

Comments

Tree Planters' Notes

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Cover: Stand of *Pinus greggii* at La Tapon, Nuevo Leon, Mexico, see page 86 (photograph by Jeffery K. Donahue, CAMCORE, North Carolina State University, Raleigh, NC).

Establish Plantations on Pastureland Now To Protect Native Forests in the Future

The world's population will likely approach 10 billion in just 55 years. A population of this size could easily consume more than 7 billion cubic meters (m^3) of wood annually. There is no doubt that in the future, wood will be harvested from both plantations and natural stands. However, how much wood is harvested from natural forests in the year 2050 will depend largely on how many plantations we establish today. The following word problem demonstrates how important it is for fastgrowing societies to plan for the future by establishing tree plantations.


Word problem. Three hypothetical islands are identical in natural resources but each is inhabited by a different society. Each island has a 5-ha pasture and 5-ha wood. Initially, each society has 4 people at year 0. Each society follows a strict ethic regarding population growth and therefore growth on each island is limited to only 2 persons per year.

The inhabitants can obtain all the food they need from the ocean. They rely on a renewable energy source for cooking and heating, using firewood at a rate of $1 m^3$ /person/yr. The native woods produce about $2 m^3$ /ha/yr and this wood can be collected on a sustainable basis without reducing the growing stock. However, the native trees are small and therefore the standing volume of the forest never exceeds $2 m^3$ /ha. To clarify, the 5-acre wood has $10 m^3$ of standing volume on January 1st and during the year, $10 m^3$ of firewood (dead branches, etc.) can be collected. On December 31, the standing volume of the forest is still $10 m^3$. If the firewood is not collected, the branches fall off the trees and either decay or are occasionally washed off the island. However, firewood can be collected and stored indefinitely without wood decay. Each society has the same major objectives: to continue cooking food and to protect the 5-ha woods.

The three societies differ in the way they manage their land. The society on island A decides to keep sheep on the 5-ha pasture. The people there collect firewood from the woods and store any unused firewood for future needs. On January 1st (year 1), they have $6 m^3$ of firewood in storage.

The society on island B establishes an exotic tree plantation on the pastureland. The plantation produces $10 m^3$ of firewood/ha/yr. On January 1st (year 1), there are $56 m^3$ of firewood in storage ($50 m^3$ from the plantation and $6 m^3$ of extra firewood collected from the woods).

The society on island C does the same as the society on island B. On January 1st (year 1), the inhabitants also have $56 m^3$ of stored firewood. However, they decide to invest time and effort into research. Although they



make some mistakes, new ways are discovered to increase the volume production from the plantation. Amazingly, each year the researchers figure out a way to increase production by $0.2 \text{ m}^3/\text{ha}/\text{yr}$. For example, the first crop was 50 m^3 , the second was 51 m^3 , the third was 52 m^3 , etc.

With the information given, how long does it take before each society depletes the storage of wood? Which society protects its 5 ha of native woods for the longest period of time?


Answer. Island A can only sustain a population of 10 people. The supply of stored wood runs out during year 6. On January 1, year 7, there are 18 people on the island and during the year they end up cutting down all of the woods for firewood.

The society on island B uses an exotic tree plantation to increase the production of firewood. With both wood from the plantation and the native woods, this society is able to produce $60 \text{ m}^3/\text{yr}$. Therefore, island B can sustain a population of 60 people (six times more than island A). The society lasts for 56 years before the firewood supply runs out. The native woods were protected for 5 decades longer than on island A.

The society on island C was able to discover new ways to increase volume growth. As a result, they protected the woods for more than a century. By conducting research aimed at improving plantation yields, this society was able to have 5 ha of native woods and sustain at least 160 people (a yield of $160 \text{ m}^3/\text{yr}$ was obtained on year 100). However, at the end of year 112 the population is 228 and there is no more wood in storage. They decided that, for the next year, some of the native woods would have to be harvested.

The ability to protect the native woods varied with the land management regimes. The two societies that relied on fast-growing exotic plantations were able to protect the native woods for much longer than the society that preferred pastureland to tree plantations. One could conclude that highly productive plantations can help protect native forests by meeting the day-to-day consumption needs of the population. I conclude that planting trees on pastureland is one way to protect wilderness or non-utilized lands from exploitation.

None of the societies can sustain a population growth of 2 persons/yr. Therefore, the real problem for all three societies is population growth. Adoption of new technology can only delay the inevitable. However, for areas with limited resources, societies must adopt appropriate ethics about population growth if the society hopes to be sustainable during the next several millennia. It also can be concluded that for any of the three islands to have a sustainable ecosystem and an unconstrained population growth either (1) per-capita wood consumption must decline in direct proportion to



the population growth (through recycling, product substitution, or reduced standard of living) or (2) technology must devise ways to continually improve yields.

A global program for planting trees on pastureland. In the past, the world's societies have encouraged the establishment of pastures. In just 4 decades, pastureland increased globally from 18% of the world's landbase in 1955 to about 26% today. The increase in pastureland was about 25 million ha/yr. Although it seems unlikely the world's society will favor a similar rapid expansion of tree plantations, perhaps a target of 5% of the world's landbase by the year 2050 would be acceptable if plantations were established on abandoned pastureland. I propose that nongovernmental organizations of the world promote large afforestation programs with the goal of planting trees on more than 8 million ha of pastures each year for the next 55 years. This would reduce the amount of pastureland to about 22% of the world's landbase. This effort would go a long way toward removing some of the expected over-harvesting pressure from natural stands in the year 2050.

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[Editor's note: The history of Easter Island, a real-life island in the east central Pacific Ocean, is a telling example of the relationship between a culture and its trees and forests. The thriving culture of the Polynesians who colonized the island in their canoes about 1500 years ago (that is, around 400 A.D.) reached its peak around 1500 A.D., when about 9,000 people lived on the island. This culture carved those huge stone heads and moved them to sites all over the island. But the statue culture declined and had nearly vanished from memory by the time that Dutch Admiral Jacob Roggeveen first saw the treeless island on Easter Sunday 1722. Archaeologists trying to discern reasons for the population crash and cultural degeneration found several clues. Pollen studies showed that trees began disappearing in large numbers around 980 A.D., and the preserved nuts of a now-extinct native palm related to the Chilean wine palm (*Jubaea chilensis*) were found. The Easter Islanders used slash and burn agriculture and went to sea in their wooden canoes to catch fish for protein. When the last palm was cut down and they had to subsist on farming alone, the large population could no longer survive, warfare broke out, and the culture degenerated. Now there are barely any trees and only 36 families that can claim descent from the old people. This story was told in a 1989 NOVA program entitled "The Secrets of Easter Island" (© WGBH, Boston, Massachusetts). -RN]



A New Feature

The *Tree Planters' Notes* team is continuing to improve our product. With this issue, we introduce a new section— the "**Species Spotlight.**" John Kuser and George Zimmerman's informative and enjoyable review of Atlantic white-cedar is our first "Species Spotlight." *Tree Planters' Notes* has a dual purpose— we want to provide interesting and informative how-to's, tips, and such for the working nursery manager as well as provide a peerreviewed and refereed outlet for nursery and outplanting-related scientific research results. **We want your articles!** Write about your favorite tree or conservation plant. Tell us about that gizmo you invented or that nifty new way you figured out to solve a nursery problem. Call and talk over any of your ideas with me or buttonhole any member of the editorial team at a meeting.

Rebecca Nisley

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Restoring Atlantic White-Cedar Swamps: Techniques for Propagation and Establishment

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There has been much recent interest in restoring white-cedar swamps along the Atlantic Coast of the United States. Awareness of the ecological role of wetlands in keeping our environment healthier has combined with demand for cedar products to produce a drive to develop better methods to propagate and establish young cedars. This paper discusses unique features of cedar swamp ecosystems, natural regeneration methods, protection from deer, the use of herbicides, and nursery propagation and cedar swamp restoration by planting seedlings or rooted cuttings. Current research is noted, with references. Tree Planters' Notes 46(3):78-85; 1995.

Atlantic white-cedar, *Chamaecyparis thyoides* (L.) B.S.P (figures 1 and 2), is an obligate wetland species occupying swamps along the Atlantic Coast from central Maine south to Florida and westward along the Gulf Coast to the southeastern corner of Mississippi (figure 3). The western Florida population is sometimes regarded as a separate subspecies, ssp. *henryae* (Li 1962; Little 1966, 1979). Most cedar swamps lie along the Coastal Plain from New Jersey southward, but a few are perched atop mountains at some distance inland, as at High Point, New Jersey (1,500 feet elevation, 90 miles inland). The largest natural areas containing cedar swamps are in eastern North Carolina, southeastern New Jersey; and northwestern Florida (figure 3).

Currently, the area occupied by cedar swamps or wetlands (5 to 95% cedar) rangewide is about 115,000 acres, according to foresters and conservationists surveyed in spring 1995. This includes typical cedar swamps from the Carolinas to Maine and sandy streamside forests in western Florida and the Mobile Bay area (Ward and Clewell 1989). At the time of European settlement, there was much more, perhaps 500,000 acres.

What happened to most of it? In North Carolina, which probably had more than half of the original cedar, much of the Great Dismal Swamp and the lands along the Alligator River were drained for agriculture beginning in the late 18th century. One of the early land speculator-agriculturists who joined a consortium to drain 40,000 acres of the Dismal Swamp was George Washington, who also bought land there in his own

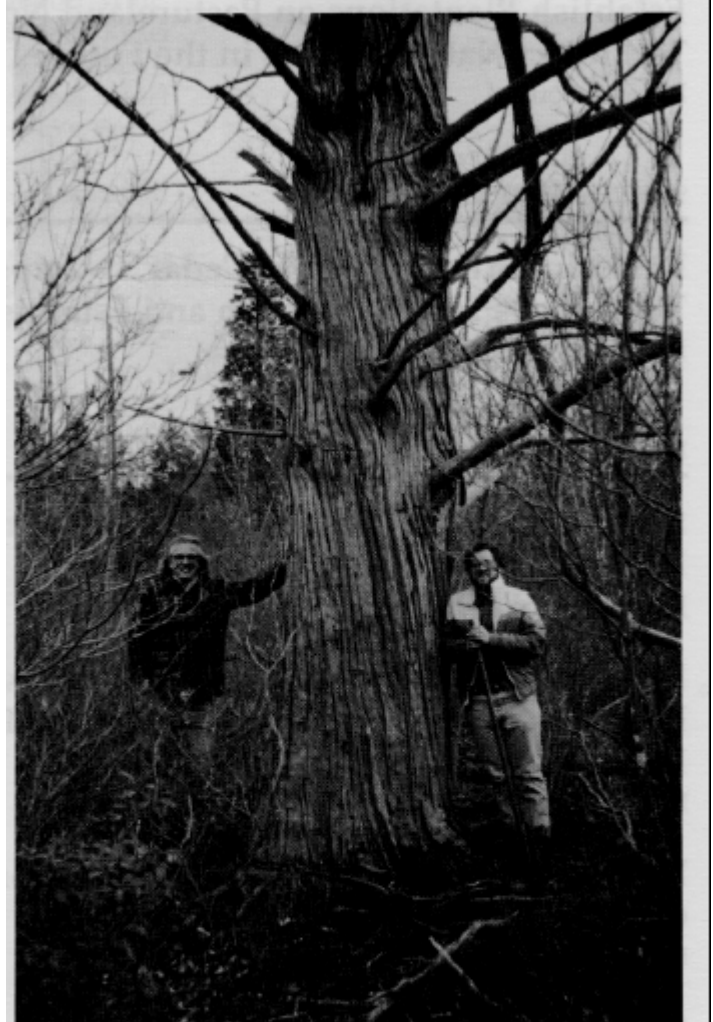


Figure 1— The New Jersey record Atlantic white-cedar—located at Nixon Branch, Cumberland County, in southern New Jersey—is 9 ft, 6 inches in circumference at breast height. This battered old tree (age is estimated at 300 years) grows not far inland from Delaware Bay and has lost its top at least once to hurricane winds. Most Atlantic white-cedars grow to 70 to 80 feet in height, with a trunk diameter of 2 to 4 feet. Few forest trees grow in denser stands, and trees in such stands have long straight trunks and narrow crowns (Collingwood and Brush 1974).

name (Frost 1995). Farming the drained lands met with varying success, and problems arose as the upper levels of the organic peat subsided because of oxidation.



Figure 2— A stand of 70-ft Atlantic white-cedars in Lebanon State Forest, New Jersey. Although cedars are usually small (a 14-inch diameter is a good size), better stands have trees with 18-inch diameters and 60-to 70-foot heights at ages of 75 to 100 years.

Hydrologic changes in the Dismal Swamp made water levels too low (or in some cases too high) for cedar, and logging without fire allowed stump-sprouting hardwoods to replace cedar. Dismal Swamp was essentially mined rather than managed for cedar as a renewable resource. Today much of the Great Dismal Swamp and the low-lying lands along the Alligator River have become national wildlife refuges, and active white-cedar revegetation programs are underway in both areas (Brownlie 1995, Johnson 1995, L. Smith 1995, S. Smith 1995, Wicker 1995).

