known to decrease effective population size for any given number of adult individuals. In plants, the breeding system plays an equivalent role in determining the reproductive contributions of individuals. For any other than strictly dioecious plants, however, calculation of N_e will not be possible with the standard two-sex formulas.

Genetic structure of plant populations

The amount of information that could be collected on the genetic structure of even a single endangered taxon is overwhelming. It is, therefore, imperative that the amount of effort spent gathering this information is commensurate with the benefit likely to be obtained from it. Cursory surveys of morphological differentiation between different populations are probably sufficient for taxa that have a reasonable number of large populations. Those taxa in which only a few individuals occur in each population, even if there are many populations, may require more careful assessment of the genetic structure. Much depends on whether the taxon has always been rare or if its range and numbers have only recently been reduced. Taxa that have always been rare will probably have genetic systems that allow them to cope with the genetic consequences of rarity. Taxa that have only recently become rare, on the other hand, will probably have genetic systems appropriate for large, extensive populations and be very susceptible to the genetic consequences of rarity.

The genetic structure of plant taxa can be inferred from information of two general types: (i) phenotypic variability, and (ii) allelic variability at allozyme loci as assessed by electrophoretic techniques. Inferences based on phenotypic variability have several advantages over those based on allelic variability. First, assessments can be made easily in the field and frequently do not require sophisticated statistical treatment. Second, assessments based on phenotypic variability will often include assessments of characters of vegetative and floral morphology that are directly important in the survival and reproduction of the plant. Third, phenotypic variation, especially in characters other than colour characters, is usually polygenic, so that a sample of many genetic loci is implicitly included in an assessment of phenotypic variability.

TABLE 3. The relationships between life history traits and the distribution of genetic variation in plant populations

Character	Factors promoting genetic differentiation between populations	Factors retarding genetic differentiation between populations
Mode of reproduction	asexual	sexual
Mating system	self-fertilisation	outcrossing
Pollination vector (for mixed or out-crossing mating system)	animal pollination, especially insects	wind pollination
Seed dispersal	gravity (no obvious adaptations for dispersal) animal dispersed, intermediate	wind (winged or plumose seeds)
Phenology	populations asynchronous	populations either seasonal and synchronous, or with extended low-level flowering
Life cycle	annual	perennial
Timing of reproduction	monocarpic	polycarpic

Modified from Loveless & Hamrick (1984).

Assessments based on phenotypic variability also suffer from some significant disadvantages, however. Foremost among these is the difficulty of determining how much of the observed phenotypic variability is due to genetic differences between the individuals plants and how much is due to differences between the environments where the individual plants grow. Most plants exhibit a great deal of phenotypic plasticity (especially in vegetative characters) in response to different levels of light, water, nutrients and wind. Thus, the phenotypic characters most readily observed and most important to the plant's continued survival are also the ones subject to most uncertainty about their genetic component. In addition, quantitative assessments of the breeding system and of inbreeding (see below) require the use of simply-inherited genetic markers, which most phenotypic characters are not.

In general, surveys based on phenotypic variation should prove most useful to managers of endangered plants. For the types of problems they are likely to encounter, phenotypic analysis is likely to be the only practical tool, and it is likely to be sufficiently accurate for the purposes intended. Assessment of population structure by more sophisticated electrophoretic analysis should be necessary only when an active programme of genetic management is necessary, and when monitoring the success of that programme requires the kind of specific, individual detail that electrophoretic analysis can provide. Electrophoretic analysis would be required, for example, if it were necessary to obtain an estimate of the number of genetic individuals found in a population of clonally-reproducing plants.

There are three types of information that a manager must have if genetic consequences of a management decision are to be understood: (i) the pattern of genetic diversity in the taxon, (ii) the structure of local populations, and (iii) the relative importance of different modes of reproduction. Even a superficial knowledge of each of these puts the manager in a much better position to evaluate management alternatives than no knowledge at all. Thus, a manager should get some feeling for each of these aspects of the taxon's biology before any comprehensive management plan is developed.

Pattern of genetic diversity

Because plants are rooted and unable to move, a great deal of genetic differentiation can occur in the space of a few tens of metres, even in the absence of significant habitat heterogeneity (Epling & Dobzhansky 1942; Epling *et al.* 1960; Schaal 1975). If there is evidence of a significant amount of genetic differentiation within local populations (e.g. different frequencies of flower colour morphs, different flowering times, distinctive vegetative morphology), it is important that every effort be made to maintain this diversity. Thus, encroachments that destroy a part of a population might be acceptable if they remove a form that is predominant in most of the population, but encroachments would not be acceptable if they entirely removed a distinctive segment of the population.

It has been known for many years that widespread plant taxa can exhibit significant ecotypic differentiation, i.e. there may be certain races that are genetically distinct from one another and adapted to specific climatic and soil conditions, as in *Achillea millefolium* (Clausen *et al.* 1948). Whether or not significant ecotypic differentiation also occurs between populations of endangered plant taxa is less certain. In general, the geographic area over which they occur is much smaller and the diversity of climates and soil types on which they are found is much smaller than it is in plants like *Achillea.* Nevertheless, it would be prudent to suspect that at least some ecotypic differentiation can occur even in endangered plant taxa that are found in only a few places. Thus, it is important that managers devote their attention to ensuring that the populations to be preserved encompass as much of the entire range of genetic diversity of the taxon as is possible. It is particularly important to preserve distinctive populations that are effectively isolated from one another with respect to dispersal.

In the process of forming an accurate assessment of how much genetic variability is present in individual populations and how much genetic variability exists between populations, two other very important pieces of information will emerge: (i) the amount of genetic diversity in the taxon as a whole and (ii) the distribution of that variation within and among populations. The first of these is important because different management strategies will be required when a taxon has much variability than when it has little. The second is important because it will determine the relative importance of preserving a few large, well-selected populations or preserving many small populations.

Structure of local populations

The number of plants in a population and their spatial distribution relative to one another have a significant impact on the genetic structure of plant populations. Animal pollinators often follow a pattern of nearest-neighbour foraging in which the plant nearest to the one just worked is chosen for the next visit. Although wind-pollinated plants tend to disperse pollen further than animal-pollinated ones, they also show the tendency for matings to occur in a fairly localized area (Levin & Kerster 1974). The result is that population may be broken up into many small breeding units or 'neighbourboods', even if it is distributed more or less continuously over an area of several hectares. This may contribute to the small-scale patterns of genetic diversity just discussed. In populations that are relatively sparse, the area covered by these breeding units may be substantially smaller. In addition, self-fertilisation may occur more frequently in self-compatible plants when populations are sparse than when they are dense. Thus, maintaining a certain number of plants in a given area may not be a sufficiently precise management objective. It is better to maintain densities at least as high as those inferred to have been present in prehistoric past. In other words, it is better to focus on the density of individuals present rather than on their number. Because of the deleterious effects drift may have when the number of breeding individuals is small, it is better to err on the side of too high a density than on the side of too low a density.

Plants that occur as widely scattered individuals, like ground orchids, are more likely to require attention to maintaining their genetic structure than those that tend to occur in discrete populations. The reasons are simple. These plants are the most likely to have their mating structure disrupted by human activity. Because they occur at very low densities over a wide area, it may be impossible to preserve the entire habitat. The result is the loss of at least some individuals and the isolation of those that remain from one another. The results may be very similar to the results of habitat fragmentation on large vertebrate populations: loss of genetic variability, inbreeding, and perhaps even extinction.

One aspect of local population structure is particularly important in perennial plants that have the potential to reproduce clonally: the number of clones or genets found in a given local population. In some clonally reproducing plants, like *Populus tremuloides* (quaking aspen), each stand appears to be composed of a single clone (Mitton & Grant 1980). In other plants, each stand is composed of a mixture of clones (Huenneke 1985). In plants where a single clone constitutes an entire population, preservation of many populations may be necessary to ensure a reasonable sample of the genetic diversity in the taxon. In plants with several clones per population, preservation of a few carefully selected populations may be sufficient to guarantee a good sample of the genetic diversity present with the taxon.

One problem that faces managers of endangered plant populations is that not all of the individuals that are actually part of the population may be visible at any one time. As discussed above, many annual plants have a seed bank in the soil with the result that only a small fraction of the genetic variability actually present in the population is expressed at any one time. Even herbaceous perennials may not show above-ground vegetative growth in every year. In fact, there may be distinct genotypes in both annuals and herbaceous perennials that are adapted to different seasonal weather conditions so that two more-or- less distinct genetic populations may inhabit the same geographical area. The manager can only make an assessment based on what is observed, but this difficulty points up the need for effective monitoring and for erring always on the side of too much protection rather than too little.

On the other hand, the existence of a seed bank may also lessen the ill effects of rarity. The mixing of genotypes produced in several different growing seasons that results from the existence of a seed bank reduces the effect of genetic drift from what would be expected based on the number of reproductive individuals alone. Thus, the existence of a seed bank buffers a population not only against environmental and demographic stochasticity, but also against the loss of genetic variability as a result of genetic drift.

Perhaps the most difficult aspect of local population strucure to infer is how the structure of local populations might have changed in the recent past as a result of human activities. It is also one of the most important to understand. As suggested above, plants that have always been rare probably have genetic systems appropriate to allow them to cope with that rarity. Their continued existence in spite of their perpetual rarity is strong evidence that they are able to cope with the genetic consequence of rarity. For example, *Clarkia springvillensis* is known only from three or four widely separated populations, but it has probably never been more common. Thus, preservation of the existing populations is probably all of the genetic management that will be necessary, at least in the near future. On the other hand, plants like Hawaiian silversword that have recently been much reduced in population size and have had their habitat greatly fragmented are much more likely to require active measures to maintain their genetic structure.

Modes of reproduction

There is one case in which it is not difficult to gauge accurately the mode of reproduction in a plant taxon (assuming that the plant in question is sexual): the case in which the plant is dioecious, i.e. stamens and pistils are borne in separate plants, as in *Populus* spp. (cottonwoods) and *Salix* spp. (willows). In this case, all reproduction obviously occurs through outcrossing. In monoecious plants (those in which stamens and pistils are borne in separate flowers on the same plant, as in *Quercus* spp. (oaks), selfing could occur but frequently does not, either because of the pistillate and staminate flowers on a single individual are open at different times or because the individuals are genetically self-incompatible. Most flowering plants are hermaphroditic: both stamens and pistils are found within a single flower. Even in this case, however, outcrossing is often enforced because of strict, genetically-controlled self-incompatibility.

Many plants are self-compatible and may reproduce by self-fertilisation to some extent. Although an accurate assessment of the frequency of self-fertilization is difficult, it is possible to get a reasonable idea about whether reproduction occurs primarily through outcrossing or primarily through selfing simply by examining the morphology of the flower (Table 4). An even better estimate can be obtained by comparing the seed set of open-pollinated flowers with those that have been bagged to prevent pollination. In this case it is also a good idea to bag some flowers that have been emasculated to see whether a significant proportion of seeds might have been produced through asexual means.

TABLE 4. Morphological features indicative of breeding systems in hermaphroditic plants

Predominantly outcrossing	Predominantly selfing
Large showy flowers	Small inconspicuous flowers
Anthers and stigma spatially separated	Anthers and stigma in close proximity
Anthers shed pollen *before* stigma becomes receptive	Anthers shed pollen *after* stigma becomes receptive
Heterostylous (two or more flower types, differing in arrangement of pistils)	

The means by which a plant reproduces is one of the most important determinants of its genetic structure. Plants that reproduce primarily through self-fertilization often have little genetic variability within populations and what genetic variability there is occurs between populations. Plants that reproduce primarily through outcrossing, on the other hand, may have as much as 90% of the variability found in the entire taxon present within populations (Gottlieb 1981; Loveless & Hamrick 1984). In addition, plants that reproduce primarily by asexual means also tend to have a more variability between populations than within populations. Of course, plants that reproduce by a mixture of outcrossing and selfing or a mixture of sexual and asexual reproduction fall somewhere between these extremes. Finally, different pollinators often move different distances between bouts of foraging with the result that mating groups tend to be more spatially localized in bee-pollinated than in butterfly-pollinated flowers (Levin 1981).

In the case of outcrossing plants, a reasonable guess about the primary pollinators of a plant can be made based on characteristics of flower colour and morphology (Table 1). This is important for several reasons. First, the type of pollination may influence the local population structure, because different pollination systems are characterised by different degrees of pollen dispersion. Second, the abundance of pollinators may affect the degree of outcrossing actually occurring in self-compatible plants. Thus, an encroachment that does no direct harm to the plants may still be undesirable if it destroys the nesting habitat of the plant's primary animal pollinator, leading to an unfavourable change in the breeding system of the plant. Third, the demographic survival of the population may depend on the presence of a specific pollinator.

MANAGEMENT OF VIABLE PLANT POPULATIONS

Critical information needed for management

In view of the demographic and genetic characteristics of plant populations, an informed management plan depends upon a sound understanding of the life history and dynamics of the target population. At a minimum, the manager should be able to describe the population in the following terms:

- life history (annual vs. perennial? monocarpic vs. polycarpic?)

- any clonal reproduction?
- any seed bank or dormant stages?
- breeding system (self-compatible?)
- number, size of other populations, and relative magnitude of within-and between-population variability
- critical requirements for habitat, germination, or microsite (adaptation to natural disturbances)
- original distribution and history of rarity
- mutualistic relations with pollinators or dispersers.

Of course, rare plants are not characterised by any single set of life -history features. A comparison of three rare plant taxa (Table 5 demonstrates that rare plants may have various histories of disturbance, partitioning of genetic diversity and demographic characteristics.

In which plant species should we attempt to manage population dynamics? Collecting such detailed information on a plant population is often intensive and expensive work. Active management of the population requires even more effort. For that reason, we should carefully evaluate whether habitat preservation is likely to be sufficient or more active steps are warranted. No single list of characters will be a foolproof indication of the need for active management, but a plant possessing one or more of the following traits should be evaluated as a candidate for such intervention.

- limited reproductive effort (e.g. monocarpic, or with some morphological constraint on seed production)
- no seed bank or dormancy
- highly specific relationship with animal mutualist (especially if mutualist is threatened)
- threshold effect or density-dependent phase of life history, coupled with low densities or population size
- dioecious or otherwise obligately outcrossing
- local differentiation and microevolution have been particularly strong-historical distribution and abundance have been drastically altered

Of course, attentive monitoring of the status of any protected population will alert the manager to the need for additional steps, regardless of the plant's life history traits, if numbers or reproduction should decline.

Management options for rare plant populations

Habitat preservation, coupled with periodic monitoring of the population, remains the primary technique of plant conservation in the field. If more direct intervention seems necessary, a first step is to identify the critical or limiting step in the life history. Population models are invaluable at this stage. The most common approach is to use a transition matrix, which summarises the changes over time in the number of individuals found in each size class (or at each stage in the life history: e.g. seeds, seedlings, juveniles, flowering adults). By using observed numbers of individuals and the observed rates of change or transition rates, one can project the future of the population (assuming that those rates remain unchanged). Thus the projection matrix allows a useful extrapolation of current trends in the population. The same matrix can be used to predict the effects of various management techniques. For example, if management is designed to increase seedling surviorship, the higher surviorship rates are used in the matrix and resulting changes in overall population size can be calculated. In this way, a matrix is used to perform a sensitivity analysis, identifying the stage of the life history that is most critical in controlling overall population fate.

TABLE 5. Examples of three rare plant species.

	Plantago cordata[1]	*Pedicularis furbishiae*[2]	*Orcuttia* spp.[3]
Life cycle	perennial	perennial	annual
Mating system	self-compatible protogynous	bee-pollinated	wind-pollinated self-compatible
Mode of reproduction	seed, vegetation	seed only	seed only
Genetic partitioning	high within populations, high among populations	?	high within populations, low between populations
History of rarity	neoendemic, formerly widespread	narrow endemic	narrow endemic
Germination	high under diverse conditions	?	specific requirements
Clonal growth	?	none	none
Seed bank	short dormancy	?	short dormancy
Dormant individuals	yes	?	no
Seedling survival	high	low	
Juvenile survival	high	low	moderate (but subject to stochastic drought-caused mortality)
Adult survival	low	high	
Reproductive pattern	polycarpic	polycarpic	monocarpic
Seed/inflorescence	low	high	moderate
Max. seed/flower	low (2)	high	low (1)
Rate of cloning	?	none	none
Seed dispersal	local, by ?	local	local

[1] Data from Meagher *et al.* (1978)
[2] Data from Menges *et al.* (1984)
[3] Data from Griggs & Jain (1983)

Once a critical stage is identified, managers may resort to a variety of direct interventions. Low germination success can be countered by collecting seeds, germinating and establishing the seedlings in the laboratory or glasshouse, and outplanting the resulting seedlings. Habitat manipulation can sometimes increase the availability of suitable microsites for seedling establishment in the field. Hand pollination can supplement inadequate natural pollination. Excluding large grazers often results in tremendous increases in survivorship (although such steps may be counter to the management of livestock or wildlife populations on the same site).

CONCLUSION

Accurate understanding of a plant's population biology may require intensive, time-consuming work. In part this is because plants are so variable in their life histories and genetic processes. We have attempted to describe these variable patterns, and to draw a few generalisations that may pinpoint those taxa in which active management is necessary. Only an understanding of the demography and genetics of a target population will enable the manager to choose the best strategy for long-term preservation.

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SEEDS IN NATURAL POPULATIONS: THEIR SIGNIFICANCE FOR PLANT CONSERVATION

JONATHAN SILVERTOWN

INTRODUCTION

A growing plant is merely a seed's way of making more seeds. This may seem an eccentric view, but it is a useful starting point from which to consider the significance of seeds in natural populations. Unlike growing plants which often have a capacity for clonal reproduction, each seed is unequivocally a genetic individual (i.e. a genet), except in the relatively rare cases where seeds are produced by apomixis. Because seeds are discretely packaged and easily counted, they are natural units for studies of plant population dynamics. The diagram of an idealised plant life-cycle in Fig.1 illustrates the potential role of seeds in plant population dynamics. The actual importance of seed production in a particular population will depend upon the relative values of the transition probabilities (triangles) between the various stages (boxes) of the life cycle. In some species, including most of the tree species of the established phase in tropical forests, post-dispersal seed mortality is very high so that the seed pool is numerically small. In other species, such as short-lived herbs and leguminous shrubs for example, adults have relatively low year-to-year survival, seeds have higher survival and there are significant numbers of seeds in the soil.

REVIEW OF THEORY

Seeds in the soil

Seed populations in soil are often described as the 'seed bank' a term which gives the erroneous impression that this is a place of safekeeping for plant genotypes. In fact the seed bank is constantly plundered by predators and is highly prone to attack by fungi. Even when they germinate, few seeds make a successful escape. Plants which do invest their progeny in the seed bank retrieve only a tiny fraction of them, and each of these is worth (in terms of fitness) much less than a seed which has successfully produced progeny of its own rather than remain dormant in the soil.

The species which are most heavily represented in the seed bank tend to have relatively small seeds, to be relatively short-lived in their growing phase, and tend to occupy ephemeral sites. Plants we consider weeds, and species of habitats where rainfall is highly unpredictable or infrequent generally have large seed banks. Trees of primary forest tend to have large seeds with little dormancy and very low survival

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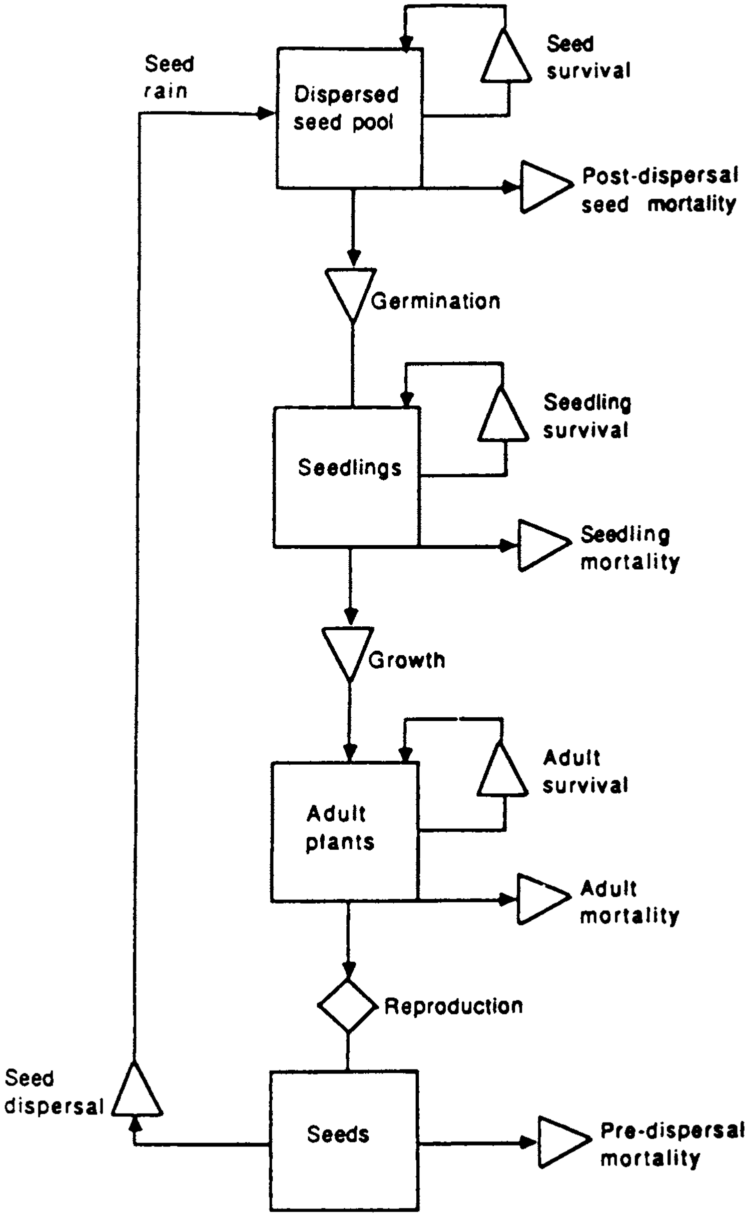
FIG. 1. A model of an idealised plant life-cycle illustrating the potential role of seeds. Boxes represent stages in the life cycle, triangles represent the average probabilities that a plant will move between two stages (or die) during a year, and the diamond represents average annual seed output per plant. The dispersed seed pool is often called the 'seed bank'.



in the soil, but pioneer tree species which occupy the early phases of succession in the forest regeneration cycle rely heavily or exclusively upon the seed bank to colonise new treefall gaps (e.g. Putz & Appanah 1987). Secondary forest and vegetation on sites with a history of disturbance or agriculture have the densest populations of seeds in the soil. Examples of tropical seed banks and their composition are given in Table 1.

TABLE 1. Seed banks of tropical habitats

Vegetation	Location	Seeds m^{-2}	Predominant species in the soil	Reference
Herbaceous vegetation				
Arable fields	Honduras	7620	Weeds	Kellman 1974
Pasture in cleared forest	Venezuela	1250	Grasses and dicot weeds	Uhl & Clark 1983
Serengeti grasslands	Tanzania	490-1225	(not specified)	Belsky 1986
Forests				
moist	Nigeria	128-211	43-68% pioneer trees	Keay 1960
wet evergreen	Ghana	163	pioneers	Hall & Swaine 1980
moist, semi-deciduous	Ghana	633	pioneers	Hall & Swaine 1980
dry, semi-deciduous	Ghana	696	pioneers	Hall & Swaine 1980
rain forest	Australia	519-1069	90% pioneers	Hopkins & Graham 1983
primary rain forest	Mexico	175-862	mostly pioneers	Guevara & Gómez-Pompa 1972
secondary rain forest	Mexico	862-4051	mostly pioneers	Guevara & Gómez-Pompa 1972

Little information has been published on the seeds in soil of tropical habitats and there are two major difficulties in interpreting data such as those in Table 1, whether collected in tropical or temperate studies. Firstly, sampling techniques used to estimate the size of the soil seed bank have typically used inadequate replication. This sampling problem arises because seed distribution tends to be very patchy. A minority of the individuals in a population often accounts for the majority of seed production in a particular year, and although seed dispersal agents do not remove seeds from the parent plant, they may concentrate them as, for example, when they are deposited in dung. Uhl & Clark (1983) found that cow pats collected in a pasture cleared from the Amazon rainforest contained twenty-times the density of viable seeds of the same species to be found in the soil.

