

# GENE CONSERVATION: AN INDUSTRIAL VIEW

B. G. McCutchan'

**Abstract:** --Gene conservation of commercial forest tree species is vital to the continued increase in forest productivity. As a critical commitment from forest industry to supplying wood for processing purposes, selective breeding and clonal preservation provide both genetic improvement and gene conservation. No concern for loss of genetic variability exists for these species due to large population sizes and diverse selection efforts. Tree improvement efforts worldwide on major species, such as loblolly pine (*Pinus taeda* L.), slash pine (*Pinus elliottii* Engelm. var. *elliottii*), and radiata pine (*Pinus radiata* D. Don), have created a multiple population breeding structure, or meta-breed, for each species. Details on the loblolly pine multiple population breeding structure is given as a case study.

Gene conservation efforts by industry for regional commercial species, such as sweetgum (*Liquidambar styraciflua* L.) and American sycamore (*Plantanus occidentalis* L.), have resulted from cyclic breeding interests in the Southeast. The perennial nature of progeny and provenance tests has allowed tree improvement efforts to resume, using these tests as the basis for a second cycle of selection.

Noncommercial species have no direct industrial conservation or development efforts, save that through *in situ* forest stands, wetland or regulated areas. Potential commercialization interests in these traditionally noncommercial species will be focused on specific genes that have use in transformation of commercial species.

Genetic resources of commercial forest species are available to industry through federally-funded tree improvement efforts. The funding of tree improvement *per se* for loblolly pine has been reduced to a maintenance level, preserving some existing progeny tests and clone banks. Federal efforts have been shifted to tree species at risk from introduced insects or pathogens and to species for specific at-risk ecosystems.

**Keywords:** Gene conservation, genetic resource, multiple population breeding structure, meta-breed, loblolly pine, *Pinus taeda* L, slash pine, *Pinus elliottii* Engelm. var. *elliottii*, radiata pine, *Pinus radiata* D. Don, sweetgum, *Liquidambar styraciflua* L., American sycamore, *Plantanus occidentalis* L, commercial species, noncommercial species, commercialization, clone hank, clonal seed orchard.

## INTRODUCTION

"Gene conservation" became a part of the SFTIC organization in 1994 with the establishment of a subcommittee on gene conservation (Rousseau 1994). This subcommittee recommended several items, including the urging of tree improvement cooperatives to develop sound gene conservation strategies for commercial species. For minor species of the southern United States, support of ecosystem-based, regional gene conservation efforts was recommended. Since 1995, the SFTIC organization has had a gene conservation specialist (Rousseau 1995).

Gene conservation is the preservation of both genes and genotypes. Genes are often preserved within the context of random or specific genotypes, through *in situ* or *ex situ* conservation stands, seed collections, grafted clone banks, seedling seed orchards or cryopreservation. In the context of tree breeding populations, the desire is to maintain alleles that exist at a given frequency such that, through recombination, these genes

---

Westvaco Corporation, Forest Science & Technology, Westvaco Research Center, Mill Road, P. O. Box 950, Covington, VA 24426-0950 USA. Email [bgmccut@westvaco.com](mailto:bgmccut@westvaco.com)

may be available for selection. An important benefit from breeding programs is that specific genotypes, with known performance values, can be preserved through clone banks.

Gene conservation efforts with forest trees, being at the beginning of the crop improvement process, have the benefit of learning from the development processes of other crops, especially the perennial commercial cultivars, such as apple or peach. In many cases the active breeding program itself has very limited genetic variation, and the commercial crop extremely limited genetic variation (Plucknett *et al.* 1987). In many crops there are now renewed efforts to go back into the undomesticated relatives and to introgress genes of interest (such as for adaptability or new processing factors) through traditional breeding or transgenics. Germplasm conservation for crops is vital to maintaining remnant genetic variability (Hancock 1998). Given that breeding cycles are multi-year events for most forest trees, it is prudent to develop gene conservation efforts in conjunction with species improvement efforts. Libby (1973) expounded on this particular opportunity twenty-six years ago. The opportunity is not lost.

The process of gene conservation has been described as either an end in itself, or as part of a breeding population. On its own, a gene conservation program for a particular species involves the following: assessment of genetic variability of the species across its range; description of a sampling process to include the variation within a collection of germplasm; identification of existing conservation programs including *in situ* stands; an archiving process; and potentially, a means to further the development of the inherent variation within each subpopulation (Namkoong 1986).

Namkoong (1976, 1984a, 1984b) described the multiple population breeding system that develops both a breeding program for a species and active gene conservation. The basic concept is that there are a number of populations undergoing differential selection criteria such that populations diverge over time. This interpopulation variance is released (or made available for selection) through advanced interpopulation hybrids (Koshy and Namkoong 1996, Namkoong and Koshy 1997). These differences can be hastened by subjecting the progeny tested population to extreme environmental conditions, such as droughty sites compared to wet sites, with subsequent selection and breeding of those specific site types. It should be noted that gene conservation is occurring within the breeding populations, rather than in commercial plantations that arise from the deployment population such as, seed orchards or clonal cutting orchards.

The genetic variability of a species provides the framework for gene conservation efforts. Measures of genetic variation, or diversity, include the variation in morphological traits, adaptive traits, allozymes, terpenes, and molecular markers. The National Forest System has a dedicated lab, NFGEL, for the collection of genetic diversity information of forest plants, using a variety of laboratory techniques (Valerie Hipkins<sup>(2)</sup> personal communications). The native population structure for wind-pollinated species, as described by the variation among allozyme loci (which are considered to represent neutral alleles), is largely without genetic division among populations; most of the variation exists within species (Hamrick *et al.* 1992). In contrast, there are many studies reporting the variation among seed sources (native populations) dealing with various traits. For example with loblolly pine, western sources tend to be slower growing, more fusiform rust resistant and more drought tolerant than eastern sources (Wells 1983, Schmidting - this issue), while mountain and Piedmont sources tend to be more cold hardy than coastal sources (Wells and Rink 1985). Additionally, monoterpene composition variation among loblolly pine provenances displayed a strong east to west clinal trend (Squillace and Wells 1981).

Prior to the onset of any active gene conservation, an assessment of the genetic resources available is essential. The Committee on Managing Global Genetic Resources (1991) provided an overview of the global forest tree genetic resource. They summarized gene conservation work and also the level of effort

---

Director, NFGEL, National Forest System, Camino, CA

As a case for the existence of a multiple population breeding structure', the loblolly pine breeding populations are examined for structure, population size and breeding direction.