In Massachusetts and New Jersey, many cranberry bogs were once cedar swamps (Korstian and Brush 1931); in the latter state, 5,500 acres of cedar swamps in the Hackensack meadowlands were burned in 1791 to elim-

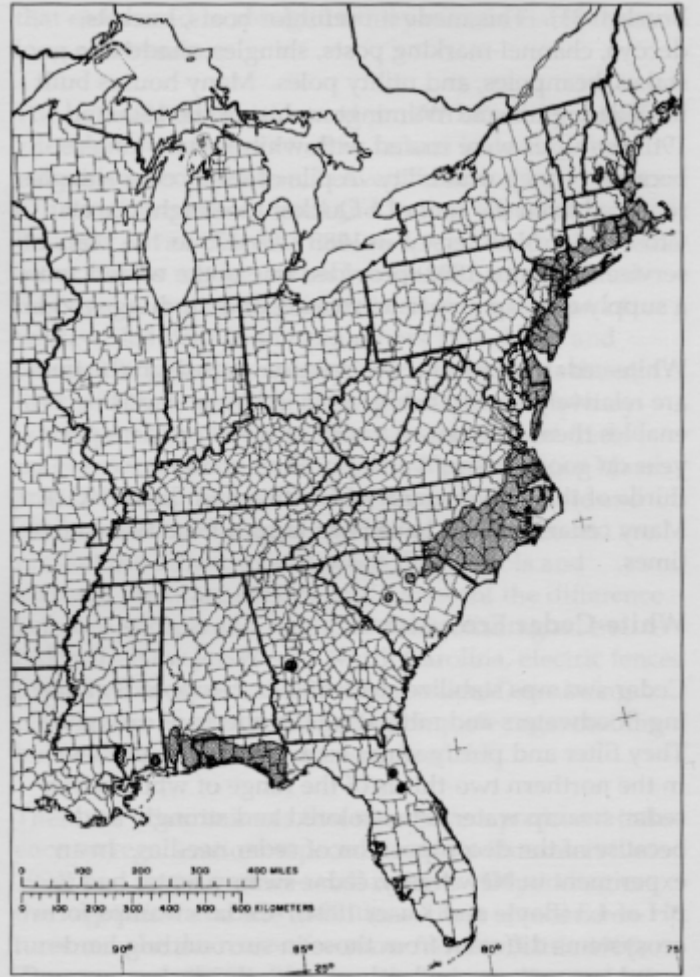


Figure 3— Range of Atlantic white-cedar (Little 1971).

inate hiding places for pirates who preyed on shipping in Newark Bay (Kantor and Pierson 1985, Schmid 1987). Lakes have been built, swamps drained, stream channels straightened (allowing saltwater penetration to kill cedars), beavers have raised water levels in some swamps, highway construction has changed water levels, and logged cedar swamps have become hardwood or brush swamps after cedar regeneration has failed because of heavy deer browsing (Little and Somes 1965).

Wood Characteristics

For the first three-and-a-half centuries after European settlement, people were interested in cedar swamps mainly for the fragrant, rot-resistant wood that could be harvested from them. The decay resistance of Atlantic white-cedar is better than that of white pine, yellow pine, yellow-poplar, and oak although probably not as good as that of redwood or chestnut (Korstian and

Brush 1931). This made it useful for boats, buckets, decoys, channel-marking posts, shingles, shade-tree stakes, beanpoles, and utility poles. Many houses built in Philadelphia and Wilmington during the 18th and 19th centuries were roofed with white-cedar shingles because of their durability. A pile of used cedar shingles removed from the roof of a Quaker meetinghouse at Crosswicks, New Jersey, in 1985 after 175 to 185 years of service (Williams 1992) provided one of the writers with a supply of crisp, dry fishsmoking and kindling wood.

White-cedar is a productive species. Although the trees are relatively small, their growth in dense stands enables them to produce a cord of wood per acre per year on good sites in North Carolina or about two-thirds of this in New Jersey (Korstian and Brush 1931). Many cedar swamps have been logged from two to five times.

White-Cedar Ecosystems

Cedar swamps stabilize streamflows, temporarily storing floodwaters and mitigating the effects of droughts. They filter and purify water as it flows through them. In the northern two-thirds of the range of white-cedar, cedar-swamp water is teal-colored and strongly acid because of the decomposition of cedar needles. In an experiment in New Jersey, cedar-swamp water had a pH of 4.3 (Boyle and Kuser 1994). Cedar swamps form ecosystems different from those in surrounding hardwood swamps or pinelands. Under the dark crowns of the cedars it is 6 to 8/F cooler in summer and almost windless (Wander 1980). Occasionally the canopy is dense enough to shade out most undergrowth, but most of the time one has to struggle through tangles of greenbrier (*Smilax rotundifolia* L.), sweet azalea (*Rhododendron viscosum* (L.) Torr.), rhododendron (*R. maximum* L.), highbush blueberry (*Vaccinium corymbosum* L.), and sweet pepperbush (*Clethra alnifolia* L.) in order to go anywhere in the swamp.

Cedar swamps are prime habitat for endangered swamp pinks, *Hellonias bullata*, in New Jersey and the Delmarva Peninsula (Zappalorti 1994, Dill and others 1987). Around the edges of cedar swamps, fringed orchids, *Habenaria* spp., turkey-beard, *Xerophyllum asphodeloides*, and curly-grass fern, *Schizaea pusilla*, can be found.

Bird species nesting in cedar swamps in New Jersey include black-throated green warblers, black-and-white warblers, brown creepers, ovenbirds (Wander 1980), and hermit thrushes (Zappalorti 1994). In North Carolina, cedar swamp nesters include prairie, prothonotary, and

hooded warblers, as well as ovenbirds and yellowthroats. Cedar swamp ecosystems support a higher density of nesting birds than maple-gum sites, nearly twice as high (Terwilliger 1987). In the Dismal Swamp, Van Velzen (1981) observed 1,312 nests/km², the highest value for birds nesting in any of 12 eastern coniferous forest habitats.

Southern red-backed voles, *Clethrionomys gapperi*, are the predominant small mammals in mature cedar swamps in New Jersey. The presence of mycorrhizal fungal spores in the fecal pellets of these voles suggests that they may play a role in dispersal of mycorrhizal fungi that may be important for successful growth of the cedars (Craig and Dobkin 1993). Hollows under the roots of cedars growing along streams are used as winter dens by Pine Barrens rattlesnakes (Reinert and Zappalorti 1988). The best known amphibian associated with cedar swamps is the Pine Barrens treefrog, *Hyla andersonii*. One butterfly, Hessel's hairstreak, uses Atlantic white-cedar exclusively; it inhabits bogs and swamps close to white-cedar from New Hampshire and Massachusetts south to North Carolina and the Gulf Coast of Florida (Zappalorti 1994, Pyle 1981).

Bringing Atlantic White-Cedar Back— the "Cedar Initiative"

With growing public awareness of the importance of wetland ecosystems, efforts to regenerate or restore cedar swamps have increased. On August 1-3, 1995, a conference on current developments with Atlantic white-cedar management drew 75 researchers, foresters, and nursery managers to Goldsboro and Washington, North Carolina. Many papers on natural and artificial regeneration were presented, and a tour was given to sites with natural regeneration, planted seedlings, planted cuttings, and a cedar sawmill. Methods of regeneration are discussed below with references to current or recent research.

Natural Regeneration

The natural regeneration of white-cedar depends on a source of seed and the factors influencing its presence, germination, and subsequent survival. The main abiotic factors influencing seed germination are moisture, light, and temperature (Korstian and Brush 1931, Little 1950). In the field the primary limiting factor seems to be moisture. A continuous supply of moisture is critical to germinate white-cedar seed. For the seedling to survive the water supply cannot be too little or too much (Akerman 1923, Little 1950). There is also a critical

interaction between moisture and substrate for successful germination. Field observations by Little (1965) and experiments by others (Greenwood 1994) have shown that cedar seed germination is earlier and more complete on sphagnum than on mineral soil. The differences in germination between substrates cannot be attributed to moisture-holding capacity or absolute moisture; unpublished experiments by Zimmermann (1993) have shown striking differences in germination between the substrates to persist when moisture is held above field capacity. The pH of the substrate is not a factor in germination (Boyle and Kuser 1994).

The amount of light needed for white-cedar germination, establishment, and growth has been the center of conflicting reports through the years (Korstian and Brush 1931, Little 1950, Hickman and Neuhauser 1978). Recent experiments with different logging slash levels by Zimmermann (1995) show cedar germination to be the densest in areas where slash is completely removed thus allowing maximal light. However, following the first year subsequent survival and growth is statistically significantly higher where slash is not removed. Indeed there is still adequate cedar regeneration and growth where logging slash has been doubled. Whether the second and subsequent year's survival and growth of cedar are due to a shift in its shade tolerance or whether there are other factors (nutrients, less inter-specific competition, etc.) remains to be seen as the 5-year experiment and analyses are finished.

These facts—combined with white-cedar's delayed germination (Moore 1939, Little 1950), variable seed crops, difficulties in obtaining adequate seed, and recent field experiment observations (Zimmermann 1995)—have led to recommendations that are contrary to those of Little (1965), who said that direct seeding can be successful more often than not. Indeed, in New Jersey, recent success has been too variable even on optimal sites (good moisture, good substrate, etc.) to recommend direct seeding.

Natural regeneration of white-cedar from seed already present in the seed bank (usually a sphagnum substrate) is, however, another matter. In New Jersey the highest probability for successful regeneration and restocking at adequate levels occurs when choosing areas where cedar was present or is near enough that the seed bank has accumulated adequate seed (Zimmermann 1995). Although Zimmermann is currently in the fifth year of a long-term experiment on cedar seed viability, field observations and experiences by Little (1990) suggest

that cedar seed in sphagnum may remain viable for as long as 14 years.

The natural regeneration and growth of white-cedar are affected by a number of other factors including fire, interspecies competition, beaver, browsing by a variety of animals, rising sea level and human disturbance (cutting and development). In New Jersey the prime reason cedar fails to regenerate and reestablish after clearcutting or similar disturbance is the high population of white-tailed deer (Little and others 1958, Little and Somes 1965, Zimmermann 1995). During the winter, deer will browse white-cedar partially or completely while leaving primary competitors untouched (red maple, *Acer rubrum* L.; blackgum, *Nyssa sylvatica* Marsh.; and sweet pepperbush). Indeed where adequate and effective deer exclosures (electric or woven fences) are present the differences between the controls and exclosed areas are striking and represent the difference between success and failure in reestablishing whitecedar. In New Jersey and North Carolina, electric fences (usually five-stranded and solar-powered) are being used where necessary to insure adequate regeneration, but in many cases they are not affordable.

There are other animals that may have a profound influence on regeneration, especially rabbits (Summerville 1994) and various other small rodents. Depending on the vegetation and site conditions, these smaller creatures may be the reason for some failures (Little 1950, Zimmermann 1995). Beaver activity according to Little (1950) may have had a major role in holding natural succession back and perpetuating white-cedar.

The role of fire in regeneration depends on a number of factors including the structure, history, and size of the cedar stand as well as the intensity and type of fire (Little 1950, Motzkin and others 1993). Frost (1995) considers cedar to have been a fire species in the Great Dismal Swamp, with nearly pure stands dependent on fire return intervals of 75 to 300 years.

In New Jersey and North Carolina, wetlands-approved herbicides have been used to control competing vegetation that may arise either from differential deer browsing or a natural consequence of successional trends in the ecosystem. In New Jersey, Arsenal® is the most commonly used herbicide providing adequate control over troublesome species like red maple while avoiding (at proper dosages) "burning" of the cedar foliage.

Artificial Regeneration

Before planting seedlings or stecklings comes into widespread use, it will be useful to increase our knowledge of the genetic architecture of *Chamaecyparis thyoides*: differences among populations, uniqueness of any populations, how far propagules may be moved from their site of origin, differences in growth rate, cold tolerance, and other characteristics among populations, stands, and clones. Variation in heterozygosity may be estimated by isozyme frequency analysis, while comparisons of growth rates, hardiness, tree form, and disease resistance require classical provenance experiments which are just being established now. Eckert (1995) has compared isozyme frequencies in different swamps in New Hampshire and Maine and estimated degrees of relatedness among cedar populations. Kuser and others (unpublished data) have compared isozyme frequencies at four swamps in New Jersey and two in North Carolina.

Provenance testing. In North Carolina, Summerville (1995) established a provenance test on two sites in spring 1993, using seedlings grown from 77 single-tree collections. In New Jersey, Kuser and Spaziano (unpublished data) planted a test of rooted cuttings of 29 clones from 10 swamps on several test sites belonging to Clayton Sand Co. at Lakewood, NJ, in May 1995. We are also comparing survival and growth of cuttings from selected tall cedars vs. random cedars vs. juvenile (3 to 4 ft) cedars, vs. seedlings from three different swamps. When results are known in 5 to 10 years, it should be possible to estimate differences in cedar growth rates due to provenance, clone, maturity state of ortet (cuttings), and method of propagation (seedlings vs. cuttings).

Seed propagation. Seed viability and germination vary widely among seedlots from different swamps (Laderman 1989, Boyle and Kuser 1994). Cedar seed is tiny, difficult to collect, and notorious for delayed germination (Schopmeyer 1974). In North Carolina, Summerville is experimentally collecting seed from a Christmas tree plantation using a cone rake. Greenwood (1994) and Jull and others (1995) have found that larger plants can be produced in less time at 30°C with high-nitrogen fertilization. Currently, bareroot seedlings furnished by the New Jersey state nursery are 2+0, 6 to 12 inches tall, and 5/32 inch in diameter, and supply is not adequate. In North Carolina, the state nursery is producing 13,000 1+0, 4-in bareroot seedlings and would produce more if possible. The best planting season in

New Jersey is thought to be April/May, and in North Carolina March/April.

