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Agricultural models and forestry practice

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Much of forestry practice is simple exploitation of the resource, much as pre-agricultural, hunter-gatherer societies utilized native plants (Figure 4). Commercial timber species are often used as they are found, and natural reproduction is relied upon to regenerate the forest. Because much of forestry still depends on wild plants growing in naturally regenerated stands, the management of wild species is an aspect of conservation unique to forestry. In agriculture, once species were domesticated, agriculturists usurped the habitat of their wild progenitors by cultivation and displaced the native vegetation. This may often have had the effect of driving the progenitors of the domesticated crop to extinction. That seems to be the case with maize in México (Mangelsdorf et al. 1964).

The origin of most major agricultural crop species is lost in prehistory. As a consequence, *in situ* conservation of crop species is hardly ever considered by agriculturists, and they have rarely used *in situ* methods even for wild relatives of their domesticated crops. An exception is the new World Bank project in Turkey to protect wild relatives of crop species and forest trees in a system of *in situ* reserves (see Box 2). In forestry, virtually every important commercial tree species, with rare exceptions such as island endemics like Mauritius ebony (*Diospyros hemiteles* L.), can still

be conserved *in situ* (Ledig 1992).

The agricultural model of conservation is one of *ex situ* conservation in huge seedbanks and in field plantations, especially for clonally propagated species and those having recalcitrant seeds. The number of wheat accessions in seedbanks alone is immense, 46,000 in the U.S. National Seed Storage Laboratory (Chang 1989). More recently, clonal archives *in vivo* or in *in vitro* tissue cultures maintained under slow-growth conditions have become a useful mode of conservation (Chavez et al. 1988).

Conversely, *ex situ* conservation is not usually as critical in forestry as it is in agriculture, nor need it be. In forestry, *ex situ* conservation can be considered a back-up, or insurance policy, to guard against the loss of especially critical or threatened populations. The main threat to forest species in North America is from deforestation that results from conversion of forest land to agricultural uses, primarily grazing, as in México. With the advent of widespread use of improved lines of commercial forest species, which is probably conceivable only in the southeastern United States or some parts of the Pacific Northwest, some *ex situ* conservation practices will be needed.

Genetic resource management of agricultural crop plants is divided into eight components: collection, documentation, characterization, storage, evaluation,

multiplication, distribution, and utilization. The list fits the forestry situation poorly. In forestry, the process of genetic resource management began with evaluation (Keiding and Graudal 1989).

In agriculture, conservation followed transport and diversification of crop plants. The process of adaptation to new environments that followed human transport and the deliberate efforts of breeders over millennia to modify crop plants to human advantage resulted in a tremendous genetic radiation. For example, broccoli, Brussels sprout, cauliflower, collards, kale, kohlrabi, marrow-stem kale, and the savoy, leafy, and heading cabbages have all been selected from the single species *Brassica oleracea* L. introduced into cultivation 8,000 years ago (Janick et al. 1969). Within each of these crops, numerous cultivars have been developed. Bread wheats (*Triticum aestivum* L.) have diverged into countless varieties of hard, soft, winter, spring, red, and white wheats, and maize (*Zea mays* L.) into flour, dent, sweet, and popcorn types.

Evaluation of the genetic resource should be an important component of any conservation program. Because no accurate record of origin exists, genebanks for major crop species undoubtedly contain many essentially redundant accessions. The National Seed Storage Laboratory in Fort Collins, Colorado has over 46,000 accessions of wheat alone; the Vavilov Institute in Russia has 63,000; and the International Rice Research Institute in the Philippines has 83,000 accessions of rice (Chang 1989). Sampling the collections for evaluation is a daunting task. If the need arises to locate resistance genes for a new pest, screening (i.e., evaluating) these huge collections is a major problem (Spagnoletti Zeuli and Qualset 1993). Forestry has followed a different model.

Conservation efforts in forestry, in contrast to agriculture, began with the process of evaluation as forestry moved from the strictly exploitive to the early stages of domestication. That is, as tree planting began to supplement natural regeneration of forests in some areas, foresters began to plant provenance tests to determine appropriate seed sources for local planting (see Box 3). Because patterns of variation in naturally regenerated forests largely reflected underlying climatic variation, trends were often clinal and it was possible to interpolate between the provenances under test. Therefore, in most major commercial timber



Figure 4. Mechanical felling of loblolly pine (*Pinus taeda* L.) forest in Florida, U.S.A. In the last century, natural stands of many tree species were harvested without regard to regeneration, and treated like other exploitive resources (e.g., oil, gold). At present, loblolly pine either is replanted after harvest or appropriate silvicultural methods are used to favor natural regeneration, treating it like a sustainable resource.

species, evaluation is well underway, and foresters are only now feeling the need to move into more formal conservation activities such as collection and storage of germplasm.