Loblolly pine is planted extensively in the southeastern United States. Breeding programs, that provide improved genetic material for planting, are largely conducted cooperatively in the United States by the North Carolina State University-Industry Cooperative Tree Improvement Program (NCSU-ICTIP) and the WGFTIP. The USDA Forest Service conducts an independent program in the southern United States (Region 8). Additionally, loblolly pine is planted as an exotic species in Argentina, Australia, Brazil, China, New Zealand and South Africa, with the greatest representation of native provenances being represented in Brazil, China and South Africa (Rogers and Ledig 1996). The genetic resource of loblolly pine, being developed in various programs around the world, is listed in Table 1.

### *Loblolly Pine – Indigenous Breeding Programs*

Cooperative breeding populations are on-going in the United States with both the NCSU-ICTIP program (McKeand and Bridgwater 1998, Hatcher 1998) and with the WGFTIP program (Lowe and van Buijtenen 1986). Both of these cooperatives are funded by dues-paying members, with genetic material and testing results remaining the property of cooperative members. In both programs, selection is for saw timber and/or pulpwood products, and field-testing is on operational and/or old agricultural fields. The NCSU-ICTIP program includes genotypes from Maryland to Louisiana, and both Coastal Plain and Piedmont provenances. This genetic material is bred in sublines for eight regions, and third-generation selections are being made. Specialty populations exist to preserve special seed sources and to generate new genetic variation, such as in elite populations. Gene conservation is the focus of the genetic diversity archives, in which all selections are preserved (Bailian Li<sup>b</sup> personal communications). The WGFTIP loblolly program includes genotypes sampled from Mississippi west to east Texas and north into Oklahoma and north Arkansas. This program is currently completing field-testing of first-generation selections with six regional populations in sublines. In addition to the breeding regions, there are specialty populations for drought hardiness and for high wood density (Bill Lowe' personal communications). The WGFTIP has a gene conservation plan that relies on preservation in grafted clone banks with a stated commitment to their preservation (Bryam *et al.* 1999 in press). Information on these genotypes is available on the Internet(8) .

The USDA Forest Service Region 8 breeding program for loblolly pine was developed as six separate breeding populations (Wells and McConnell 1984). Natural stand and some plantation selections in national forests, which are in general not represented in collections by cooperative efforts, were completed in 1990. The 934 selections were made across the southeastern USA (Anonymous 1994), with intensive selection criteria, consistent with those used by industry, for growth, straightness and fusiform rust resistance (Table 1). Since 1995, the loblolly (and slash) pine breeding populations are no longer progressing. Genetic material remains in selected progeny tests or in selected seed orchard blocks; although there are no plans to regenerate original selections in aging seed orchards. Emphasis has shifted to gene conservation, in particular for species that are at risk or to species within at risk ecosystems, although active tree improvement programs do remain for some species (Jay Kitzmiller<sup>9</sup> personal communications, Richard

---

<sup>5</sup> The collection of populations is a "structure", rather than a "system" since the populations were not intentionally designed nor are they to be maintained as a "system" (Richard Barnes of Oxford Forestry Institute personal communications).

NCSU-ICTIP Associate Director, Raleigh, NC

WGFTIP Geneticist, College Station, TX

<http://www.ars-grin.gov/misc/wgftip/index.html>

<sup>9</sup> Regional Geneticist, Pacific Southwest Region (R-5), Genetic Resource Center, Chico, CA.

**Table 1.** Assessment of loblolly pine genetic resources.

Country: Program (Contact)	Provenance Sources	Breeding Status	Selection Criteria	Population Structure No. Sublines	Total Population Size (Avg. size)	Germplasm Preservation Methods	Information Access
Indigenous Programs							
USA: NCSU-ICTIP cooperative (Baillian Li, McKeand and Bridgwater 1998, Hatcher 1998)	Coastal Virginia through the upper and lower Gulf Coastal plain in MS.	1950's 1st cycle selections; 1970's 2nd cycle selections; 1999 completing 2nd cycle field testing with completion of 3 <sup>rd</sup> cycle selections by 2003. Special populations for elite breeding of cold hardiness and growth traits and also for geographic recombination.	Growth, form, fusiform rust resistance & wood density; cold hardiness in Piedmont.	8 separate regions.	3834 2nd cycle (480/region).	Clonal seed orchards, clone banks and progeny tests. Genetic archiving of all genetic material.	Genetic material, pedigree and breeding value: Not publicly available.
USA: WGFTIP cooperative (W.J. Lowe, Lowe and van Buijtenen 1986)	Arkansas, Louisiana, Mississippi, Oklahoma, and Texas sources.	1950's 1' cycle selections; 1969 cooperative organized; 1999 completing 1st cycle field testing. Special populations for drought hardiness and for wood density.	Volume, form, disease resistance.	6 regions, 115 total sublines (25 trees/subline).	3000 1" gen (500/region); 2" gen 170/region at this point.	Clone banks.	Genetic material, pedigree and breeding value: Not publicly available.
USA: USDA FS Region 8 (Tom Tibbs, Anonymous 1994)	NC to east Texas, both Coastal and Piedmont sources.	1995 1" cycle selections but only few 2" cycle selections, program halted.	Growth, form and fusiform rust resistance.	6 separate populations, independent of cooperative programs.	934 1st gen (156/region).	Clonal seed orchards, clone banks, progeny tests.	Genetic material, pedigree and breeding value: publicly available.
Exotic Programs							
Argentina: CIEF cooperative (BB&W 1997, Báez 1997)	Plantations with unknown sources; 1968 & 1982 prov trials, n-FL & s-LA sources preferred; 1990 USFS n-FL and LA sources 44 OP families & 100 controlled crosses from e-TX to e-NC; Southern Africa introductions; 1997 new collection planned.	1984 cooperative formed; 1986 - 1997 1' cycle selections made.	Volume growth & straightness (pulp and solid wood).	12 sublines.	600 1' gen (50/subline).	Clonal seed orchards, OP progeny tests.	--

Table 1. (Continued)