Stecklings (rooted cuttings). Nursery managers have been propagating cultivars of related species of *Chamaecyparis* as stecklings for a long time, and the advent of modern mistbed technology together with the use of rooting hormones has made it easy (figure 4). Recent research at North Carolina State University (Hinesley and others 1994) and Rutgers University (Boyle and Kuser 1994) aims to optimize techniques for rooting cuttings. With a mistbed, rooting hormones, and bottom heat during cooler months, our experience has been that cedar can be rooted with about 90% success at any time of year. Commercial production of stecklings is well underway in North Carolina, where Weyerhaeuser can produce up to 400,000 a year, 6 to 8 in high, in tubes and bareroot. Within the last year or two, experiments in North Carolina have shown that mistbed rooting of cedar can be accomplished outdoors using sandy soil and fogging/ irrigation spray regulated by evapotranspiration sensors (Hinesley 1995). Outdoor mist-rooting is also being done by Weyerhaeuser, using a different technique (Miller, personal communication).

Planting and establishment. If the site is a swamp where natural regeneration has failed or is inadequate, the first step is reduction of competing vegetation by cutting and applying herbicide (if there are small cedar seedlings underneath brush, herbicide alone may work). Seedlings or stecklings should be planted at medium elevation on hummocks (Ehrenfeld 1995) where the root collar will be dry but the lower ends of roots moist. Cedar is “picky”— it tolerates neither inundation nor drought. If the site is a hardwood swamp slated for conversion or mitigation, the hardwoods must be controlled first because cedar is intolerant and will not grow up underneath them. If the site is a newly constructed lakeshore (such as along worked-out sandpits) or stream-edge, the planter should match as closely as possible the microsite conditions under which cedar naturally and often aggressively colonizes such places: the roots must be within easy reach of water, but the stem never inundated.

After planting, young cedars must be protected against deer and/or rabbits. In small plantations or where rabbit clipping may be a problem, plastic mesh collars (figure 5) are effective. In larger plantations with high deer populations, fencing is necessary exactly as with natural regeneration.



Figure 4 — Cedar cuttings in a mistbed at Rutgers University.

Seedlings vs. stecklings. Comparison of the growth of outplanted seedlings and stecklings (rooted cuttings) in North Carolina showed that seedlings usually grew somewhat faster but not always so (Gardner and Summerville 1992, Phillips and others 1993). In New Jersey, we planted seedlings and stecklings resulting from Boyle's experiments (Boyle and Kuser (1994), averaging 4 to 7 cm high in June 1992 in a swamp at the Jackson tree nursery. In November 1995, 41 stecklings averaged 131 cm tall and 24 seedlings averaged 128 cm after four growing seasons. The most obvious difference between the two groups was in winter color: all seedlings were copper-maroon on 20 March 1995, but 36 of 40 stecklings were green. The 3 tallest plants in the plot were all seedlings, (246, 227, and 205 cm).

One advantage of seedlings is that no two are exactly alike, and thus would seem less likely to be affected by pathogens such as those that have decimated single-clone plantations of hybrid poplar. If stecklings are planted, this risk can be minimized by planting blocks of up to 20 selected clones or a multiclone mixture.

Several advantages of stecklings are that cuttings are easy to collect, easy to root, and the supply does not depend on variable pollination, seed production, and viability.

In British Columbia, the entire provincial reforestation program with Alaska yellow-cedar, *Chamaecyparis nootkatensis* (D. Don) Spach, has switched from seedlings to stecklings in the last 10 years, and currently produces about 750,000 per year. Russell and others (1990), Karlsson and Russell (1990), Grossnickle and Russell (1993), and Russell (1993) provide good summaries of this situation. In North Carolina, Weyerhaeuser's white-cedar cutting/rooting facility at Trenton had doubled its capacity to 400,000 stecklings/year in April 1994. It was then providing year-old rooted cuttings of North Carolina, Delaware, and New Jersey clones.

Which will be the method of choice in the future for white-cedar? The verdict is not in, but the British Columbia and Weyerhaeuser examples may foreshadow

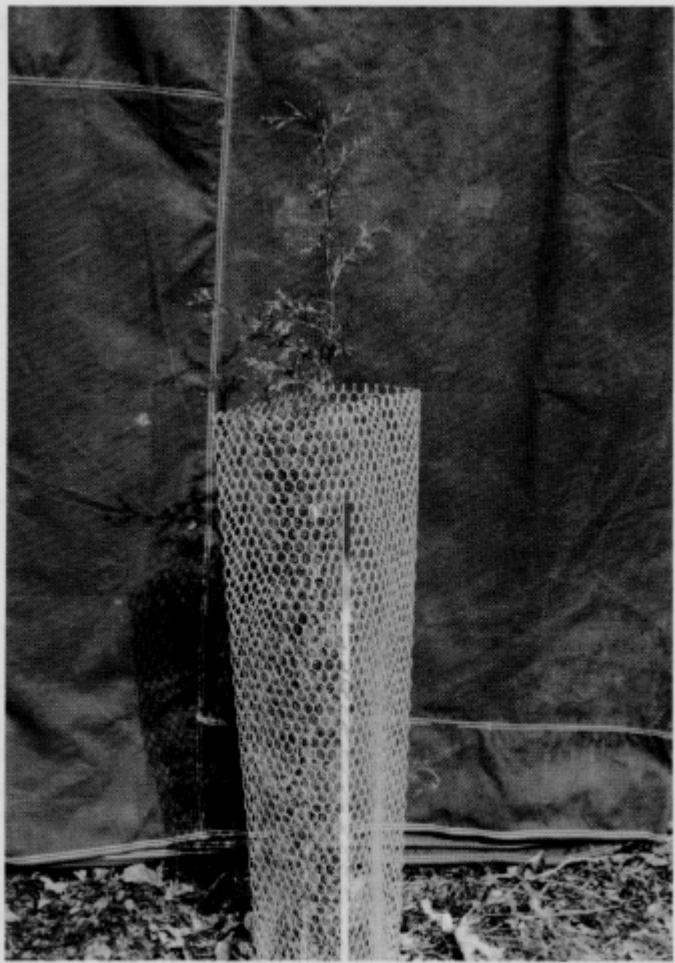


Figure 5— Plastic mesh collars around cedar seedlings at Clayton Sand Co., Lakewood, New Jersey.

future mass regeneration techniques of known genetic material.

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Seed Production of *Pinus greggii* Engelm. in Natural Stands in Mexico

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Five cones of *Pinus greggii* Engelm. were collected from each of 117 trees at 12 widely separated sites in Mexico to examine their seed potential and efficiency. Seed efficiency of *P. greggii* in natural stands was 63% rangewide. Differences were found in seed-yield traits related to geographical location. Trees in southern stands in the states of Hidalgo and Queretaro had greater seed potential (117 versus 91 seeds/cone) and produced more filled seeds per cone (74 versus 46) than trees in northern stands in Coahuila and Nuevo Leon. Trees in northern stands had more first-year aborted seeds per cone (42 versus 32) and three times more insect-damaged seeds than trees in southern stands in 1993. Tree Planters' Notes 46(3):86-92; 1995.

Pinus greggii Engelm. is a closed-cone pine that grows in two disjunct regions of the Sierra Madre Oriental in Mexico (figure 1). The species' northern region includes the states of Coahuila and Nuevo León, while the southern region consists of San Luis Potosi, Queretaro, Hidalgo, Puebla, and Veracruz (figures 2 and 3). The northern and southern locations have distinct environments. Northern *P. greggii* sites are usually at higher elevations (2,300 to 2,800 m versus 1,200 to 2,300 m) and have lower rainfall (650 mm versus 800 to 1,600 mm) than most southern sites, and have near neutral or slightly alkaline topsoils (Donahue 1993). Soil pH at southern *P. greggii* sites tends to be more acidic. Environmental details are listed in table 1.

Many stands of *P. greggii* have been disturbed by selective cutting and burning, particularly in northern stands. The largest, least disturbed stands are in the state of Queretaro, in the southern region, where the trees grow faster and appear to have less disease and insect problems than at northern sites.

Pinus greggii is a precocious species. It produces seed cones in natural stands at 3 to 5 years of age (Lopez-Upton 1986) and in exotic field trials after the first year (Dvorak and Donahue 1992). It is quite prolific when mature, producing large cone crops on a regular basis (figure 4). Cone buds mature and pollination occurs in April-May in the southern stands, and May-June in northern stands. Seed cones begin to mature in

December of the following year, with seed dispersal delayed primarily until the hotter months of April and May, varying among stands and trees. The slow opening of *P. greggii* "closed-cones" allows for an extended seed collection period beginning in January, and continuing through March or April.

The objective of this study was to determine the species' variation in seed potential and production in natural conditions, over the range of environments where it grows. The study was done in conjunction with a rangewide survey of *P. greggii* to study the morphological variation and terpene chemistry of the species.

Materials and Methods

In 1993, a project was initiated between the Colegio de Postgraduados, Montecillo, Mexico, and the Central America and Mexico Coniferous Resources (CAMCORE) Cooperative, North Carolina State University, USA, to study geographic variation in cone, leaf, and seed morphology of *Pinus greggii*. A rangewide sample was collected from 12 sites (figure 1), from a total of 177 trees. Cones from 15 trees were obtained at most sites (table 1), with the sample covering the majority of the targeted stand.

Cones were collected from healthy dominant and codominant trees, spaced at a minimum of 100 m. A cone was collected from five distinct locations in the upper third of the crown of each tree (5 cones/tree). The cones were oven-dried for approximately 48 hours at 50 °C to facilitate opening, and the seeds were counted and classified (by dissection) as filled, empty, first-year aborted, second-year aborted, or insect-damaged following the methodology described by Bramlett and others (1977). The number of fertile cone scales was counted to calculate seed potential and determine seed efficiency. Seed potential is the number of cone scales multiplied by two. Seed efficiency is the total number of filled seeds divided by the seed potential.

Site and individual tree means and coefficients of variation were computed for each seed-yield trait. An analy-

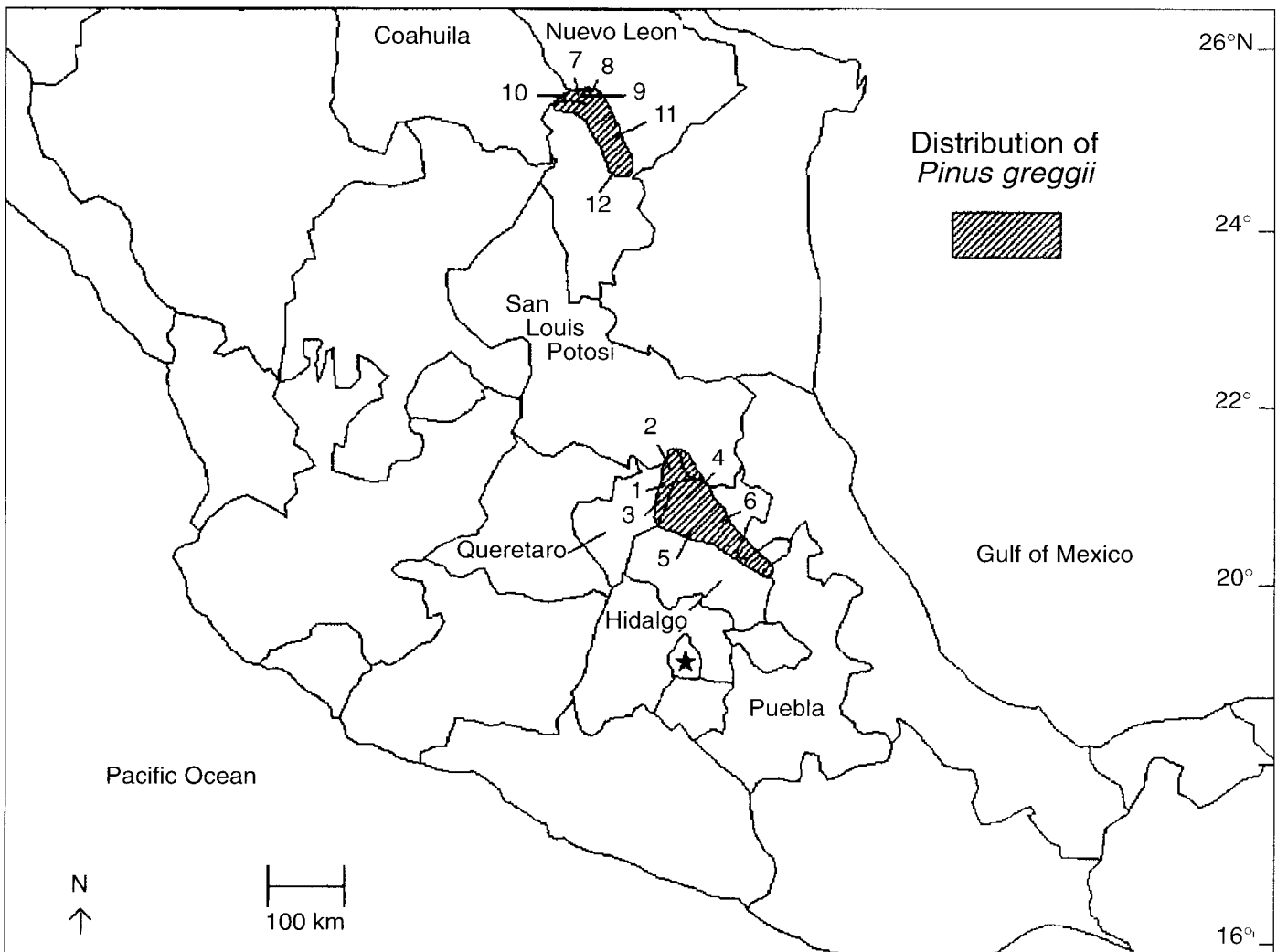


Figure 1—Location of the seed production study sites in Mexico.

sis of variance was conducted on the individual tree means using the GLM procedure of the Statistical Analysis System Institute (SAS 1989), with a nested model; trees, sites, and sites within region (north and south regions). Waller-Duncan comparisons were done on site means to detect differences among sites, and to look for trends across regions.