In estimating soil seed densities a large number of small soil samples is preferable to a few large samples. Grieg-Smith (1983:31-32) describes a method for determining the number of samples required to obtain any desired level of accuracy. Fewer samples will be needed to obtain an estimate of the density of a common species than of a rare species to the same level of accuracy.

This may be an important consideration if one is particularly interested in the conservation of a rare species with a seed bank, although rarity in the vegetation does not necessarily imply rarity in the soil. Indeed, there may be a negative correlation between above and below-ground abundance in some situations.

The second problem with simple estimates of seed density in the soil, even if these have been accurately made, is that on their own they tell us nothing about the importance of the seed pool as a reservoir from which plants can be recruited. To know how important the seed pool is, as distinct from how large it is, we need to know something about the turnover of seeds in the soil. This involves making numerical estimates of all inputs to and outputs from the seed pool that are shown in Fig. 1. If the annual input of seeds in the seed rain is larger than the outputs due to mortality and germination, then viable seeds must accumulate. On the other hand, if the annual seed rain is about the same size as the outputs, then the seed pool is merely transient. Where seed production is seasonal, it may be possible to sample the soil just before seeds are shed. This will give an estimate of the size of the accumulated seed pool after a year's seed mortality and germination have taken their toll of the previous year's seed rain.

Seeds have a vertical distribution in the soil, and sampling should be deep enough to ensure that the estimate of seed density includes any seeds that have a chance of reaching the surface to germinate. Whilst it is usually thought that deeply-buried seeds have little chance of successful germination, burrowing animals and uprooted trees may bring these to the surface.

A choice of methods is available for estimating seed numbers in soil samples. The simplest is to spread the soil out in trays, protected from pests and contamination from any local seed source, keep the soil watered, and identify and count emerging seedlings over a period of months. Alternative methods involve physically separating seeds from soil by flotation, sieving or other methods, followed by viability or germination tests. Roberts (1981) describes various methods in greater detail. Garwood (1983) studied the seasonality of seed germination at Barro Colorado Island (BCI), Panama by monitoring the *in situ* appearance of seedlings along trails in the forest. This little-used method could be adapted to estimate soil seed pools in experimentally disturbed plots, if seedlings could be identified and removed regularly, and measures could be taken to protect plots from animals and to estimate the incoming seed rain.

Each of the stages of the life cycle represented by a box in Fig. 1 can be broken down into sub-compartments representing particular age classes within the seed, seedling or adult stages. Whether, and exactly how, this refinement of the model should be carried out depends largely upon the ecology of the species in question and on the purpose of the study. A full population model will allow predictions to be made from estimates of the values of transition probabilities and seed production in Fig. 1. Matrix models are the most commonly used type of model for this purpose (e.g. Piñero *et al.* 1984), and for which there are statistical guidelines about how the life cycle should be divided into stages (Moloney 1986). For short-lived plants such as weeds it is more convenient to frame a model to predict seed numbers than adult numbers (Mortimer 1983; Silvertown 1988).

Seed dormancy

For plants which have a numerically significant seed pool, it makes sense to divide this into sub-compartments for seeds with different types of dormancy. Seed dormancy is a highly changeable phenomenon. Seeds from the same plant may exhibit different germination behaviours when collected, seeds may change their behaviour with time and do so in different directions depending upon storage conditions; and all these difference may themselves vary between populations. The development and evolutionary causes of this lability in seeds have been discussed by Silvertown (1984).

Baskin & Baskin (1985) suggest a scheme of classification for seed dormancy states which explicity allows for changes in dormancy state. The scheme divides seeds into those with *primary dormancy*, which are unable to germinate when shed from the plant and those with *secondary dormancy*, which acquire dormancy after leaving the parent. Seeds with primary dormancy may become non-dormant and then acquire (secondary) dormancy again. Many temperate annual weeds exhibit a seasonal dormancy cycle. Both primary and secondary dormancy are divided into two sub-categories: **innate dormancy** and **conditional dormancy.** Innately dormant seeds will not germinate under any normal environmental conditions. Seeds with conditional dormancy will germinate in only a narrow range of the conditions in which the germination of non-dormant seeds takes place. When innately dormant seeds alter their dormancy state they usually do so by a gradual change which takes them through a stage of conditional dormancy.

An important form of innate primary dormancy caused by a hard seed coat is found in many legumes. With the passage of time in the soil this kind of dormancy may be broken by the decomposition of the testa. Fire or passage through the gut of a vertebrate dispersal agent will frequently break this kind of dormancy, too. It is a kind of dormancy likely to be important in savannas and heathlands, although little is known about the population biology of plants in these tropical habitats.

Conditional secondary dormancy is induced in many species which will normally germinate in the dark but which become light-requiring when exposed to light filtered through a leaf-canopy. Half of a sample of 32 common East African weed species tested by Fenner (1980) showed this behaviour. In seeds of the Nigerian tree *Hildegardia barter* low humidity caused innate secondary dormancy, which became conditional when humidity was raised to 90% (Enti 1968).

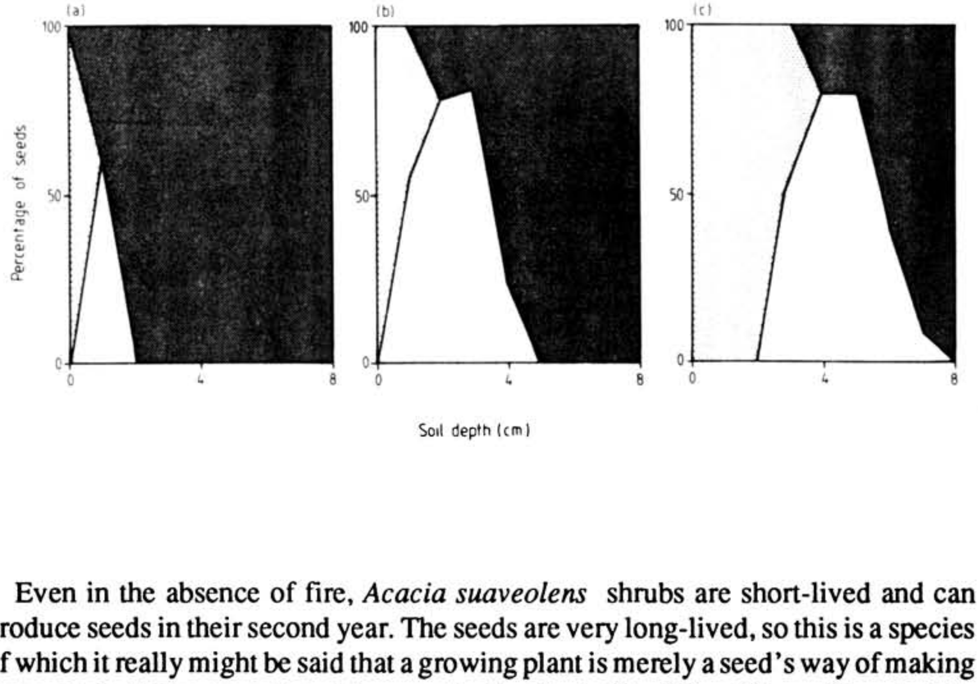
Although seed dormancy is likely to be important in the semi-arid tropics, it remains to be seen how important it is in wetter tropical areas. The only two extensive studies are by Ng (1983) and Garwood (1983) on forest species in Malaysia and Panama, respectively.

CASE STUDIES OF THE ROLE OF SEEDS IN POPULATION AND VEGETATION DYNAMICS

Acacia suaveolens in S. Australia

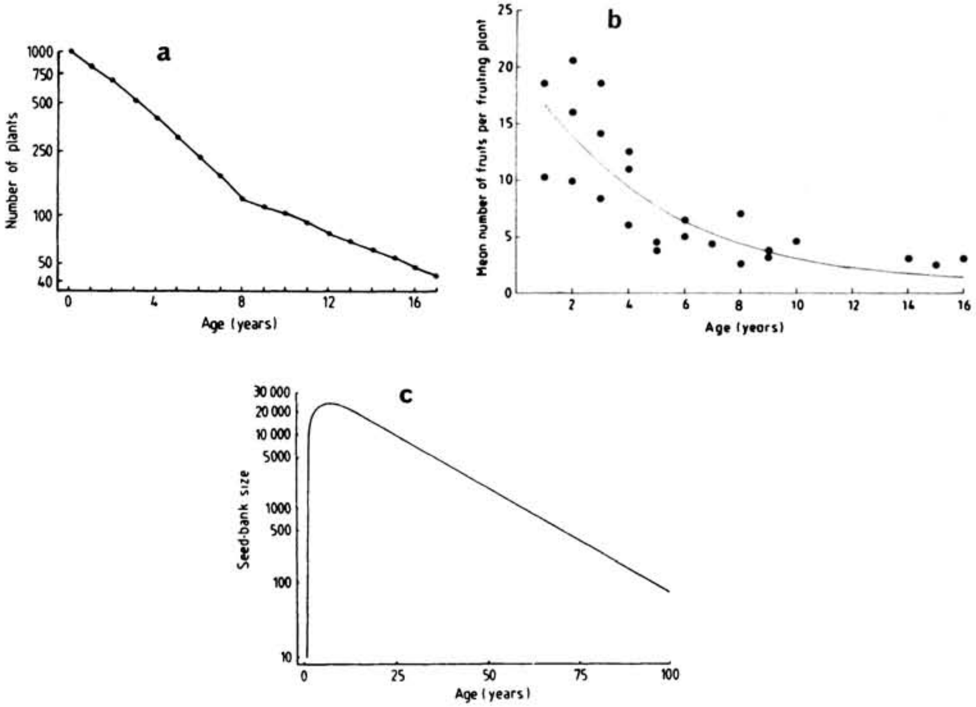
Acacia suaveolens is a legume shrub which, although not a tropical species, is both ecologically and taxonomically closely related to the savanna species found in the tropics. *Acacia suaveolens* has been intensively studied by Auld (1986a, b, 1987; Auld & Myerscough 1986) who estimated values for all of the transition probabilities shown in Fig. 1. Fire is crucial to the ecology of this species because it kills the shrubs and stimulates the germination of buried seeds. Ants are also very important because they transport and bury seeds. Ants of a *Pheidole* species removed 38% of seeds from the soil surface to their underground nests and buried 82% of these deeper than 5cm. Only 5% of the seeds not taken by ants were buried as deep as this. The depth of seed burial and the intensity of a fire determined the fate of seeds. Low-intensity fires killed few seeds but also caused few to break dormancy. More intense fires caused more seed mortality and more germination (Fig. 2).

FIG. 2. The effect of fire intensity and depth of burial upon the fate of *Acacia suaveolens* seeds in the soil; (a) low intensity fire (b) high intensity fire, (c) very high intensity fire. Light shading = % mortality, no shading = % germination, heavy shading = dormant. From Auld (1987).



Even in the absence of fire, *Acacia suaveolens* shrubs are short-lived and can produce seeds in their second year. The seeds are very long-lived, so this is a species of which it really might be said that a growing plant is merely a seed's way of making more seeds. Using a survivorship curve for the shrub (Fig.3a) and fecundity schedule (Fig.3b) which records seed production changes with the age of the plant, Auld (1987) calculated how the size of the *Acacia suaveolens* seed pool would change in hypothetical population of 1,000 shrubs inhabiting an area where no fire occurred for 100 years. After 16 years only 48 of the original cohort of 1,000 shrubs would still be alive, but in those 16 years the 1,000 would have produced nearly 45,000 seeds between them. This huge pulse of seeds in the seed pool would long outlive its shrubby progenitors and there would still be 1,000 viable seeds left in the soil 60 years after the fire which saw their parent's birth (Fig.3c).

FIG. 3. (a) The survival and (b) reproduction of 1,000 *Acacia suaveolens* recruited from seed following a fire and (c) the dynamics of the resulting seed pool, assuming no further fires. From Auld & Myerscough (1986) and Auld (1987).



With information on a population as detailed as that Auld collected on *Acacia suaveolens* it is possible to make firm predictions on how different kinds of management would affect the abundance of a plant. Unless intense fires were very frequent or very infrequent, it is unlikely that *Acacia suaveolens* would be in any danger of going extinct. How other factors such as grazing or disease might affect a population is of course another question, but with such a long-lived seed pool it does seem fairly invulnerable to short-term threats in the growing phase. Probably its weakest link is the species' dependence upon ants. If these were to disappear for any reason (and there could be many), then seeds would no longer be buried and, as Fig. 2 makes clear, this would spell extinction for *Acacia suaveolens* in a fire-prone environment.

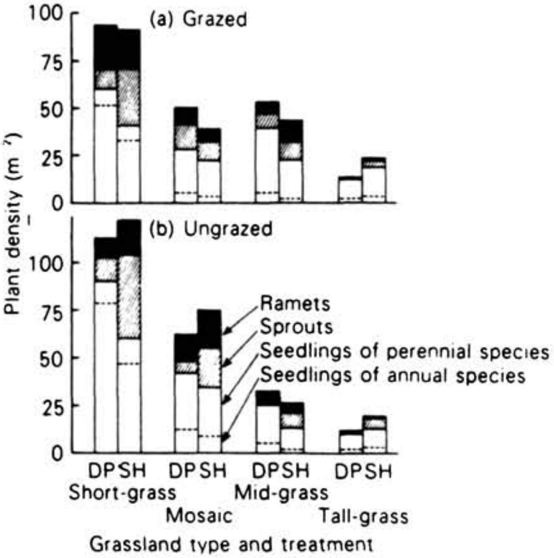
Vegetation dynamics in the Serengeti

Regeneration from seed is important in many of the Serengeti's vegetation types where fire, grazing and soil distrubance by grazing animals create the conditions required for seedling recruitment by the dominant grasses. *Themeda triandra* is a major grass species found throughout the savanna regions of the Serengeti and which is dominant in six of the seventeen grassland communities distinguished by McNaughton (1983). This species was studied in Uganda by Lock & Milburn (1971), who observed that naturally occurring seedlings appeared only after burning. *Themeda triandra* seeds have a long hygroscopic awn which drills them into cracks in the soil. The mean depth of burial of 100 seeds was found to be 11mm, which was sufficient to protect them from damage by surface fires. In an experiment, Lock & Milburn found that clipping the vegetation to the soil surface or burning produced the same densities of *T. triandra* seedlings, suggesting that the positive effect of fire was due to the removal of plant cover. A similar experiment by McNaughton (1983) in the Serengeti found that burning produced a significantly greater number of seedlings (of *T. triandra* and other spp.) than clipping (44.2 m^{-2} and 3.8 m^{-2}, respectively, 2.1 m^{-2} in controls). Seedling densities were the highest of all in animal hoofprints in the burned area, where they reached 316 m^{-2}. Plant recruitment from seed may be affected by interactions between fire and grazing, particularly if animals are attracted to grass regrowth following fires.

Belsky (1986) studied the recolonisation of experimental disturbances made in four plant communities in the Serengeti: short-grass *(Digitaria scalarum* and *Sporobolus* spp.); a short-grass/mid-grass mosaic *(Panicum coloratum* and *Pennisetum mezianum / Justicia exigua* and *Sporobolus spicatus)*; mid-grass (*Themeda triandra* and *Heteropogon contortus)*; and tall-grass *(Diheteropogon amplectens, Elyonurus argenteus, Hyparrhenia filipendula* and *Themeda triandra).* She created two kinds of disturbance in plots 2m x 1m: one kind in which the soil was broken up, mixed to a depth of 15 cm and had above-ground and below-ground plant parts removed, and another in which plots were hoed to a depth of 1-2 cm, removing only the plant parts in this shallow zone. Disturbance treatments were factorially combined with grazing treatments: plots were either open to grazing or situated in the grazing exclosures. Wildebeest, zebra and Thompson's gazelle were the dominant herbivores in all four plant communities which were situated along a south – north gradient of moisture availability. Plots were set up at the beginning of the growing season and the number of seedlings, vegetative sprouts from underground rootstocks and ramets attached to rhizomes invading from outside plots were recorded at the end of the season in May. Unfortunately, only percentage cover was recorded in completely undisturbed plots, and not the appearance of seedlings, vegetative sprouts or ramets, so there were no controls with which to compare the overall effect of slight disturbance with that of severe disturbance and the interaction of grazing with these treatments.

As the results in Fig. 4 show, seeds were an important source of recolonisation at all sites and in all treatments, and comprised between 58% and 76% of recruitment. These results over-emphasise the importance of recruitment from seed to perennial species because they take no account of the subsequent survival of seedlings relative to that of sprouts and ramets. Higher mortality can be expected among seedlings relative to that of sprouts and ramets which are attached to established plants. The type of disturbance had a significant effect upon seven of eleven species at the short-

FIG. 4. Mean density of seedlings (□), sprouts (▧) and ramets (■) in disturbed plots made in four grassland communities; (a) grazed treatment, (b) ungrazed treatment. DP = deep disturbance, SH = shallow hoeing. From Belsky (1986).



grass site, two of eight species at the mid-grass site, one of four species at the tall-grass site, but no significant effect on any of the eleven species found in plots at the mosaic site. Grazing effects on the consequences of disturbance were similarly absent from the mosaic site and affected only 2/10, 4/9 and 1/4 species at the other sites. These results do *not* mean that neither grazing nor disturbance were important for seedling recruitment at these sites (because there were no undisturbed controls in the experiment), but refer only to differences between types of disturbance.

A total of thirty-seven annual species occurred in the undisturbed vegetation at the four sites but, surprisingly, a smaller percentage of these than of available perennials colonised the disturbances. This was probably because the annuals had only small populations in the undisturbed sward. One species of annual, *Gutenbergia petersi*, was rare in the undisturbed Serengeti grassland community, but dominated the deeply disturbed plots in the year following disturbance and then returned to its previously low abundance. The perennials which colonised, such as *Themeda triandra*, tended to be the most abundant species in the undisturbed vegetation.

Six species occurred significantly more frequently in deeply disturbed plots than in shallow ones, and all but one of these was annual. This suggests the importance of a buried seed pool for these plants. Belsky took soil samples to estimate the persistent seed bank and found 490-1225 seeds m^{-2} in the top 2.5 cm of soil. Unfortunately, these soil samples were too few and too shallow to draw any conclusions about the seed pool. Belsky suggests that regeneration from seed is the dominant strategy in the plant communities she studied, but that recruitment tends to be from recently produced seed and not from a persistent seed pool. The lack of proper no-disturbance controls in this experiment limits the conclusions which can be drawn from it, but there is no doubt that regeneration from seeds is important in many of grassland communities of the Serengeti.

Cecropia obtusifolia in Mexico

Seeds are the principal source of recrutiment in secondary forest succession in the tropics (Bazzaz & Pickett 1980; Whitmore 1983). Although the seed dormancy mechanisms of several tropical pioneer species have been studied (Vázquez-Yánes & Orozco-Segovia 1984), the mere existence of such mechanisms is not sufficient to guarantee the importance of dormancy and recruitment from the seed pool in the life cycle of a plant.

Cecropia obtusifolia (Moraceae) is a dioecious pioneer tree which has been studied in some detail in the tropical rainforest of Los Tuxtlas, in the state of Veracruz, Mexico. Female trees produce their first fruit at about 3 years and increase their fecundity with age (cf. *Acacia suaveolens* (Fig. 3b) which does the reverse). *Cecropia* fruits are produced at two seasons of the year (Carabias & Guevara 1985) and are eaten by a large number of different birds and mammals which also disperse the seeds. Martínez & Alvarez-Buylla (1986) found that dispersal agents produced a highly patchy seed rain amounting to 371 m^{-2} in gaps 10-15 years old, 226 m^{-2} in gaps a year old, but only 53 m^{-2} under a mature forest canopy.

The fate of dispersed *Cecropia* seeds depends upon where they land. Vázquez-Yánes & Smith (1982) found that conditional dormancy caused *Cecropia* seeds that were placed near the periphery of a gap to remain dormant while those placed in its centre germinated rapidly. This behaviour is controlled by the spectral composition of light (ratio of red/far red) at the periphery and in the middle of a canopy gap (Vázquez-Yánes & Orozco-Segovia 1985). Seeds which do not germinate may enter the seed pool, but the probability of this happening is not known. Seeds can remain in a viable state in the soil for at least two years, although Bosch & Vázquez-Yánes (1985) found that rates of seed mortality were extremely patchy and some seed samples they buried in experiments lasted a much shorter time. *Cecropia obtusifolia* was not a very frequent species in soil samples taken by Guevara & Gómez-Pompa (1972 and Table 1), was missing from many of them, and was altogether absent for much of the year. Martínez & Alvarez-Buylla (1986) conclude that the seed rain is more important than the seed pool in the providing recruits to the *Cecropia* population at Los Tuxtlas. Seedling survival as well as seed germination is dependent upon gaps. No seedlings planted at Los Tuxtlas in gaps smaller than 100 m^{-2} survived to one year of age (Martínez & Alvarez-Buylla 1986).

CONCLUSIONS

Inadequately replicated soil samples tell us little about the seed pool, although the marked absence of primary forest species from virtually all forest sites which have been sampled (Table 1) does indicate the fragility of primary tropical rainforest. The absence of a seed pool means that seed-bearing adults are essential to the regeneration of primary-forest trees. A seed pool of significant size and longevity can buffer changes in a population. However, even in a species such as *Acacia suaveolens* this does not make a population invulnerable to, say, the extinction of a dispersal agent.

Seed pools may be a significant repository for the genetic variation in a population and may buffer genetic as well as numerical changes. The genetic significance of seed pools has scarcely been investigated for either temperate or tropical plants, although its theoretical importance has been considered by several authors (e.g. Templeton & Levin 1979). The *field* (as distinct from laboratory) germination conditions which a plant requires are a key to understanding the role of seeds in a plant's life history. Indeed, if recruitment is confined to certain kinds of micro-environment (e.g. gaps >100 m^2) or only occurs after certain events (e.g. fires), the frequency of these can be used to calculate how seed numbers will translate into future plant numbers. The abundance of species such as *Gutenbergia petersi* in the Serengeti or *Cecropia obtusifolia* in Mexican rain forest will obviously be influenced by the frequency of disturbances. The same may be true, though less obviously so, of longer-lived species which have rather specific regeneration requirements and which have no significant seed pool.

The strongest conclusions to be drawn from Table 1 and the three case studies is that seeds are potentially of great importance in the biology and conservation of tropical plants, but that more thorough studies are needed. Such studies should be aimed at estimating the relative importance of the seed rain and the seed pool in the context of the rest of the plant life cycle (Fig. 1).

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PLANT-ANIMAL INTERACTIONS

M.J. CRAWLEY

INTRODUCTION

The fundamental links between the producers in an ecosystem (the green plants) and the consumers (the animal and fungal life) are between living plants and their herbivores, and dead plants and their detritivores. The plant – herbivore link involves potentially the most interesting dynamics, because herbivores are likely to have a substantially greater impact on the future rate of production of green plants than are the detritivores (although the decomposer organisms have a vital role to play in nutrient cycling). This chapter is concerned with eight questions about plant – herbivore interactions, and with the practical means of answering these questions in the context of conservation in the tropics. The questions are these:

1. To what extent is plant recruitment limited by vertebrate and invertebrate herbivory?
2. To what extent is the competitive ability of plant species affected by the herbivory?
3. How do recruitment and competition influence plant species richness?
4. How many of the plants owe their persistence to herbivores?
5. What determines the abundance of different herbivorous animals?
6. How many herbivores are food limited and by what plant species are they limited?
7. How many plant species do the most influential herbivores consume (do they eat just one plant – monophagy, or many -polyphagy)?
8. To what extent is herbivore diversity determined by plant species richness?