Country: Program (Contact)	Provenance Sources	Breeding Status	Selection Criteria	Population Structure (No. Sublines)	Total Population Size (Avg. size)	Germplasm Preservation Methods	Information Access
Australia: Queensland & New South Wales state programs (Garth Nikles, Mark Dieters, BB&W 1997)	1917 North of Ocala NF (FL); 1936 Australian land race development from ne FL, se GA and n Ocala NF was initiated; 1955 SSPSS 13 prov; 1956 test of Marion Co, FL source, Marion Co. surpassed land race in growth but not stem straightness.	1940s mass selection implemented; 1953 planting stopped on coastal lowlands; 1967 CSO from land race selections with of ne FL - se GA origin; late 1970's planting stopped on subcoastal uplands; 1994 CSO destroyed by wildfire; 1997 OP PT USA and South African sources; 1999 little to no planting.	Stem straightness, secondly on vigor.	No breeding program, only one OP PT left intact.	N/A.	Small plantations and plots still exist. CSO grafts of land race selections effectively lost to fire.	No structured genetic material remains in QLD; archived information is available pending retrieval expense.
Brazil: former IPEF cooperative and private industries (Jarbas Shimizu, Heuzer Guimaraes, BB&W 1997)	1940 early plantations unknown origin; 1960's majority of plantations still with unknown origin; 1975 - 1982 provenance and family trials from WGFTIP and NCSU-ICTIP with FL, LA, coastal SC, and coastal GA, preferred; Zimbabwean and South African land race OP seed.	1978 CSO with 1" gen selections, now rogued; 1993 cooperative for loblolly pine disbanded; some companies with 1 <sup>st</sup> cycle CSO while others field testing 2nd cycle selections.	Vigor, volume, stem straightness, form, wood density and adaptability.	6 populations, separate by company.	100 1 <sup>st</sup> gen /population, unknown number of 2" gen selections.	Clonal seed orchard, clone banks, and field trials.	Access is according to individual companies.
China: national program, 21° N to 33° N (BB&W 1997, Bridgwater 1997)	1920's initial introduction; 1974 unknown origin; 1981 prov trial (unimproved); 1983 1 <sup>st</sup> gen SO lots from SE USA & cold hardy lots; 1988/9 limited range collection; 1989 SO lots from Australia and Zimbabwe; 1995 & 1996 USDS-FS controlled crosses from SE USA. Preferred sources south of 32° N n FL, s GA, AL, MS, LA; coastal GA and SC to 34° N; Piedmont or upper coastal where freeze damage occurs	1983 first clonal seed orchard; 1997 more orchards being established with preferred selections (1 <sup>st</sup> , 1.5 and 2" gen orchards); elite population exists; 1997 breeding strategy designed, 1 <sup>st</sup> gen selections being made.	Fast growth and form; no fusiform rust selection pressure.	One breeding region, sublines of size 20.	Not known at this time.	CSO and clone banks.	--

Table 1. (Continued)

Country: Program (Contact)	Provenance Sources	Breeding Status	Selection Criteria	Population Structure (No. Sublines)	Total Population Size (Avg. size)	Germplasm Preservation Methods	Information Access
New Zealand: national program, 38° S (Rowland Burdon)	1912 initial introduction of unknown origin; 1955 prov trial, Queensland, Australian land race (n Fl origin) preferred.	NZ land race from initial introductions; no breeding program developed due to preference for radiata pine in plantations.	Growth, tree form and wood density.	N/A.	N/A.	1996 less than 500 ha plantations remain; some remaining grafts of Queensland land race selections.	N/A.
Southern African: South Africa national program (CSIR & SAFCOL, formerly Dept. of Water and Forestry), Zimbabwean national program and private industries (Steve Verryn, Marianne Hettasch, Isaac Nyoka, Richard Barnes, Eric Kietzka, BB&W 1997)	South Africa 1880's initial introduction of unknown origin; 1901 & 1930 unidentified seedlots; Zimbabwe 1920 trial plots of South African seed; South Africa 1931 & 1932 GA and LA sources; Zimbabwe and South Africa 1960-69 Improved seed from TX, AL, FL, GA, SC, NC, preferred southern-most provenances not in original introductions; 1971 Marion Co, FL source imported as resource stands.	South African Land race, sent to other southern African countries. South African and Zimbabwean National: 1959 selection of plus trees, CSO, progeny tests; mid-1960's - 1983 progeny tests; 2" gen selections, none tested. Private industry: 1968 1" gen selections made; 1974-96 2" gen selections, clone banks, CSO and progeny tests. Mid-1980's cessation of planting species In South Africa: "bottle-shaped" trees, abnormal wood, drought proneness, baboon damage and susceptibility to black aphid ( <i>Cinara cronartii</i> ). 1999 South African national breeding on hold; Zimbabwean breeding strategy recently completed; private industry 2" gen progeny testing. 1999 loblolly planting likely to increase.	Volume, stem form, crown form, wood density, resistance to abnormal wood; resistance to introduced aphid pests.	MPBS in Zimbabwe with 7 2" gen sub-populations, 1" gen was one population; 3 other breeding populations.	Total of 702- 1" gen; total of 646 - 2" gen.	CSO, progeny tests, clone banks.	Zimbabwe: available without charge pending request.--

Abbreviations used above

BB&amp;W 1997 - Bridgwater, Barnes and White 1997

CSO - clonal seed orchard

Gen - generation

MPBS - multiple population breeding structure

N/A - not applicable

NF - National Forest (referring to the United States National Forest)

OP - open pollinated

Prov Trial - provenance trial

PT - progeny test

SSPSS - Southwide Southern Pine Seed Source (trial)

Meier(10) personal communication, Tom Tibbs' personal communications). The pedigree, genetic material and breeding value information are public knowledge and are available(12).

### *Loblolly Pine – Exotic Breeding Programs*

Three countries, Argentina, Brazil and China, each have active breeding and deployment programs for loblolly pine.

The Argentinean loblolly population is a cooperative effort (Baez and White 1997). A first-generation breeding population of 600 selections was assembled from introduced seedlots of various provenances. Primary emphasis was on selections arising from the Florida and Livingston Parish sources (70%). Selections were also made in commercial plantations with unknown origin (20%), other American provenances (5%) and South African and Zimbabwean sources (5%). Open pollinated and control pollinated seedlots were received from the USDA Forest Service, contributing both to preferred and other USA provenances (Bridgwater *et al.* 1997). Clonal seed orchards preserve the selections and progeny tests will be converted to seedling seed orchards. Volume growth and stem straightness were the primary selection criteria (Baez and White 1997).

Several companies in Brazil plant loblolly pine derived from land race populations. Currently there are six populations that were developed both by individual company and cooperative efforts, the latter no longer existing (Bridgwater *et al.* 1997, Jarbas Shimizu(13) communications). These tree improvement programs are based on provenance test results, with the Florida, Louisiana, coastal South Carolina and coastal Georgia sources being preferred. Selections were predominantly from these preferred provenances, but other provenances are also represented in the selections. Selection criteria for these programs were for growth and form traits, but without any pressure on resistance to fusiform rust infection. The level of advancement differs by company (Jarbas Shimizu personal communications).