The genetic resources for forest tree species have a different geographic pattern than do crop plant resources. While the genetic resources for most crop plants are concentrated in centers of diversity in warm temperate areas, genetic resources for forest tree species are globally distributed, spanning the range from tropical to temperate to boreal regions. Furthermore, the genetic resources for forest tree species are still abundant, for the most part, on publicly owned land,

Box 2

Global Environment Facility supports *in situ* conservation of forest trees and wild crop relatives in a pilot project in Turkey

Turkey is a major center of biological and cultural diversity and it is highly appropriate that the country was chosen for the development of a pilot project of the Global Environment Facility (GEF). The project targets habitats which contain concentrations of biological resources of great importance for human use and for the maintenance of biological diversity. As a pilot project, it promises to show how complex conservation activities can be managed and will generate new information about biodiversity. The project is unique in addressing conservation of both forest and wild crop genetic resources in their native habitats. Turkey is the center of origin for many woody and bulbous species that are exploited by extractive harvests. The country has the most northern extension of the formerly great forests dominated by cedars of Lebanon (*Cedrus libani* A. Rich.) and harbors many plants of known or potential medicinal values. Its flora of wild crop relatives is truly amazing, including woody-horticulture progenitors of apple, plum, almond, pear, walnut, pistachio, chestnut, and others. Understorey species in forest lands include wild relatives of numerous important world crop plants, including barley, wheat, chickpea, and lentil and many forage grasses and legumes.

The GEF project is funded for three years with the World Bank providing

\$5,500,000. The end date is March, 1997 which will be marked by an international conference in southern Turkey on *in situ* conservation. Ministries of the Government of Turkey are providing personnel and facilities to the project. Three areas were selected for study: 1) the Kazdagi National Park in the Aegean region of northwestern Turkey, a mountainous area containing many forest species and crop relatives; 2) the Amanos Mountains in southcentral Turkey which is the confluence of Euro-Siberian, Mediterranean, and Irano-Turanian flora and the northern extremity of the Fertile Crescent; and 3) the Ceylanpinar State Farm, a 1.69 million ha facility in southeastern Turkey which includes many annual crop relatives in its 48,000 ha of rangelands and in borders of cropped lands. Three ministries participate in the project, including the Ministry of Agriculture and Rural Affairs (MARA), the Ministry of Forestry (MOF), and the Ministry of Environment (MOE). MARA has overall management responsibility and conducts the work on agricultural crop plant relatives, MOF handles forestry, and MOE is involved in drafting a national plan for biodiversity conservation and public awareness.

The project has a strong element of human resources development through on-site training, short-courses, and external training. Funds are provided for insti-

tutional development, including laboratories and equipment. The first goal of the project was to undertake biological surveys in the targeted areas, using traditional inventory methods linked to geographical information systems. A major activity of the project is the development, from the survey data, of gene management zones (GMZs). These will be defined for the array of selected plant species and each will have its own management plan designed to maintain the natural genetic composition of the protected species. Each GMZ will have a scientific and technical team from the various government agencies responsible for carrying out the conservation activities on site. These initial GMZs will become the basis for a nationwide program to be initiated in the near future for a much broader *in situ* conservation of wild plants. Thus, this project has potential for great impact on conservation of Turkey's rich heritage of biological resources and will serve as a model for other countries. It is, perhaps, the first example of the comprehensive use of *in situ* resources for conservation of agricultural crop plants and their wild relatives.

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while the habitat of the wild relatives of crop plants has been largely eliminated by agriculture and urbanization.

Another way in which forestry differs from agriculture is in the inherent variation of tree species relative to annual crop species. In agriculture, cultivars have been bred for specific traits, soils, climates, and cultural regimes, and that has resulted in narrow genetic bases within cultivars or strains (U.S. Committee on Genetic Vulnerability of Major Crops 1972). For-

est tree species have been relatively little influenced by selection of this sort, and genetic variation within populations is usually high. In fact, variation within populations of tree species is, on average, much higher than that in annual plants, even wild annuals (Hamrick and Godt 1990). One reason for greater within-population variation in forest species may be that trees are predominantly outcrossing (Schemske and Lande 1985) while many annuals are selfing. Another reason may be that trees must endure fluctuating environ-

Box 3

Evaluation of genetic resources in forestry

Even before Darwin had formulated his theory of natural selection, and while the typological concept of species still reigned, foresters knew that tree species graded into series of races that differed for economic characteristics, such as bole straightness. In 1759 the Royal Swedish Admiralty issued a communiqué about oak, which said that the farther north that acorns could be collected, the better would be the shape of the tree (Langlet 1971).