THEORY

Theory on plant – herbivore interactions has been developed at the ecosystem level and at the population level. At the ecosystem level, a number of generalisations have been made (although it should be noted that these are highly controversial, and not generally accepted):

1. because the wet tropics are green, herbivorous animals cannot be food limited;
2. since every group of organisms is limited by something, the herbivores must be limited by their own natural enemies (predators, parasites and diseases);
3. since the herbivores are not food-limited, they have little impact on plant abundance; therefore,
4. plants must be limited by interspecific competition for space.

This argument, originally proposed by Hairston, Smith & Slobodkin (1960) has been called 'the world is green hypothesis'. An extension to this reasoning has been proposed by Oksanen (1988). He suggests that plant productivity affects the impact of herbivory on plant communities. In very unproductive environments like deserts,

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there is too little plant material to support herbivore populations, so the impact of herbivory is negligible. In very productive environments, there is sufficient energy flow to support not only herbivores, but also their natural enemies; the enemies will be so abundant that herbivores are kept scarce, and the impact on plant populations will again be negligible. Only in environments of intermediate productivity will herbivores have an important effect on plant dynamics. Here, there is sufficient energy flow to support herbivore populations, but herebivore productivity is insufficient to support populations of natural enemies. Thus the herbivores are food-limited, and have an important effect on the plant community.

At the population level, theory has followed developments in predator – prey dynamics. Much of the theory is based on the opposite hypothesis to that held by the ecosystem theorists, namely that herbivores are food-limited. There are two reasons for this: (1) mathematical models that form the backbone of this theory typically consider only two trophic levels (plants and herbivores) and (2) there is little theoretical interest in plant – herbivore dynamics unless plants are affected by herbivores, and vice versa. Neither of these reasons is at all persuasive. Nevertheless, there is a substantial body of theory which allows many predictions to be made for those cases where herbivores numbers *are* food limited. Note that while the earliest theoretical models assumed symmetrical dynamics (e.g. Lotka-Volterra models), where the plant affected the abundance of the herbivore and the herbivore affected the abundance of the plant, modern theories stress the asymmetry of most interactions. There are a good many cases of invertebrate herbivory, for example, where the herbivore has shown to be food-limited, but where its impact on plant dynamics has been negligible (e.g. the interactions between the cinnabar moth and ragwort; Crawley & Nachapong (1985)). Again, for polyphagous vertebrate herbivores, there is ample evidence that certain, preferred plant species may be excluded from the plant community, or kept at very low densities, without any reciprocal effect on herbivore numbers (e.g. rabbits can eliminate tree seedlings from grasslands; see Crawley 1983). Perhaps the most important general point about plant – herbivore dynamics is that while it is easy to measure the impact of herbivore feeding on plant performance (on growth and seed production, for instance), it is very difficult to determine the effects of herbivory on plant population dynamics. Just because an insect destroys a great many seeds does not mean that it necessarily reduces the number of plants in the next generation; just because deer browse most of the individual plants does not necessarily mean that those plants would be bigger, or would leave more offspring if the deer were excluded.

On an evolutionary note, it is evident that herbivores have had a profound effect on plant morphology and chemical composition. Defences against herbivory range from toxic chemicals through spines and glandular hairs, to exquisite symbiotic relationships with ants (as in the ant acacias; Janzen 1977). This evolutionary evidence, however, tells us nothing about the importance of herbivory in plant population dynamics. Genotypes possessing anti-herbivore defences would prosper wherever there was selective herbivory, whether or not the herbivores were food-limited. A second potential area of confusion centres on the notion that herbivores might be good for plants. The argument goes that without herbivory, grasslands would turn into forests, therefore herbivory must be good for grassland plants. This is a group selectionist argument, and betrays a misunderstanding of the mechanism of evolution. Individual plants almost always leave fewer offspring when they are attacked by herbivores; herbivory reduces their fitness. In grasslands, certain species prosper because their individuals suffer smaller reductions in fitness than are suffered by the potential woodland species. These grazing-tolerant plants are not competitive in the absence of herbivores because they cannot grow tall and are not shade-tolerant.

FIELD TECHNIQUES

In order to answer the eight questions listed in the Introduction, we need to undertake *manipulative field experiments*. There is only a limited amount we can learn by observation: e.g. by correlating the abundance of a particular herbivore species with the abundance of its food plants. If we want to understand the dynamics (and this is the essence of good biological conservation) we need to know what would happen to the plants if the herbivore were to increase or to decrease in abundance, and what would happen to the herbivore if the plants were to become more or less common. The essence of the experimental technique involves *exclusion*. It is much easier to keep herbivorous animals out of certain areas than it is to increase their numbers. Attempts at density-enhancement usually cause unrealistic changes in animal behaviour (density stress) and therefore alter the impact of herbivore feeding on plants. They are also technically difficult, and expensive in terms of manpower (collecting, rearing and tending the herbivores).

Two simple techniques can be employed. Fences constructed of wire mesh can be used like sieves to exclude vertebrate herbivores of different sizes. For example, an outer, single-strand barbed wire will keep out cattle, an inner, 2-cm mesh fence will keep out larger rodents and lagomorphs, while an innermost, small plot (of, say, 2m x 2m) fenced with fine metal mesh can be used to exclude the smallest rodents. Herbivorous birds can be excluded by netting across the top of the fenced enclosures. Note that it is very important to have large cage controls. Because the fence can affect the microclimate (especially if a netting roof is used), it is vital to know how much of the observed effect on plants is due to this, so that the response due to herbivory can be estimated accurately. A cage control consists of the top and walls of the enclosure, but with gaps built in to the bottom of the fence to allow free movement of the animals. It is a good idea to trap inside both the cages and the cage control (using a Longworth or similar trap): this will demonstrate whether animals really are being excluded or not, and also if they are entering the open cages.

The second technique involves using chemical insecticides to exclude insect herbivores from natural vegetation. There are risks with this approach, in that it is possible that insect natural enemies prove to be more susceptible to pesticide than herbivores, in which case it may that herbivore numbers actually increase following application. Unless herbicide resistance develops, however, frequent application should reduce insect herbivore numbers to low levels. With this kind of experiment it is important to have controls that check for direct effects of the chemical on plant performance; many insecticides, for example, are known to have slightly depressive effects on plant growth. If the chemical turned out to stimulate plant growth, then yield improvements could not be attributed to reduced herbivore numbers. Rapid, non-persistent, knock-down insecticides (such as pyrethroids) are preferable to systemic insecticides (such as dimethoate) because they have less impact on internal plant biochemistry.

Points to be borne in mind in designing exclusion experiments include

1. natural habitats are extremely heterogeneous, so large numbers of replicate plots are vital if results are to be representative;
2. historical effects, such as differences in the composition of the soil seed bank, should be taken into account;
3. randomisation is important to eliminate bias.

At a practical level, fences will need to be regularly checked and repaired *before* herbivores get into the enclosures. Once animals have gained access, the plots are essentially useless, because one does not know how much plant material they have eaten.

Data to be collected include: (i) germination rate; (ii) seedling survival schedules (measured as frequently as possible given the available manpower); (iii) probable cause of seedling death (shading, desiccation, fungi, mollusc, insect or vertebrate herbivore); (iv) plant growth rate (this is best estimated by periodic (e.g. monthly) destructive sampling followed by dry weight determination; (v) plant size; (vi) seed production; (vii) phenology (the timing of all different life stages – differences in phenology can have profound effects on plant herbivore dynamics). For the herbivores: (i) the number of individuals of different species (methods for insects in Southwood 1976); (ii) estimates of the amount (dry weight) and type of material taken from plant species (this is technically difficult for sucking herbivores like Homoptera); (iii) the phenology of damage; (iv) the effectiveness of the exclusion technique.

Successful vertebrate exclusion experiments have been carried out all over the tropics. They have tended to be carried out in grassland and savanna, and it would be profitable to extend these studies to tropical forests. Responses in vegetation are almost always profound and are usually noted in the first year after the fences are erected.

Insect exclusion in natural vegetation is much more recent, and the published cases are all from temperate environments (see Crawley 1989 for a review). Exclusion of invertebrate herbivores can have important effects on plant population dynamics, but it appears generally to be the case that these effects are substantially less profound than those resulting from exclusion of vertebrate herbivores. Insect herbivores typically have subtle effects on plant dynamics; vertebrates have relatively obvious effects (excluding certain plants altogether, altering competitive ability of others, etc.).

TRAINING METHODS

1. Demonstration exclosures and insecticide trials need to be set up to show students

the effects of herbivory on plant communities, diversity and relative abundance.

2. Sampling techniques (use of sweep nets, suction traps, pitfall traps, etc.) and marking techniques (tagging, mark/recapture analysis) need to be demonstrated.
3. Plant demographic techniques: working with seeds and seedlings; understanding seed dormancy and seed-bank heterogeneity need to be grasped.
4. Simple graphical models of population dynamics (requiring no computing or mathematical skills) should be mastered (see Begon, Harper & Townsend 1985).
5. Demonstration of the monophagy of most insect herbivores and the polyphagy of most vertebrates; the fact that increasing body size is associated with increasing polyphagy; other background concepts of herbivory (see Crawley 1983).
6. Reinforce the importance of determining whether a particular herbivore population is food-limited or not. It is much more likely to have a profound effect on plants if it is food limited. If it is not food-limited, it may be important to understand how it is limited, and to predict what would happen to plants if regulation were to break down (if, say, the herbivore's major natural enemy were to go extinct locally as a result of altered managment practices).

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BREEDING SYSTEMS OF PLANTS

SEXUAL SYSTEMS, POLLINATION MECHANISMS AND GENETIC DIVERSITY IN TROPICAL FOREST PLANTS

K.S. BAWA

INTRODUCTION

Information about the modes of reproduction in plants is important for conservation of biological resources in the tropics for two reasons. First, modes of reproduction determine the level of inbreeding and outbreeding and consequently the genetic structure of populations. Conservation of genetic resources depends upon knowledge of the patterns of genetic variation and the factors underlying these patterns. Second, reproduction in most tropical plants involves mutualistic interactions with a diverse array of animals, which serve as pollen and seed vectors. Effective conservation of biological communities in the tropics is virtually impossible without an understanding of the key mutualistic interactions. Here I review results of recent studies on the modes of reproduction and the patterns of genetic variation in tropical woody species. My purpose is to identify the major trends and to provide key references in these two areas.

SEXUAL SYSTEMS

Plant sexual systems can be distinguished into two broad categories, sexually monomorphic systems and sexually dimorphic systems Bawa & Beach 1981).

Sexually monomorphic systems

Sexually monomorphic systems are characterised by only one gender class of individuals. In such systems all reproductive individual function as both pollen and seed parents to a greater or lesser extent. The sexually monomorphic species may be (a) hermaphroditic, with all the flowers being bisexual, (b) monoecious, with separate male and female flowers, or (c) andromonoecious, with bisexual and male flowers on the same plant. No tropical tree species is known to be gynomonoecious, a condition exemplified by plants with bisexual and female flowers. The vast majority of tropical trees are sexually monomorphic, and an overwhelming majority of these species are hermaphroditic. Bawa & Opler (1975) found that 68% of tree species in a tropical lowland deciduous forest are hermaphroditic and 10% monoecious. Comparable figures have been reported for a lowland wet evergreen forest in Costa Rica (Bawa, Perry & Beach 1985), a southeast Asian Dipterocarp forest (Ashton 1969) and a lowland dry deciduous forest in Mexico (Bullock 1985). Andromonoecious

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species are difficult to detect without quantitative studies of floral variation. The figures cited above for both hermaphroditic and monoecious species include an undetermined, though probably low, proportion of andromonoecious taxa.

Self-incompatibility

Controlled pollinations have revealed that the vast majority of hermaphroditic species in tropical lowland forests are self-incompatible (Bawa, Perry & Beach 1985). In the montane forests, the proportion of self-incompatible species is significantly less than in the lowland forests (Sobrevila & Kalin-Arroyo 1982). The reasons for this disparity are not known, but unpredictability in pollinator services due to the frequent inclement weather in montane forests may select for a higher degree of self-compatibility.

There appears to be a wide range of variation in the strength of the incompatibility barrier. Thus, in practice, the distinction between self-compatibility and self-incompatibility is quite arbitrary, because the self-incompatibility barrier is often breached. The distinction is further obliterated if inbreeding depression, especially during early embryogeny, is considered as another manifestation of self-incompatibility (Seavey & Bawa 1986).

Little is known about the genetic control of self-incompatibility in tropical forest trees. There are some data for *Theobroma cacao* which suggests a gametophytic-sporophytic type of system (Cope 1962a, b). In this species, self-pollination has been shown to result in 25%, 50% or 100% ovules receiving male nuclei, but not undergoing fertilization. A series of alleles showing independence and dominance are believed to control the self-incompatibility. Gametes that contain similar dominant or independent alleles do not fuse with each other. Incompatibility reaction is presumed to occur in the ovules.

Monoecy

Many tree species, especially in such large families as Anacardiaceae, Araliaceae, Euphorbiaceae, Meliaceae, Palmae, Sapindaceae and Sterculiaceae are monoecious. The ratio of male to female flowers in monoecious species varies considerably over time during a flowering season (e.g. Bawa, Webb & Tuttle 1983). Overall, the number of male flowers greatly exceeds that of female flowers. Most important, in many monoecious species male and female flowers mature at different times (Bawa 1977). The lack of temporal overlap in the flowers of the two sexes results in complete outcrossing.

Distyly

In distylous species, although all mature plants act as pollen and seed parents, there are two types (morphs) of plants in the population. One morph bears flowers with long styles, called "pin" flowers and the other morph bears flowers with short styles or "thrum" flowers. The long and short-style flowers have short and long stamens, respectively. Not only is each morph usually self-incompatible, but also similar morphs are cross-incompatible. Thus, seed and fruit set occurs only when pollen from the short-style morph is transferred to the long-style morph and vice versa. The family Rubiaceae contains a notable number of distylous species. Bawa & Beach (1983) document in detail the crossing relationships, nature of self-incompatibility and pollination mechanisms of several distylous species in the Rubiaceae of the Costa Rican lowland wet evergreen forests.

Sexually dimorphic systems

Sexually dimorphic systems are characterised by the presence of two gender classes in the population. The two types of plants may be male and female (dioecy), female and hermaphroditic (gynodioecy) and male and hermaphroditic (androdioecy).

Dioecy

Dioecy is widespread among tropical forest trees, particularly in such common families as Anacardiaceae, Aquifoliaceae, Araliaceae, Burseraceae, Combretaceae, Ebenaceae, Elaeocarpaceae, Euphorbiaceae, Flacourtiaceae, Guttiferae, Lauraceae, Meliaceae, Nyctaginaceae, Polygonaceae, Rubiaceae, Rutaceae, Sapindaceae, Sapotaceae, Simaroubaceae, Sterculiaceae and Tiliaceae. The families Caricaceae, Datiscaceae and Myristicaceae exclusively consist of dioecious tropical trees.

At the community level, the percentage of dioecious tree species has been shown to range from 20% to 40% in lowland tropical forests (Bawa & Opler 1975).

A notable feature of dioecious species is that most of them have small (less than one centimetre across), inconspicuous, green, pale yellow or white flowers that lack morphological specialization (Bawa & Opler 1975) and seem to be collectively pollinated by a wide variety of generalist insects such as small bees, beetles, flies, wasps and butterflies. A disproportionate number of dioecious species also have flesh fruits (Bawa 1980a). These fruits are generally few-seeded and dispersed mostly by specialized fruvigores.

In many dioecious species, male and female flowers have incompletely or fully developed organs of the opposite sex that mask sexual dimorphism (Bawa & Opler 1975). In the genus *Saurauia* (Dilleniaceae), for example, the flowers on female plants in dioecious species have well-developed stamens with anthers that dehisce to release pollen which is collected by bees, the pollinators (Harber & Bawa 1984). However, this pollen once it lands on stigma does not germinate and is thus non-functional in fertilization. Because of the presence of opposite sex organs in male and female flowers, many dioecious tropical tree species have been, until recently, described as hermaphroditic (Bawa & Opler 1975; Bawa 1980a).

There are, on the other hand, some dioecious species that show conspicuous differences between male and female flowers. These differences are extreme in trees of the family Caricaceae. In both *Jacaratia* and *Carica*, for example, the male flowers have a long corolla tube formed by the union of petals. The tube terminates in five white petal lobes (Bawa 1980b). The female flowers, by contrast, lack a corolla tube: the petals are free and green in colour. However, the ovary at the tip bears five white petaloid lobes that closely resemble the lobes of the corolla tube of the male flower.

In general, regardless of the morphological differentiation between male and female flowers, the two sexes in dioecious species show often profound differences in many reproductive traits (e.g. Opler & Bawa 1978; Bawa 1980b). The male flowers are more numerous because male plants have more flowers per inflorescence and more inflorescences per plant than do the female plants. The male and female plants also differ in the timing, duration and frequency of flowering. In several species, male plants start flowering earlier, flower over a longer period and more frequently than do female plants.

The male and female flowers have also been shown to differ in nectar production. Bawa & Opler (1975) reported greater nectar production in female flowers of several species, but additional data indicate that usually male flowers secrete more nectar than female flowers. In *Jacaratia dolichaula* (Caricaceae) only male flowers secrete nectar; female flowers, which are devoid of nectar, mimic male flowers in order to get pollinated (Bawa 1980b).

Gynodioecy and androdioecy

There are no thoroughly documentated examples of gynodioecy or androdioecy among tropical forest plants. Some species which were earlier suspected of being androdioecious on the basis of a morphological criterion have been shown to be dioecious. A detailed study of *Xerosperum intermedium* (Sapindaceae) reveals that there are two sexual phenotypes which normally function as male and female parents (Appanah 1981). However, the flowers on female trees also bears stamens, which can release pollen the second or third day after anthesis. It is thus difficult to determine if this species is dioecious or androdioecious.

Sex ratios

The data on sex ratios of tropical trees show several species to have male-biased sex ratios. Opler & Bawa (1978) have offered several explanations for the biased sex ratios.

Mating systems

Studies of sexual systems in tropical trees, based on floral morphology and compatibility relationships, indicate that these trees are very strongly outcrossed. However, even in outcrossing individuals, limited gene dispersal can result in considerable inbreeding. Thus, to assess the exact degree of outcrossing, quantitative estimates are required.

Plant mating systems can be quantitatively analysed by measuring the amount of outcrossing at marker loci. The use of genetic markers allows one to partition the progeny of an individual into outcrossed and selfed or inbred (Clegg 1980). The outcrossing is measured by the parameter *t*, the value of which can range from 0 (for complete selfing) to 1 (for complete outcrossing). Genetic markers in the form of allozymes have been used to estimate the rate of outcrossing in several tropical tree populations. All these estimates indicate a high outcrossing rate, ranging mostly from 0.849 to 1.089 (Bawa 1992).

Implications for conservation

The data from floral sexuality studies and the analysis of mating systems indicate that tropical fruit trees are widely outcrossed. This means that gene flow within populations of most tropical forest trees is widespread. A very large number of tree species in the tropical rain forests occur in low population densities, with one or less than one reproductive individual per hectare (Hubbell & Foster 1983). Apparently, breeding populations of such species, if widely outcrossed, occur over very large areas. Natural reserves to conserve these species would have to be of sufficient size to contain the breeding populations. The size may range from 20 km^2 to 200 km^2 or more depending upon the spatial distribution of individual trees (Bawa, unpublished).

POLLINATION MECHANISMS

Tropical forest plants are pollinated by a wide variety of animals. Pollination by wind is uncommon and restricted to a few plant species in a particular community (Bawa & Crisp 1981). Pollination by animals involves both vertebrates and invertebrates. Among vertebrates, the major groups of pollinators are bats and birds, and to a lesser extent small non-flying mammals. The primary pollen vectors among invertebrates are bees, moths, beetles, butterflies, wasps and flies. The following description of pollination mechanisms is adapted from Bawa (1990).

Pollination by vertebrates

Bat pollination

Bat-pollination has been reported in a number of tree species in both the old and the new world (Heithaus 1982). These species constitute a diverse assemblage from a taxonomic point of view, but bat-pollination appears to be especially common among the members of the Bombacaceae and Sonneratiaceae. Apart from trees, bats are also known to pollinate several species of epiphytes in tropical forests. At community level, the exact proportion of bat-pollinated tree species is generally not known. Bawa *et al.* (1985) estimate that three percent of all three species in a tropical lowland rain forest may be pollinated by bats. In a tropical lowland deciduous forest with about 160 tree species, Heithaus *et al.* (1975) found 13 (eight percent) of the tree species to be bat-pollinated.

Floral syndromes associated with bat-pollination have been described in detail by Faegri & van der Pijl (1966) and Baker (1973). The two types of bat flowers, "shaving brush" and "campanulate", have been distinguished by Baker (1973). In general, bat flowers are large, white or pale yellow in colour, borne on stout, relatively exposed branches. The flowers bear abundant quantities of pollen and large amounts of nectar. Opler (1983) reports that bat flowers are among the largest and have the highest amount of nectar per flower among plant species of a tropical lowland dry deciduous forest.

The order Chiroptera to which bats belong is divided in two suborders: Megachiroptera and Microchiroptera. The Megachiroptera are confined to the Old World and Microchiroptera occur in both the Old and New Worlds. According to Baker (1973), the Megachiroptera are exclusively vegetarian; nectarivory in Microchiroptera is of more recent origin than in Megachiroptera. Baker also describes some interesting differences in foraging behaviour between the bats of the two suborders. The Megachiroptera start visiting flowers immediately after sunset and spend many minutes in the vicinity of the tree, whereas the Microchiroptera initiate visits to the flowers about an hour after dusk and may not spend more than a few seconds on a particular tree.

Pollination by non-flying mammals

Rourke & Wiens (1977) have documented pollination by arboreal marsupials and rodents in many plants from Australia and South Africa. Sussman & Raven (1978) have presented circumstantial evidence for pollination of several tree species in Madagascar by lemurs, especially in areas where bat-pollination is absent or rare. They are uncertain about any specific adaptations involved in pollination by non-flying mammals and consider the system to be a relic that has survived from ancient time in certain areas. Janson *et al.* (1981) have also implicated non-flying mammals, e.g. opossums, kinkajous and monkeys, in the pollination of several tree species such as *Ceiba pentandra, Ochroma pyramidale* and *Quararibea cordata* (all in Bombacaceae) in an Amazonian forest. Their evidence consists of observations that these animals visit flowers and move from one tree to another, thereby transferring pollen. However, as Janson *et al.* themselves note, two of these three species *(C. pentandra* and *O. pyramidale)* are known to be bat-pollinated and the presumed non-flying mammals do destroy a number of flowers.

Substantial evidence for pollination by non-flying mammals exists only for *Mabea occidentalis* (Euphorbiaceae), a small tree in the Central American lowland forests. Steiner (1981) found that the red woolly opossum, *Caluromys derbianus*, is a common visitor to the inflorescences of *M. occidentalis* which are also visited by noctuid and pyralid moths, Cerambycid beetles, Trigona bees and bats. According to Steiner, the inflorescences are "clearly adapted" to pollination by bats. Steiner also reports visits of the opossum to the flowers of the balsa tree, *Ochroma pyramidale* (Bombaceae), which is also bat-pollinated.

Bird pollination

There are several anecdotal accounts of bird-pollination in tropical rain forest trees (e.g. Skutch 1962). Among the common tree species in which bird-pollination has been reported are: *Bombax malabaricum*, *Bernouillia flammea*, *Ceiba pentandra*, *Erythrina* spp., *Spathodia campanulata* and *Eucalyptus* spp. In the neotropics, Trochilidae (humingbirds) and Icteridae (orioles) are significant pollen vectors and in the paleotropics, Nectariniidae (sunbirds), Meliphagidae (honeyeaters), Dicaeidae (flowerpeckers), Coerebidae (honeycreepers) and Drepanidadae (Hawaiian honeycreepers) act as important groups of pollinators (e.g. Stiles 1981).