Loblolly pine has also been imported into China, including large provenance studies and the development of breeding programs. The effort is coalescing with the knowledge of preferred sources for the various growing regions of China. One breeding population is being developed with a number of sublines based on different preferred provenances. Initial introductions, upon which the Chinese land race was based, are inferior to the recent selections from preferred provenances (Bridgwater *et al.* 1997, Bridgwater(15) personal communications).

In Australia, New Zealand and southern Africa, loblolly pine has been planted and evaluated but is no longer commercially planted or is planted on a much reduced scale.

Loblolly pine was introduced to Queensland, Australia in 1917 to provide for future wood supply, particularly for the infertile coastal lowlands where indigenous hoop pine (*Araucaria cunninghamii*) could not be grown. The initial Australian land race, developed from introductions originating just north of the Ocala National Forest, northeast Florida and southeast Georgia, was later found to be inferior in growth to

---

<sup>10</sup> Regional Geneticist, Northeastern Region (R-9)  
USDA Forest Service, Region 8, Atlanta, GA.

<sup>12</sup> Personal communication from Elizabeth Estill, Regional Forester, USDA Forest Service, Atlanta, GA, to Stephen Coleman, Boise Cascade, Jackson, AL, August 11, 1998.

EMBRAPA-Florestas (Centro Nacional de Pesquisa de Florestas), Parana, Brasil.

Rigesa, Forest Research Director, Tres Barras, Santa Catarina, Brasil.

<sup>15</sup> USDA Forest Service, College Station, TX.

Marion County, Florida sources. Loblolly pine plantation establishment on coastal lowlands halted in 1953 due to poor performance on phosphate-deficient sites; until that time breeding efforts were just as intensive as those accorded to slash pine (Haley 1957). Plantings on subcoastal uplands continued on a small scale until the late 1970's. A clonal seed orchard, established in 1967 with pedigreed selections originating from the initial land race, was destroyed by fire in 1994. Some plantations and plots and one recent open-pollinated progeny test still exist. Selections were shared with the New South Wales state program, where substantial plantations still exist. (Information from Bridgwater *et al.* 1997, Garth Nikles<sup>(16)</sup> personal communications, Mark Dieters<sup>(17)</sup>;

Loblolly pine was introduced to New Zealand with the oldest plantation established in 1912 (Rogers and Ledig 1996, Box 9). Fewer than 500 ha of plantations now exist, which are of unknown seed origin. Radiata pine is the preferred plantation species and consequently there is no breeding effort for loblolly pine (Rowland Burdon<sup>(18)</sup> personal communications). An interesting story, however, arises from a provenance trial established in 1955 that covered the range of native loblolly pine, plus Queensland, Australia and New Zealand land races. Results were consistent with provenance differences reported elsewhere, with coastal and southern sources growing the fastest, northern and western sources growing more slowly. The Queensland land races (derived from northern Florida sources) were preferred due to improved growth and stem form from the one generation of selection (Shelbourne 1971 unpublished).

The South African loblolly pine land race, originating from unknown sources introduced in the late 1880's, was found suboptimal through subsequent provenance testing (Bridgwater *et al.* 1997). Material from this program has been sent to various other countries in southern Africa. Despite high production on fertile sites with adequate rainfall, problems with wood abnormalities, site requirements and baboons in the early 1980's halted the planting of loblolly pine in South Africa, and consequently the breeding by the South African national program (9) (Steve Verry and Marianne Hettschi<sup>(20)</sup> ;

personal communications, Bridgwater *et al.* 1997). Control of the pest responsible for the abnormal wood is likely to increase the planting of loblolly pine in both South Africa and Zimbabwe, replacing patula pine (*Pinus patula* Schiede and Deppe) on good sites at medium altitudes (Richard Barnes personal communications). A multiple population breeding system has recently been established for the Zimbabwean second-generation population (Isaac Nyoka<sup>(22)</sup> personal communications). Private companies operate two independent breeding programs that are still ongoing (Eric Kietzka<sup>(23)</sup> personal communications, Richard Barnes personal communications).

### *Loblolly Pine - Meta-Breed Resource*

The three indigenous programs comprise twenty different breeding populations that differ in terms of original seed sources sampled, and in independent sampling in same areas. The two cooperative programs sampled separate areas of the loblolly pine range. The USDA Forest Service Region 8 program sampled different stands within the same range of the two cooperative programs. Additionally the two cooperative programs are advancing in breeding cycles for the selection of genotypes (and their alleles) that are suitable for specific planting areas. In total there are 7768 selected genotypes in 20 separate populations, with most of these genotypes preserved. Additional genetic material is preserved in progeny tests or provenance trials.

<sup>16</sup> Senior Principal Research Scientist-Genetic Resources, Queensland Forest Research Institute (QFRI), Australia.

<sup>17</sup> Principal Geneticist, Tree Improvement Group, Queensland Forestry Research Institute, Australia.

<sup>18</sup> New Zealand Forest Research Institute, Rotorua, New Zealand.

<sup>19</sup> Department of Water and Forestry, now operated by SAFCOL and CSIR jointly.

<sup>20</sup> CSIR, Pretoria, South Africa.

<sup>21</sup> Oxford Forestry Institute, Oxford, United Kingdom.

<sup>22</sup> Manager, Research and Development, Forestry Commission, Highlands, Harare. Zimbabwe

<sup>23</sup> Tree Breeder, Tree Improvement Research, Mondi Forests, Pietermaritzburg, South Africa



The various exotic loblolly pine populations are not necessarily independent in terms of the germplasm sampled from the three indigenous programs, since the exotic populations were initiated with some seedlots from these programs. However, forward selections were indeed made with differential selection criteria in each of the environments. The actively advancing programs are those in Argentina, Brazil and China, which include eight independent breeding populations with at least 1200 selections clonally preserved. In addition, the four southern Africa first-generation populations contain approximately 702 clonally preserved selections. This array of separate programs has a number of independent selection criteria advancing the initial populations away from the unimproved or introduced populations, such that different allelic combinations are being selected for and differential arrays of mutations may occur across these populations. A recent report of five alleles in the Zimbabwe loblolly pine population, which are not present in the ancestral populations, illustrates this point (Williams *et al.* in review). These differences arise from both different selection criteria and environmental conditions. For example, no selection emphasis is placed on fusiform rust resistance in Brazil, southern Africa or China whereas resistance is part of the NCSU-ICTIP criteria within the same provenance sources. Analogously, drought resistance is important for loblolly in Texas compared to wet soil adaptability in eastern North Carolina and selection for wood quality and resistance to aphids are paramount to the future of loblolly pine in southern Africa.