Results and Discussion

Table 2 gives the results of the analysis of variation of the data in which the sources of variation were sites and individual trees within sites. Highly significant statistical differences were found for both sources of variation for all traits analyzed (table 2). In general, there was considerable tree-to-tree variation among traits, as indicated by the high coefficients of variation. The extreme

coefficient of variation for second-year abortions coincides with a highly extreme CV for insect-damaged seeds, indicating insect damage as the principal cause for the high number of second-year abortions. In the southeastern United States, second-year abortions are caused primarily by *Leptoglossus corculus* Say, the leaf-footed pine seedbug (Bramlett and others 1977). *Leptoglossus occidentalis* Heidemann has been reported to attack *P. greggii* in native stands and is considered one of the most important pine cone and seed pests in Mexico (CibrianTovar and others 1995). There were no significant statistical differences between northern and southern groups of sites for any traits. There are some apparent north-south trends in the data for number of fertile cone scales, number of insect-damaged seeds, and first and second-year aborted seeds,

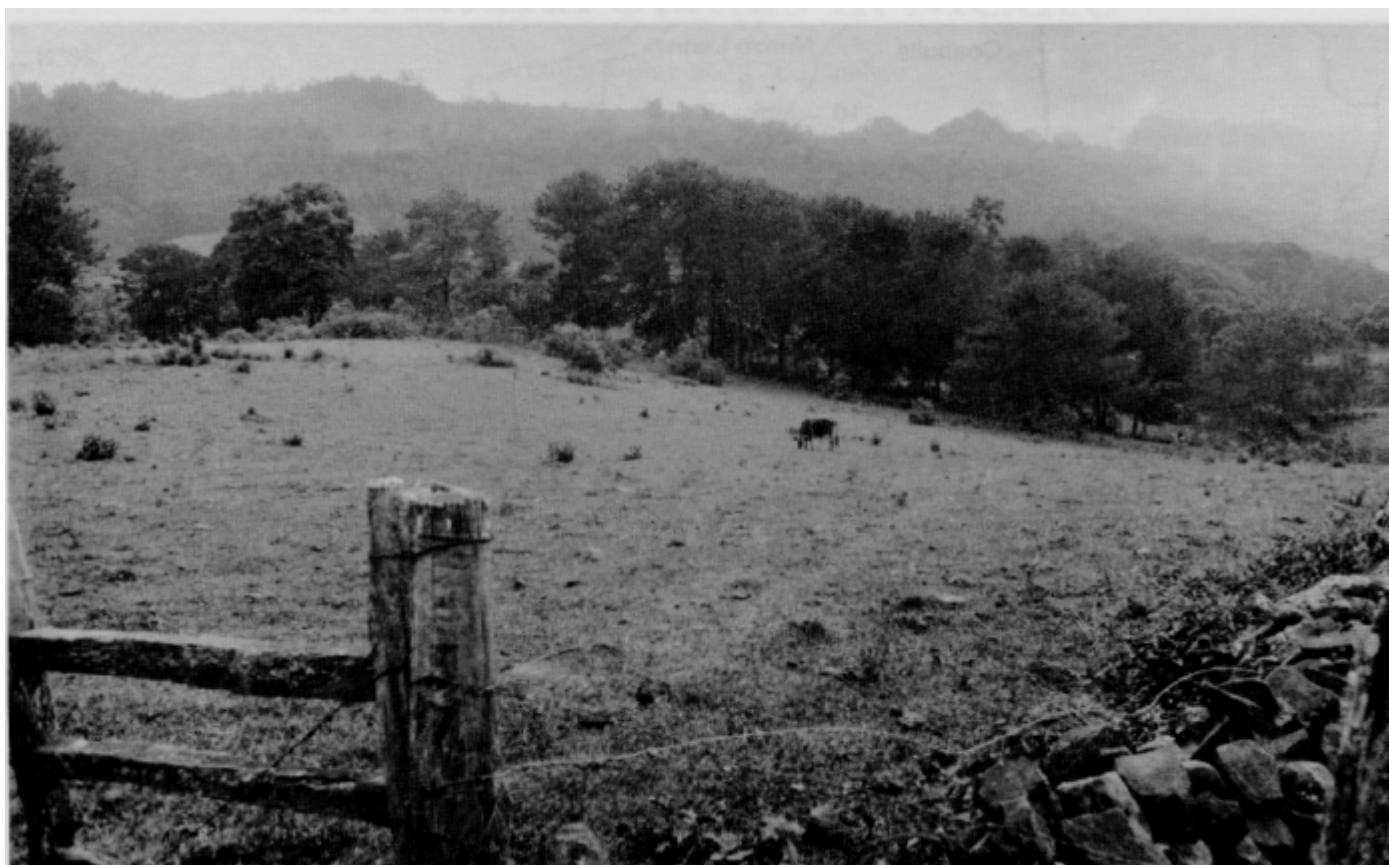


Figure 2—*Pinus greggii* in a typical stand of small groups of trees scattered about pasturelands (Laguna Atezca, in Hidalgo, Mexico).

where 4 of 6 sites in a region cluster together (table 3). Because the cones were collected for a morphology study, those that were obviously deformed were rejected. These results are for seed-yield traits of normal cones.

The average number of fertile cone scales across all sites was 52, giving an average seed potential of 104 seeds/cone for the species. Based on the number of fertile cone scales, seed potential at southern region sites was 28% higher than northern region sites; 117 seeds per cone versus 91 seeds/cone (table 3). Although not statistically significant at the region level, southern sites tended to have higher numbers of fertile cone scales, except for Laguna Atezca. This site had the lowest average, and also had the lowest number of filled seeds. Laguna Atezca is the study site located nearest to a *Pinus patula* stand (Jalamelco, at 3 km distance). Introgression may have occurred between the two species in the past, resulting in altered cone and seed development. Trees from this site are statistically distinct from trees of other southern stands in cone and seed morphology, and resemble trees of *Pinus patula* from Zacualtipan, Hidalgo in some traits (Donahue and

Upton 1995). The Laguna Atezca stand is also one of the more fragmented; most of the trees are growing in small groups, scattered about pasture land (figure 2). Trees from El Madrono had the highest number of fertile cone scales. This site has the largest, least disturbed area of *P. greggii* in the southern region, encompassing nearly 10,000 ha.

Information on "per-cone" seed production in natural stands is not readily available for Mexican pines. Bello-Gonzalez (1983) reported on two other closed-cone pines, *Pinus pringlei* Shaw, and *P. oocarpa* Schiede, in a survey conducted in the state of Michoacan in 1981. The sample was comprised of 5-tree bulks from one site for each species. His results showed a seed potential of 36 seeds/cone for *P. pringlei* and 60 seeds/cone for *P. oocarpa*. Seed viability per cone was 26 and 55%, respectively, for the 2 species. Dvorak and Lambeth (1993) reported a seed potential for *Pinus tecunumanii* (Schw.) Enguiluz et Perry in Guatemala and Chiapas, Mexico of 90 seeds/cone. Narvaez-Flores (1993) found a seed potential for *Pinus arizonica* Engelm. in Chihuahua of 88 seeds/cone.

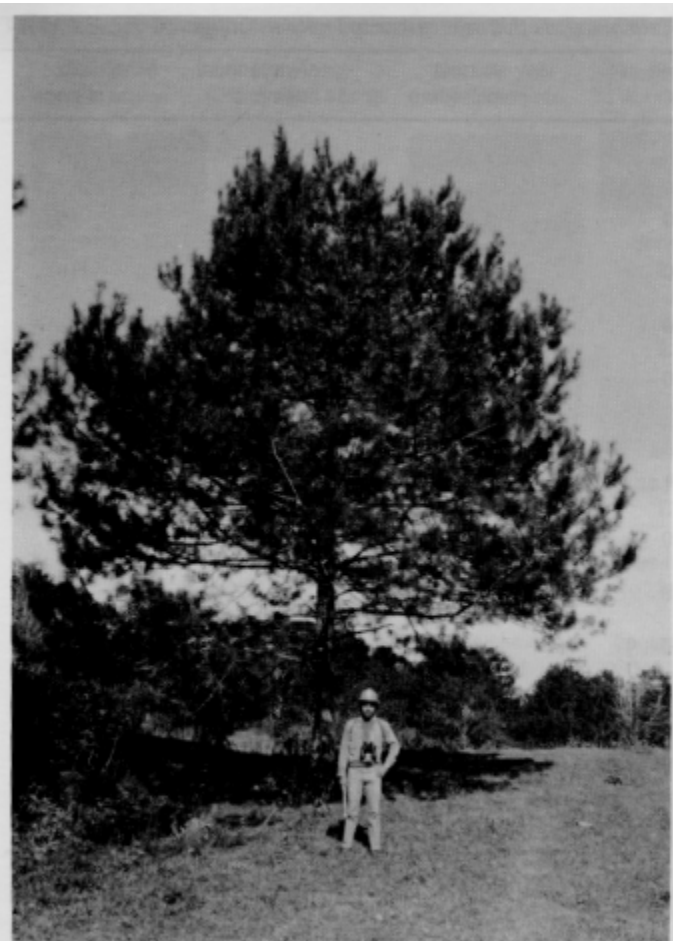


Figure 3—*Pinus greggii* showing the high stem diameter to tree height ratio common on many sites (Laguna Atezca, in Hidalgo, Mexico).



Figure 4—Closed mature (bottom) and immature (top) cones of *Pinus greggii* (Las Placetas, Nuevo Leon, Mexico). Cones may be produced in clusters of up to 10 to 12 and multiple flushes do occur in one year.

Seed efficiency, the number of filled seeds as a ratio to the seed potential, averaged 63% for all sites. This compares favorably to seed orchards in the southeastern United States, where a seed efficiency of 55% is considered good (Bramlett and others 1977). Trees at El Madroño had the highest seed efficiency, and those at La Tapona, a northern stand, the second highest. Like the stand at El Madroño, the stand at La Tapona is the least disturbed in its region and covers an area of approximately 220 ha. The stand at San Joaquin had the lowest seed efficiency of all sites. This stand is at the highest elevation reported for *P. greggii* in the southern region and also is among the most affected by human activities. Stand density is very low, and the trees are scattered about in small groups, interspersed among pasture areas over an area of approximately 150 ha. Inadequate pollination may be the cause for low seed efficiency at San Joaquin, as indicated by its having the highest number of first-year aborted seeds (table 3). The stand at Valle Verde, in the south, also ranked low in

filled seeds. This is interesting due to the fact that like the stand at El Madroño, it covers a large area (nearly 10,000 ha) but stand density is very variable, ranging from dense to widely dispersed. This site is located approximately 10 km north of El Madroño, at the lowest elevation reported for the species (1,150 m). The stands appeared to be in general poor condition based on the large number of trees observed with shoot borer attacks and cone pests. Based on casual observation, no other southern stand had this amount of insect problems. Seed efficiency in *P. greggii* was much higher than *Pinus arizonica* Engelm. in Chihuahua. Narváez-Flores (1993) reported an efficiency of only 19%, and first- and second-year abortions together averaged 44%.

The number of filled seeds per cone averaged 28% more in southern stands of *P. greggii* than northern stands (73.5 versus 57.2). Both the highest and lowest amounts of filled

Table 1- Summary of the *Pinus greggii* sites included in the study, with site numbers that reference map locations in figure 1

Site	Latitude & longitude	Elevation (m)	Annual precip. (mm)	Ave. annual temp. (°C)	No. of trees
Southern region					
1. El Madroño, Queretaro	21/ 16' N 99/ 10' W	1,650-1,730	1,200	17	15
2. Valle Verde, Queretaro	21/ 29' N 99/ 12' W	1,150-1,250	1,400	17	15
3. San Joaquin, Queretaro	20/ 56' N 99/ 34' W	2,310-2,380	1,100	16	15
4. Laguna Seca, Hidalgo	21/ 02' N 99/ 10' W	1,670-1,830	820	18	12
5. Cerro Perico, Hidalgo	20/ 44' N 99/ 02' W	1,830-1,970	800	17	15
6. Laguna Atezca, Hidalgo	20/ 49' N 98/ 46' W	1,250-1,420	1,642	19	15
Northern region					
7. Santa Anita, Coahuila	25/ 27' N 10/ 34' W	2,515-2,620	650	13	15
8. Mesa del Rosario*, Coahuila	25/ 26' N 100/ 28' W	1,920-2,325	650	13	15
9. Cañon Los Lirios, Coahuila	25/ 22' N 100/ 29' W	2,260-2,460	650	12	15
10. Loma El Oregano, Coahuila	25/ 22' N 100/ 55' W	2,310-2,350	600	13	15
11. Las Placetas, Nuevo Leon	24/ 55' N 100/ 11' W	2,370-2,520	750	16	15
12. La Tapona, Nuevo Leon	24/ 43' N 100/ 10' W	2,090-2,350	650	15	15

Source: INEGI (1980).

*This includes the dispersed stands that occur between Agua Fria (25/ 24'N, 100/ 25'W) and El Tarrillal (25/ 27'N, 100/ 31'W).