The flowers pollinated by birds or the bracts subtending the flowers are generally red in colour. Morphologically, the bird flowers are of two types: brush (e.g. *Calliandra* spp.) and tube (e.g. *Erythrina* spp.); this dichotomy however is not restricted to the bird flowers (Stiles 1981). As compared to insect-pollinated flowers, the bird flowers contain less dilute but more nectar (e.g. Stiles 1978; Opler 1983). There also seems to be a direct relationship between nectar and flower weight (Opler 1983).

The characteristics of birds that act as pollinators are summarised by Stiles (1981). Briefly, the birds involved are small, less than 20 g, with slender bills, and their breeding behaviour and seasonal migration is particularly sensitive to flower abundance. Stiles' studies of pollination of tropical rain forest plants by hummingbirds are the most detailed investigations of bird-pollination in the tropics.

Pollination by invertebrates

The vast majority of trees are insect-pollinated. The principal groups among insects are bees, beetles, butterflies, moths, thrips, wasps and a diverse array of generalist insects. Together, these groups may pollinate more than 80% of tree species in a community (see below).

Bee pollination

Among insects, bees constitute perhaps the most important group in terms of number and diversity of tree species pollinated. The vast majority of tree species in such common families as Araliaceae, Burseraceae, Dipterocarpaceae, Euphorbiaceae, Leguminosae, Sapindaceae and Rutaceae are bee-pollinated.

Bees in the families Anthophoridae and Apidae have been found to be the major pollinators of neotropical forest trees (Frankie *et al.* 1983). In the forests of southeast and south Asia, species of *Apis* pollinate many trees. Small, stingless bees, especially in the genus *Trigona*, also pollinate a number of species, particularly in the understorey.

The diversity of bee-pollinated trees is so large that no generalisation can be made with respect to flower morphology or flowering pattern. Bee flowers, especially those that are pollinated by small bees can be relatively small, inconspicuous, white, pale or green in colour. Flowers pollinated by medium-sized to large bees may, however, be relatively large, brightly coloured and morphologically specialised, as in many species of the Bignoniaceae and Leguminosae. Flowering may extend from a few days in some species to several months in others (Frankie *et al.* 1983).

Moth pollination

Moth-pollination is particularly prevalent in the Rubiaceae (Bawa & Beach 1983). The large white flowers with narrow corolla tubes and with nocturnal anthesis in many species of such families as Apocynaceae, Leguminosae, Mimosoideae and Solanaceae suggest that moths are important pollen vectors in these groups. Moth-pollinated trees are mostly found in the understorey and subcanopy. There are, therefore, no large canopy trees in which moth-pollination has been reported. On the basis of flower syndromes, it is conceivable that some canopy tree species in the Mimosoideae in the New World and in the Apocynaceae in the Old World are moth-pollinated.

The number of moth species involved in pollination is not known. Pollinating moths may be distinguished into two broad categories, the large sphinx moths and small moths in the Noctuiddiae and possibly other families. Virtually nothing is known about the biology of the interactions that the latter group have with tropical trees. The flowers pollinated by sphinx moths are generally white or pale yellow in colour; corolla tubes open in the late afternoon or after dark, are sweet-scented and offer nectar as the main reward to the moths (Faegri & van der Pijl 1966; Haber & Frankie 1989). Two types of flowers may be distinguished: tubular flowers with narrow corolla tube terminated by four to six corolla lobes, and brush type of flowers with reduced corolla and many exserted stamens.

Although sphinx moth-pollinated plants may be found to flower at all times of the year, Frankie and coworkers (Frankie 1975; Haber & Frankie 1989) have observed peak flowering in the wet season. Frankie has explained this seasonality on the basis of plants serving as sources of food not only for adults but also for the larvae. The larvae are dependent upon the leaves which in the case of most plant species in the dry deciduous forest are borne only during the wet season. The sphinx moth-pollinated species may flower in highly synchronous episodes lasting only 4 to 5 days or they may bloom for as long as 10 months.

Beetle pollination

Pollination by beetles is common in the Annonaceae, Myristicaceae and Palmae. A wide variety of beetles is involved in pollination, but detailed information is available for only a couple of species pollinated by scarab beetles (Beach 1982, 1984). Flowers pollinated by beetles lack bright colourations, are of diverse shapes and sizes, and have strong odours.

Wasp pollination

The classical example of pollination by wasps is the genus *Ficus* in the Moraceae. All of the 700 or more species of figs are pollinated by species-specific wasps (Wiebes 1979). The interaction between wasps and figs has been described in detail by Wiebes (1979) and Janzen (1979). Wasps other than pollinating fig wasps probably also pollinate tropical plants but such cases have not been adequately documented.

Pollination by other insects

Flies and butterflies constitute two other groups of pollinators in tropical forests. In addition, many species of tropical plants possess inconspicuous pale white, green or yellow flowers that are collectively visited by diverse array of small insects such as bees, butterflies, beetles, wasps and flies (Bawa *et al.* 1985). It is not known if all of these groups or just one of them are the effective pollinators. There are few detailed studies of pollination by flies, butterflies or the last, the diverse insect, category, although these groups pollinate a number of tropical forest plants. Beamen *et al.* (1988) have recently described the pollination by flies of the endangered species of the genus *Rafflesia* (Rafflesiaceae).

Pollen flow

Information about pollen flow is essential to define the boundaries of a population. Pollen flow in plant populations is a function of the plant density and the distances to which pollinators may fly (Levin & Kerster 1974). Bats, large bees and sphinx moths that pollinate a vast majority of tropical forest plants are known to fly over long distances (e.g. Heithaus *et al.* 1975). However, precise data on the extent of pollen flow in tropical plants are lacking. Fluorescent dyes to monitor the movement of pollen (Webb & Bawa 1983) or the pollinator (Frankie, Opler & Bawa 1976) as well as genetic markers (O'Malley & Bawa 1987) have been used to study pollen flow in tropical forest plants.

Implications for conservation biology

Because almost all tropical forest plants are animal-pollinated, their conservation in fact requires the conservation of plant-pollinator as well as other mutualistic plant-animal interactions. Equally important, as several studies have shown, groups of plant species that share the same pollen vectors may interact with each other through their pollinators (Stiles 1978; Frankie *et al.* 1983). The effect of the removal of some plant species from these guilds on the pollinator and the concomitant effects on other species of the guild are unknown. It is also important to keep in mind that conservation of a pollinator may be contingent upon the heterogeneity of the resources as well as the habitats on a large scale. Janzen (1987) points out that many species of sphingid moths that pollinate plant species in the dry forest migrate to the wet evergreen forests or montane forests during the dry season. Thus, very large conservation areas are required to prevent disruption of plant-animal interactions.

GENETIC DIVERSITY

In plants, modes of reproduction have been shown to be primary determinants of the population genetic structure (Loveless & Hamrick 1984). In general, the outcrossing populations are much more variable than populations with high levels of selfing. However, little is known about factors that regulate distribution of genetic variation between populations.

In recent years, genetic markers in the form of allozymes have been used to measure the degree of genetic diversity within and between populations (Hamrick *et al.* 1979; Schoenwald-Cox *et al.* 1983). To determine the level of genetic variability, three parameters are usually estimated: proportion of polymorphic loci, average level of hetrozygosity, and the average number of alleles per locus. Hamrick & Loveless (1988) provide data on genetic variability in several tropical tree populations of central America. They note that tropical species vary with respect to the amount of genetic variability within populations; in general, the level of variability is high and in many species comparable to that in the temperate-zone conifers. The latter are among the most genetically variable group of plants (Hamrick *et al.* 1979).

Very little is known about the degree of genetic differentiation within and between populations. There is increasing evidence that even the local populations of plants are often genetically structured. Evidence for genetic structuring of tropical tree populations has been presented by O'Malley & Bawa (1987).

There is a wide variety of measures to estimate the extent of genetic variation between populations. Usually, H_t, the total genetic variability is partitioned into within (H_s) and between population components (G_{st}), and G_{st} is expressed as a fraction of the total genetic variability, or $G_{st} = H_t - H_s/H_t$ (Nei 1975). The value of G_{st}, estimated tropical tree species so far, is very low, indicating little or genetic differentiation among populations, (Bawa & Krugman 1989; Hamrick & Loveless 1989).

In summary, the data on genetic diversity within and between populations of tropical forest trees are quite limited. Further, much of the available information is based on the study of allelic variants of genetic loci coding for specific enzymes. The relationships between this biochemical variation and variation in morphological traits that are of direct survival value is obscure. Clearly the process of documenting patterns of genetic variation in tropical plants which has barely begun will require a multiplicity of approaches to measure genetically based variation in biochemical, morphological and physiological traits.

Implications for conservation biology

Effective conservation of genetic resources requires information about the amount and pattern of genetic variation. For example, if a species is highly variable and much of the variability is distributed within the population, then the conservation of one or a few populations might preserve a large proportion of genetic diversity. If, on the other hand, a large proportion of the genetic variability is accounted for by the between-population component, then conservation of multiple populations may be necessary for the preservation of genetic diversity within species. Furthermore, the sampling design for collection of seed material for conservation of genetic resources *ex situ* depends upon the population genetic structure.

CONCLUDING COMMENTS

The data from floral sexuality, pollination biology and the studies of genetic diversity reveal that most tropical forest trees are widely outcrossed. Because many tropical tree species have low population densities, the wide outcrossing implies that scattered individuals could interbreed with each other over a wide area. Thus, the breeding populations of tropical trees could occupy large areas and their conservation may require reserves up to a few hundred km^2 in size. Moreover, most of tropical forest plants have pollen or seed or both dispersed by a wide variety of animals. Effective conservation of forest resources therefore requires identification of key mutualistic interactions and the conservation of all interacting partners. The breeding systems of plants, their pollination and seed dispersal mechanisms interact in a wide variety of ways to influence the genetic structure of plant populations. An understanding of the factors regulating genetic diversity is important for the sound management and conservation of forest genetic resources.

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PHYSIOLOGY OF PLANTS

PHYSIOLOGICAL ASPECTS OF *EX SITU* SEED CONSERVATION

E.H. ROBERTS

SUMMARY

The main physiological characteristics of seeds, which affect the technology of harvesting, drying, storing, monitoring and regenerating seed accessions for genetic conservation, are described. It is essential that those who are practically involved have access to various key publications and it is preferable that, in addition, they receive specialist practical and theoretical training.

INTRODUCTION

The purpose of this chapter is to draw attention to some of the more important physiological and genetical principles which influence the practice of seed storage for genetic conservation. It is not possible here to discuss the problems in detail, and so anyone who intends to be practically involved in this type of storage should, at least, read the first and second of the *Practical Manuals for Genebanks* published by IBPGR (Hanson 1985; Ellis, Hong & Roberts 1985a) and have the third manual to hand for reference (Ellis, Hong & Roberts 1985b) together with the IBPGR publication on the design of seed stores (Cromarty, Ellis & Roberts 1982) with updated material and additions published by IBPGR (1985). For general background reading, useful chapters will be found in Holden & Williams (1984).

PRACTICAL METHODOLOGY

Orthodox, recalcitrant and intermediate seeds

So far as their storage characteristics are concerned. seeds may be divided into two categories – orthodox and recalcitrant. Most seeds are orthodox, i.e. decrease in moisture content and temperature predictably increase longevity according to certain quantitative rules, which are now well understood. All arable and forage species produce seeds in this category, as probably do most wild herbaceous species and many tree species. However, some large, fleshy seeds produced by various tree species, and seeds produced by some of the species from aquatic habitats are recalcitrant, i.e. desiccation kills them and, even when stored moist, they usually do not survive for more than a few weeks or months. Many of the trees of tropical rain

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forests, some important industrial crops (e.g. rubber and cocoa) and many tropical fruit trees (e.g. mango, durian) produce recalcitrant seeds.

Recalcitrant seeds can seldom be stored, even under ideal conditions (cool, moist with access to air) for more than a few weeks or months. As a result, the genetic resources of such species have to be conserved by *in situ* conservation, although it may be possible, eventually, to store some as tissues or organ cultures, but there are still many problems to be solved before these *in-vitro* systems can be routinely used.

Finally an intermediate category of seeds has now been identified in which seed can be dried with benefit – typically to about 10% moisture content – but storage at cool temperatures (<10°C) shortens lifespan. Examples include coffee, oil palm and papaya. Such seeds may be stored for several years, but not in long-term cold stores.

A useful list of species with their seed storage characteristics is available (Ellis 1984), although this was published before the intermediate category had been identified.

Handling orthodox seeds

In most cases, the cheapest, safest and most convenient way of conserving genetic resources of crop plants and their wild relatives is by long-term seed storage, provided, of course, the seeds are orthodox. Similar methods can be used for conserving the germplasm of endangered wild species. The potential longevity of a seed depends on its initial quality, and the extent to which that potential longevity is maximized depends on the storage conditions.

When a seed is first formed it is quite moist – usually 50% of its total weight is water. Then when it reaches physiological maturity – defined as the stage when its dry weight reaches its maximum value – the seed begins to dry out. As soon as it reaches physiological maturity it is at the ideal stage for harvest for long-term storage because from now on the seed begins to deteriorate, even while it is still on the mother plant in the field. The rate at which it deteriorates depends on the same factors which influence deterioration in the seed store, i.e. moisture content and temperature. Initially, when the seed is still fully hydrated, the rate of deterioration is slow but as the moisture content decreases, so the rate of deterioration increases, reaching a maximum rate of deterioration at a particular moisture content which is probably about 30% in most non-oily seeds and about 15-18% in oily seeds. Below this level, the rate of deterioration decreases with further decrease in moisture content, at least down to 5% in most species and down to at least 2.5% in many oily seeds.

Harvesting and drying

Accordingly, it is important to harvest seeds as soon as they have physiological maturity and then dry them as soon as possible so that they pass rapidly through the vulnerable zone – say, between 45% down to 12% moisture content – without delay. For long-term storage the drying will need to be continued down to 5% moisture content, but it will not matter if there is a temporary delay, say, in a field-collecting expedition, at 12% moisture content (or less) where good drying facilities may not be available. In the field it is often possible to achieve 12% moisture content by sun drying. Storage over dehydrated silicia gel is even better. In the genebank the use of a drying room or cabinet run at about 15°C and 15% relative humidity is advocated. If a hot-air drier is used the air temperatures should not exceed 40°C but when using this temperature in many warm and humid climates it may not be possible to achieve the low moisture contents required for long-term storage.

The importance of reducing moisture is exemplified by considering the factor by which it increases seed longevity. In cereals, for example, at around 8-9% moisture content, seed longevity doubles for each 1% decrease in moisture content. But by time the moisture content has reached 5% the factor has risen to a trebling of longevity for a 1% decrease in moisture content. In commercial grain storage, seed is often stored at about 13% moisture content; but at the same temperature longevity would be about 275 times greater at 5% moisture content (the moisture content recommended by IBPGR for long-term seed storage).

Storage

Seeds take up, or give off, water vapour to the air until they reach equilibrium with it. In almost all natural environments very dry seeds will therefore absorb water vapour and increase in moisture content if allowed to do so. Accordingly, as soon as seeds have been dried sufficiently, they should be put in containers which are impermeable to water vapour. Suitable containers include heat-sealed laminated-foil packets of good quality, or cans or bottles with screw-cap tops and rubber seals. Polyethylene bags are not good enough for long-term storage, because they are not completely impervious to water vapour.

Seed longevity can be increased further by maintaining a low temperature during storage. In typical tropical conditions with average temperatures in the range 20 – 30°C, seed longevity doubles for each 5°C decrease in temperature. When the temperature has fallen to 5°C, the advantage falls to about an increase in longevity by a factor of 1.5 for a further5°C decrease in storage temperature. Nevertheless, providing facilities are available, it is clearly well worth decreasing the storage temperature by as much as is economically and practically feasible. This is why for the long-term storage of base collections IBPGR recommends storing seeds at about -20°C. For small collections it is feasible and relatively cheap to use conventional domestic deep-freeze chests which operate at about this temperature (Cromarty, Ellis & Roberts 1982; Ellis & Roberts 1982; IBPGR 1985). Storing at -20°C as compared with 20°C would be expected to increase seed longevity by a factor of about 40. Thus the combined effect of using IBPGR-preferred conditions for long-term seed storage (-20°C and 5% moisture content) as compared with a typical farm storage in the tropics averaging, say, 20°C and 13% moisture content would be to increase longevity by a factor 40 x 275 = 11,000.

Consideration is now being given to ultra-dry storage, i.e. drying seeds to moisture contents in equilibrium with about 10% relative humidity (moisture contents between 2 and 4% depending on whether the seed is oily or non-oily). This will increase longevity in cold stores even more, or make long-term storage in some species feasible without refrigeration (Roberts 1991).

Regeneration of accessions

Although under IBPGR-preferred conditions seed deterioration is very slow, it still occurs. Most aspects of sub-cellular structure and metabolism are affected so that, not surprisingly, as seeds deteriorate so they lose 'vigour', i.e. they germinate more slowly, frequently show morphological abnormalities and are less able to withstand stressful conditions in the seed bed. So far as genetic conservation is concerned, the most important of the sub-cellular changes which take place is the damage to chromosomes which results in the accumulation of heritable mutations. Generally speaking, the greater the loss of viability and the lower the moisture content at which it occurs, the greater the damage (Rao, Ellis & Roberts 1987). This one of the reasons why IBPGR recommends that seed accessions should be regenerated (grown to produce a fresh stock of seeds) before viability has fallen very far: 85% viability is the arbitrary regeneration standard recommended for most species. In genetically heterogeneous accessions there is additional reason for adopting a high regeneration standard which derives from the fact that some genotypes survive better than others. Accordingly, any loss of seed viability in a genetically heterogeneous accession will inevitably lead to selection of longer-lived genotypes and therefore to some change in the genetic constitution of the accession as a whole.

Monitoring seed viability

Seed accessions in store, therefore, need to be monitored regularly, but infrequently, in order to determine percentage viability. The monitoring needs to be infrequent not only to minimise work load but, even more importantly, to minimise depletion of accessions. This is because currently the only satisfactory method of monitoring viability is to carry out germination tests which are, of course, destructive. Each test, therefore, in addition to being no more frequent than is necessary, should also employ the minimum number of seeds consistent with an acceptable level of accuracy. A reasonable probability of taking the right decision as a result of the test is important because, on the one hand, it is important not to regenerate too soon (because the cost of regeneration is high), whereas, on the other hand, the danger of not regenerating soon enough could at best result in genetic changes in the accession or, at worst, complete loss. The best technique available which takes into account these conflicting pressures is a seed-testing procedure designed for the purpose (Ellis, Whitehead & Roberts 1980) known as the Sequential Probability Ratio Test and described in the manuals (e.g. Ellis, Hong & Roberts 1985a). Further improvements in the technique are described by Ellis & Whitehead (1987).

In addition to these statistical techniques, it is most important that appropriate practical procedures are adopted for the germination tests. Erroneous results can arise through three major causes – imbibition injury, seed hardness and seed dormancy. All three factors are likely to pose much greater problems in genebanks than in commercial seed technology because the first two problems are exacerbated by very dry storage, and the last by cold storage, because cold storage of dry seeds preserves dormancy as well as viability. Furthermore, seed hardness and dormancy are greater problems in wild species. And dormancy will also be more pronounced in seeds promptly harvested and stored (to maximize seed quality, as advocated earlier for genetic conservation) because dry 'after-ripening', which proceeds faster under warm conditions in most species, will be minimised. Because of these special circumstances, the methods prescribed by the International Seed Testing Association (ISTA) or the American Association of Seed Analysts (AOSA) are often inadequate for application in genebanks. However, using appropriate techniques, all three problems can be overcome.

Imbition injury is a problem which is less well-known than the others, but it is particularly important in genebanks where seeds are stored under conditions which are much drier than those with which most people are familiar. When dry seeds are set to germinate, the rate of water uptake can be very rapid, and this can lead to seed injury and often to death. It can be avoided by ensuring that the seeds take up water slowly as water vapour (instead of as liquid water) by placing them in a closed container kept at 100% relative humidity for a day or so before they are set to germinate. A layer of water at the bottom of a container, but separate from the seeds, will serve the purpose. After the moisture content of the seed has been raised to, say, 12% moisture content or more by humidification, the seed can safely be transferred to the standard germination tests.

Seed hardness is more of a problem in some families than others (e.g. Leguminosae, Malvaceae). During drying the seeds develop coats which are impermeable to water and consequently the seeds are unable to germinate until the seed coat has been damaged in some way. It is important while damaging the seed coat not to damage the embyro. Various techniques are available.

The third problem, seed dormancy, is often the most difficult of the three because different species respond to different methods and, while satisfactory methods have been worked out for common crop species (e.g. rice and temperate cereals), satisfactory methods have not yet been developed for all species – especially some of the wild ones. Nevertheless, general guidance is given in Ellis *et al.* (1985a) and specific information and guidance, family by family, has also been published for ease of reference (Ellis *et al.* 1985b).

Clearly a short article such as this cannot attempt to do more than alert the reader to some of the main technical problems in *ex situ* seed conservation. The technology has developed rapidly in recent years and any person involved in seed storage for genetic conservation should ideally receive some specialist training, including practical work. Short courses have been organised from time-to-time by IBPGR. When such courses are not available, some study of the literature mentioned in the Introduction should at least provide most of the information required.

PROPOSED TRAINING METHODS

It is suggested that a training course should include a series of lectures and discussion groups which cover at least the following topics:

(i) Seed morphology and germination, criteria of germination and seedling evaluation;

(ii) Seed moisture content/relative humidity equilibria, the determination and expression of seed moisture contents;

(iii) Main factors affecting loss of viability, seed survival curves and decisions concerning frequency of monitoring tests;

(iv) Some of the main factors which prevent the germination of viable seeds and methods of overcoming or avoiding them: dormancy (especially in relation to temperature, light, surgical intervention and chemical additives), seed hardness (methods of scarification), water sensitivity, imbibition injury, empty seeds and their detection;

(v) Methods of testing seed viability: standard germination tests, the sequential probability ratio test, tetrazolium tests.

Lectures and discussions on these topics should be linked to laboratory classes which should provide all students with 'hands-on' experience in performing and interpreting germination tests on seeds of several species. The students should also be set practical problems in the diagnosis of seed dormancy, seed hardness and imbibition injury, and methods of dealing with these problems, and distinguishing these conditions form loss of viability. Exercises should be undertaken on the determination of seed moisture content.

Basic information on all these topics will be found in Ellis *et al.* (1985a, 1985b). Students should be provided with copies of Hanson (1985). All three publications may be obtained from: International Plant Genetic Resources Institute, c/o FAO, Via delle Sette Chiese 142, 00145 Rome, Italy.

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PHYSIOLOGICAL CONSIDERATIONS IN CONSERVATION WITH SPECIAL REFERENCE TO PROPAGATION AND GROWTH ASSESSMENT

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SUMMARY

The main aspects of the physiology of plant conservation are discussed. Propagation, in particular vegetative propagation, is especially important and is discussed in some detail. Other topics such as the assessment of growth, the responses to water and nutrient supply are considered as well as the effects of the physical factors of the environment such as light, temperature, photoperiod. For the detailed methodologies required for the several techniques involved, reference must be made to the special texts, which should be available for the training programme.

INTRODUCTION

Of the very large number of plant species in the world only a very small proportion is presently utilised by man as crops. Other species are exploited destructively from the wild (e.g. timber trees) or their products are collected (e.g. fruits or nuts). However, it seems certain that when their properties are examined and assessed that more direct and important uses will be found for many other species. This is likely to apply particularly to species with pharmacological properties, or plants yielding such products as latex, oils, etc. Others which should (must) be conserved will include species of particular scientific interest, or of ecological importance or of amenity value.