Industry has contributed a substantial portion to the loblolly pine meta-breed. Genetic variation, the source of future genetic gain, is being increased through this multiple population structure. Worldwide, roughly 9,670 select trees are clonally preserved in 32 breeding populations at this time. The entire range of loblolly pine, including outlying populations, has been sampled and differential selection criteria (both trait and environment) are being applied to the individual breeding populations around the globe. Since the individual programs are separately funded, there is no foreseeable situation when they would be merged and overall genetic variation contained by the meta-breed reduced. Private funding of many of these breeding efforts has resulted in limited public access to the resulting resource, although the USDA Forest Service genetic material and information remain publicly available. The loblolly pine genetic resource is well conserved, with industry moving populations into advanced generations.

### Germplasm Conservation Methods

The most common form of germplasm conservation has been grafting selections in clone banks. The specific genotype is grafted in one or more locations, although not maintained necessarily for seed production. Early in tree improvement, there were not clone banks *per se*, instead selections (with no progeny test information) were grafted into clonal seed orchards. The disadvantage of this strategy was that as progeny test information accumulated and poorer genotypes were removed from the orchards, these genotypes were not maintained. Later, as research in forest genetics progressed and there was a need to access genotypes with unique or poor characteristics, many such genotypes did not exist. Consequently, the separation of germplasm preservation from deployment gains has been realized with establishment of a few ramets of all genotypes in clone banks, as compared to many ramets of few genotypes in seed orchards.

Progeny tests also contain the genes in the population, and are used as a gene conservation method, for example in the USDA Forest Service Region 8 loblolly program. Seed collections are stored in many other types of gene conservation programs, however, these genes are not necessarily packaged in the most advantageous form unless a select tree is identified from the resulting seed. There is greater emphasis from an industrial view on maintaining genotypes with known performance information, such as growth traits or disease resistance (or susceptibility). Clone banks offer this possibility. In addition to clone banks, other forms of genotype preservation, such as tissue culture or cryopreservation are possible, particularly with material started through a vegetative propagation effort (Ahuja 1997).

Provenance resource stands (PRS) were developed for *Pinus caribaea* var *Hondurensis* in Queensland, Australia (Nikles and Newton 1984, Nikles 1984) as a means to broaden the inherent genetic variation available for the development of this exotic species. These plantings of known provenances (recorded on maps) over a large land area can be used as a genetic resource for the breeding program.

These efforts are indeed forms of germplasm preservation. A grafted clone bank on its own is a stagnant situation. However, in conjunction with an active tree improvement program, new selections (either offspring or parental) that are grafted into clone banks add to the overall composition and collection of genotypes preserved and enhanced.

### **Advantages of Clone Banks (Genotype Preservation)**

There is indeed a direct economic purpose for the establishment of clone banks. A large investment of money has been made in determining the breeding values of these genotypes. The information can be kept and retrieved. If a genotype is, at some point in time, desired but has not been maintained, the effort to test the genotype has not yielded a direct benefit. For example, by preserving all genetic material, the opportunity exists to use selections for a pollen mix that was not part of the breeding population. As land bases change, trees that were not previously wanted for plantation seed sources have become desirable. For example, as Westvaco's landbase has shifted northward in the interior part of the United States, cold hardiness in loblolly pine has become more important. Although genotypes were previously rogued from production orchards due to other undesirable traits, they were still available in clone banks. In other examples, not all first-generation parent genotypes existed when they were later needed, hence the desire to preserve this genetic material in well-documented clone banks.

A corollary to this practice of clone banking genetic material is that if it is preserved at several locations then the probability of losing the genotype due to insects, diseases or catastrophes is reduced. For example, Hurricane Hugo decimated the USDA Forest Service Region 8 Francis Marion genetic conservation areas for breeding populations 4 and 5, which were not grafted elsewhere (Anonymous 1994). Grafting parents at several locations is also beneficial for breeding purposes. Pollen can be collected from within a clone bank or can be collected earlier from more southern clone banks and used fresh.

### Utilization and Commercialization

The driving force for gene conservation by industry is to be able to plant adaptable, consistent high productivity planting stock with desirable quality characteristics that will yield healthy, high performing stands at rotation. To avoid the risk of plantation failure, diversity of planting stock via diversity of pedigree is a guiding factor in the choice of planting stock (McCutchan *et al.* 1994). Additionally, with many plantations being established in family blocks (most commonly, open-pollinated families), diversity of the mitochondrial DNA (maternally inherited in loblolly pine according to Neale and Sederoff in 1989) is an issue affecting risk. The benefit of genetic preservation is that access to genetic material to meet the needs of the operational landbase is maintained.

Access to genetic material with known performance by industry is important for either basic research or commercialization opportunities. Progeny carrying a mutant lignin allele were found to have increased stem elongation (Wu *et al.* in press). The genetic control of loblolly pine wood specific gravity is being studied based on crosses of high by low value grandparents (Knott *et al.* 1997). Further, genetic material with a particular array of desirable traits can be subjected to transformation, with the resulting transformants propagated for commercialization. Recently, a joint venture among Westvaco, International Paper, Monsanto and Fletcher Challenge was announced with this purpose (April 6, 1999 news release).

## NONCOMMERCIAL SPECIES

Noncommercial species are omitted from the industrial perspective for gene conservation due to a lack of benefit from the efforts required to conserve genetic material. Selection of genotypes and subsequent characterization or maintenance efforts require funding. If it is not possible to plant a species in a widespread fashion or to meet a given level of return on investment, then there is no interest in developing that species.