Table 2- Means and variances for cone and seed-yield traits across all sites

Trait	Mean	Min.	Max.	CV
No. of fertile cone scales	52.0***	9	111	34.4
No. of filled seeds	64.8***	0	221	62.1
No. of empty seeds	10.1***	0	73	94.7
No. of insect damaged seeds	0.5***	0	9	281.4
No. of aborted seeds-1st year	37.1 ***	0	132	57.0
No. of aborted seeds-2nd year	1.7***	0	24	140.2
Seed efficiency	62.6***	0	100	59.3

*** Differences among sites and trees within site significant at P#.001.

Laguna Atezca, respectively. Again, there could be a seed development problem at Laguna Atezca due to the reasons mentioned previously. The low number of fertile cone scales and number of first-year aborted seeds appear to be the dominant factors affecting the number of filled seeds at Laguna Atezca. Las Placetas, possibly the largest stand in northern Mexico (approximately 400 ha), had the second lowest number of filled seeds. This site had the highest incidence of insect attacks, both shoot borers and cone pests, of all sites inspected in 1993. The trees appeared to be under stress— top dieback and bark beetle attacks were frequently

observed in the stand. Precipitation usually increases in May in this zone. In 1993 rains were delayed until midJune, indicating that the region perhaps was in a prolonged dry-season cycle, putting the trees under moisture stress, leading to pest problems and reduced seed yields.

Upton and others (1993) got similar results for *P. greggii* from a collection done in 1990, when they sampled a total of 11 populations; 5 in southern region stands and 6 in northern region stands. Trees in southern stands had 17% more filled seeds than trees in northern stands. His results showed 75 and 46 filled seeds/cone for El Madroño and Molango (same site as Laguna Atezca), respectively. Trees at Las Placetas, in northern Mexico also had 46 filled seeds/cone. Plancarte (1988) sampled the stand at Molango in 1988 and got 97 filled seeds/cone. His results were based on bulked multipletree samples. Dvorak and Lambeth (1993) reported 6 filled seeds/cone for *P. tecunumanii* in Guatemala, and 30 filled seeds/cone in Nicaragua. Comparative data are unavailable for other species, but Flores (1969) reports 60 to 80 "viable" seeds per cone for *Pinus arizonica*, *P. durangensis* Mart. and *P. engelmannii* Carr in the northern

Table 3— Site means and Waller-Duncan groups for seed-yield traits of *Pinus greggii* in natural stands.

No. fertile cone scales	No. insect-damaged seeds	No. first-year aborted seeds	No. second-year aborted seeds	No. empty seeds	No. filled seeds	(%) Seed efficiency
El Madroño 74.7 a	Santa Anita 2.27 a	San Joaquin 64.0 a	Valle Verde 4.31 a	Cerro Perico 15.2 a	El Madroño 122.6 a	El Madroño 82.1 a
Cerro Perico 68.3 b	Mesa Rosario 1.10 b	Laguna Seca 44.5 b	Santa Anita 2.37 b	San Joaquin 14.6 a	Cerro Perico 95.1 b	La Tapona 73.1 b
Laguna Seca 65.5 c	La Tapona 0.55 c	Valle Verde 44.1 bc	Los Lirios 2.11 c	Los Lirios 13.6 b	Laguna Seca 85.4 c	Cerro Perico 69.5 b
San Joaquin 56.6 d	Laguna Atezca 0.53 c	Cerro Perico 39.6 cd	Cerro Perico 1.88 d	Laguna Seca 12.4 c	La Tapona 77.6 d	Laguna Seca 65.0 bc
La Tapona 52.5 e	Loma Oregano 0.36 d	Santa Anita 38.7 de	Las Placetas 1.73 d	Las Placetas 10.3 d	Santa Anita 59.6 e	Loma Oregano 63.0 cd
Santa Anita 50.9 f	Las Placetas 0.21 e	Las Placetas 35.6 def	Mesa Rosario 1.38 e	Santa Anita 10.1 de	Mesa Rosario 56.2 f	Santa Anita 61.9 cde
Valle Verde 48.6 g	Los Lirios 0.21 e	Los Lirios 34.1 ef	Loma Oregano 1.29 ef	Loma Oregano 9.4 e	Los Lirios 52.5 g	Los Lirios 59.0 de
Mesa Rosario 44.7 h	Cerro Perico 0.19 e	Laguna Atezca 31.6 fg	El Madroño 1.29 ef	La Tapona 7.9 f	Loma Oregano 51.5 g	Mesa Rosario 57.6 ef
Los Lirios 44.4 h	Valle Verde 0.19 e	Mesa Rosario 31.6 fg	Laguna Seca 1.27 ef	Valle Verde 7.4 fg	Valle Verde 48.6 h	Laguna Atezca 55.2 ef
Las Placetas 41.4 i	Laguna Seca 0.18 e	Loma Oregano 28.6 gh	San Joaquin 1.16 f	Mesa Rosario 7.0 gh	San Joaquin 47.9 hi	Las Placetas 54.7 ef
Loma Oregano 40.9 i	San Joaquin 0.13 e	La Tapona 27.5 gh	Laguna Atezca 1.11 f	Laguna Atezca 6.8 gh	Las Placetas 45.9 i	Valle Verde 50.0 fg
Laguna Atezca 37.2 j	El Madroño 0.09 e	El Madroño 25.5 h	La Tapona 0.47 g	El Madroño 6.3 h	Laguna Atezca 41.3 j	San Joaquin 42.3 g

The values shown represent average per cone. Shaded blocks are sites from the southern region, all others are northern region. Means in a column with the same letter are not significantly different at the 0.05 level.

Mexico states of Chihuahua and Sonora. The lower and upper values correspond to typical and abundant seed years respectively.

Northern stands of *P. greggii* had almost triple the amount of insect-damaged seeds per cone as southern stands— 0.62 versus 0.22. The highest incidence of insect damage was at Santa Anita, which had double the amount found at the second highest ranked site, Mesa del Rosario. Except for the one outlier southern site, Laguna Atezca, the results show a geographical trend; northern sites had more insect-damaged seed than southern sites. This could be attributed to moisture stress on the drier northern Mexico sites. Averaged

across sites, *P. greggii* had only 0.4% insect-damaged seed. This compares favorably to the *P. arizonica* study done by Narváez-Flores (1993), which showed 8% insect damage due to seed chalcids (*Megastigmus* sp.).

A slight geographical trend also appears in the first-year data on aborted seeds. On average, southern stands of *P. greggii* had 28% more first-year aborted seeds than northern stands (41.5% versus 32.3%). This trait was the dominant loss effect on seed efficiency. San Joaquin had the highest average of first-year abortions, possibly due to inadequate pollination, while El Madroño, the apparently healthiest stand, had the lowest average. It appears that the southern stands may have a general

problem of inadequate pollination. Usually, first-year seed abortions are attributed either to a lack of pollination or to insect attack. In this study, the southern stands had fewer insect-damaged seeds on average, thus indicating inadequate pollination as the major cause of first-year aborted seeds. The study reported by Lopez-Upton and others (1993) showed 40% more aborted seeds (1st- and 2nd-year combined) in southern stands of *P. greggii* than in northern stands. The stand at Valle Verde stands out as having the highest number of second-year aborted seeds. It also ranked high in first-year abortions, and subsequently low in seed efficiency. It is possible that the seeds are having developmental problems related to the apparent stress that the trees were suffering. As mentioned, a high incidence of shoot borer and cone pest attacks was observed in the field, but the site ranked low in the number of insect-damaged seeds. As such, the cause of this stress is unclear.

Conclusions

Seed efficiency for *Pinus greggii* in natural stands appears to be high in comparison to other pine species, and appears to have fewer and less severe seed insect problems. Adequate seed production in orchards located in the species' natural range should not be a problem. Sound seed production and seed efficiency is higher in southern stands than in northern stands. This may be due to genetic differences in numbers of fertile cone scales among populations, to the better soils and higher rainfall found at southern sites, or fewer pest problems than at northern sites. Further research is required to determine the actual cause of first-year seed abortions, which was the primary seed loss factor in this study. These results indicate a potential for insect problems in seed orchards of *Pinus greggii*. Close monitoring and control programs should be included in seed orchard management for this species.

Stands that were least disturbed by human activities, and growing under optimum conditions, had higher amounts of filled seeds. El Madroño (a southern site) and La Taponá (a northern site) had the highest seed efficiencies. Both stand out as large, homogeneous stands in their respective regions. Stands at elevational and precipitation extremes produced fewer sound seeds.

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Effect of the Antidesiccant Moisturin® on Conifer Seedling Field Performance

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Two concentrations of the antidesiccant Moisturin® were applied to Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings after lifting by either dipping or spraying. Seedlings were outplanted to 5 typically dry sites in Oregon and to a garden plot at Oregon State University. Seedling performance was assessed at the end of the first growing season. Despite trends in plant moisture stress measurements that suggest reduced transpirational loss, there were no significant treatment effects on height growth, survival, or stem diameter growth at any of the study sites nor in the garden plot. These results are consistent with most found in the literature in which conifer seedling field performance was not significantly or consistently improved by application of an antidesiccant product. Tree Planters' Notes 46(3):97-101; 1995.

Considerable research as well as practical knowledge indicate that a seedling's ability to use water efficiently is crucial to outplanting survival (Rietveld 1989, Burdett 1990). After being transplanted to the field, a seedling must recover from any damage, reestablish root-to-soil contact, and resume water and nutrient uptake in a new environment. During this adjustment period, the seedling continues to transpire, resulting in a stressed condition of physiological drought. It would be useful if a seedling could be protected from water loss during its establishment phase in the field.

Englert and others (1993) found that deciduous seedlings treated with the latex emulsion Moisturin® had significantly less water loss than non-treated controls. The success of Moisturin in trials with hardwood seedlings warranted further research with this compound to assess its utility in forest nurseries and forest outplantings. Moisturin, developed by Burke's Protective Coatings (Washougal, WA), is non-toxic to plant stems, roots, or foliage when applied at the recommended concentration. The white emulsion is visible when applied but dries to a transparent, flexible coating. Theoretically, the coating allows for the transmission of vital gases such as oxygen and carbon dioxide

while reducing water loss and retains its effectiveness for several months on dormant plants, or until plants "outgrow" the covering (Badertscher 1991).

This study examined seedling field response to Moisturin applied at differing rates and times. The following null hypotheses were tested: (1) application of Moisturin does not increase seedling field survival and growth, (2) there are no differences in seedling survival and growth between 1:3 and 1:7 concentrated applications of Moisturin, (3) there are no differences in seedling survival and growth when Moisturin is applied before or after lifting, and (4) there are no differences in seedling survival and growth when Moisturin is applied to seedling shoots only or to the entire seedling.

Materials and Methods

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) and ponderosa pine (*Pinus ponderosa* Dougl.) seedlings of varying stocktypes were operationally grown at four different nurseries (table 1). The following 7 treatments were applied at each of the nurseries:

1. Control
2. Spray shoots at 1:7 (Moisturin to water, vol:vol) concentration before lifting, in nursery bed
3. Spray shoots at 1:3 concentration before lifting, in nursery bed
4. Dip shoots in 1:7 concentration after lifting and grading, before storage
5. Dip shoots in 1:3 concentration after lifting and grading, before storage
6. Dip shoots and roots in 1:7 concentration after lifting and grading, before storage
7. Dip shoots and roots in 1:3 concentration after lifting and grading, before storage

All seedlings were lifted and treated in January 1992, with the exception of the ponderosa pine seedlings from Bend Pine Nursery, which were lifted in early March. Moisturin was applied to seedlings in the nursery bed

Table 1-Nurseries, species, stocktypes, and outplanting sites of seedlings in the study

Nursery	Species and stocktype	Outplanting site
Oregon State Department of Forestry, D.L. Phipps Nursery, Elkton, OR	2+0 Douglas-fir	USDI Bureau of Land Management, Roseburg District
International Paper Company, Kellogg Nursery, Oakland, OR	plug+1 Douglas-fir	USDI Bureau of Land Management, Medford District
USDA Forest Service, Deschutes National Forest Bend Pine Nursery, Bend, OR	1+0 ponderosa pine	USDA Forest Service, Mt. Hood National Forest
USDA Forest Service, Rogue River National Forest, J. H. Stone Nursery, Central Point, OR	2+0 ponderosa pine	USDA Forest Service, Fremont National Forest
J. H. Stone Nursery	2+0 Douglas-fir	USDA Forest Service, Umpqua National Forest

(treatments 2 and 3) with a hand-held compression sprayer. The compound was applied 1 day before lifting to allow adequate drying time. Efforts were made to apply the compound while temperatures were greater than 4.5 °C in order to ensure optimum coverage. For the other treatments (47), Moisturin was applied by dipping seedlings into one of the various concentrations of the compound. Dipping was done outdoors if the temperature was warm enough or in a large, well-ventilated room. After being dipped, seedlings were laid out to allow the coating to dry. To avoid excessive root exposure, seedlings were placed in cold storage within 1 hour, whether or not the compound had thoroughly dried. All seedlings were labeled and kept in cold storage until outplanting.

Seedlings were outplanted to 5 different sites in Oregon (table 1). Each site was selected because of its typically dry environment. Douglas-fir seedlings were planted February 1992, and ponderosa pine seedlings were planted early April 1992. The study design at each field site consisted of a randomized complete block design with 4 blocks, 7 treatments /block, and 10 seedlings/treatment/block.

Initial height, stem diameter, and survival were measured 2 weeks after planting. Total height, stem diameter, survival, and a damage/vigor assessment were recorded at the end of the first growing season.