In order to maximise the benefit from such species, they need not only be protected but must also be brought into cultivation. This will permit breeding for higher productivity or the investigation of useful properties in general. Hence, once a species is chosen, detailed physiological investigations are required before it can become a 'crop', and even established crops still require further research. For example, the oil palm is an established crop, but it has a long breeding cycle, so that no more than a few generations have been passed in cultivation, compared with, perhaps, 3000 in the cereals; yet even in cereal breeding there is no suggestion that genetic variability and physiological potential have been fully exploited. In fact, with the big advances expected from the new methods of biotechnology in the next few decades, the possibilities seem endless. What are the physiological implications for conservation in this context?

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Basically, they comprise the need for (i) maintaining and increasing the plant material and (ii) understanding the plant's requirements as far as its physical external environment and supply of water, CO_2 and nutrients are concerned. This will have to be supplemented by an understanding of the internal control mechanisms determining morphogenesis affecting shape and size of the organs and their optimal functioning. Most probably, studies may also be needed on the enemies (pests and diseases) of the plant which will interact with the plant's physiology. All such studies will generally have to focus on the particular aspects of importance to man, which may be the growth of plant as a whole, or of particular parts which constitute the desired product, leaves, seeds, fruit or wood.

Some of these aspects will be considered in this chapter with particular reference to propagation, nutrient and water requirements, determination of optimum environmental conditions, and optimisation of the plant's efficiency in producing the desired product by manipulating the environment or the plant's behaviour.

PRACTICAL METHODOLOGY

Propagation

There are three common methods available to the propagator: propagation from seed, vegetative propagation from cuttings, offsets, bulbs or many other types of plant organ, and propagation by tissue culture. Each of these techniques has its advantages and disadvantages. These will be discussed briefly when giving some detail of the several methods available.

Seeds

Only a few comments on propagation by seeds need to be made here because most aspects of significance of seed behaviour have already been covered in the chapter by E.H. Roberts (this volume) and also in the papers by Ellis *et al.* (1985a, 1985b) in which methods for overcoming seed dormancy are discussed. Techniques commonly employed include the following: various methods of abrasion or chemical treatment to disrupt hard seed coats, short exposure to ultrasonics, prolonged chilling treatment, or heat treatment including brief immersion in boiling water or even exposure to burning material such as straw or litter. There is a whole range of chemicals promoting germination of imbibed seeds, comprising nitrates, thio-urea, high oxygen levels, plant hormones such as gibberellins, ethylene or cytokinins. Also inhibitors of respiration such as carbon monoxide, sodium-azide, -fluoride, -cyanide, iodoacetate, etc. have been used successfully with some species. Of course, conditions during germination must be satisfactory as far as water supply, oxygen availability and suitable temperature conditions are concerned; some species may require light for germination, while others may need total darkness. In order to optimise conditions for germination, a range of treatments may thus have to be tried. Much fuller information on these aspects will be found in Khan (1982) and Bewley & Black (1978, 1982).

Vegetative propagation from cuttings and other plant organs

Many plant species have natural methods of vegetative propagation which may be exploited in their multiplication; these comprise all plant parts, stems, leaves, roots and flowers. A number of these arise from special reproductive organs: bulbils, mammillae, runners, stolons, rhizomes, suckers, etc. (examples are given in Schwabe 1971).

The most common term applied to plant parts used to grow into complete new plants is, of course, 'cuttings', which may be derived from all kinds of source material. The methods described below for their propagation will, therefore, depend to some extent on their origin and this will be indicated. In an article such as this, it is only possible to draw attention to the important criteria and basic methods. Detailed techniques used for particular species are given in such textbooks as Hartmann & Kester (1968).

Vegetative propagation, whatever the method used, is, of course, clonal in nature and the plant material raised by these methods will be genetically identical with the mother plant. Generally this is of advantage and desirable, but implies a lack of genetic variability. Occasionally, of course, so-called 'sports' arise, and in tissue-cultured material somaclonal variation is not uncommon. The clonal, vegetative propagation makes it imperative to ensure that only healthy mother plants are employed so as not to propagate diseased material (especially if virus-infected).

The following aspects deserve particular attention when propagating from cuttings:

(i) Mother plants

Cuttings should only be taken from healthy mother plants, although under special circumstances it may be possible to free the cutting of virus diseases if subjected to high-temperature treatment, or if the cutting consists of only the apical shoot tip and is propagated in sterile tissue culture.

The plant age may be important in determining the ability of the cutting to root. Juvenile material is usually easier to root; and in this context (e.g. in trees) the oldest part which is also nearest to the roots may have retained a more juvenile response. Adventitious shoots formed on root cuttings can often be detached and rooted separately much more readily than similar shoots from the top of the plant.

The state of development of the individual cutting may be of decisive importance to successful rooting. Often very young or soft growth may root more readily than matured tissue with mature leaves (e.g. oaks and beech), yet in other species the opposite may be the case. Thus, seasonal variation in the ability to root may be an important factor.

(ii) Environment for rooting of stem cuttings

Because a stem cutting normally lacks roots, it will lose water by transpiration, etc. without the ability to take up water to compensate for the losses. Hence, a very humid environment is required during the rooting process. This may be achieved by enclosing the cuttings in a very humid or saturated atmosphere (e.g. under polythene) or spraying the cuttings at frequent intervals with a mist of fine water droplets (the frequency of this can be linked to a timer, or sensed by evaporation from a so-called 'artifical leaf'). In a further refinement, only minute droplets are injected into the atmosphere (fogging), which causes less deposition of water on the leaf surface of cuttings, something which has often been found to be detrimental.

The maintenance of optimal temperature may be equally crucial and this would need to be determined for the particular species to be propagated. Moreover, quite commonly the optima are higher for the basal part of the cuttings where the roots are forming; these may benefit from higher temperatures than the tops in the humid atmosphere of mist, etc.

The provision of light to the cuttings during the rooting process on the bench must be adequate for leafy cuttings to allow photosynthesis and yet it must be low enough to prevent excessive transpiration occurring with direct radiation even under humid conditions.

Although the precise reasons are still not known, it is essential to provide good aeration at the cutting base to facilitate rooting; this may be achieved by use of an appropriate rooting medium but actual air flow and even oxygen injection have been used. The airspace for the upper parts of the cuttings also need ventilating, in this case to supply the necessary carbon dioxide for photosynthesis and also to remove any possible accumulation of ethylene produced by the cuttings themselves. Such accumulation may occur in enclosed spaces and can lead to premature leaf abscission and subsequent failure of the cuttings to root and survive.

The rooting medium must have a good moisture-holding capacity while allowing maximum aeration and drainage (under misting), also it should not support fungal and bacterial growth. While peat/sand mixtures are often employed, coarse vermiculite and/or perlite media are generally preferable. In any case, good hygiene is required such as the immediate removal of any dead leaf or other plant material.

(iii) Pre-treatments

The cuttings should be prepared before insertion into the rooting medium on the bench, by clean cuts, sometimes with a length of tissue (heel) from which roots may arise, by removal of all injured or surplus leaf tissue, which may sometimes be cut back, etc. However, probably the most effective pre-treatment to promote rooting, is the application of plant hormones or synthetic growth regulators of the auxin type. Usually applied to the base of the cuttings, they generally improve and accelerate the formation of new adventitious roots. Indol-3yl-butyric acid is the most commonly used active substance and can be given in aqueous solution or in a 50% alcoholic solution or mixed with talc as a 'rooting powder'. The best method of application will need to be determined for each species. Generally, relatively low concentrations are used with aqueous application when cuttings are stood with their bases (about 1 cm deep) in the solution for up to 24 hours, concentrations ranging from 10 to 100 parts per million. With the alcoholic solutions only a very short immersion of the cutting bases is needed, i.e. a few seconds only, but the concentrations of the 'quick dip' methods are usually much higher i.e. 1000 to 10,000 parts per million. In the case of pistchio *(Pistacea vera)* only concentrations of more than 25,000 ppm were successful (Bazari & Schwabe 1982). The application as 'rooting powder' is used again at rather lower concentrations but in this case the powder is left in contact with the moistened cutting bases for the entire rooting period. Sometimes application to a low leaf rather than the stem base is more effective and the optimum method will need to be determined for each species to be propagated.

Grafting, budding, layering, marcottage

Another group of common techniques of vegetative propagation involves the grafting of the desired species onto root-stocks which may or may not be of the same species; these may often be seedlings, or they, too, are clonal in origin. There are numerous methods for effecting the junction between the two partners. The scion may be a shoot in the dormant or active state, or a bud; it may be placed to abut the stem or be inserted under the bark of the stock, etc. The main criteria for a successful graft are suitability of scion wood, compatibility between stock and scion, a good junction to allow cambial activity and tissue fusion, prevention of desiccation during graft development and subsequent pruning treatment. Details will found in texts such as *The Grafter's Handbook* (Garner 1968).

Other techniques such as layering or marcottage may be used for vegetative propagation, though only on a small scale. These involve the induction of roots on shoots or branches of growing plants by wounding (sometimes followed by hormone application) and subsequent enclosure with a moist substrate such as peat or soil. When root formation has occurred the rooted branch can be severed completely and will exist independently.

Propagation by tissue culture

The third method for propagation of plant material is by tissue culture. This method generally permits a much higher rate and degree of multiplication, but it may be more difficult to achieve and requires specialised equipment and conditions. The practical details of tissue culture for purposes of clonal propagation have been described in numerous texts and cannot be given here in detail. However, the crucial stages may be listed: The taking and preparation of explants, the surface sterilisation process, the provision of the initial medium leading to survival, growth and cellular proliferation of the explant as organised tissue or callus, the provision of media of different composition (usually hormonal) for the purposes of differentiation, often followed by a further change of medium to promote rooting of shootlets, the establishment of the plantlets, the weaning from the test tube to the soil, and eventually full establishment.

The two modes of propagation referred to are based either on the use of organised tissue from the mother plant (e.g. stems or shoot tips from which new plant material arises as organised shootlets or branches) or by way of disorganised proliferation from the explant to give callus from which new organised material is raised as adventitious shoots or as embryoids. Before either can be cultured it is necessary to surface-sterilize the explants, which will then need to be induced to grow or proliferate. There are now many texts available which describe the techniques of sterilisation, the details of media with their constituent macro- and micro-mineral nutrients, organic components and other adjuvants including the all-important growth hormones, which are suitable for inducing particular types of growth, establishment, proliferation, organization of new plantlets or induction of embryoid formation. There are special conditions, usually hormone treatments promoting rooting of the new shootlets, which then behave as miniature plants. Once these have reached an adequate size, they need to be taken out of the sterile test-tube environment and be weaned to grow in drier conditions than the usually saturated atmosphere in culture, while the roots need to be established in the soil. Protocols for all these aspects are found in texts such as Bhojwani & Razdan (1983) or Thorpe (1981). Nonetheless, difficulties may be encountered and the available methods or 'recipes' may prove inadequate, so that further research will be needed to develop methods suitable for species not previously used in tissue culture.

Requirements for water, nutrients and optimum environment

Assessing the requirements of water, nutrients and soil pH for optimum growth of crop plants is usually the next stage to be investigated, once plant material in adequate numbers is available. Again, this can only be done by experimentation, and commonly such tests are done on different scales. Small-scale trials of young plants in pot culture can reveal symptoms of deficiency and/or toxicity in relatively short-duration experiments. Similarly, the water requirements of young plants may be assessed in the same way when stress can easily be brought about and maintained. For nutrient studies on a small scale, sand or gravel culture or water culture, possibly involving nutrient-flow techniques, are useful for detailed studies. More often, of course, fertilizer experiments must be done in the field where the addition of ions to the soil will be the basis of experimentation. The scale of experimentation, the plot size, degree of replication, etc. will, of course, depend on the crop under investigation (e.g. different considerations will apply when a cereal crop is grown or when a tree crop is to be studied). For experiments on water relations, it is usually easier to supply additional water, say by irrigation, but it may also be possible to reduce the available water by shielding plants with canopies from the rain, or preventing water falling on the soil from reaching the roots. The water status of the plant as well as the soil will usually have to be assessed. Such measurements, for instance of the water potential of plants and soil, will, of course, require the necessary equipment such as pressure bomb, porometers, neutron probe, etc.

It cannot be stressed too much for all experimentation that a sound statistical design is one of the most important aspects of such work, which will usually include factorial combinations of the different treatments involved. Suitable information on design and analysis will be found in most textbooks on elementary biological statistics.

Much of the same applies to the study of optimum environmental conditions. Where this is possible, optimum temperature, light intensity, photoperiod and other conditions can be tested in controlled conditions such as in a phytotron. Generally this may not be possible, and inferences made from the natural environment to which the species in question is adapted may be the only means, and may in fact be adequate. However, it is essential that this aspect is not overlooked, as, for instance, the provision of an appropriate photoperiod may make all the difference between flowering and fruiting or its failure.

Assessment of physiological functions in the plant

Once the species of interest has been established and the optimum conditions defined in which it will grow, it is usually necessary to gain information on its physiological activities, particularly inasmuch as these will be affected by the growth conditions. Here it is generally important to measure the photosynthetic efficiency and define whether the plant has a C_3 or a C_4 mechanism. Use of infra-red gas analysis apparatus will be invaluable for such studies. However, in the field an estimate of efficiency can usually be obtained by way of growth analysis, for which no sophisticated equipment is required. Basically the requirements are for some means of determing fresh- and dry-weights as well as leaf area. Three of the most frequently used measures are given here, where L_A = area, W = dry weight, P = ground area; ln is the natural logarithm; numerical subscript of T (time) refer to the sampling occasion.

	Instantaneous	Mean over T_2-T_1
Relative growth rate:	$R = \frac{1}{W}\frac{dW}{dT}$	$\frac{\ln W_2 - \ln W_1}{T_2 - T_1}$
Net assimilation rate:	$E_A = \frac{1}{L_A}\frac{dW}{dT}$	$\frac{W_2 - W_1}{T_2 - T_1} \times \frac{\ln L_{A_2} - \ln L_{A_1}}{L_{A_2} - L_{A_1}}$
Leaf area index:	$L = \frac{L_A}{P}$	$\frac{L_{A_2} - L_{A_1}}{P}$

A much fuller treatment and formulae for other useful measurements and determinations are given in *Plant Growth Analysis* (Hunt 1978).

The integrative processes in the plant, and particularly morphogenetic effects, are believed to be under control of internal hormone levels, their distribution and sensitivity to their action. Hence, in the later stages of investigations into a species or crop, it will become necessary to investigate these aspects. This is particularly so where it is desirable to modify metabolic processes, e.g. breaking dormancy, altering apical dominance patterns, changing stem elongation, promoting fruit set, etc. Usually such studies involve the external application of the five naturally occurring hormones (auxins, gibberellins, cytokinins, abscisin and ethylene) or synthetic growth regulators. These may eventually permit the manipulation of crop growth in desired directions. Valid determination of natural hormone levels are fraught with difficulties and usually require sophisticated techniques and equipment; nonetheless such studies may eventually be required.

SUGGESTIONS FOR PRACTICAL TRAINING EXERCISES

(1) A simple experiment would be performed with, say, *Pyrethrum* or some similar species of economic importance. The traditional method of propagating this species has been to dig up a 'clump', break it into 2-3 pieces which are then replanted. When this is done 3-4 times per year a multiplication of X10 is achieved. If, however, with more careful handling and under mist or high humidity, single-node cuttings are rooted (i.e. by cutting up a leafy shoot to yield cuttings consisting of 1 leaf, 1 axillary bud and a piece of stem as unit), the multiplication rate rises to nearly 1 million times. Such an experiment could encompass different lengths of unit cutting (i.e. different node numbers), different hormone concentrations to induce rooting, different durations of treatments, etc.

(2) Training in mineral nutrition and growth analysis could be combined in one experiment. Seedlings of any one conveniently available species (preferably one with no particular germination or dormancy-breaking problems) could be planted in sand culture, and the effects of partial or complete deficiency of one or more mineral elements could be demonstrated, e.g. full nutrition, 1/3 and 1/9 of the full dosage. A factorial arrangement of more than one element deficiency would be more instructive. In making up the necessary salt solutions, attention will have to be given to the balancing of the ions in solution, so that equal amounts of all major ions (except of course the deliberately deficient ones) are provided.

Provided enough seedlings can be grown, regular 'sampling' can be carried out to determine fresh and dry weights, leaf areas, rooting dry weights, stem lengths, etc. Secondary data can then be derived, e.g. water contents, relative growth rates, net assimilation rate, leaf area index and so on.

These two examples may suffice to indicate what may be done, and also how easy it is to do.

CONCLUSION

In an article of this nature it is impossible to give detail for all areas of interest referred to, but for some aspects such as propagation it seemed worthwhile to go into somewhat greater depth. In other areas it is only possible to draw attention to what may or may not be desirable or appropriate to investigate. Nevertheless, some guidelines are provided as to what physiological studies will be required in the establishment of a new 'crop' or preservation of a desirable species not presently cultivated when transferred to a new environment or geographic area.

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BIOLOGICALLY ACTIVE NATURAL PRODUCTS OF PLANT ORIGIN

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SUMMARY

There is a wide diversity of plant germplasm resources with multifarious biological activities, as medicines, pesticides, plant-growth promotors, attractants, repellants and antifeedants, *inter alia*. The compounds responsible for these bioactivities include most classes of chemical compounds and many of them play important functions in the plant for defence against pathogens, pests, herbivores, and other plants, and as pollinator attractants, etc. Although some of these plants are known, many of them and their future potentials have not yet been identified. Thus, all attempts must be made to conserve these valuable germplasm resources before they are completely destroyed by irrational human activities.

INTRODUCTION

Plants are composed of a diverse group of chemical compounds, some of which are involved in primary metabolism. For example, carbohydrates, proteins, fats, and nucleic acids are involved in photosynthesis, respiration, fatty acid metabolism, protein biosynthesis, etc. Other chemical constitutents in plants are the secondary metabolites which are biosynthesised by the plant and are involved in a variety of plant processes. Most of these secondary metabolites (natural products) exist in the plant for specific purposes. For example, some confer defence against pathogens, pests and other plants while others act as attractants or repellants (Harborne 1988).

The tropics are extremely rich in plant species, but this richness is being reduced at a phenomenal rate, especially since we still do not know how to combine development of plant resources with conservation (Aysenu *et al.* 1984). Rational exploitation of plant resources with biologically active compounds can contribute to meeting the commitment of UN-FAO, WHO and others to self-sufficiency in food and health for all by the year 2000 A.D.

Although 200,000 of the 300,000 or so plant species that have been identified on Earth are found in the tropics, not much work has been accomplished to date in disseminating information about their uses and in characterizing them chemically and biologically. Thus, there are abundant plant resources in the tropics which are far from being exhausted with respect to potential biologically active substances which can be useful as core structures in future drug design (National Academy of Sciences

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1975, 1978) and in pesticide and other developments, in order to optimise the desired therapeutic action or to minimise the adverse effects by structural modifications. These compounds can also throw light on the relationship between plants, animals and man from their chemical perspectives and can also be used in chemotaxonomy. Crude plant extracts can also be developed for their desired usefulness. It must, however, be remembered that 25% of the drug prescription in the USA contain one or more important plant-derived chemicals (Farnsworth & Soejarto 1985) and that pyrethrum, an insecticide, originates from the tropical plant *Chrysanthemum cinearifolium* (Harborne 1988).

Plant germplasm resources include the total array of living species, subspecies, genetically defined stocks, genetic variants and mutants whose continuing availability is important for present and future health and welfare of mankind. The Earth is composed of this array of plant germplasm together with millions of animal and microbial germplasm all interacting together to form complex ecosystems. These interactions have been going on for millions of years by mutation and selection. However, with increase in population, slash-and-burn farming practice, increased need for food, living space and sources of energy, some natural habitats are being lost by deforestation; by genetic erosion, there is the possibility of losing valuable plant species that are important to meet long-term human needs. This may include species we already know about and some we do not know about as yet. It may also include wild relatives of crops containing biologically active compounds which confer resistance against pathogens and pests (Green & Hedin 1986). Hence, genetic diversity must be conserved.

The collections of varieties of economically important organisms on Earth serve as reservoirs of genes. It is the preservation of the basic genetic material, i.e. the DNA which has the unique quality of carrying information and the capacity to make identical copies of itself, that is being sought. This rich diversity of genetic material present today that has been provided by natural mutation and evolution must be saved from catastrophe. No doubt this diversity of germplasm is an essential resource. But so far, most conservation priority has been accorded to the seven staple crops with the biggest tonnage, i.e. wheat, maize, rice, potatoes, barley, sweet potatoes and cassava. Next are vegetables and fruits, then species which are sources of industrial end-products such as fibres, waxes, gums, oils, pharmaceuticals and insecticides, beverages and stimulants, forage plants, etc.

Plants utilise radiant energy from the sun to biosynthesize a variety of chemical susbstances of varying complexity; e.g. compounds that determine the colour or the scent, which may determine the kind of pollinators, i.e. compounds that attract specific insects towards specific plants (insect pheromones). In addition, plants produce various compounds that defend them from insects, pathogens and other pests (Green & Hedin 1986; Harborne 1988). Apart from physical defences like spines and thorns, they produce chemical toxins and repellants of one type or another. Notable examples of plant insecticides are pyrethrins, rotenoids and nicotine. Other toxins produced by plants include non-protein amino acids, cyanogenic glycosides and various alkaloids. There are also oestrogenic compounds produced by some plants, while others contain biologically active carbohydrates (oligosaccharides) and proteins on the cell wall together with lignin and glycoproteins that may play some role in plant-defence mechanisms. Also, plant steroids are involved in promoting growth of certain plant species. Thus the chemical diversity of plants is undoubtedly phenomenal.

PLANTS IN MEDICINE

In Africa, for example, over 70% of the people of most countries rely on traditional medicine as their health-delivery system, and there appear to be claims of cures for almost all diseases and illnesses (Soforowa 1982). Traditional medicine in Africa and elsewhere has always relied to a large on the vast diversity of plants in tropical rainforest (Ayensu 1978; Macfoy & Sama 1983) and most bioactivity have been attributed to chemicals present in these plants, either in their roots, stem, leaves, bark, or in their resins, etc. (Watt & Breyer-Brandwijk 1962; Wagner & Wolff 1977; Soforowa 1982; Krossgaard-Larsen *et al.* 1984; Steiner 1986). There is now a lot of evidence that many of these plants contain active chemicals responsible for bioactivity and these compounds include all major classes of chemicals – alkaloids, tannins, terpenes, flavonoids, essential oils, etc. (Soforowa 1982; Oliver-Beaver 1986). In fact, quite a lot of drugs from plant origin are now in the market in Africa and even the West (25%). For example, pure compounds from higher plants include codeine, atropine, digoxin, digitonin, resperpine, ephedrine, and plant extracts include belladonna, opium, citrus biflavonoids, rauwolfia, digitalis and others (Farnsworth & Morris 1976). *Maytenus buchananii* from East Africa (Kokwaro 1966) has been shown to contain a compound called maytensine which can suppress the growth of cancer-causing organisms. *Catharanthus roseus* (periwinkle), used against blood cancer, contains alkaloids called vincristine and vinblastine which have been developed into drugs that are being used today in cancer chemotherapy, while *Zanthoxylum zanthoxloides* (Fagara) has been shown in Nigeria to contain the compounds p-aminobenzoic acid, other benzoic acids and zanthoxylol which have anti-sickling activity and are used against sickle-cell anemia (Soforowa 1982). More recently, seeds of *Cajanus cajan* (pigeon pea) have also been shown to contain anti-sickling activity. The leaves are also been shown to contain anti-sickling activity (Ekeke & Shode 1985). The leaves are also popularly used in Sierra Leone against measles (Macfoy 1983). In 1977, seventy-six different chemical compounds of known structure derived from higher plants and used very frequently were listed (Farnsworth & Bingel 1977); only six of these were produced by synthesis (Ford-Lloyd & Jackson 1986).

In realisation of this vast potential some research is being conducted in almost all African countries, some of which have research institutes specifically for medicinal plants. Work in Africa is supported by various international organizations such as the WHO, UNIDO, FAO, UNESCO, UNEP, IBPGR, IFS, CSC, OAU, and some Governments. This support cannot be timely, especially when one considers the escalating cost of drugs in these developing countries, even though there exists a vast resource of valuable plant species, and the phenomenal rate of deforestation in the tropics.