Lack of interest by industry in the active gene conservation for particular forest tree species does not, however, indicate no future commercial interests nor lack of importance in an ecosystem. There are several tree species in southeastern forests that are at risk due to introduced pests (Fryar 1996, page 128 - 129). Without intervention, species could be lost via introduced pests or pathogens. An example is the elimination of butternut (*Juglans cinerea* L.) by the exotic fungus *Sirococcus clavigigentijuglan-daceareum* that causes a lethal canker. The USDA Forest Service Region 8 is doing limited work on species under imminent threat, also called at-risk species. An example includes the work being done with flowering dogwood (*Cornus florida* L.) that is endangered by anthracnose (Tom Tibbs personal communications). In a separate assessment of North American temperate forest genetic resources, Rogers and Ledig (1996) point out that there may be future commercial interests in what are now noncommercial species. The case is made with the Pacific yew (*Taxol brevifolia* Nutt.) that was valueless until taxol from the bark was found to be effective in treating cancer (Rogers and Ledig 1996, page 3 and Box 1). Most North American forest tree species are managed *in situ* (Rogers and Ledig 1996). Additionally, land use regulations, such as in wetland or wildlife areas, and natural regeneration result in leaving stands of a variety of species, but not in a coordinated effort or conscience manner. Reliance is consequently placed on public agencies to provide gene conservation of noncommercial species (Namkoong 1986).

## CONCLUSIONS

Gene conservation efforts for commercial species are in the interest of industry. Commercial species are being developed in a number of breeding programs about the world, each with differential selection criteria, resulting in a global multiple population breeding structure for these species. The populations are collectively large, sample a range of native stands and are likely to diverge in subsequent breeding populations. A case study is presented for the loblolly pine populations. This is a clonally preserved population, where information on pedigree and performance is also being collected for these genotypes. This species has approximately 32 populations totaling approximately 10,000 selections. Germplasm conservation is consequently in good state for this species. Since these selections were developed in the context of a breeding population, both pedigree and performance information is developed in this process. Genetic material and information derived through private funding, however, remains privately held.

The caveat to the private funding of gene conservation by industry is the lack of motivation to provide a genetic resource for unspecified purposes to future generations. Lacking collective gene conservation efforts among all industrial concerns, there are no future plans once a species falls from commercial interests. Gene conservation efforts from industry for noncommercial species *per se* do not exist, although species are being conserved in special land use areas and by natural regeneration. There is no financial motivation to conserve genetic material that does not contribute to the bottom line of the industry. Exception to this would be noncommercial species containing genes that could be used in creating transgenic plants. Fortunately, the USDA Forest Service is focusing their gene conservation efforts on at-risk species, which may be a valuable resource in the future for industry.

## ACKNOWLEDGMENTS

The support of Westvaco Corporation in the writing and presentation of this paper is appreciated; the review comments of Dave Gerwig, Victor Steel, Randy Rousseau and Bill Hammond were helpful. The following persons graciously provided information on loblolly pine populations and also valuable review comments: Bailian Li (NCSU-ICTIP, USA); Tom Tibbs (USDA-FS Region 8, USA); Bill Lowe (WGFTIP, USA); Tim White (University of Florida) for Argentina; Garth Nikles and Mark Dieters (QFRI, Australia); Heuzer Guimarães (Rigesa) and Jarbas Shimizu (EMBRAPA) for Brazil; Floyd Bridgwater (USDA-FS) for China; Rowland Burdon (NZFRI, New Zealand); and Richard Barnes (Oxford Forestry, Institute), Steve Verryn and Marianne Hettasch (CSIR), Eric Kietzka (Mondi Forests) and Isaac Nyoka (Forestry Commission, Zimbabwe) for southern Africa.

## LITERATURE CITED

- Ahuja, R. M. 1997. Biotechnology in Forestry: Expectations and Challenges. Pp. 45-56 in *Perspectives of Forest Genetics and Tree Breeding in a Changing World. I. Aspects of Tree Breeding* (Sopron, Hungary. Vienna, Austria: International Union of Forestry Research Organizations).
- Anonymous. 1994. Chapter 10 - Genetic Resource Plans. *Forest Service Handbook 2409.26g - Tree Improvement Handbook, Region 8 Amendment 2409.26g-94-I*.
- i
- Northeast Region of Argentina. Pp. 110-117 in *Proceedings of the 24th Biennial Southern Forest Tree Improvement Conference* (Orlando, Florida).
- Balocchi, C. E. 1996. Gain Optimisation Through Vegetative Multiplication of Tropical and Subtropical Pines. Pp. 304-6 in *Tree Improvement for Sustainable Tropical Forestry, QFRI - IUFRO Conference, Caloundra, Queensland, Australia, 27 October -1 November 1996* (Caloundra, Queensland, Australia. Gympie, Queensland, Australia: Queensland Forestry Research Institute).
- Behm, A., A. Becker, H. Dorflinger, A. Franke, J. Kleinschmit, G. H. Melchior, H.-J. Muhs, H. P. Schmitt, B. R. Stephan, U. Tabel, H. Weisgerber, and TH. Widmaier. 1997. Concept for the Conservation of Forest Genetic Resources in the Federal Republic of Germany. *Silvae Genetica* 46(1):24-34.
- Boomsma, D. 1997. Development of the Southern Tree Breeding Association Radiata Pine Breeding Population. Pp. 211-16 in *Proceedings of IUFRO '97 Genetics of Radiata Pine, Conference, 1-4 December 1997, Workshop 5 December 1997, IUFRO Working Party S2.02. 19, Pinus Radiata Provenances and Breeding, Rotorua, New Zealand* (Rotorua, New Zealand. Rotorua, New Zealand: New Zealand Forest Research Institute Ltd).
- Bridgwater, F. E. 1997. Consultancy on Breeding Theory and Strategy and Establishment and Management of Advanced Seed Orchards of Slash Pine and Loblolly Pine, October 3 - October 18, 1997. *United Nations Development Program, Project of the Government of the People's Republic of China, Project Number CPR/91/I 53*.
- Bridgwater, F. E., R. D. Barnes, and T. White. 1997. Loblolly and Slash Pines As Exotics. Pp. 18-32 in *Proceedings of the 24th Biennial Southern Forest Tree Improvement Conference* (Orlando, Florida).
- Byram, T. D., W. J. Lowe, and G. D. Gooding. 1999 in press. Western Gulf Forest Tree Improvement Program Gene Conservation Plan for Loblolly Pine. *Forest Genetic Resources*.
- Burdon, R. D. 1986. Clonal Forestry and Breeding Strategies - A Perspective. Pp. 645-59 in IUFRO Conference, A Joint Meeting of Working Parties on Breeding Theory, Progeny Testing and Seed Orchards (Williamsburg, Virginia, R. J. Weir. Raleigh, NC: North Carolina State University - Industry Cooperative Tree Improvement Program).
- Burdon, R. D., M. H. Bannister, H. A. I. Madgwick, and C. B. Low. 1992. Genetic Survey of *Pinus Radiata*. 1: Introduction, Description of Experiment, and Basic Methodology. *New Zealand Journal of Forestry Science* 22(2/3):119-37.