The earliest record of tests to evaluate a species' genetic resources are for Scots pine (*Pinus sylvestris* L.), a highly variable species with a wide range. Between 1745 and 1755, H.L. Duhamel du Monceau grew plants from seeds from several regions in Europe together in France. In the next century, Pierre Philippe André de Vilmorin assembled a seed collection from several geographic areas and, beginning in the 1820s, planted them side by side on his estate at Les Barres in the Loire Valley. This experimental approach is the classic 'common garden' (or 'uniform garden') test used in all field evaluations of crop cultivars. Some of de Vilmorin's trees can still be seen in the Arboretum National des Barres. As the trees matured, it was obvious that the geographic variation observed in the forest was, in part, hereditary; i.e., when grown together, trees from different origins, called provenances, differed in growth rate, straightness, branching habit, and foliage color.

Early in this century, Cieslar (1907) demonstrated differences among seed sources that were much closer in proximity than the widely separated geographic races planted by de Vilmorin. Segments of more-or-less continuous populations of Norway spruce (*Picea abies* (L.) Karst.) drawn from an altitudinal transect in the Tyrol were adapted to their altitudinal zone of origin despite an apparent lack of major barriers to gene flow over the transect. Cieslar's test was a 'reciprocal transplant' study; in this case, replicate experiments with

seeds from different elevational zones were planted back across the range at low, middle, and high elevation.

The concept of species as a series of populations adapted by selection to local climate and edaphic conditions was almost fully matured by 1925. The term 'genecology' was coined by Turesson (1923) to signify the study of racial variation resulting from the hereditary response of the population to the environment. In the United States, several evaluation trials (now called seed source or provenance tests) were established in the decades of the 1920s and 1930s. One of these (Wakeley 1944) convincingly demonstrated the loss of forest productivity that could accompany use of the wrong seed source in plantation forestry. Wakeley planted four provenances of loblolly pine (*Pinus taeda* L.) in Louisiana in 1926 and harvested part of the test in a thinning in 1948 (Figure 5; Wakeley and Bercaw 1965). The dramatic difference among provenances in timber yield was a

graphic argument for conservation of local seed sources because provenances from Texas, Georgia, and Arkansas produced much less wood than those from Louisiana.

In California's classic ponderosa pine (*Pinus ponderosa* Laws.) elevational transect study planted in 1938, low-elevation seed sources grew well at the high-elevation planting site for many years (Mirov et al. 1952; also see Ledig and Kitzmiller 1992). They were overtaken by high-elevation sources only after the test had been subjected to a range of climatic conditions over two to three decades. By 29 years of age, low-elevation provenances were best at a low-elevation planting site, mid-elevation provenances were best at mid-elevation, and high-elevation provenances were best at high elevation (Conkle 1973).

The overwhelming result of provenance testing in North American forest tree species has been to demonstrate clinal patterns of variation (making interpolation possible) and the near-optimality of local races.

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Figure 5. Loblolly pine (*Pinus taeda* L.) pulpwood harvested in a thinning from a 22-year-old plantation at Bogalusa, Louisiana, U.S.A. The plantation provided an opportunity to evaluate performance of seed sources from Louisiana (LA), Texas (TEX), Georgia (GA), and Arkansas (ARK). The local, Louisiana seed source (i.e., the seed source closest to the planting site) obviously grew best, a common result in evaluation trials. (Photo from Wakeley and Bercaw 1965.)

mental conditions (and therefore, fluctuating selection pressures) over decades or centuries, which may maintain variability within the population. In addition, tree species may have a higher mutation rate per generation, which generates higher levels of variation than is possible in annuals (Ledig 1986, Klekowski and Godfrey 1989).

Because of the high levels of genetic variation available for selection, forest tree breeders have not given 'wild relatives' as much consideration as have agricultural breeders. The term has a broad range of meaning in forest tree species (see Box 4). Wild relatives could mean noncommercial congeners of commercial timber species; e.g., Table-Mountain pine (*Pinus pungens* Lamb.) could be considered a wild relative of the partially domesticated loblolly pine. Noncommercial tree species may have value for hybridization with commercial species by traditional sexual means, or through other techniques now being explored by biotechnologists. At the current stage of domestication in many forest tree species, noncommercial relatives (i.e., nondomestic, conspecific populations) are perhaps the most meaningful interpretation of wild

relatives. Together with populations of noncommercial species of forest trees, they are recognized both as currently or potentially valuable, and yet are vulnerable to loss because they are not represented in breeders' collections.