Thus, several of these plants have been investigated by scientists for their claimed bioactivity. Both phytochemical and pharmacological studies have been conducted and the literature is replete with various examples. A few may be mentioned.

Teclea triocarpa (Rutaceae), which is used in both East and West Africa against wounds and sores, has been shown to contain three 9-acridone alkaloids in its stem bark, called melicopine, tecleanthine and 6-methoxytecleanthine (Lwande *et al.* 1983). All three compounds possessed antifungal activity against the fungus *Cladosporium cucumerinum*; antibacterial activity against the bacterium *Bacillus subtilis*, and antifeedent activity against the armyworm *Spodoptera exempta*.

Tephrosia spp. (Papilionoideae) are notably used as fish poisons, arrow poisons and insecticides. They are also used in folk medicine against various diseases and illnesses (Dalziel 1937; Lwande *et al.* 1987). The dried roots of *Tephrosia hildebrantii* yielded a new 6a-hydroxypterocarban called hildecarpin (Lwande *et al.* 1987) similar to many legume phytoalexins such as pisatin from peas, medicarpin from alfalfa and clover, phaseollin from french beans and glyceollin from soyabeans (Harborne 1988). Hildecarpin showed antifungal activity against *Cladosporium*, antifeedant activity against the cowpea insect pest, *Maruca testulalis*, and no antibacterial activity against five bacterial species (Lwande *et al.* 1987). Another new 6a-hydroxypterocarpan called hildecarpinin has since been isolated from the same plant.

Also, plants in the *Aspilia* genus are generally used against wounds and skin diseases in both East and West Africa. Lwande *et al.* (1985) isolated three kaurenoic acids from *Aspilia pluriseta* which were active against gram negative and gram postive bacteria.

Ageratum conyzoides (Compositae) is popularly used in West Africa to heal wounds and burns. Aqueous and methanol extracts of the leaves of this plant has been shown to contain antibacterial activity. In Nigeria, the aqueous extract has recently been shown to possess haemostatic activity, i.e. arrests bleeding (Akah 1988). *Azadirachta indica* (Meliaceae), called the Indian neem tree, is abundant in India and Africa and has worldwide interest. It has a variety of traditional uses including antimalaria (oral decoction), as chewing stick, etc. The compound azadirachtin (limonoid structure) from this plant and its close relative *Melia azadarach* shows insect antifeedant bioactivity against the desert locust (*Shistocerca gregaria*) and a variety of insects (Harborne 1988). This plant has also shown antiplasmodium, antibacterial, insecticidal, antiviral and other activities (Oliver-Beaver 1986).

The African plant *Phytolacca dodecandra* contain saponins which kill the snails that transmit the worms causing the important tropical disease schistosomiasis (or bilharzia) in many countries in Africa (Harborne 1988).

CONSERVATION

In Africa, medicinal plants are mostly cultivated in the same way as in the ancient past; thus with a few exceptions they have not yet been domesticated. In other words, it is the wild population of these plants that still make up the major genetic resource. The genetic resources of medicinal plants are usually found in forests, natural reserves, uncultivated lands and backyards, where they are vulnerable to varying degrees, resulting in genetic erosion.

As far as conservation goes, not much is known about their phytogeographical distribution patterns, modes of reproduction, breeding systems, storage potential of the propagules, etc., thus making effective conservation difficult. Nevertheless, some medicinal plants which are already highly commercially exploited are treated in some straightforward manner, e.g. *Papaver somniferum* (opium poppy) which yields morphine and codeine pain killers. Thousands of acres of this crop are grown for these products and several accessions have been collected and stored in genebanks in Turkey and India. In addition, some have already been characterised and evaluated for dwarfing genes and susceptibility to fungal diseases such as powdery and downy mildews, as well as for latex, morphine and codeine yields (Ford-Lloyd & Jackson 1986). Work in this area should, however, be improved, and seeds and vegetative parts such as corms, bulbs, rhizomes, tuber and roots should be collected and stored where possible.

Apart from the above *in situ* and *ex situ* methods of storage, some of these useful plants can also be stored as tissue cultures, while others can be maintained in an agroforestry system where they can provide a sustainable use. Furthermore, many more natural reserves should be set aside now, before the genetic diversity is further reduced by unwise land and water use; in other words, maintaining natural ecosystems like botanical gardens and arboreta and taking an inventory of all useful plant species. These can also serve in the study of these ecosystems and ensure the future supply of currently used drug plants and potential sources of biologically useful plant species. These latter conservation methods are usually more valuable, because many tropical seeds are usually too large and moist to survive in most present-day seed banks.

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POPULATION MAINTENANCE AND MONITORING

THE SIGNIFICANCE OF COMPETITION IN THE MAINTENANCE AND EVALUATION OF PLANT ACCESSIONS

R.W. SNAYDON

INTRODUCTION

Competition occurs when plants share a common resource (e.g water, mineral nutrients or light) which is in limiting supply. The severity of competition increases as the number of plants sharing the limiting resource increases. Competition between plants causes a reduction in the growth, reproductive capacity and/or survival of plants, compared with their performance in the absence of competition, i.e. when plants are grown widely spaced.

Plants very rarely occur in the complete absence of competition, i.e. as isolated individuals, either in the wild or in agricultural systems. On the contrary, plants normally occur in dense stands of complex mixtures of species in the wild, while in agriculture they occur either in dense monospecific stands (e.g. most arable crops in developed countries), or in dense stands of species mixtures (e.g. crops with weeds, mixed pastures, and mixed cropping). In all of these conditions, one or more environmental resources (mineral nutrients, water or light) are usually present in limiting supply. As a result, intense competition normally occurs between plants of a single species, and often between plants of different species. Because competition is so ubiquitous, and has such a large effect on plant performance, no consideration of the ecology or ecological genetics of plant species is complete without some consideration of plant competition. Plant competition is particularly important in the context of genetic conservation, and especially in maintaining and evaluating plant collections.

COMPETITION AND MAINTENANCE

One of the most important objective in maintaining plant accessions, whether *in situ* or *ex situ*, is to ensure that their genetic structure remains as constant as possible. Since competition has such large affects on the size of plants (see below), and so on their survival and reproductive capacity, it can have large effects on the genetic composition of populations. As a result, competition is an important factor to consider in the maintenance of accessions.

Competition and maintenance *ex situ*

Most accessions are maintained *ex situ* as seed. In this state, they can be kept for

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long periods, but not indefinitely (Ellis *et al.* 1985), so that occasionally they must be grown from seed, and resultant seed harvested; it is during this phase that competition is likely to have important effects on the genetic composition of accessions.

Competition, plant size and reproduction

Competition for limiting resources reduces the size of individuals. For example, when wheat plants are grown at usual crop densities, the average plant size is about 5% of that achieved when they are grown in the absence of competition, i.e. grown at wide spacing (e.g. Donald 1963). This would not create a problem if all plants responded similarly, but the differences between initially large and small individuals usually increases greatly under competition (e.g. Black 1958); in addition, the small plants usually produce fewer seeds, relative to their size, than large plants (e.g. Hawthorne & Cavers 1982). As a result, the less-competitive individuals in the population produce fewer seeds, and so form a smaller proportion of the next generation.

Competition and plant survival

There is increasing evidence (e.g. Hawthorne & Cavers 1976) that, in many cases, competition for limiting resources is a more important cause of plant death than extreme climatic conditions. Under intense competition, small plants are more likely to die than large plants (Schmitt *et al.* 1987). If the differences in plant size are genetically determined, this difference in mortality will mean that the less-competitive individuals will die without leaving offspring, so changing the genetic composition of the population.

Competition and genetic shift

When populations consisting of mixtures of genotypes are grown in dense stands, large changes in genetic composition occur, because of the effects of competition on plant survival and reproduction. These changes can occur within a single generation (e.g. Charles 1970), probably as a result of differences in mortality (Bazzaz *et al.* 1982). Even larger changes in the genetic composition of such populations occur when they are grown for several generations (e.g. Blijenburg & Sneep 1975; Snaydon 1978), probably as a result of differences in both mortality and seed production. It is, therefore, extremely dangerous to multiply and maintain genetically heterogeneous populations under competitive conditions, if the intention is to keep the genetic composition of accessions constant.

Genetic shift can occur even in the absence of competition, i.e. at wide spacing, because genotypes differ in seed production under those conditions (e.g. Laude *et al.* 1958). As a result, the only safe way to maintain and multiply accessions is to grow them as spaced plants, to harvest equal quantities of seed from each plant, and to mix these equal quantities to provide a composite seed sample.

Competition and maintenance *in situ*

In the absence of competition, plant species and populations can be grown over a much wider range of environmental conditions than when competition occurs. This is clearly apparent from the fact that agricultural and horticultural plants can be grown successfully in habitats widely different from those in which they naturally occur, as long as they are protected from competition from other species. Ellenberg (1958) recognised this phenomenon and coined the terms 'physiological tolerance range' and 'ecological tolerance range' to describe the different conditions. Because the physiological tolerance range, i.e. the range in the absence of competition, is normally much broader than the ecological tolerance range, i.e. the range in the presence of competition, many plant accessions are maintained in the absence of competition, i.e. *ex situ*. This may be essential in some cases, where the natural habitat has been destroyed, is threatened, or is changing, but is often convenient in other cases since, for example, plant material may be multiplied more rapidly and can be evaluated under those conditions. However, there is a limit to the number of accessions that can be maintained in this way; most species and populations must be maintained *in situ* or not at all. It is, therefore important to recognise the importance of competition in determining the composition and, indeed, the very survival of species and populations, in their native habitats.

Genetic shift

There is considerable evidence that plant populations change rapidly in both time (e.g. Snaydon & Davies 1982) and space (Liu & Godt 1983); obviously populations are genetically very plastic, when growing in their native habitats. This rapid genetic change in populations is due to the action of natural selection. Although we know very little about the mechanisms of natural selection, it seems likely that competition is an important component of the selection process, as was recognised by Darwin.

If the natural habitat of a population changes appreciably, either the genetic composition of the population must change adaptively or the population will become extinct. Surprisingly small changes in the habitat can bring about genetic change or extinction, as is seen by the wide diversity of ecotypic differentiation in plant species, and by the subtle changes in the species composition of plant communities. If species and populations are to be conserved unchanged *in situ*, therefore, conditions in the habitat must be maintained in the same state as before. This has proved to be especially difficult where it involves active management, i.e. where a previous management regime is to be maintained (e.g. Wells 1973), or where a natural regime is to be simulated. This is hardly surprising, because the requirements of populations and species are so specific, our knowledge of the limiting factors affecting individual species and populations is so inadequate, and our knowledge of competition between individuals, both within and between species, is even more rudimentary. In such situations, we cannot hope to control competition *per se*, though we may be able to influence the outcome of competition by manipulating environmental conditions. Conservation *in situ* is likely to be most successful where no human interference is required, although the changes that occur in natural habitats (e.g. succession or climatic change) can also lead to population extinction (Soulé 1983).

COMPETITION AND EVALUATION

The ultimate objective of conserving crop populations, such as landraces or wild progenitors, is to provide material for breeding programmes. If the accessions are to be used successfully, they must be evaluated. Therefore, we need to consider methods of evaluation, and how competition may affect evaluation.

Accessions may be used in widely different ways in breeding programs. At one extreme, they may be screened and the most satisfactory accessions released as cultivars; at the other extreme an accession may be used only as the donor of a single gene, using various techniques to transfer the gene to an otherwise suitable existing cultivar. Between these two extremes lies a spectrum of degrees of genetic transfer by crossing and selection. The method of evaluation will depend, to a large extent, upon the use to which accessions are put, because selection for the presence of a single gene will obviously involve different evaluation methods than selection of a potential cultivar. In this paper, I shall concentrate more on the selection of potential cultivars, because this is where the effects of competition are most apparent.

Types of competition

Agricultural plant communities are almost always grown in dense stands, i.e. under conditions of intense competition, because these are the conditions that give the highest yields per unit area (Willey & Heath 1969). However, agricultural species are grown in a wide diversity of stand conditions, ranging from complex and largely uncontrolled species mixtures (e.g semi-natural grassland), through simple and controlled species mixtures (e.g. mixed-cropping and sown grassland) and single species but multi-genotype stands (e.g. landraces of most crops, cultivars of outbreeding crops like rye, and cultivars of most pasture species), to single genotype stands (e.g. cultivars of inbreeding crops and pasture species, and F_1 hybrids of inbred lines of outcrossing species like maize). These conditions determine the nature of the competition experienced by individuals; for example, in species mixtures, competition will be largely inter-specific, while in single species multi-genotype stands it will be largely inter-genotypic, and in single genotype stands it will be intra-genotypic.

The nature of competition has important implications in evaluation. As a general rule, accessions should be evaluated in the same competitive conditions as those in which they will ultimately be used, i.e. as mixed species, mixed genotype or single genotype, and at the same density that they will experience. This has rarely been done in the past. For example, it has been conventional to evaluate accessions of outbreeding pasture species either as spaced-plants or in wide-spaced rows, in spite of the fact that they will ultimately be grown in dense species mixtures, while genotypes of inbreeding crop species have usually been evaluated in multi-genotypes stands, although they will ultimately be used in single genotype stands (Donald

1981). We need, therefore, to consider each of the various types of crops separately.

Single genotype stands

A wide range of crop species, such as inbreeding species, vegetatively reproduced species, and F_1 hybrids of inbred lines, are normally grown in single species and single genotype stands. Few pasture species are grown in such stands because: (i) they are normally outbreeding and populations are genetically heterogeneous, and (ii) they are normally grown in mixed species stands.

Accessions of species which will ultimately be grown in single genotype stands are often genetically heterogeneous (e.g. landraces, natural populations or the result of artifical crossing). These genetically heterogeneous populations are usually evaluated as a whole, either in dense stands or in wide-spaced rows. The accessions are then usually selected on the basis of populations means, although this gives little indication of the potential value of the best individual genotypes within the populations. The alternative approach, often used by plant breeders, is to select the best individuals within the mixed population. However, this is dangerous, because there is an unpredictable relation between performance in mixtures and performance in monocultures (Donald 1981); there is sometimes little correlation (e.g. Bell 1963), sometimes a positive correlation (e.g. Spitters 1974), and sometimes a negative correlation (e.g. Hamblin & Donald 1974). This lack of a consistent relation occurs because competitive ability is not necessarily correlated with yield (Donald 1981). Some breeders have attempted to circumvent this problem by growing isolated plants, i.e. by eliminating competition altogether. This is no solution, because the performance of plants in the absence of competition is poorly correlated with that in dense stands (e.g. Knight 1960; Syme 1972).

Ideally, each genotype should be tested in a single genotype stands at the optimum density, although it is clearly a counsel of perfection because: (i) there is not enough seed of each genotype, (ii) it would require vast numbers of plots, and (iii) the optimum density for each genotype is not known. Numerous studies have shown that cultivars differ in their response to plant density (e.g. Carlone & Russell 1987), i.e. cultivars differ in their response to the severity of competition, so the density used during evaluation is likely to affect the ranking of genotypes. Since we cannot hope to test each genotype at a range of densities, the best way that is likely to be achieved is to assess each genotype at a single realistic density, usually that used in local practice, if that is known. Even this is usually too great a task, in view of the large number of accessions, each consisting of many genotypes. As a result, most evaluations will continue to be of the yield of the mixed genotype stand at a realistic density; we must recognise, however, that this may give us little indication of the genetic potential hidden within each accession.

Mixed genotype stands

This type of stand is probably the easiest to evaluate, although it rarely occurs, at least in intensive agriculture; however, it is quite common in subsistence agriculture, where genetically heterogeneous landraces are still widely used. It is also fairly common in pastures where single species stands of genetically heterogenous populations are often sown; however, these stands are usually invaded by other species (see below). Where mixed genotype, single species stands are used, the whole populations must be compared, rather than individual genotypes. This greatly simplifies evaluation, because we do not need to consider competition between genotypes, which bedevils the evaluation of genotypes that will ultimately be used in pure stands (see above). In the case of pasture species it is not even necessary to find the optimum density, because the stand reaches its own equilibrum density.

Although it is relatively easy to evaluate species in the same mixed genotype stands in which they will later be grown, it is surprising how often they have been tested under other conditions. For example, it has been conventional to test pasture species in spaced-plant conditions, in spite of the generally poor correlations between performances in swards and performance in spaced-plant conditions for genotypes and cultivars of pasture species (e.g. Knight 1960; Copeman & Swift 1966). However, the practice seems to be declining, as the lack of correlation is recognised.

Mixed species stands

This type of stand is more common than is generally recognised. Most pasture species occur in mixed species stands, being either sown in that form or being invaded by other species (Morrison 1979). Similarly, many crop species are invaded by weeds, while most of the crops grown in subsistence agriculture are grown in mixed species stands (Francis 1986). It is, therefore, important to evaluate accessions of these species in mixed species stands, though it is surprising how often they are evaluated in single species stands. For example, pasture species and species normally grown under mixed-cropping are usually evaluated and selected in single species stands, in spite of the fact that there is usually a poor correlation between yield in single species stands and yield in mixed species stands, because yield is poorly correlated with competitive ability (Donald 1981).

The nature of correlation between yield in single species stands and yield in mixed species stands will depend on the type of mixture and how yield is measured. For example, in cases where the total yield of the stand is important, e.g. the mixtures of legumes with non-legumes that are commonly used in both pastures and mixed-cropping, there may sometimes be a modest correlation between pure stand and mixture yields, so that differences in pure-stands are less than those in mixtures (e.g. Stewart *et al.* 1966), or they may be no correlation so that differences disappear entirely in mixtures (Cowling & Lockyer 1965), or there may even be a negative correlation, so that the differences are reversed in mixtures (e.g. van Keuren 1961). It is, therefore, important, where accessions will ultimately be used in mixtures and the total yield of the mixture is important, to evaluate accessions on the basis of the total yield of the relevant mixtures, rather than on the basis of single species stands.

If only one component of a mixture is agriculturally useful (e.g. a crop with weeds), it is important to evaluate accessions of that component on the basis of their individual performance in mixtures. It is probably not necessary to evaluate the accessions in competition with particular weed species, because competitive ability seems to be general rather than specific (e.g. Williams 1962; Welbank 1963), i.e. if one accession has a higher competitive ability than another, when both are grown with a particular weed, it will also have a higher competitive ability when grown with another weed. This makes the evaluation of accessions for competitive ability against weeds more convenient and simple, because they need only be grown with one weed. There is even evidence (e.g. Kawano *et al.* 1974) that accessions with a high competitive ability against other accessions of the same species also have a high competitive ability against weeds, indicating that intra-specific and inter-specific competitive abilities are closely correlated.

In evaluating and selecting accessions, it is important to recognise that attributes other than yield may be important. For example, persistence is important in pasture species, which are only occasionally resown. Quality is a very important attribute, both in pasture species, where quality affects animal production (Snaydon 1987), and in crop species, where quality affects both the nutritional and financial value of the crop. Other attributes, such as resistance to pests and pathogens, must also be considered and are sometimes the most important attributes sought among accessions.

EVALUATION AND ENVIRONMENT

So far, evaluation has been considered mainly in the context of competitive conditions, but the relative performance of accessions is also affected by other biotic conditions (e.g. pests and pathogens) and by abiotic conditions (e.g. soils and climate); this is usually termed genotype x environment interaction (GxE). Plant breeders have long recognised the importance of GxE (Hill 1975). The various factors that affect relative performance cannot be considered in isolation, because they interact with one another. In particular, competitive conditions interact with physical conditions, so that competition between populations affects their relative response to environmental conditions (e.g. Snaydon 1962). As we have already seen, species and populations usually have a wider range of tolerance in the absence of competition, i.e. their ecological tolerance range is narrower than their physiological tolerance range.

The most common way to evaluate accessions (G) comprehensively is to test them at a number of different environments (E), i.e. several sites in several years. Numerous such evaluations have shown that, in general, GxE interactions are large, compared with overall differences between accessions (Table 1), indicating that a given accession is rarely best in all environments. The other important conclusion to be drawn is that interactions involving predictable components of the environment, i.e. genotype x site, are less important than those involving unpredictable components, i.e. genotype x year and especially genotype x year x site (Table 1). As a result, it is clear that accessions should be tested over several years, and that selection should normally be for general-purpose accessions, i.e. ones that will perform well should be tested over several years, and that selection should normally be for general-purpose accessions in a range of environments. It is also clear that is more important

TABLE 1. Estimated components of variance (%) for various crops grown in the UK (Talbot 1984).

Component of variation	Winter wheat	Spring barley	Perennial ryegrass	Potatoes	Spring beans
Cultivars	7.2	2.3	4.5	6.1	2.5
Cultivars x sites	0.5	1.4	0.4	1.8	0.3
Cultivars x years	1.6	3.0	3.0	1.6	1.1
Cultivars x sites x years	8.2	6.7	11.2	9.3	3.5
(Number of sites x year combinations)	174	214	54	178	38

to evaluate accessions roughly in a range of environments (years and sites), rather than accurately evaluate them, by heavy replication, in a single environment.

It is clear that GxE interactions occur very widely, and their effects are large, relative to the genotype (or accession) effect. What is less clear is the extent to which competition (GxG) affects GxE interactions, i.e. the extent of GxGxE interactions, although there is certainly evidence that competition affects the relative responses of species and populations to environmental conditions (e.g. Austin & Austin 1980). There is also evidence that differences between accessions in response to density, i.e. the severity of competition, are affected by environmental conditions (e.g. Carlone & Russell 1987). Evidently, therefore, the conditions under which studies of competition are carried out are likely to affect the response of accessions to both interspecific and intraspecific competition.

CONCLUSIONS

Competition greatly affects the relative performance of accessions. This is true of competition between genetically identical individuals, between different genotypes, and between species. As a result, assessments made under one set of competitive conditions, e.g. mixed genotype stands cannot be extrapolated to another set of conditions, e.g. single genotype stands, or even to another density. Accessions should therefore be tested under competitive conditions as close as possible to those under which they will ultimately be used.

In addition, the relative performance of accessions is greatly affected by the environmental conditions (soil and climate) in which the test takes place, and competition interacts with the effects of these environmental factors. Accessions should, therefore, be tested in a wide range of environmental conditions (sites and years).

There is no possibility that the multitude of accessions currently being accumulated could be assessed in all the possible environments and competitive conditions in which they might possibly be used. The most that might be achieved would be to test some of the accessions in some conditions; the skill comes in deciding which accessions to test, and which environments to use, given our very limited knowledge of the accessions, and of the likely magnitude of the various interactions. In view of the large effects of competitive interactions, which can often reverse the ranking of accessions, it is certainly necessary to evaluate accessions in the competitive conditions in which they will ultimately be used, i.e. in single genotype stands, mixed genotype or mixed species stands, and at realistic densities.

It is also necessary to identify the relevant selection criteria clearly. For example, if it is a crop accession growing with weeds, it is the yield of the accession itself? If it is an accession to be used in mixed-cropping or pastures, it is yield of the whole stand that is important? The importance of other criteria, such as quality in both crops and pasture species, or persistence in pasture species, should not be underestimated.

In the past, much evaluation in plant breeding and in plant introduction has been carried out in artificial conditions of competition. For example, accessions have often been evaluated in spaced-plant trials or wide-spaced rows, instead of at dense spacing. Similarly, plants that would ultimately be grown in single genotype stands have been evaluated in mixed genotype stands, while those that would be used in mixed species stands have commonly been evaluated in single species stands. To some extent these errors continue, but, as the nature of the problem is recognised, more valid methods of assessment will be used.