- Burdon, R. D. and G. Namkoong. 1983. Short Note: Multiple Populations and Sublines. *Silvae Genetica* 32(5-6):221-22.
- Critchfield, W. B. and E. L. Little, Jr. 1966. Geographic Distribution of the Pines of the World. *U.S. Department of Agriculture Forest Service Misc. Pub. 991*.
- Committee on Managing Global Genetic Resources: Agricultural Imperatives, Subcommittee on Managing Plant Genetic Resources Forest Genetic Resources Work Group Board on Agriculture National Research Council. 1991. Managing Global Genetic Resources. Forest Trees. Washington, D.C.: National Academy Press.
- Eldridge, K. G. 1997. Genetic Resources of Radiata Pine in New Zealand and Australia. Pp. 26-41 in *Proceedings of IUFRO '97 Genetics of Radiata Pine, Conference, 1-4 December 1997, Workshop 5 December 1997, IUFRO Working Party 52.02.19, Pinus Radiata Provenances and Breeding, Rotorua, New Zealand* (Rotorua, New Zealand. Rotorua, New Zealand: New Zealand Forest Research Institute Ltd).
- Fryar, R. 1996. Genetic Conservation Programs. Pp. 129-31 in *Southern Appalachian Man and the Biosphere (SAMAB) The Southern Appalachian Assessment Terrestrial Technical Report, Report 5 of 5*, Atlanta, GA: U.S. Dept. of Agriculture, Forest Service, Southern Region.
- Haley, C. 1957. The present status of tree breeding work in Queensland. QLD. For. Dept. Paper to Seventh British Commonwealth Forestry Conference, 23pp.
- Hamrick, J. L., M. J. W. Godt, and S. L. Sherman-Broyles. 1992. Factors Influencing Levels of Genetic Diversity in Woody Plant Species. *New Forests* 6:95-124.
- Hancock, J. 1998. Critical Issues Involving Crop Germplasm Diversity and Conservation: Introduction to the Colloquium. *HortScience* 33(7):1120-1121.
- Hansen, C. P. 1996. Making Available Information on the Conservation and Utilisation of Forest Genetic Resources: the FAO World-Wide Information System on Forest Genetic Resources. Pp. 37-41 in *Tree Improvement for Sustainable Tropical Forestry, QFRI - IUFRO Conference, Caloundra, Queensland, Australia, 27 October - 1 November 1996, Volume 1* (Caloundra, Queensland, Australia. Gympie, Queensland, Australia: Queensland Forestry Research Institute).
- Hatcher, A. 1998. Cooperative Database Documentation. *N. C. State University - Industry Cooperative Tree Improvement Program*.
- Jayawickrama, K. J. S. and L. C. Balocchi. 1993. Tree Improvement in Chile: Two Decades of Progress. *Journal of Forestry* 91(6):43-47.
- Jayawickrama, K. J. S., M. J. Carson, P. A. Jefferson, and A. Firth. 1997. Development of the New Zealand Radiata Pine Breeding Population. Pp. 217-25 in *Proceedings of IUFRO '97 Genetics of Radiata Pine, Conference, 1-4 December 1997, Workshop 5 December 1997, IUFRO Working Party S2.02.19, Pinus Radiata Provenances and Breeding, Rotorua, New Zealand* (Rotorua, New Zealand. Rotorua, New Zealand: New Zealand Forest Research Institute Ltd).
- Kellison, R. C., G. Leach, and M. Young. 1996. A Tree Improvement Plan for Sweetgum and Sycamore in the Southern United States. *North Carolina State University Hardwood Research Cooperative, Raleigh, NC, Working Document*.
- Knott, S. A., D. B. Neale, M. M. Sewell, and C. S. Haley. 1997. Multiple Marker Mapping of Quantitative Trait Loci in an Outbred Pedigree of Loblolly Pine. *Theoretical and Applied Genetics* 94(6 / 7):810-820.
- Koshy, M. P. and G. Namkoong. 1996. Futuristic Breeding - Some Plausible Options. Pp. 333-37 in *Tree Improvement for Sustainable Tropical Forestry, QFRI - IUFRO Conference, Caloundra, Queensland, Australia, 27 October - 1 November 1996* (Caloundra, Queensland, Australia. Gympie, Queensland, Australia: Queensland Forestry Research Institute).
- Libby, W. J. 1973. Domestication Strategies for Forest Trees. *Canadian Journal of Forest Research* 3:265-276.
- Lowe, W. J. and J. P. van Buijtenen. 1986. The Development of a Sublining System in an Operational Tr Improvement Program. Pp. 98-106 in *IUFRO Conference, A Joint Meeting of Working Parties o*