In addition to the field sites, a garden plot consisting of seedlings from each nursery (with the exception of the Douglas-fir seedlings from the J.H. Stone Nursery) was established at Oregon State University (OSU). The

study design for the garden plot consisted of a randomized factorial block design with 4 blocks, both species in each block, 7 treatments/species, and 6 seedlings/species (3 from each nursery)/treatment/block. In addition to taking the same measurements as those taken at the field sites, days to budbreak were monitored.

A small sample of 15 Douglas-fir seedlings (2+0 stock from the D.L. Phipps Nursery) were potted and placed in an OSU greenhouse. Five seedlings were dipped in a 1:3 concentration of Moisturin, 5 were dipped in a 1:7 concentration, and 5 were dipped in water (control). Needles from these potted seedlings were photographed after treatment using scanning electron microscopy (SEM). After approximately 2 months without water, these seedlings were measured with a pressure chamber to determine plant moisture stress (PMS).

Data were analyzed with analysis of variance (ANOVA) procedures to determine if there were differences among treatments. SAS software was used for all analyses (SAS 1989).

Results and Discussion

Application of Moisturin was a fairly simple process requiring very little concentrated product to treat seedlings for the entire project. Air temperatures were above 4.5°C when Moisturin was applied to the seedlings, as recommended by the manufacturer. However, in a few instances, after applying the spray treatments, overnight temperatures dropped below freezing. When lifting these seedlings the following morning, it was observed that the treated seedlings

tended to have more frost on them than the surrounding trees. Also, frozen blue-tinted droplets of Moisturin were visible on the seedlings.

The highly magnified SEM images clearly show the Moisturin coating on the needles (figure 1).

Although the results were not statistically significant ($P = .28$), the seedlings that were potted and then not watered for 2 months showed encouraging results. The untreated, control seedlings had the lowest mean readings (- 1.95 MPa), that is, the greatest plant moisture stress. Seedlings treated with Moisturin applied by spraying had the next lowest mean readings, with the 1:7 concentration having slightly lower readings (- 1.60 MPa) than the 1:3 concentration (- 1.53 MPa). Seedlings treated with Moisturin applied by dipping had the highest readings (that is, least plant moisture stress), with the 1:7 concentration again exhibiting slightly lower readings (1.56 MPa) than the 1:3 concentration (- 1.43 MPa). These trends suggest that seedlings dipped in a high concentration of Moisturin may have reduced transpirational loss.

Despite trends of reduced transpiration in the potted seedlings, there were no significant treatment effects on height, survival, or stem diameter at any of the study sites (table 2) nor in the garden plot (data not shown). In addition, there were no effects of treatment on budbreak in the garden plot trees. These results lead to an inability to reject the null hypotheses.

Most of the literature addressing research of this nature have found results consistent with the current study. Research with various antidesiccant products show that treatments did not significantly or consistently improve survival or growth of conifer seedlings (Jack 1955, Fowells and Schubert 1955, Roy 1966, Magnussen 1986, Odum and Columbo 1987, Poljakoff-Mayber and others 1967, Vera-Castillo 1995, Williams and others 1990).

Interestingly, research has shown that some antidesiccant applications seem to be most effective in reducing water loss under moist soil conditions. However, when soils are dry (that is, when plants actually need protection against water loss) the treatments are no longer effective. In a series of growth chamber, greenhouse, and field experiments with *Pinus halepensis* Mill. seedlings, Poljakoff-Mayber and others (1967) found that antitranspirant treatments were "of little value ...if the soil around the roots of the plants was allowed to dry." In fact, they concluded that plastic mulching was the only treatment that effectively protected seedlings

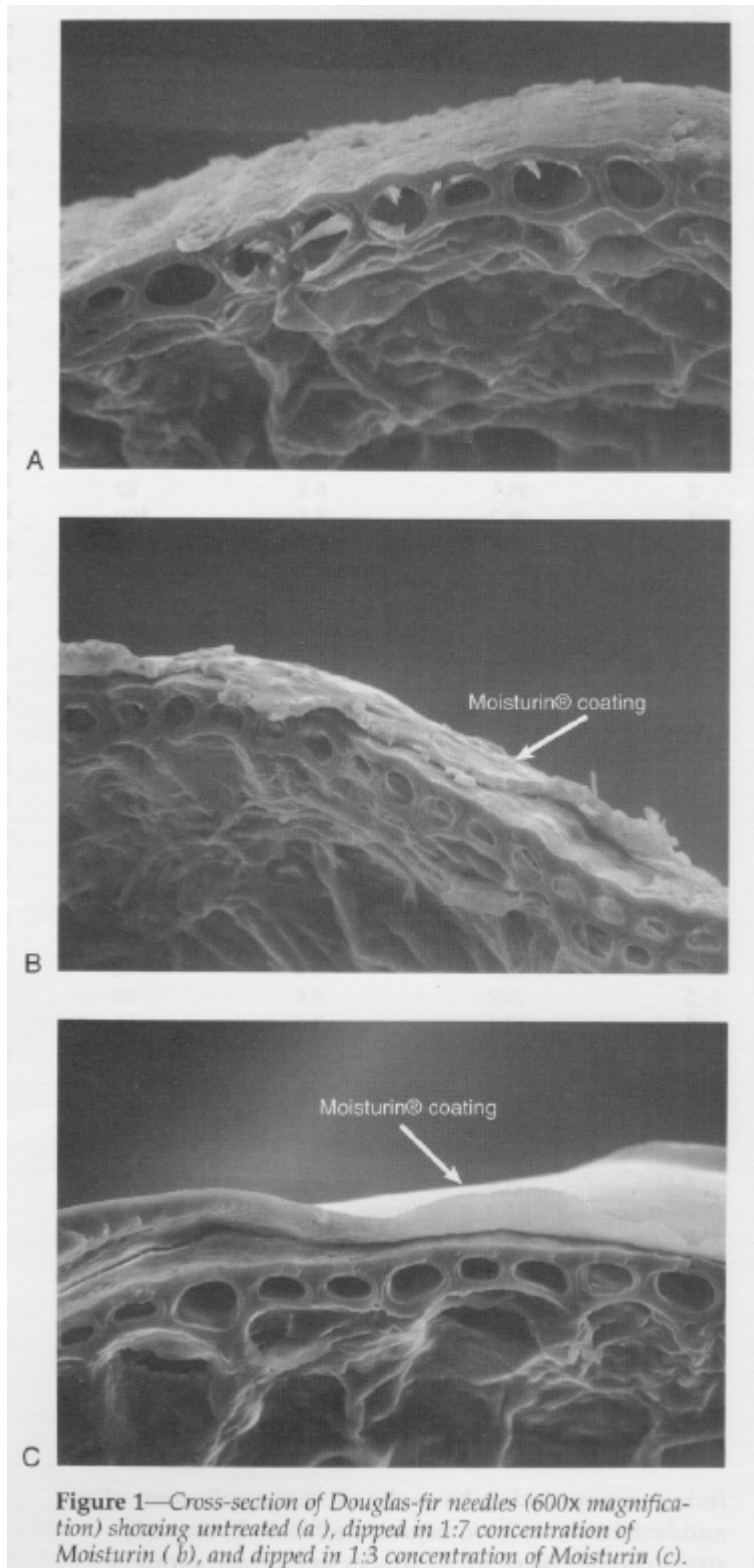


Figure 1—Cross-section of Douglas-fir needles (600x magnification) showing untreated (a), dipped in 1:7 concentration of Moisturin (b), and dipped in 1:3 concentration of Moisturin (c).

from moisture loss and increased field survival. Magnussen (1986) found that root-coated white spruce (*Picea glauca* (Moench) Voss) seedlings had improved

Table 2- Mean height, stem diameter, and survival after one growing season.

Site & treatment (cm)	Height	Stem diameter	Survival
	(cm)	(mm)	(%)
Douglas-fir			
BLM-Medford			
1	47.7	8.0	100
2	48.7	8.1	100
3	52.2	8.2	97
4	48.0	7.8	100
5	49.0	8.1	100
6	48.4	8.0	100
7	52.4	8.1	97
BLM-Roseburg			
1	36.1	7.5	100
2	35.7	6.5	89
3	38.1	6.2	92
4	39.2	6.6	100
5	41.1	7.0	90
6	37.4	6.7	92
7	39.5	7.1	100
Umpqua National Forest			
1	42.3	6.9	95
2	45.2	7.2	100
3	44.6	6.7	100
4	44.4	7.0	100
5	43.6	6.5	100
6	38.6	6.0	95
7	44.2	7.1	97
Ponderosa pine			
Mt. Hood National Forest			
1	13.6	3.7	74
2	13.3	3.8	90
3	12.2	3.3	77
4	13.7	3.6	75
5	13.2	3.6	82
6	13.4	3.4	85
7	12.2	3.5	74
Fremont National Forest			
1	12.9	4.6	23
2	16.1	5.1	20
3	16.5	5.1	18
4	14.4	4.5	18
5	16.3	5.2	8
6	14.1	4.3	43
7	n/a	n/a	0

survival when exposed to no more than 2 weeks of post-planting drought. However, the root coating had no effect when soils were shielded from natural precipitation for more than 2 weeks.

In fact, many studies have shown that application of an antidesiccant can have negative effects. In an early study on the use of foliar sprays to increase drought resistance of conifer seedlings, favorable reductions in transpiration were offset by unfavorable effects such as increased mortality (Shirley and Meuli 1938). Simpson (1984) noted that antitranspirant treatments that effec-

tively reduce moisture stress also tended to have the most negative effects on root growth and field performance of conifer seedlings. Odlum and Colombo (1987) found that antitranspirants greatly decreased survival of black spruce (*Picea mariana* (Mill) B.S.P) seedlings despite reduced plant moisture stress. Vera-Castillo (1995) found that application of Moisturin after lifting delayed budbreak in ponderosa pine seedlings by 15% in comparison with the untreated control. In addition, antitranspirants can elevate leaf temperatures due to decreases in transpiration (Gale and Hagan 1966) and can decrease the rate of photosynthesis (Olofinboba and others 1974). Furthermore, antidesiccant applications to conifer seedlings can even result in higher stomatal conductances than untreated control seedlings (Vera-Castillo 1995). In a study of six antitranspirants on black spruce container seedlings, Colombo and Odlum (1987) found mixed results. Although some treatments showed promise for reductions in water loss, the effects were also either phytotoxic or short-term.

Conclusions

Moisturin did not show promise for improved conifer seedling field performance. Furthermore, the literature demonstrates that there does not appear to be any product to date that effectively improves growth and survival of outplanted forest tree seedlings on a consistent basis.

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Shoot:Root Ratio Is of Limited Use in Evaluating the Quality of Container Conifer Stock

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The ratio of shoot dry mass to root dry mass, or shoot:root ratio, is sometimes used to evaluate the drought avoidance potential of container conifer stock. A review of published data from plantation trials reveals, however, that this relationship does not hold for container conifer seedlings. It is argued that the particular cultural conditions of container production favor root proliferation beyond strict physiological needs and that, once outplanted, the root plug-soil interface imposes a stronger limit on water and nutrient absorption by the seedlings than the roots themselves. Tree Planters' Notes 46(3):102-106; 1995.

The evaluation of seedling stock quality is one of the primary tools for ensuring the success of plantations. This evaluation usually relies on the measurement of attributes that are then compared against contract specifications or preset standards for the selection or rejection of nursery stock. Morphological attributes such as height, diameter, and dry mass are on the front line of seedling evaluation, and account for most of the variability among seedling stocks (D'Aoust and others 1994).

One of these morphological attributes is the ratio of shoot dry mass to root dry mass, or shoot:root ratio. Conventional forestry wisdom holds that shoot-root imbalance is one of the primary causes of transplanting shock. The objective of this text is to discuss the shoot:root ratio concept and to evaluate its usefulness as a predictor of seedling survival and growth in container conifer seedlings.

The Significance of Shoot:Root Ratio

The shoot:root ratio is a morphological attribute that is commonly used for the evaluation of bareroot seedlings and, to a lesser extent, of container stock. The basis for the use of this attribute is derived from a water balance perspective: a certain amount (surface area or dry mass) of transpiring foliage needs a certain amount (surface area or dry mass) of roots to absorb soil water and offset transpirational losses. A low shoot:root ratio means that

roots are abundant with respect to the foliage area, and that the seedling has a high water stress avoidance potential. A high ratio means that the roots are not as abundant, and that the seedling is more likely to suffer from water stress after planting, particularly in droughty sites or under conditions of high evaporative demand. Shoot:root ratio is thus used to evaluate the drought avoidance potential of seedlings.

The importance of this attribute for bareroot stock has been criticized (for example, Burdett 1990, Racey and others 1983). However, its relationship with seedling survival has been well demonstrated on seedlings planted in generally dry soil conditions (for example, Haase and Rose 1993, Boyer and South 1987, Rowan 1987, Larsen and others 1986, Thompson 1985, Lopushinsky and Beebe 1976). Usually, a shoot:root ratio of about 2 g/g is viewed as desirable.

The use of shoot:root ratio in container stock is based on the same water balance reasoning as in bareroot stock. As for bareroot stock, a shoot:root ratio of 1.5 to 2.5 g/g is also viewed as desirable (for example, figure 4 in Rose and others 1990; Romero and others 1986). However, judging from current experimental and field observations, we believe that shoot:root ratio is of limited value in the evaluation of container conifer stock.