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MANAGEMENT OF PLANT POPULATIONS AND PROBLEMS OF EROSION IN GENETIC DIVERSITY

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INTRODUCTION

The maintenance of genetic diversity in managed populations has become a major issue in conservation biology since Frankel (1970) postulated that genetic diversity is essential for the long-term survival of managed species. Foremost, genetic variation is important for the immediate fitness of many plant species which maintain fitness as heterozygotes; reduction of genetic variation results in a corresponding loss of heterozygosity and fitness. Furthermore, genetic variation is essential for any subsequent adaptive change. Altered environments or new pests or diseases pose challenges to species. Without adequate genetic variation a species cannot adapt to these new aspects of the habitat. For conservation practices to be ultimately successful, the genetic variation of a species must be preserved. Even if the number of individuals in a managed population is high, the population may eventually become extinct if the management plan has not carefully provided for the maintenance of genetic diversity. In addition, the maintenance of genetic diversity is essential for preserving genetic resources for future applied uses. Recombinant DNA technologies now allow the transfer and expression of genes from one plant species into another. Such transgenic plants hold promise for producing new crop varieties with enhanced yield, physiological tolerance or disease resistance, and for the production of important compounds with pesticide or medicinal value. It becomes important, therefore, to conserve the genetic diversity of a large number of plant species, so that the genetic resource base for future biotechnology remains as broad as possible. Conservation of genetic resources thus is essential for two reasons: it promotes the long-term survival of the species under management by maintaining both its fitness and natural evolutionary potential, and it provides genetic variation for genes which can be used in future genetic engineering of plants with beneficial traits.

Unfortunately, the conditions under which populations are placed during management are often those very conditions which lead to erosion of genetic diversity. Species which are confined to preserves are often limited both in the number of individuals within a population and in the total number of populations preserved. Even when the number of individuals is not small, there may be a very small number of genotypes maintained, due either to asexual reproduction or sampling from a limited seed source. Both low population size and few total populations result in erosion of genetic diversity, although by slightly different mechanisms. Below we will consider each factor in turn, show how genetic diversity

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can be lost, discuss how the genetic structure of a plant species can affect this loss, and finally make recommendations for managed plant populations.

POPULATION SIZE

Problems in erosion of genetic diversity in managed populations often result from small population sizes. Managed populations are frequently reduced in size over previously unmanaged ones as a result of only a few captured individuals, such as in a zoo or botanical garden, or because of a habitat so restricted in area that relatively few individuals are included in a preserve. This reduction in numbers over previous levels often leads to a loss of genetic diversity within the population. Such processes as inbreeding, genetic drift and fixation or loss of alleles can all occur when population sizes are dramatically reduced. If population sizes become very small, inbreeding, the mating of relatives, becomes unavoidable. A consequence of inbreeding is to increases the homozygosity of individuals within populations. Thus a species which may have previously contained individuals with high levels of heterozygosity might, after restriction in population size and the resulting inbreeding, comprise individuals which are now predominantly homozygous. Such increased homozgosity may be accompanied by inbreeding depression. Inbreeding depression is the result of deleterious, recessive alleles being expresed as homozygotes, where prior to inbreeding, deleterious alleles were maintained in the heterozygous state and not expressed. The loss of viability in restricted animal populations, such as observed in zoos or in some breeds of dogs, is a result of inbreeding depression (e.g. Templeton & Read 1983). So, restricted population size may have an immediate effect on the fitness of individuals in managed populations. Accompanying inbreeding will be increased effects of genetic drift due to small population size. As the number of individuals within a population decreases, the effects of chance changes in gene frequency become increasingly more important. In very small populations gene frequencies can be altered by such genetic drift. In very restricted populations alleles become fixed; that is, alternative alleles at loci are lost due to drift. Genetic drift within small populations leads to an erosion of genetic diversity by reducing the number of alleles.

We can ask: What is a desirable population size based on theoretical grounds? Franklin (1970) considered a 1% increase in the inbreeding coefficient, F, per generation as a tolerance level of inbreeding. Substitution in the formula which relates the change in inbreeding coefficient to population size, $F=0.5N_e$, yields a population size of 50. However, Franklin points out that this does not consider additive genetic variance and that a population size of 500 is a more realistic minimum. It is encouraging that population sizes of 500 are obtainable in many preserves. Even in highly dispersed species, such as a hyperdispersed tree of one plant per km^2, a reserve of 20 km x 25 km would contain 500 individuals.

A population size of 500 plants, for many species, may actually contain several breeding units (groups of individuals which have a fairly high probability of crossing with each other). Because of limited gene dispersal in plants (Levin & Kerster 1974), many plant populations are genetically subdivided into neighbourhoods, a neighbourhood being the number of individuals which form a randomly mating unit. Neighbourhoods may be genetically differentiated from each other by both allele frequency and allele composition. Estimates of neighbourhood size in plants are in the general range of 50-300 plants (Crawford 1984). Neighbourhood size in plants depends on a number of species characteristics, such as the level of gene flow and breeding system. Small neighbourhoods are a result of limited gene migration and autogamy; very large neighbourhoods are observed in outcrossed species with widespread gene flow, such as in some trees. In species with small neighbourhood sizes, those with restricted gene flow and self-compatible breeding systems, a preserve which contained 500 plants would usually be adequate to avoid increased inbreeding; such population numbers would maintain the genetic structure characteristic of natural populations of the species. On the other hand, a population size of 500 may be barely adequate for some species which are dioecious and have wind dispersed pollen. Here gene flow may be very great. A population size of 500 individuals might not reveal the genetic structure of natural populations.

Finally, it should be pointed out that we are considering here N_e, the effective population size. The effective population size can be quite different from the number of individuals. Populations of asexually reproducing species may contain very few genotypes, yet be extensive in number. Likewise, artifical populations from a limited seed source (only a few plants) would have a low effective population size.

NUMBER OF POPULATIONS

The next critical issue for management of plant species is to determine the number of populations necessary to maintain adequate genetic diversity. Genetic diversity is a function of both allele frequencies and number. A frequently used measure diversity is that of Nei (1973). For a given polymorphic locus, the total allelic diversity is determined by $H_T = 1 - p_i^2$ where H_T is the allelic diversity, p_i is the mean frequency of the i th allele at a given locus. The total diversity can be apportioned into the diversity within populations, H_S, and the diversity among populations, D_{ST}, with the following relationship

$$H_T = H_S + D_{ST}$$

The proportion of diversity due to among population differences, G_{ST}, is given by

$$G_{ST} = D_{ST}/H_T$$

Such measures of diversity are critical for assessing the number of populations which must be prepared in order to maintain a good representation of the genetic diversity of the species. G_{ST} specifically determines how much of the diversity occurs among populations; that is, how genetically different are populations from each other. When G_{ST} values are low, there is little genetic differentiation among populations and only a few populations provide a large fraction of the total genetic diversity of the species. On the other hand, if G_T values are high, there are substantial genetic differences among populations and a few populations will not provide an adequate representation of the total species diversity.

Data on the apportionment of genetic diversity within and among populations have been collected for many plant species. These studies are based on allozyme data and have been conducted for hundreds of plant species, so that generalisations about genetic diversity are beginning to emerge. In general, these studies have found that most diversity resides within populations. However, G_{ST} values range widely, from 0.91 for the cocklebur, *Xanthium strumarium* to 0.001 for eel grass, *Zostera marina*. These represent the extremes of G_{ST} values; values of 0.1 to 0.3 are by far the most typical for plants (Hamrick 1983). These values mean that characteristically 10 - 30% of the total genetic diversity found in a plant species is due to differences among populations. Conversely, 70 - 90% of the diversity is usually found within plant populations. These values can be used, then, as a working assumption about other species which have not been studied electrophoretically. But one should use caution because the *Xanthium* and the *Zostera* examples clearly show that a small number of species occur outside the typical range.

In order to make an informed estimate of genetic differences among populations, and to have an idea of how many populations to preserve, one can examine life history features. Life history characters clearly influence genetic differentiation among populations. Hamrick and his coworkers have compiled data for a very large number of plant species and examined the factors which influence genetic diversity among populations. Using the available allozyme literature, they correlated plant life history features with genetic characteristics, such as G_{ST}, number of alleles per locus, population substructure, and heterozygosity of the plant species (Hamrick 1983; Loveless & Hamrick 1984). Table 1 lists a portion of their data and relates species characteristics to genetic traits. It is evident that numerous features affect genetic diversity and the proportion of total diversity which is due to differentiation among populations. Such factors include geographic range of the species, mode of reproduction, mating system, seed dispersal and succession stage. These factors are examined in greater detail in the extensive tables of Loveless & Hamrick (1984).

Thus, to determine the number of populations to be conserved one needs to look at the life history characteristics, breeding system, and other species characters. Only three or four populations of an outcrossed wind-dispersed species are needed to maintain 99% of species diversity, where average G_{ST} is 0.056. For selfed species, with average G_{ST} of 0.437, about eight populations are needed. Table 1 also indicates the proportion of total alleles found within single populations; to preserve 99% of alleles, four selfed and six outcrossed populations are needed. In general, to conserve a given number of alleles requires slightly greater population numbers (see Table 1). It is recommended to use number of alleles for determining number of populations. This is a more conservative estimate of number of populations required and, in addition, it is a goal of conservation to preserve the different kinds of alleles. Conservation of alleles is particularly important, because often it is the rare alleles which are of most interest in plant breeding. Table 1 presents data which are average for a particular type of plant. The range of values within a class is not apparent; if one

TABLE 1. Life-history traits and genetic diversity in plant populations (Hamrick 1983).

Characteristic	H_T	H_S	G_{ST}	A_P	P_A
Geographical range					
Endemic	0.275	0.208	0.200	3.26	0.639
Narrow	0.261	0.177	0.275	2.96	0.609
Regional	0.238	0.154	0.312	3.23	0.573
Widespread	0.380	0.293	0.253	3.70	0.702
Modes of reproduction					
Asexual	0.172	0.159	0.080	3.29	0.652
Sexual	0.280	0.194	0.284	3.17	0.620
Both	0.325	0.257	0.209	3.30	0.732
Mating system					
Selfed	0.250	0.141	0.437	3.02	0.559
Mixed– animal	0.284	0.181	0.304	2.68	0.644
Mixed – wind	0.712	0.560	0.189	16.03	0.425
Outcrossed – animal	0.352	0.238	0.221	3.37	0.633
Outcrossed – wind	0.256	0.248	0.056	3.29	0.737
Seed dispersal mechanism					
Large	0.260	0.181	0.350	3.07	0.635
Animal-attached	0.262	0.155	0.425	3.77	0.504
Small	0.312	0.196	0.349	2.81	0.846
Winged or plumose	0.260	0.238	0.073	3.28	0.706
Animal-ingested	0.344	0.210	0.330	3.63	0.526
Stage of succession					
Weedy or early	0.295	0.172	0.394	3.37	0.574
Middle	0.262	0.196	0.236	3.15	0.613
Late	0.299	0.275	0.071	3.14	0.786

H_T = total allele diversity; H_S = mean allelic diversity within populations; G_{ST} = proportion of total diversity due to differences among populations; A_P = mean number of alleles at polymorphic loci; P_A = proportion of the total number of alleles found within a single population.

examines the individual species used to determine averages in Table 1, there is a great deal of heterogeneity. As an example of this, our own work on endemic species with populations restricted to isolated glade communities shows very different levels of variation for same DNA sequences (ribosomal DNA). Two species, *Clematis fremontii* and *Rudbeckia missouriensis* are both obligately outcrossed, perennial, insect pollinated and restricted to the same sites. *Clematis* is highly variable with subdivided populations (Learn & Schaal 1987), while *Rudbeckia* shows little variation with minor differentiation among populations (King & Schaal, unpublished data). These results indicate that generalisations about the genetic structure of plant species based on life history, breeding systems or other characters may not be appropriate in some individual cases. The only way of accurately measuring genetic diversity is to conduct an allozyme analysis of diversity where G_{ST} and the number of alleles are determined directly for a given plant species. Such studies are, of course, not feasible for all of the plant species that a manager may wish to preserve. We are again left with the generalisations about diversity related to species characteristics as the most reasonable basis for making informed decisions on the management of diversity. If one applies the information from Table 1 in a conservative way, by adding a few more populations, most species will have a very good representation of diversity. The addition of more populations would be particularly important when the emphasis on conservation is preservation of alleles for future plant breeding. Additional populations increase the probability of including rare alleles.

A possible way of increasing genetic diversity of managed populations is to add migrants from other populations. Such an approach is appropriate for some animal species, but is in general ill-advised for plant species (James 1982; Clegg & Brown 1983; Hamrick 1983). Because of the diverse genetic structure of plant species and the vast differences between the genetic organisation of different populations of the same species, the addition of migrants may be harmful by disrupting genetic mechanisms which maintain heterozygosity and adaptive gene complexes. A management approach which uses migrants should be done only after very careful genetic analysis of population structure and breeding system. By far the best approach for conserving genetic diversity of plant species is to preserve established, natural populations. Establishing populations from seed is less desirable, due to the necessity of sampling and due to the difficulty of adaptation to a new locale. However, with very rare species, artificial populations are the only alternative to extinction.

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BIOLOGICAL CROPPING SYSTEMS AND GENETIC CONSERVATION

B.R. TRENBATH

INTRODUCTION

For the purposes of this paper, 'cropping' means the exploitation of populations of any plant or animal species by humans. Exploitation usually involves removing some biomass, with or without killing the individual organism(s) that produced it. The level of impact on the ecosystem affected varies greatly. The biotic diversity within forests inhabited by low densities of hunter-gatherers (e.g. parts of Amazonia) is hardly influenced by man's presence, whereas that of land planted with intensively managed cereals may be much reduced.

Within any system of biological exploitation, there are usually one or more cropped 'target' species, some unwanted competitor 'weed' species, and then other 'non-weed' species whose presence does not interfere with the cropping operation. In an agricultural cropping system, the target is often a single plant species of which just the fruits are removed; in a grazing system, the targets are one or a group of preferred plant species together with (usually) one species of herbivore, whose products are removed. In forest exploitation or deep-sea fishery, the targets may be numerous: a series of species all of varying commercial value, and then other species considered 'trash'. The commercial species are harvested while the trash species are left more or less damaged by the harvesting procedure, in a sometimes profoundly altered environment.

As the biological resource is managed more intensively, more and more of the energy flow through the ecosystem is intentionally concentrated into the target organisms. To achieve this, usually any remaining wild habitat is utilised, weed and other associated species are suppressed, and parastic and predatory organisms are controlled using agrochemicals. Such interventions may lead directly to the elimination of many species. However, by disrupting the original pattern of biological interactions (e.g. the food chains, pollination and seed-dispersal mechanisms), man's activity leads also indirectly to the disappearance of further species populations. In such impoverished ecosystems, the biological diversity is low. The species which persist tend to be only those specialized parasites, predators and weeds which can tolerate the (sometimes extreme) physical and chemical measures used in managing the system. Within any cropping system, there are, nevertheless, opportunities for conservation of germplasm. In the harvested parts of the habitat, richer communities of plants and animals may be achieved in various ways. The four main ways are:

(i) genetic diversification of target species (e.g. reintroduction of old local cultivars

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and stock breeds, where they still exist; integration of undomesticated species into the cropping system; intercropping of cultivars within fields; mixed stocking of pastures or fish ponds);

(ii) strictly controlled harvesting of any 'keystone species' (a keystone species is one on which depends the survival of many others in the habitat);

(iii) acceptance of low densities of weed species, parasites and predators of the target species (rather than aiming at elimination), and thus the use of less-intense control measures. The common result of this is that populations of their natural control agents increase and gain in effectiveness. Integrated pest management is the ideal approach;

(iv) encouragement of the survival of non-weeds, especially those with known uses.

Outside the harvested part of the habitat but still within the overall cropping system, negative effects of cropping on wild species can be reduced by making the placement of any agrochemicals more accurate. Non-persistent biocides are recommended. Lower application rates of biocides (in line with (iii) above) will imply less pollution of non-harvested habitat and reduced down-stream effects. In agricultural systems, where almost no unharvested habitat exists, the diversity of the now-critical residual parts can often be increased by judicious neglect and/or plantings of selected trees. Native multi-use trees can be grown, to avoid interfering with cropping, on terrace and field edges, along tracks and within shelter belts.

Planned agricultural developments should include the setting aside of suitably large and species-rich conservation areas, with arrangements for the monitoring of wildlife there, and appropriate measures to provide for long-term protection from disturbance. Protective measures include the provision of game wardens, a research component, and buffer zones surrounding the core areas. Cropping activities, human habitations and infrastructure should be located in such a way as not to interfere with populations of conserved species in reserves and other protected areas. Thus, patches of habitat which are outside the reserve but necessary to wildlife within the reserve should not be developed; corridors between patches of wildlife habitat should be retained; and cropping and processing activities should be sited so as to protect reserves from any down-stream effects. It is vital to design environmentally benign and sustainable cropping systems for use within the extensive buffer zones around large reserves.

REVIEW OF THEORY

Some further background to the above is now given in three sections, the first two relating to conservation within an illustrative agricultural system, and the third referring more generally to other exploitation systems.

The importance of *in situ* conservation of domesticated germplasm

Only a minute proportion of the world's estimated 10 million species can be conserved in special *ex situ* facilities. Such expensive treatment is reserved for rather small samples of some hundreds of species of animal domesticates and their relatives, and for larger samples of actual or potential plant cultivars and relatives. The cheapest way to conserve not only a much wider range of species – both animals and plants – but also a range of genotypes from within each species, is by habitat conservation (FAO 1985). While inclusion of undisturbed habitat within cropping sytems will contribute very significantly to conservation of wildlife, there are pressing reasons for trying to conserve germplasm of useful animals and plants within harvested habitat, even in 'modern' systems.

In agriculture, the breeding of new high-yielding crop cultivars and types of stock has led to the numerous locally adapted races being progressively replaced by just a few successful genotypes (Okigbo & Greenland 1976). The consequent loss of germplasm ('genetic erosion') threatens the future development of new crop and stock types for new uses and for the time when pests and disease organisms have overcome the resistance of the present types. The loss is especially serious near the centres of natural diversity of relatives of crops or stock types. *Ex situ* conservation of a wide range of genotypes is only available in designated genebanks for the 40 or so plant species grown on a large scale, whereas some 3000 plant species are known to be useful as food or in other ways. Genebanks of vegetatively reproduced plants are very costly to maintain and so such species are under-represented in world collections. The wealth of vegetable types and of the wild relatives of major crops is also relatively poorly conserved. Similarly, conservation of some animal species of critical significance (e.g. goats in Africa) has been seriously overlooked (OAU/STRC/IBAR 1985).

Since genes for local speciality effects and those giving local adaptation are constantly in demand, the planned inclusion of some use of traditional cultivars and stock breeds within agricultural projects seems likely to contribute vitally to their sustainability and further development.

In situ conservation of wildlife germplasm

Within a cropping system, the fate of associated wildlife depends greatly on what target species are cropped. Considering the case of agricultural systems based on field crops, in parallel with the concentration on the most successful genotypes of each crop, intensification of cropping leads usually to concentration on only one or a few types of crop species. As traditional crop rotations are replaced by more simple ones or monoculture, mechanisation and ultimately agrochemicals are extensively used to maintain yields. Consequently, the variety of weed floras and types of wild animal normally associated with each of several crops in a rotation is lost.

With this situation in view, measures to favour wild species in agricultural cropping systems seem to fall into two groups relating, respectively, to harvested and non-harvested habitat. For harvested parts, the following modifications of the cropping system can realistically be considered:

- reduce the use of broad-spectrum biocides and, preferring selective types, aim for integrated pest management (IPM) (Brader 1979; Goodland *et al.* 1984);

- diversify the crops grown in different areas of the holding, possibly within an IPM framework, and aim for maximum compatibility and synergy between any introduced crop and those originally present;
- introduce some intercropping/agroforestry, possibly with an animal component and/or the use of a variety of cover crops and green manures (to select the most useful and convenient) (Kang *et al.* 1984);
- cultivate separate small plots of old cultivars, or less desirable, a single mixed plot, as a 'museum strip'. Use traditional techniques (i.e. do not spray);
- where hand-hoeing is practised, allow non-weeds with known or suspected uses to continue growth until harvest. Some species may later be identified as useful.

For non-harvested parts of a cropping system, the following ways of increasing biological diversity could be

- to encourage the development of a diversity of habitats on unused land. Aware of the implications for human disease, allow thicket and all stages of forest re-growth to appear, possibly using live fences to prevent casual grazing and poaching. In wet areas, a variety of aquatic habitats could be created and stocked with native water plants and edible fish species (Goodland *et al.* 1984). If conservation areas are likely to receive spray drift from crops, dense hedges should be planted. Any relatively undisturbed habitat will probably become a reservoir for natural enemies of crop pests (Greenwood 1987), but they may also harbour pests. Waste land near field boundaries will probably provide habitat for weedy relatives of the crop species, and so could act as a reservoir of potentially useful genes for crop improvement;
- to plant a variety of multi-use tree/shrubs with appropriate ground cover on field boundaries, exposed erodible areas and along tracks (von Carlowitz 1986). If possible, trees should be raised from planting material obtained from local threatened natural forest. Indigenous species are preferred because they are likely to support a richer fauna (but there could be difficulties over ownership);
- to plant any areas of problem soils with ameliorative tree species (Prinsley & Swift 1986), together with a possible addition of livestock. Areas of undisturbed problem soils could allow the appearance of wild species useful in managing such soils;
- to encourage the development of protected home gardens containing both diverse woody multi-storey vegetation and herbaceous traditional vegetable crops (IITA 1986). As the vegetation comes to resemble natural forest, the gardens are likely to be colonised by diverse insects and birds.

Principles of conservation of diversity in ecosystems

Returning to the full range of biological cropping systems, it is clear that the above consideration of the conservation needs of a field-crop based agricultural system can do no more than suggest how to treat other systems. Indeed, agricultural systems themselves are too diverse to receive a full consideration here.

There are, however, some guiding principles on how to retain species diversity.

The first principle relates to the control of potential monopolist species: if, in the absence of predation, one species outcompetes the others in its trophic level, the loss from the system of a carnivore that preys heavily upon it will probably allow it to dominate the community. As has been seen in several types of community (intertidal zones and coral reefs (cf. Harper 1977), too heavy an exploitation of such a carnivore will lead to a loss of species richness.

A second guiding principle is related to the first: that keystone species should be retained, these being in many cases the easily identifiable top carnivores (large predators not preyed on by others). The importance of these principles was seen in a Chinese Nature Reserve where heavy poaching for sale of a vulture allowed squirrel populations to explode and destroy the forest (Jianming 1987). (Sometimes, however, a keystone species may provide the structural basis for the habitat, for instance the mangroves in coastal swamps.)

If the exploitation is directed at the potential monopolist itself, this will probably lead to increased species richness. Cutting a sward for fodder often has this effect. However, the outcome in a grazed pasture is determined by the relative palatabilities of the species present (and their response to grazing, the intensity and timing of the grazing, etc.). Grazing may lead to either a near-pure stand of an unpalatable species, or a species-rich sward worthy of special protection (cf. Harper 1977). A common finding is that moderate grazing intensity increases the number of species while heavy grazing reduces it, possibly exposing the sward to destruction by soil erosion.

PRACTICAL METHODS FOR CROP-BASED AGRICULTURAL SYSTEMS

A selection of measures for the conservation of parts of the ecosystem is noted here and training exercises based on them are given in the next section.

Crops:

- government subsidies to encourage farmers to retain some area planted to traditional (often mixed) cultivars, cultivated using traditional techniques;
- government action to curb excessive promotion of homogeneous cultivars and exotic stock types for the benefit of commercial interests (where it is known that this encourages genetic erosion without compensating benefit to small-scale farmers);
- government-funded research to establish more clearly the merits and demerits of the use of several cultivars and stock breeds within farmers' holdings, either in mixtures or not, under various levels of intensification;
- government extension agents to raise farmers' awareness of the rich diversity of domesticated genetic material, encouraging farmers to show the agents examples of local variants and unusual plants/animals to be recorded in appropriate databases;
- farmers to diversify the types of cultivar used on their holdings to include traditional varieties either in their main fields or in separate plots within museum strips;

- retain uncultivated strips within holdings as habitat for weedy relatives of crop plants (especially in their centres of diversity).