- Breeding Theory, Progeny Testing and Seed Orchards* (Williamsburg, Virginia, R. J. Weir. Raleigh, NC: North Carolina State University - Industry Cooperative Tree Improvement Program).
- McCutchan, B. G., C. B. Talbert, T. L. White, and F. E. Bridgwater. 1994 Presentation & Abstract. Regulations and Trends Worldwide in Genetic Deployment of Commercial Forest Plantations. *Southern Region Information Exchange Group Meeting, 'Genetic Diversity in Commercial Forest Tree Plantations'* (Clemson University, Clemson, South Carolina).
- McKeand, S. E. and F. E. Bridgwater. 1998. A Strategy for the Third Breeding Cycle of Loblolly Pine in the Southeastern U.S. *Silvae Genetica* 47(4):223-34.
- Namkoong, G. 1976. A Multiple-Index Selection Strategy. *Silvae Genetica* 25(5-6):199-201.
- \_\_\_\_\_. 1984a. A Control Concept of Gene Conservation. *Silvae Genetica* 33(4-5):160-163.
- \_\_\_\_\_. 1984b. Strategies for Gene Conservation in Forest Tree Breeding. Pp. 79-89 in *Plant Genetic Resources, A Conservation Imperative*, Editor C. W. Yeatman, D. Kafton, and G. Wilkes. Boulder, Colorado: Westview Press, Inc.
- \_\_\_\_\_. 1986. Genetics and the Forests of the Future. *Unasylva* 38(152):2-18.
- \_\_\_\_\_. 1997. A Gene Conservation Plan for Loblolly Pine. *Canadian Journal of Forest Research* 27(3):433-37.
- Namkoong, G., R. D. Barnes, and J. Burley. 1980. A Philosophy of Breeding Strategy for Tropical Trees. *Tropical Forestry Papers. No. 16, Department of Forestry, Commonwealth Forestry Institute*:67 pp.
- Namkoong, G. and M. P. Koshy. 1997. Managing the Genetic Variance. Pp. 9-16 in *Perspectives of Forest Genetics and Tree Breeding in a Changing World. I. Aspects of Tree Breeding* (Sopron, Hungary. Vienna, Austria: International Union of Forestry Research Organizations).
- Neale, D. B. and R. R. Sederoff. 1989. Paternal Inheritance of Chloroplast DNA and Maternal Inheritance of Mitochondrial DNA in Loblolly Pine. *Theoretical and Applied Genetics* 77:212-16.
- Nikles, D. G. 1984. Broadening the Genetic Base: A Case Study With *Pinus Caribaea* Var. *Hondurensis* in Queensland. Pp. 571-73 in *Provenance and Genetic Improvement Strategies in Tropical Forest Trees* (Mutare, Zimbabwe, Editors R. D. Barnes and G. L. Gibson. Oxford, England and Forest Research Centre, Harare: Commonwealth Forestry Institute).
- \_\_\_\_\_. 1996. The First 50 Years of the Evolution of Forest Tree Improvement in Queensland. Pp. 51-64 in *Tree Improvement for Sustainable Tropical Forestry, QFRI - IUFRO Conference, Caloundra, Queensland, Australia, 27 October - 1 November 1996, Volume I* (Caloundra, Queensland, Australia. Gympie, Queensland, Australia: Queensland Forestry Research Institute).
- Nikles, D. G. and R. S. Newton. 1984. Provenance Resource Stands (PRSSs) of *Pinus Caribaea* Var. *Hondurensis* in Queensland. Pp. 582-83 in *Provenance and Genetic Improvement Strategies in Tropical Forest Trees* (Mutare, Zimbabwe, Editors R. D. Barnes and G. L. Gibson. Oxford, England and Forest Research Centre, Harare: Commonwealth Forestry Institute).
- O'Malley, D. M. and S. E. McKeand. 1997. Marker Assisted Selection for Breeding Value in Forest Trees. Pp. 27-44 in *Perspectives of Forest Genetics and Tree Breeding in a Changing World. I. Aspects of Tree Breeding* (Sopron, Hungary. Vienna, Austria: International Union of Forestry Research Organizations).
- Plucknett, D. L., Nigel J. H. Smith, J. T. Williams, and N. M. Anishetty. 1987. Gene Banks and The World's Food. Pp. 3-18 in Princeton, New Jersey: Princeton University Press.
- Purnell, R. C. and R. C. Kellison. 1987. Tree Improvement Program for Southern [U.S.] Hardwoods. *Forest Genet. Resources Inform. No. 15:72-76 [England]*.
- Rogers, D. L. and F. T. Ledig. 1996. *The Status of Temperate North American Forest Genetic Resources*. Davis, CA: Genetic Resources Conservation Program.
- Rousseau, R. J. 1995. Minutes: Business Meeting, Southern Forest Tree Improvement Committee, Asheville, North Carolina, June 22, 1995. *SFTIC Archive*.
- \_\_\_\_\_. 1994. Minutes: Business Meeting, Southern Forest Tree Improvement Committee, Clemson, South Carolina, July 19, 1994. *SFTIC Archive*.
- Schmidting, R. C. 1999. Revising the Seed Zones for Southern Pines. *Proceedings of the 25th Biennial*

- Southern Forest Tree Improvement Conference, New Orleans, Louisiana, July 12 - 14, 1999* - this proceedings.
- Shelbourne, C. J. A. 1971(Unpublished). Provenance Variation in Growth Rate and Other Characters in 13-Year-Old Loblolly Pine (*P. Taeda* L.) in New Zealand. *NZ Forest Research Institute GT1 Report No.* 54.
- Squillace, A. E. and O. O. Wells. 1981. Geographic Variation of Monoterpenes in Cortical Oleoresin of Loblolly Pine. *Silvae Genetica* 30:127-35.
- Toon, P. G., M. J. Dieters, and D. G. Nikles. 1996. Components of a Slash Pine (*Pinus Elliottii* Var. *Elliottii*) Breeding Strategy for the Continued Improvement of Its Hybrids. Pp. 388-90 in *Tree Improvement for Sustainable Tropical Forestry, QFRI - IUFRO Conference, Caloundra, Queensland, Australia, 27 October - 1 November 1996* (Caloundra, Queensland, Australia. Gympie, Queensland, Australia: Queensland Forestry Research Institute).
- Wells, O. O. 1983. Southwide Pine Seed Source Study - Loblolly Pine at 25 Years. *Southern Journal of Applied Forestry*:63-71.
- Wells, O. O. and C. C. Lambeth. 1983. Loblolly Pine Provenance Test in Southern Arkansas. *Southern Journal of Applied Forestry* 7(2):71-75.
- Wells, O. O. and J. L. McConnell. 1984. Breeding Regions in the R-8 Tree Improvement Program. *Progeny Testing: Proceedings of Servicewide Genetics Workshop* (Charleston, SC. Washington, DC: U.S. Forest Service: United States, Department of Agriculture, Forest Service, Timber Management).
- Wells, O. O. and G. Rink. 1985. Planting Loblolly Pine North and West of Its Natural Range. Pp. 261-65 in *Proceedings of the Third Biennial Southern Silvicultural Research Conference* (Atlanta, GA. New Orleans, LA: Southern Forest Experiment Station).
- White, T. L., G. R. Hodge, and G. L. Powell. 1993. An Advanced-Generation Tree Improvement Program for Slash Pine in the Southeastern United States. *Silvae Genetica* 42(6):359-71.
- Williams, C. G., C. G. Elsik, and R. D. Barnes. In review. Microsatellite Analysis of *Pinus taeda* L. in Zimbabwe
- Williams, C. G., J. L. Hamrick, and P. O. Lewis. 1995. Multiple-Population Versus Hierarchical Conifer Breeding Programs: a Comparison of Genetic Diversity Levels. *Theoretical and Applied Genetics* 90:584-94.
- Wu, R., D. M. O'Malley, D. L. Remington, J. J. Mackay, and S. E. McKeand. In press. Average Effect of a Mutation in Lignin Biosynthesis in Loblolly Pine. *Theoretical and Applied Genetics*.
- Yanchuk, A. D. and Lester. D. T. 1996. Setting Priorities for Conservation of the Conifer Genetic Resources of British Columbia. *Forestry Chronicle* 72(4):406-15.