The longevity of forest trees, especially as it determines the long rotation (i.e., interval between harvests), is significantly different from any situation in agriculture, even in orchard species such as apples (*Malus* spp.). Simple economics makes it very difficult to practice forestry on the level of intensity customary to agriculture. The necessity of compounding interest over a rotation of 20 or more years before any return is realized makes all but the most profitable investment impossible. Therefore, foresters are usually unable to provide the intensive inputs in cultivation, fertilization, and irrigation that are standard in agriculture. Foresters rely on genetic diversity within stands rather than cultural practices to buffer against environmental heterogeneity.

Perhaps, the most important way in which forestry differs from the agricultural model is in the 'slippery' or noncommodity values of forests. The noncom-

Box 4

The concept of 'wild relatives' as applied to temperate forest tree species

The concept of 'wild relatives' has its origin in agriculture, referring to the undomesticated conspecific or congeneric populations of modern crop plants. The application of the concept to forestry was addressed in workshop discussions, from which this text is extracted. Because of both the longer breeding cycles of forest tree species relative to agricultural crop species, and the shorter period of domestication of the former relative to the latter, domesticated forest trees are less differentiated from their progenitor populations than is the case in agriculture. Therefore, wild relatives have not attracted the same interest as in agriculture. If this concept is to be applied to forest tree species, it could provisionally be used in the following hierarchical sense:

1. Related species—this concept of wild relatives, although not a

common term in forest biology or forest tree breeding, would most logically include undomesticated species that were congeneric to domesticated species;

2. Wild populations—populations from natural regeneration that have not been in any way incorporated into domestication programs. An example from forest tree species might be an unimproved, natural population of loblolly pine (*Pinus taeda* L.).
3. New germplasm from previously sampled wild populations—unsampled trees from populations that have been incorporated into domestication programs. These may be an important arena for natural selection for disease resistance, for example.

As domesticated forest trees are, for the most part, not genetically far-removed from their progenitor populations, wild relatives are a source of both potential opportunities and problems. While providing natural sources of genetic variation, they are also a source of genetic contamination (in seed orchards, for example) that may degrade gains achieved by breeding in domesticated populations. Conversely, domesticated populations, in plantations, for example, may affect the genetic diversity of natural populations (e.g., by vegetative spread into natural populations or gene flow by seed or pollen if the plantations are not harvested prior to reproductive maturity) (e.g., Millar and Libby 1989).

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modity values of forests may be more critical than the commodity values. Claire G. Williams, one of the workshop participants, was thinking of esthetic values when she noted: "What makes forest tree breeding different from agricultural breeding is that foresters are ambivalent about whether they want to domesticate trees at all or whether they want to save the wild forest." For some segments of the public, particularly in the United States and Canada, esthetic values and recreational use of the forest are inconsistent with harvest and with evenly spaced, cultivated, tree plantations.

Other slippery values are ecologic values. A field of maize is very efficient at carbon dioxide uptake during the months that it occupies the field. However, forest cover is continuous, and on an annual basis, forests are the most efficient vegetational form for offsetting carbon dioxide emissions (Ledig and Linzer 1978). Furthermore, carbon sequestering is immensely more effective in forestry than in agriculture because of the longevity of trees and the relatively permanent products to which they contribute, compared to the relatively rapid turnover (oxidation by metabolism) of agricultural products. Forests and forest cover are more effective at controlling erosion and reducing siltation of streams, reservoirs, and reefs than agricultural crops because forest cover may be disturbed only once every 20 to 100 years or longer, whereas agricultural crops such as forage or pastures persist for 3 to 15 years and most others are cultivated annually or even more frequently. Forests provide habitat for native wildlife, particularly threatened wildlife, whereas agri-

cultural crops are relatively unimportant in this regard. Many other values of forests, ecological and cultural, might be mentioned, and all provide a rationale for conserving forests *in situ*. Foresters, especially those dealing with native forests, are hardly ever able to manage for commodity values alone, in contrast to agronomists.

The practice of forestry, which recognizes the diversity of forest values, suggests that *in situ* conservation will be the dominant strategy for conservation of forest genetic resources, compared to the reliance on *ex situ* conservation that has characterized agriculture. *Ex situ* conservation should be employed in forestry to ensure against loss of genetic resources, especially for species where natural ranges are small and populations are being lost.

The number of accessions needed to backup *in situ* methods of conservation will generally be orders of magnitude less in forestry than in agriculture because forestry has pioneered in provenance evaluation. Seedbanks of agricultural crops include many accessions from the same locality or even the same field. In the absence of prior evaluation, collectors of agricultural crop plants generally feel that more are better than fewer (Chang 1989). By contrast, collectors of forest tree seeds can be quite confident about encompassing the range of available variation in their species by systematically sampling populations based on a long history of provenance testing. Geographic and elevational patterns of variation are known for some forest tree species and can be extrapolated to others that have not been specifically tested.