Weeds:

- farmers to retain weeds with traditional uses and to show them to extension agents for inclusion in nationally coordinated inventories of potential new crops.

Wild species:

- government research to find acceptable methods of integrated pest management in order to protect wildlife and natural enemies of crop pests from damage by unnecessary spraying;
- avoid dispersal of fertilizer/herbicide onto any relatively undisturbed habitat (especially in water-courses and wetlands);
- extension agents to raise farmers' awareness of local plant and animal resources, especially if near a centre of diversity or protected area;
- when clearing, leave strips of original forest/bush (possibly useful to farmer as windbreaks, for firewood collection, or for maintaining already useful wild species);
- leave some undisturbed habitat on holdings (including wetland if present);
- plant multi-use native woody species in waste land;
- use native species as live fences for livestock exclusion and security purposes.

TRAINING METHODS

A selection of training exercises is suggested below. The choice of those to be attempted will depend on the local conditions and the needs of the student.

1. Carry out a survey of progressive farmers' motivations in changing over to the use of modern cultivars and stock types. Explore the conditions under which they would retain some use of traditional genotypes (e.g. in home gardens for marketing locally). Using the results, draft a memorandum to be sent from Central Government to extension agencies in the student's locality explaining the need to balance the needs of national genetic conservation against an individual farmer's desire to modernise.
2. Using a provisional table of the advantages and disadvantages of using several genetic types of plant or animal on one holding, together or separately, write a pamphlet addressed to extension personnel describing situations where it could be in a farmer's interest to use this sort of diversity.
3. If trainees are unfamiliar with the use of mixed cultivars, grow (say) three recognizable popular cultivars as a mixture and as separate pure stands at a range of sites. Compare yields and costs. Say whether or not the results suggest conditions under which it could be advantageous to grow mixtures. Use the results to evaluate the desirability of trying to conserve cultivars in a mixed museum plot.

4. List local outbreeding crops commonly growing with associated weedy relatives. Visit sites and search for evidence of cross-breeding between crops and weeds. Compare crops and weeds for susceptibility to pests and diseases. Do the results indicate that habitats carrying weeds could act as a reservoir for noxious species? In what ways could local weedy forms be useful in the short or long term?
5. List weeds locally retained in crop fields as 'non-harmful' or useful. Specify all the ways in which they are used. Compare the fauna associated with the weeds with that associated with the crop to find to what extent weed presence adds to species diversity.
6. Make a draft wall chart to show the range of diversity of locally used crop and stock types. Survey those used by local farmers and comment on rates of loss of diversity, identifying threatened types.
7. Survey wild species populations in uncultivated patches of habitat on farm holdings. Attempt to find how frequency of disturbance (and type) and the area of the patch affects species diversity.
8. As part of an effort to identify new useful plant species (and to increase awareness of the potential value of plant conservation), conduct a trial of (say) six selected native woody species for their capacity to coppice and strike from cuttings; easily reproduced coppicing species could be useful firewood material in deforested areas. An alternative would be to test six species with traditional medicinal uses as possible pesticides.
9. Using a reasonably homogeneous uncultivated area, carry out a trial to find the effect on species composition of several (relevant) kinds of disturbance (e.g. low levels of fertilizer and pesticide application, trampling, grazing, burning etc).
10. If an exotic weed has become abundant in the region as a result of intensified farming, carry out a trial with selective removal of the weed to estimate the likely past impact on floristic diversity of the weed's introduction there, and thus estimate the likely loss of diversity as a result of further spread of the weed to other regions. Which types of species are the most affected by the presence of the weed?
11. If shifting cultivation is practised in the area, compare the species richness of forest/bush regrowth of various ages and estimate the impact of levels of intensification of the system (e.g. shortening of the fallow phase) on plant and animal species. If primary forest is still present, this can be used as a point of reference. What is the response of the cultivators to your suggestions of ways in which they might slightly modify their practices so as to conserve more species?
12. If a few types of agriculture are practised in your area, compare the species richness in holdings managed in the different ways, relating differences to the intensity, frequency and type of disturbance to which the land is subjected. Report results under the categories domesticates/'weeds'/wild 'non-weed' species, considering both plants and animals. Are there any key types of

disturbance which determine most of the differences? What is the response of the farmers to your suggested modifications of their practices in order to conserve more wild or domesticated genotypes?

13. If you can find or create sites, otherwise comparable, varying in the intensity or frequency of some single sort of disturbance (e.g. grazing pressure or fire frequency), compare species richness in the sites to find the level associated with maximal richness. Try to explain your result, and say how general it is. Are any species selected by high intensity of disturbance in your area which could possibly be useful in other areas?

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DOCUMENTATION

DOCUMENTATION

S. BLIXT

SUMMARY

Documentation in this chapter means the procedure by which the information relevant to genetic resources preservation is collected, stored and made accessible using computers as main storage and processing media for data. Not dealt with is the actual handling of seeds, plants, herbaria, books, journals, etc., i.e. the 'physical documents'.

It is argued that, to fulfil its purpose, documentation should be designed according to a scientific, accepted biological theory, a theory which is also expected to form the basis for international conservation strategy as well as national conservation policy. The theory remains perhaps to be formulated, but the view that planet Earth forms one undivisible 'mega-ecosystem' and that nations are primarily responsible for preserving their own genetic resources are key ideas expected to be part of such a theory. Another essential part is that preservation is centred on the gene, which is the functional unit of heredity. On this basis, major requirements and components considered necessary in an adequate documentation system are very briefly presented. This includes, among other things, considerations on levels of registration and data processing expected from such a system, the organisation of genebanks and collections, *in situ* and *ex situ* conservation. Criteria for deciding what kind of material may be relevant for conservation are discussed on different levels, e.g. the characteristics of material that may be handled by genebanks and what should not, and genetic properties of different kinds of material.

Finally, some of the main technical aspects of a computerised documentation system are very briefly presented, e.g. databases, descriptors, codes, and different ways to structure the biological information based on genetic, taxonomic and/or character descriptors.

INTRODUCTION

Conserving and utilising genetic resources in a scientific rational way means not only collecting and storing the biological material. It also involves collecting, storing, and integrated utilisation of information and knowledge of a biological, geographical, meteorological, cultural and bibliographical nature to an extent that would 10 years ago have been unrealistic to consider. Computers are indispensible tools in advanced documentation work and the following presentation is consequently

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based on the assumption that electronic media are used for documentation relating to genetic resources conservation. This does not mean that valuable basic documentation cannot be done in a manual system.

THEORY RELEVANT TO CONSERVATION METHODOLOGY AND DOCUMENTATION

Documentation of genetic resources of cultivated plants is much more than recording seed bags on shelves. It is a complex and essential recording of a vital part of human knowledge concerning the entire environment and should, as such, be an essential part of a World Conservation Strategy. In designing in detail a documentation system for plant genetic resources, a National Conservation Policy should have been formulated. Such a policy is considered to include:

- acceptance of a national responsibility for the preservation of the endemic and indigenous genepool and for the exogenous genepool of such species that, although not endemic or indigenous, through natural selection and/or selection by man have developed specifically adapted genotypes.
- recognising that the plant genetic resources are a result of the development of the vegetation and agriculture in the country as well as the cultural and scientific development of its human population, including cultivated plants, i.e. cultivars, landraces and genetic stocks, as well as wild plants (Blixt & Kjellqvist 1988).

For the long-term planning of genebank activities it is therefore essential to be able to define what is comprised within the obligation to preserve genetic resources of agricultural and horticultural plants, in quantitative as well as qualitative terms. To achieve this a genebank needs to have access to information relating to:

- the development of the vegetation of the area during a considerable period of time until the present; this information can probably be obtained from or developed by disciplines such as plant geography, systematics, palynology, and others.
- the development of farming within the area from the gatherer – hunter stage to the present time; such information can come from disciplines of history, cultural history, archaeology and museum institutions of different kinds.

In fact, evolution of crops seems inseparable from evolution of human culture. Conservation of genetic resources, therefore, also has a humanistic, cultural and historical side, whether we recognise it or not. Full understanding and appreciation of conservation problems, therefore, necessitates taking also such aspects into consideration (Vavilov 1926).

Scientific basis

To develop a documentation system requires a formulated theory of genetic resources conservation. Such a theory is also needed for establishing criteria for the collection of relevant data and the development and use of expert computer software capable of utilising these data. Present theory of genetic resources conservation relies much on N.I. Vavilov's thinking (Valilov 1926; Whitaker & Robinson 1949/50), and a modem comprehensive scientific theory taking account of recent advances in molecular and classical genetic remains perhaps still to be formulated. The concept of gene centres or centres of diversity, the origin of cultivated plants, and the utility of genetic resources for breeding have been fairly well documented. (Frankel & Bennett; Frankel & Hawkes 1975; Zeven & VanHarten 1978; Zeven & Zhukovsky 1975). Less adequate, however, is the integration of this information and knowledge with the day-to-day routines of genebank management as well as with the utilisation, i.e. plant breeding. The main work relating to documentation has been done by or under the auspices of IBPGR which has published a series of documents available on request (Blixt & Williams 1982; Konopka & Hanson 1985), including a bibliography (Hawkes *et al.* 1983). Also largely lacking seems to be expert computer software utilising modem genetic theory, in plant breeding as well as in plant breeding processes, in order to utilise genetic resources. This is felt as a major gap in present development of applied plant science.

Level of registration and data processing

In contemplating how to design a computerised genebank management system capable of an adequate scientific documentation of genetic resources, it is very useful to think in terms of computerisation on different levels (Blixt *et al.* 1982):

- the recording and retrieval level (R & R), at which the data and processing are not used for creating new data, and
- the analytical level (A), where data are used to create new data and new information to be derived (Blixt 1982).

Most of the discussion going on today regarding computerisation of genebank management relates to the R & R- level at which advantages and gains are mainly of a practical nature, such as time saving and better overview and insight. Most of the scientific advantages of computerisation are, however, at the A-level. This, however, requires that the practical management of the material is so organised as to yield high-level quality data with high-level information content (Blixt 1978).

Organisation of preservation

With regard to designing a documentation system, the organisation of the material in the *ex situ* collections of the genebank is important. It is customary to divide it on different collections for different purposes and subsequently with different management requirements:

Safety Collection, as a safeguard against any accidental loss of material;

Base Collection, with main objective of maintaining the material at as high genetic quality as is ever possible;

Active Collection, with the main objective of providing seed for the distribution and material for characterisation and other work relevant to genebanks;

Working Collections, which are in the hands of breeders and other institutions outside the genebanks and therefore not considered in this context.

Criteria for preservation of material and information

For both practical and scientific reasons it is imperative to have the best possible definition of what genetic resources are possible to preserve in a genebank and what are not, and what, consequently, should be the responsibility of the genebank and what should not (Blixt 1988). Concerning agricultural and horticultural plants, material can be roughly separated into the following categories, of which only the first one should be considered the responsibility of genebanks:

- genebank material proper, here defined as material which is endemic or indigenous or specifically adapted to the geographic area for which the genebank has accepted responsibility to preserve genetic resources;
- plant breeding material; characterised by a dynamic decrease from often extreme genetic diversity to extreme uniformity and therefore subject to extensive loss of genetic diversity through natural and artificial selection;
- plant introduction material; normally the responsibility of another genebank to preserve;
- seed for plant production; used in agriculture or horticulture to produce a crop and therefore available through normal channels;
- plant products; as intended for consumption or processing, such material is normally available on the open market.

BASIS FOR STRUCTURING THE BIOLOGICAL INFORMATION

Genetic

The gene is the unit of mutation and recombination, i.e. variation; this variation exists as alternative states of the gene – alleles – and as different recombinations of the alleles and of different loci in adapted complexes. Genotypes and populations are distinguished by different gene complexes. The number of genes and their alleles is finite and limited, whilst the number of gene and allele combination is infinite. Consequently it is quite possible to preserve and document all genes but practically impossible to preserve and document all gene and allele combinations. What may be preserved in a genebank, in terms of material and information, is, therefore:

- genes: the aim should be to preserve all known alleles within a species and try to maintain as many as possible of the ones not yet identified, which is possible with a relatively limited number of accessions;
- geneblocks, when justified, for instance in the case of adaptive blocks;
- chromosomes, when justified by special value; for example, aneuploid lines, translocations or other chromosome changes;
- genotypes, when justified; for example, varieties of self-fertilized or vegetatively propagated crops;
- groups of genotypes, when justified; for instance, cultivars of cross-pollinated crops, representatives or relatives of cultivated species.

The main implication of all these genetic considerations for designing computerised databases is first of all that the systems need functions to handle genes and genotypes, both in terms of descriptors and in terms of other software functions. This does not present any major problems, but considering the fact that a plant may harbour some thousands of genes to be dealt with, it certainly deserves specific consideration in the design of genebank management systems.

Taxonomic

For many of our cultivated plant species – and almost all of of the wild ones – little detailed genetic knowledge seems to be available; more species have been dealt with botanically and taxonomically. It is rather self-evident that characters of plants constant enough under different environmental conditions to be useful in taxonomic classification must have a genetic background (Blixt 1979b; Lehman & Blixt 1984). For cultivated plants, therefore, an infraspecific taxonomic treatment is a scientifically valid base for a genebank management system.

Character

The utility of plant characters as defined by breeders and farmers in a documentation system depends entirely on the care taken in defining the characters on a sound genetic basis. Selecting from a genebank database those desired traits or combinations of traits to use in a breeding programme is most efficient when a trait is a monogenically or at least oligogenically inherited character. The more genes and gene interactions that are involved in determining the character, the more random the selection of accessions in the genebank database and the more random also the effect of selection in a breeding programme.

DESIGNING OR ACQUIRING A GENEBANK MANAGEMENT SYSTEM

Approximately the same criteria should be applied in acquiring existing software for handling one's genetic resources documentation as are applied when developing such a system from scratch. Some of the more important criteria relating to policy, its biological and scientific aspects, were presented above. Some of the main technical aspects will be briefly treated below.

Databases: designation

A database is a body of data, organised in records which are, in their turn, structured in a certain way. The conventional mode of establishing a database for use in computers is to define for each unit of information, each datum, to be stored, a *descriptor*. This descriptor will define what the datum represents, in case of fixed-format databases the number characters assigned to the datum, the position in the record, the field, and in addition the type of the datum, whether integer, decimal number, string, etc. In a free-format database, it has similar functions except there is not supposed to be a fixed length of the field.

A database may, in a simple form, be constructed of a fixed number of descriptors, one such sequence of descriptors forming a record, one record describing, say, one accession. To manage genebank material includes the handling and description of biological material, i.e. living organisms. The description includes the history of the material as well as its biological constitution. Considering the complexity of biology, it should not come as a surprise that a genebank management system that has any serious aspiration to succeed in handling and, with a reasonable accuracy describing, living organisms, becomes quite complex.

In computerising the management of a collection, the information on the collection can be organized in different ways depending on the hardware (machinery) available, particularly the data-storage capacity. With no restrictions on storage space and with fast computers it may be most convenient to have one big database with the information relating to the Base, Active, and duplicate Base Collections as different states of the accession. A hardware constellation with restricted storage capacity and longer disk access times may take advantage of the fact that normally all descriptors describing a collection are not used simultaneously, and keep a separate database for each function of the collection, dividing the descriptors in a logical fashion between the databases and thereby achieve on that particular constellation more manageable system.

It must, therefore, suffice for this presentation to outline broadly (i) the information required for documentation and (ii) the major kinds of descriptors to be used.

Databases: content

The information for which descriptors will have to be designed, i.e. the information relevant to genetic resources conservation, is extremely broad. It will, therefore, have to suffice to mention some databases of general interest:

- Species Inventory Database; to include information on species occurrence in reserves, infraspecific genetic diversity, needs for conservation, etc.
- *In situ* Database; to include information on reserves, relevant phytogeographical and paleobiographical data, species composition in reserves, etc.
- Biological Accession Database(s); to include information on genetics, taxonomy and characters – morphological, physiological, biochemical, and any other.
- Documentation Accession Database; to include information on the documentation relating to individual accessions, such as herbarium vouchers, photographs, literature references, etc.
- Management Accession Database; to include information on breeding systems, types of reproductive patterns, role of vectors in pollination, isolation requirements, maintenance of genetic diversity and integrity, life cycles, minimum population size, seed viability and dormancy, etc.
- Library and reference functions; databases on literature, addresses, etc. are useful complements in a computerised documentation and information system.

Descriptors

For practical reasons it is useful to categorise descriptors, to group them in different ways. The author has found the following grouping quite useful for many purposes. For information on descriptors used for specific crops the reader is referred to the IBPGR series of Crop Descriptors.

The biological characteristics of accessions have as a rule been recorded in character descriptors, including, when applicable, genes as well as botanical taxa. Particularly if looking ahead for a more sophisticated A-level use of genebank information, it seems, however, advisable to make special genetic and taxonomic descriptors, since an efficient use of such descriptors demand a specialised, more 'intelligent' or expert, software. This amounts to designing gene-symbol descriptors and taxonomic descriptors as categories to be identified as such by the computer system.

Passport

Conventionally, the history of the accession is described using descriptors called Passport Descriptors. These will include such data as name of cultivar, country of origin, habitat of collections, etc. This is information supposed to accompany the sample when it enters the genebank. There is little variation between different species of plants, more may be between different types of material within a species as to the quality or quantity of passport information considered essential for a genebank. Data referring to the collection sites are sometimes included in the passport information, sometimes kept in a separate database.

Management

Perhaps the most important kind of information for the actual management or handling of the material in the genebank itself – and what seems at present too-little used – is what can be called Management Descriptors. What particular descriptors should be included here varies perhaps more between species than in the case of passport descriptors. The particular importance of such descriptors for genebank management may be elucidated by the following considerations.

A genebank should, by definition, preserve genetic resources for the future. Obviously this must mean a long-term commitment. At the same time, the longest possible interval between rejuvenating material is recommended to minimise genetic distortion. With current preservation methods, it is quite possible for some crops that 50 years may elapse before decreasing germinability forces a rejuvenation, in which time the entire genebank staff may have been changed more than once. Also, many genebanks have responsibility for a great number of species but a very limited staff, who can not be expected to be experts in all crops. Further, all accessions of the same species cannot be handled in the same way. Everything considered, it is essential for a reasonably continued correct handling of the material that all information pertinent to the cultivation, observation, storing and distribution of the material is recorded in the information system in as much detail as is needed.

Conventionally, such data regarding harvest year, quantity harvested and stored, germinability tests, and storage location are included in most genebanks. There is much other needed information that seems not to be. For instance, with regard specifically to autogamous crops, such as peas and barley at northern latitudes, a large number of accessions are to be kept as 'pure lines', and thus to be pedigree-propagated. This requires, for instance, that some plants are always to be harvested individually for the further propagation. In most species, cultivars have certain defined characteristics which require particular measures, such as weeding a particular rogue or a frequent mutant. Collected populations of heterogamous plants should be so handled as to maintain the genetic diversity. Collected samples of autogamous plants, 'pseudopopulations', i.e. mixtures of lines, should either also be maintained as mixtures or separated into individual pure lines. Accessions defined to carry male sterility or other sterility or lethality-causing genes must be kept through the heterozygotes. The important thing is that each of these different types of accessions has to be correctly handled to maintain their genetic identity.

Also belonging here are descriptors recording the distribution of material. With the growing number of genebanks and accessions involved in exchange of genetic resources, the need to avoid unnecessary duplication in maintaining material increases, and it becomes more and more important to be able to track the movements of distributed material.

Many of these problems are taken care of by experienced curators and experience is normally carried on by a person-to-person transfer. However, the development of present cultural patterns seems not to go
in the direction of favouring such person-to-person transfer, and it seems therefore essential that as much as possible of such experience is transferred to the computerised genebank management system – although admittedly experience is too complicated a phenomenon to be ever entirely captured this way.

Genetic

The use of genes and gene symbols in genetic resources preservation have been implemented in the pea to a rather large extent. This could be done because the pea is comparatively well investigated genetically (Blixt 1969, 1972a, 1972b, 1975, 1977; Blixt *et al.* 1978; Lamprecht 1974). Thanks to this, a certain level of expert computer programs has been developed (Blixt 1979a, 1984). The fact that one can work directly on the gene and the allele makes the selection of accessions from the database relevant to the breeding problem to be solved extremely efficient. Also, the use of the database for selecting relevant material for research in general increases greatly. In fact, the genetic resources database becomes a quite powerful tool in itself for research, particularly in fields such as genetics and plant physiology. Considerable genetic information, of the same kind as in peas, is available for maize (Coe *et al.* 1982; Neuffer & Coe 1974), rice (Khush 1974), wheat (Hart 1982; McIntosh & Cusick 1982; Sears 1974), barley (Nilan 1974; Tsuchiya 1982), cotton (Phillips 1974), *Cucurbita* (Whitaker 1974), *Cucumis* (Whitaker & Robinson 1974) and tomato (Rick 1977, 1982), as well as for other species, but seems hitherto not have been utilised in genetic resources documentation.

Taxonomic

It has been shown in the pea that a good infraspecific taxonomic classification is approaching a genotypic description (Lehman & Blixt 1984). Therefore, Taxonomic Descriptors may be considered a valuable substitute for genetic descriptors in species where genetic information is presently scarce, either due to not having been investigated or not having been collected, systematised, and/or been put to use. Infraspecific classification in many crop species has been carried out particularly in east Europe, not least in the USSR.

Character

The biological characteristics of an accession are handled by Character Descriptors. Many such have been designed and the IBPGR have issued lists with recommendations for definition and use, largely based on current use in breeding programmes, etc. As a result, the genetic content of these descriptors varies, and although not necessarily causing any particular problems on the R & R-level the use of many of them at the A-level can be problematic.

CODES

Having discussed what can be seen as the central structure of a genebank management system, it remains to mention something about all the auxiliary software and database devices that will be needed to make a computerised system work efficiently. Much information to be stored and used in databases is most conveniently stored and worked with as codes. This calls for code key databases of different kinds. Some of these, dealing for instance with country abbreviations and similar matters, are easily set up, so easy that the temptation is great for each genebank to make its own. For the benefit of common communication, standard codes, as recommended for instance by IBPGR, should be used whenever available. Gene symbols and taxonomic names are, on the other hand, rather special cases. These are both codes in themselves, which require a very specialist constructed code key. A gene-symbol code key or list should contain as a minimum information the name of the symbol – the code – and the manifestation of the gene in the plant. Also essential is information on chromosomal location, and interactions with other genes. Extremely useful is information regarding the author of gene symbol and chromosomal location, in what accessions different alleles can be found, and important literature references. Only the fact that the number of genes known in species like maize, barley, pea and tomato now exceeds (or approximates) 500 in each species makes it almost necessary to code this information.

With regard to taxonomic names, these are, in contrast to gene symbols, often long, particularly as the author name is to be considered part of a taxonomic name. It is, therefore, often useful to make one more level of the code – for instance through convenient abbreviations of the name. Such codes have been constructed at least for specific and higher taxonomic levels. A code key would in such case require a minimum information, comprised of the code, the full name including author, and description – definition – of the taxon. Also here, further information such as publication and date would be useful. Such a taxonomic code key is probably most efficiently constructed as a standard botanic key to be read backwards.

Also passport and character descriptors are most conveniently used in a computerised system as codes, and then code keys for such descriptors must also be stored and handled by the system. Minimum information here would be code, full name of descriptor, maximum field length (when appropriate) and full definition of the meaning of the descriptor.

In fact, the capacity of working with codes and code key databases are probably such an important requirement for reaching the A-level of data processing in genebank documentation that this requirement should become a major criterion in choosing hardware and software.

LITERATURE

One way of looking on documentation of genetic resources is to see it as handling two separate systems of literature. One is written on paper in books and journals – or nowadays more and more often on computer disks – with letters forming words. The other is written in DNA in chromosomes, with nucleic acids making up triplets. In order to implement the second, we have to first make the knowledge and information hidden in the first accessible. Therefore, an adequate literature database and workable literature handling software is invaluable in genetic resources documentation.

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