Review of Results on Shoot:Root Ratio

A survey of existing literature reveals conflicting results with respect to shoot:root ratio and either growth or survival of container seedlings. In all the studies we could find (table 1), only one using seedlings subjected to drought stress in sand beds showed the negative relationship between survival and shoot:root ratio expected from a water balance reasoning (van den Driessche 1991). A subsequent experiment, also in sand beds but involving different levels of fertilization (van den Driessche 1992), produced a positive relationship between shoot:root ratio and survival. The reversal in relationship was attributed to an interaction with the

Table 1- Studies reporting on the shoot:root ratio of container conifer seedlings

Studies	Species	S:R ratio (g/g)	Effect of increased S:R ratio		Drought-induced mortality?
			on growth	on survival	
Endean and Hocking 1973	Lodgepole pine (<i>Pinus contorta</i> Dougl. ex Loud.)	1.9-5.8	Increased	None	None
Hocking and Endean 1974	White spruce (<i>Picea glauca</i> (Moench) Voss)	2.3-3.1	None	None	None
Walker and Johnson 1980	Lodgepole pine	1.0-3.6	Increased	None	None
	White spruce	1.5-3.6			
	Engelmann spruce	1.5-1.9			
	(<i>Picea engelmannii</i> Parry ex Engelm.)				
McGilvray and Barnett 1982	Southern pines	1.5-6.0	Increased	None	Limited
Maass and others 1989	Black spruce	2.9-4.8	None	None	None
	(<i>Picea mariana</i> (Mill) BSP)				
	White spruce	1.7-5.3			
	Norway spruce	1.3-3.5			
	(<i>Picea abies</i> (L.) Karst.)				
	Red pine	2.1-3.1			
	(<i>Pinus resinosa</i> Ait.)				
Zasada and others 1990	Jack pine	2.0-5.3	None	None	None
	(<i>Pinus banksiana</i> Lamb.)				
	Sitka spruce	1.8-4.7			
	(<i>Picea sitchensis</i> (Bong.) Carr.)				
van den Driessche 1991	Douglas-fir	1.8-2.8	NA	Decreased	Yes
	(<i>Pseudotsuga menziesii</i> (Mirb.) Franco)				
	Lodgepole pine	1.5-1.9			
van den Driessche 1992	White spruce	1.8-1.9	NA	Increased	Yes
	Douglas-fir	1.9-2.3			
	Lodgepole pine	1.7-2.0			
	White spruce	1.8-2.3			
Lamhamedi and others (in press)	Black spruce	1.5-4.5	None	None	None

fertilization treatment. Finally, in one recent sand bed experiment (Lamhamedi and others in press), physiological and growth measurements revealed no relationship between shoot:root ratio and drought avoidance in the seedlings.

All other studies reported (table 1) were outplanting experiments in which drought-induced mortality was either low or absent. In most of these, no relationship was found between shoot:root ratio and growth. An example of such results, presented in figure 1, was obtained from the data sets from several plantation trials in British Columbia (Simpson 1991, 1994). Although shoot:root ratios were related to seedling height at planting ($r^2 = 0.33$ to 0.46), these relationships did not persist for more than 2 years after planting.

Finally, a few studies reported a positive relationship between shoot:root ratio and growth (table 1), which is contrary to the water balance reasoning. However, the

greater ratios were mostly due to the larger shoots (McGilvray and Barnett 1982, Walker and Johnson 1980, Endean and Hocking 1973). The positive relationship therefore resulted from the normally greater absolute growth of the larger shoots, and not from a water balance-related advantage or disadvantage. Under conditions such as these, measurements of height or shoot mass offer a simpler and better evaluation of future growth.

Interpretation of Shoot:Root Ratio

The results reviewed above show that a strict control of root mass inside the peat plug in the nursery is of limited importance for the post-planting water balance of container seedlings. During seedling cultivation, the high levels of nutrients, water, and temperature of the rooting medium and its low density favor root proliferation (Prevost and Bolghari 1989, Friend and others 1990). When container seedlings are planted, intimate

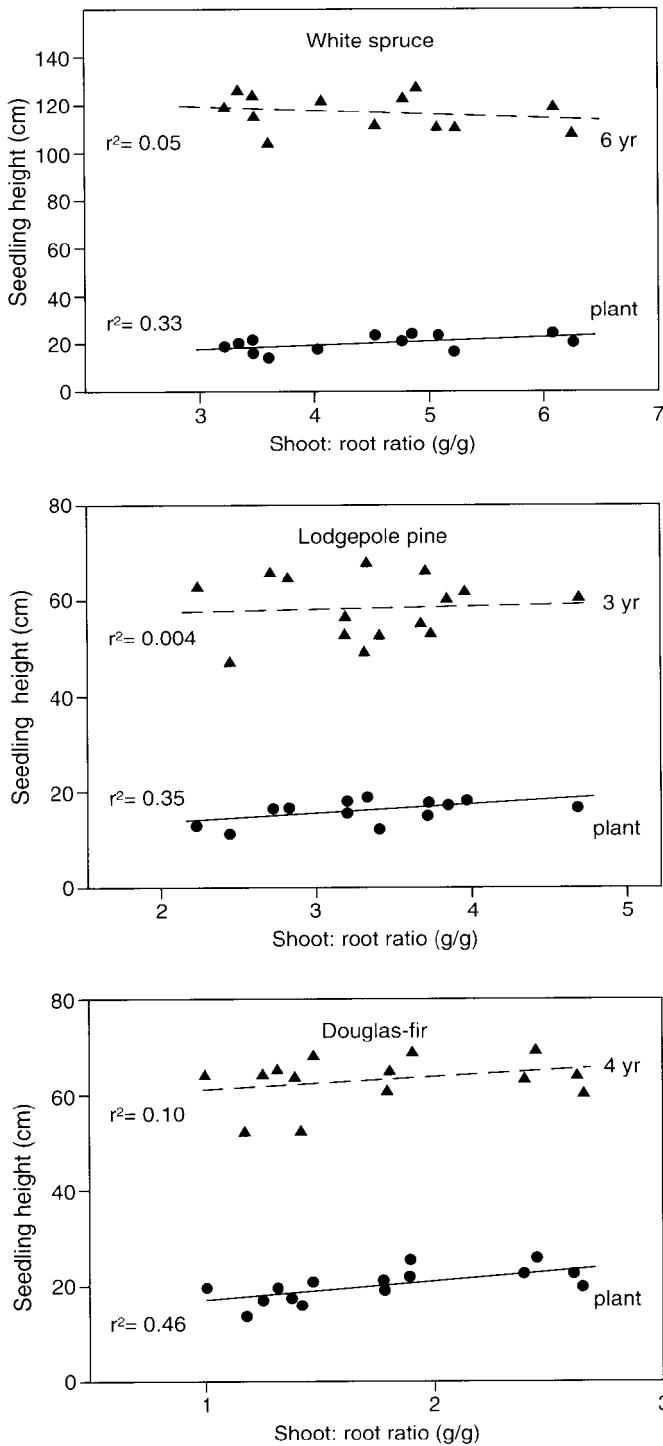


Figure 1—Relationships between shoot:root ratio and seedling height at planting time and after 3 to 6 years in the field for white spruce, lodgepole pine, and interior Douglas-fir container seedlings.

contact between the root and the rooting medium is maintained. The limiting factor then becomes the transfer of water and nutrients from the soil to the root plug as a whole because of the physical constraints imposed by the peat in the root plug to the movement and absorption of water (Bernier 1992, Bernier and others 1995).

In the longer term after planting, drought avoidance potential is related to the speed at which the seedling is capable of producing roots that extend outside the original root plug into the surrounding soil. Current evidence from white and black spruce shows a lack of a significant relationship between root dry mass in the peat plug and root growth potential (D'Aoust and others 1994), further weakening the link between shoot:root ratio and seedling quality.

In the field, extensive distribution of roots is more important than mass (Burdett 1990). For example, a comparison of shoot:root ratios of natural and container 2+0 black spruce seedlings planted on a boreal cutover site (unpublished data from P.Y. Bernier) is shown in figure 2. Measurements were taken in September. Natural seedlings have a much higher shoot:root ratio than the newly planted container seedlings, but the soil volume explored by their roots is far greater than the confined volume of the peat plug. The ratio in planted seedlings increases over the years, following the carbon allocation pattern dictated by local environmental con-

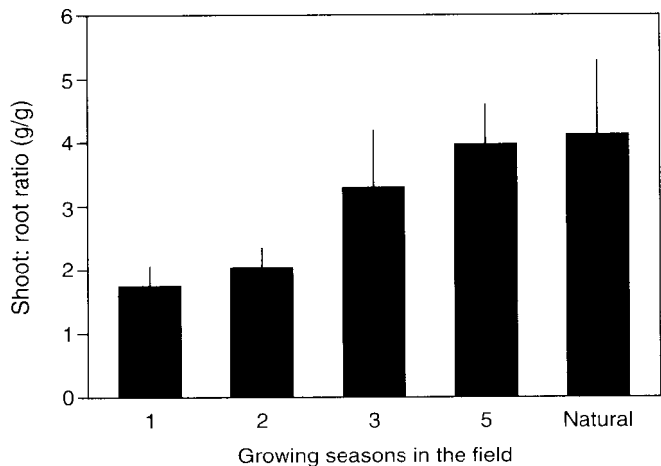


Figure 2—Shoot:root ratios of planted container black spruce and natural black spruce seedlings on a boreal site. The vertical bar is one standard deviation from the mean (n = 14).

ditions. Similar evolution of shoot:root ratio is reported by Walker and Johnson (1980). One also expects the final shoot:root ratio to be higher in a cool and humid climate, as in the figure 2 data, than in a hot and dry one.

This does not mean that any shoot:root ratio is acceptable. Values at either extreme can lead to problems. For a given shoot size, a very small ratio might mean an overly developed root system with mostly large suberized roots tightly clumped inside the container. A very large ratio might mean a poorly developed root system, with poor plug extractability, low potential for new root initiation, and reduced water and nutrient uptake. We think, however, that the range between these extremes is large, and that within this range, there is no relationship between this ratio and the survival or performance potential of container seedlings on most planting sites. In addition, the dramatic improvement in seedling survival when shifting from bareroot to container stock (for example, Walker and Johnson 1980) further narrows the range of field conditions under which moderate differences in shoot:root ratios might influence seedling survival.

Alternatives to the Shoot:Root Ratio

Apart from physical constraints such as plug extractability or root binding, the adequateness of a root system in container stock depends primarily on its ability to extract water from the peat plug and to quickly grow roots into the surrounding soil. Both of these functional properties are quite hard to ascertain with a static, morphological measurement. Neither appears to be adequately described by either root dry mass or shoot:root ratio. Traditional measurements of root growth capacity either at room temperature or at some lower equivalent of field temperature and concomitant physiological measurements of water movement in the plant currently offer the most information on the functional quality of the root system (Grossnickle and Folk 1994).

Measurements based on root architecture might also yield information on the growth potential of the root system. Alterations to the architecture of roots in the nursery influence the field growth of roots once the seedlings are outplanted. In container systems, copper-coating of containers is used to improve root architecture, with known positive effects on root and shoot growth after planting (Burdett and Martin 1982, Ruehle 1985). Air pruning of lateral roots in slotted containers can also achieve a similar effect. Studies have used the

architecture of root systems to compare the development of seedlings (for example, Grossnickle and others 1991). There has also been some work done relating root architecture to field performance in bareroot stock (for example, Hatchell and Muse 1990) and container stock (Simpson 1990). More work needs to be done in this field to ascertain the usefulness of this approach.

Conclusion

In conclusion, for sites with low drought-induced seedling mortality, shoot:root ratio is of limited value as a descriptor of container seedling quality because (1) the warm, moist, low-density and nutrient-rich environment of peat-based growing media favors root proliferation beyond strict physiological needs, and (2) upon planting, the soil-root plug interface becomes the controlling factor for water and nutrient transfer. Although extreme values of shoot:root ratios might indicate potential problems, values between such extremes appear unrelated to the water stress avoidance potential of the seedlings, or to the ability of the seedlings to produce soil roots. Other properties such as root system architecture or nutrient content exert more control over such functions.

The limited number of experiments in which shoot:root ratio was related to mortality does not permit us to evaluate conclusively the usefulness of this ratio under extreme conditions. However, the results from all other studies reporting on seedling growth suggest that the water balance reasoning applied successfully under such conditions to bareroot stock cannot be carried over to container stock.

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Variable Chlorophyll *a* Fluorescence as a Potential Indicator of Black Spruce Seedling Freezing Tolerance Under Nursery Conditions

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*Autumnal developmental decline in photosynthetic efficiency as measured by chlorophyll *a* variable fluorescence (Fv/Fm) was not found to correlate well with the freezing tolerance of black spruce (*Picea mariana* Mill. B.S.P.) seedlings produced in nursery greenhouses. A late-seeded (so-called extended) greenhouse crop maintained under a warmer temperature regime retained the potential for efficient photosynthesis, yet was tolerant of freezing to -30°C. Variable chlorophyll *a* fluorescence can, however, serve as a quick and convenient measure of a degree of damage suffered by seedlings following a -30°C freezing test. This measurement may complement the more laborious index of injury determination in current use. Tree Planters' Notes 46(2):107-111; 1995.*

Tree nursery seedlings in northwest Ontario suffered significant losses to freezing damage during outdoor overwinter storage in 1988 and 1989. Since then, storage in large-scale freezers at -2°C has been implemented by many growers. Based on early experience with longterm storage of bareroot stock at 0 to -2°C, no problems with this approach were anticipated. An understanding of the physiology of the seedling dormancy cycle is fundamental to any operational nursery overwintering regime. In this study, we use commercially grown black spruce (*Picea mariana* Mill. B.S.P.) seedlings to evaluate dormancy in terms of (a) freezing tolerance (index of injury, defined below) and (b) photosynthetic efficiency measured by chlorophyll *a* variable fluorescence (Fv/Fm, defined below). In doing so, we evaluate the reliability and utility of the fluorescence method to determine the dormancy status of greenhouse-grown seedlings.

Much of our understanding of the dormancy and freezing tolerance cycles in woody plants discussed by Weiser in 1970 remains unchanged today. While the basic model described below still applies, various tree species and ecotypes differ in timing and morphological detail. The first stage of low temperature acclimation results in morphological changes (for example, bud set),

depends on active photosynthesis and other metabolism, and is generally initiated by shortening daylength. The second stage, of increasing physiological dormancy measured as increasing freezing tolerance, is induced by near-freezing temperatures and is characterized by metabolic adjustments in no-longer-growing tissues. The end result is a tolerance of desiccation, as well as the ability to tolerate sub-freezing temperatures (Mazur and others 1972). Commercially grown seedlings of black spruce belong to a group of conifers capable of tolerating freezing temperatures to -70°C (Sakai 1983). From a practical perspective, seedling physiological dormancy, that is, freezing tolerance, is generally tested, at most, down to -40°C and the basic freezing tolerance onset characteristics have been confirmed by the extensive work of Colombo and associates (Colombo and others 1989, Colombo 1990).

One aspect of seedling physiology that changes during the onset of dormancy is the capacity for and the efficiency of photosynthesis. The latter parameter is readily measured using chlorophyll *a* variable fluorescence, that is, the ability to release excess photosynthetic energy as light. This fluorescent (longer wavelength) light arises from dark-adapted needles due to a temporary overexcitation of the photosynthetic apparatus with saturating light flash. Capacity for this fluorescence emission has been shown to correlate well with photosynthetic efficiency (the ratio between amount of light energy and the amount of photosynthetic product, usually oxygen). By coincidence, the photosynthetic efficiency values of active and therefore efficient photosynthesis (0.7 to 0.8) coincide with a commonly used measure of fluorescence, the ratio of variable to maximal fluorescence (Fv/Fm). These ratios also range around 0.7 to 0.8 for plants capable of normal photosynthesis and decrease to 0, as photosynthetic efficiency decreases. This decrease may be due to either damage to, or disassembly of, the photosynthetic apparatus as dormancy develops.

Commercially available fluorometers measure and display the Fv/Fm ratio directly and their manuals explain how the parameters are calculated (Sivak and Walker 1985, Lichtenthaler 1988). The relationship between tree seedling dormancy and chlorophyll *a* variable fluorescence (photosynthetic efficiency) was demonstrated for Douglas-fir by Hawkins and Lister (1985) and white spruce by Vidaver and others (1989). The operational use of chlorophyll *a* variable fluorescence is gaining gradual acceptance in British Columbia (Vidaver and others 1991). Some nursery applications and potential pitfalls are discussed by these authors. Fluorometer applications in seedling production are also under active investigation by Binder (British Columbia Ministry of Forests, Victoria, BC, Canada) and Mohammed (Ontario Forest Research Institute, Sault Ste. Marie, Ontario, Canada).

This report discusses research on variable chlorophyll *a* fluorescence as a suitable and quick measure of seedling freezing tolerance under nursery conditions, firstly by measuring decline in fluorescence (decline in Fv/Fm) with the onset of dormancy, and secondly by measuring damage sustained following a freezing test which exceeds the freezing tolerance of the seedlings. The damage sustained in these treatments was also measured by determining the leakage of ions from the tissue and the resulting conductivity of the solution in which the tissue is bathed. The electrolyte leakage-based index of injury test (Flint and others 1967, Colombo 1990) is in current standard use in Ontario. Dormancy-related developmental changes reflected in the fluorescence data were compared to this index of injury.

Materials and Methods

Seedling production and crop characteristics. Black spruce seeds collected from northwestern Ontario, stock # 3425003, were sown in vent block trays (Beaver Plastics, Edmonton, AB) at Hills Nursery, Murillo, and grown to shipping size in 1991 and 1992. In the fall of 1991, two crops were studied. One, the so-called current or regular crop, was sown in March and kept outside in shaded cold frames during the period of the study. Maximum and minimum temperatures are shown in figure 1 (solid triangles). The second, "extended crop," which effectively doubles the production capacity of an individual nursery, was sown in June 1991 and maintained in a heated greenhouse well into the autumn (figure 1, open triangles), with the windows opened and heating shut off the week of October 19 (figure 1, open triangles) to induce bud set and freezing tolerance (temperatures in the ventilated greenhouse were comparable to those in the cold frame during this time period, figure 1). Operational harvesting and packaging for frozen

storage took place in the week of December 2, after which time a few trays from each crop were placed in a warm greenhouse at natural short photoperiod (4 to 14 °C, figure 1a) to induce flushing. The stored crop was not investigated further. Similarly grown and treated seedlings were studied in 1992-1993. Measurements of fluorescence as Fv/Fm and sampling of shoots for the index of injury test were done every 1 or 2 weeks on the dates indicated in figure 2.

Chlorophyll *a* variable fluorescence. The Plant Stress Meter (BioMonitor, Sweden) was used to measure fluorescence. The fluorescence parameter Fv/Fm (10 readings were taken per treatment on randomly selected seedlings from several locations in the greenhouse) was measured weekly in 1991, at three separate times, early morning, mid morning and afternoon to determine any variability. As most stable readings were obtained at 8 to 9 am (data not shown), all readings in 1992 were taken at this time of day. All samples were dark-adapted for 15 minutes in a clamp supplied by the manufacturer and subsequently exposed to a blue excitation beam of 300 μmol/m²/s carried by a fiber-optic cable. Red fluorescent light in turn is carried back through the cable for measurement by the photomultiplier and display of values calculated by the instrument.

Determination of shoot frost hardiness. Shoot frost hardiness was determined using the index of injury electrical conductivity technique (Flint and others 1967, Colombo and others 1984), which quantifies leakage of electrolytes (EC = electrical conductivity) known to be proportional to freezing-induced damage (and compared to total leakage from boiled samples) to seedling tissues as described in this paragraph. The terminal 3 cm of the main shoot of 16 randomly selected seedlings were used in quadruplicate. Following 16-hr control leaching (at which time "EC control" was measured), shoot tips were frozen at a rate of 2 °C/hr to -30°C. Prior to returning samples into the pre-freezing leachates, chlorophyll *a* fluorescence was measured. After further 16 hrs of incubation, the electrical conductivity of the water was measured to determine "EC frozen." Then the test tubes containing water and shoot tips were capped and placed in 90°C oven for 4 hrs to kill the tissue and allow complete leakage to occur in subsequent 16 hours ("EC heat-killed"). Index of injury (I_t) was calculated in % as:

$$I_t \text{ (in \%)} = \frac{(\text{EC frozen} - \text{EC control})}{(\text{EC heat-killed} - \text{EC control})} \times 100$$

Low percentage values approaching 0 indicate decreasing damage, that is, a high degree of physiological dormancy and freezing tolerance. A value of 10% or less

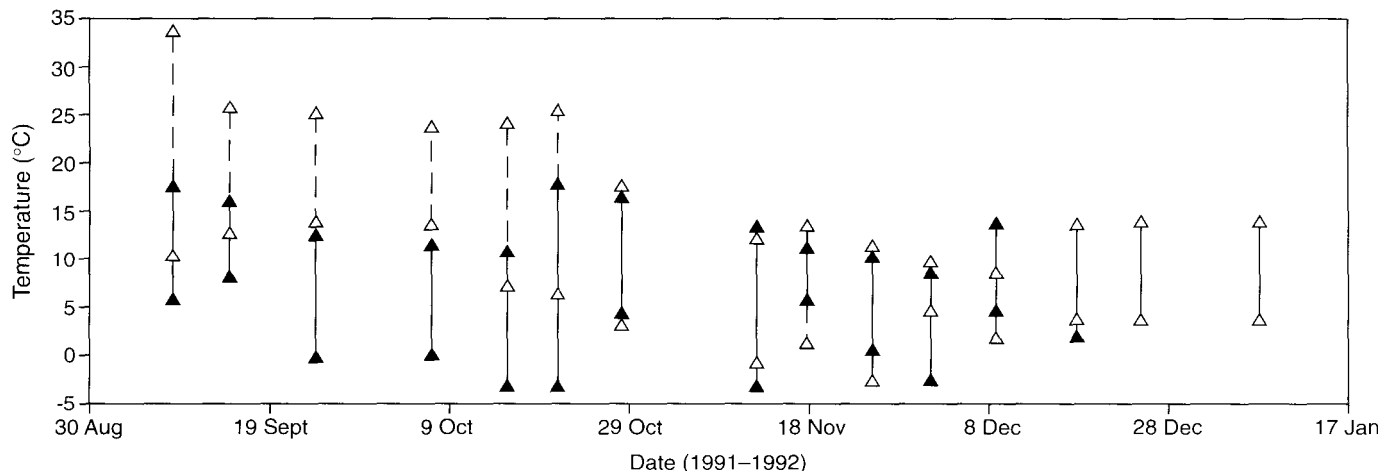


Figure 1—Maximum and minimum air temperatures for the current crop (solid triangles) and extended crop (open triangles) in 1991–1992.

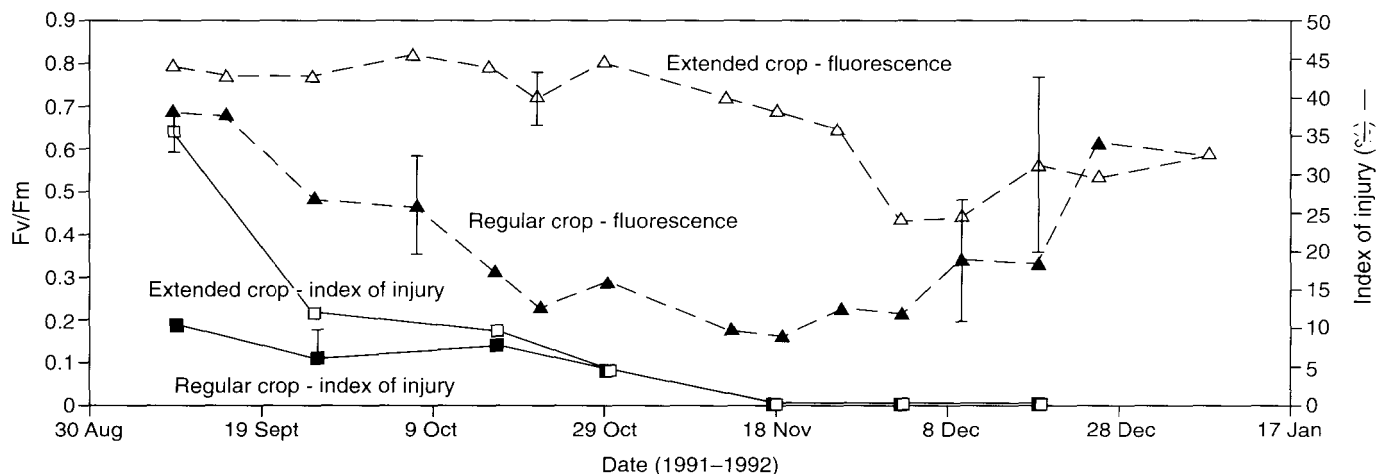


Figure 2— Seasonal changes (1991–1992) in variable chlorophyll a fluorescence (F_v/F_m , dashed lines, triangles) and freezing tolerance index of injury, solid lines, squares). Current crop (solid symbols) and extended crop (open symbols). Averages of at least 10 measurements \pm SE. For clarity, only the largest error bars for each treatment are presented.

has been selected as acceptable level of freezing tolerance for seedlings overwintered out of doors.

The fluorescence data following freezing treatments (figure 3) are not presented as a simple F_v/F_m ratio (as described in the Introduction and Section 2), because this parameter changed (declined) in the course of the study with developmental time (onset of dormancy) of seedlings (see figure 2). Instead, a difference is reported (designated as Greek letter delta, Δ) between the final (after freezing test) F_v/F_m and initial (prior to freezing test) F_v/F_m for measurements made on a particular date. Negative values for extended crop $\Delta F_v/F_m$ in September indicate damage to the photosynthetic apparatus, that is, difference between readings of 0 in damaged seedlings after freezing test and 0.6 to 0.7 initially. Values for extended crop $\Delta F_v/F_m$ near 0 in late

November result from the small difference between prefreezing values of dormant seedlings near 0 and postfreezing values in undamaged dormant seedlings still giving readings near 0.

Results

Two major findings emerged from this study. Firstly, decreasing photosynthetic efficiency (measured as declining F_v/F_m) and increasing freezing tolerance (measured as declining index of injury) changed simultaneously in the current crop (figure 2, solid symbols), although relatively high degree of freezing tolerance was measured in this crop in early September. In contrast, the extended crop that was grown in greenhouses under natural photoperiod but at elevated temperatures until late October (figure 1, open triangles), does not

show this parallel between increased freezing tolerance (rapid decrease in the index of injury during September, figure 2, open squares) and photosynthetic efficiency (Fv/Fm values remaining high at above 0.8 until late November, figure 2, open triangles). A decline in photosynthetic efficiency of the extended crop (figure 2) took place only when open greenhouse minimum temperatures started dropping below 0°C in early December, figure 1, open triangles). This was about 2 months after freezing tolerance (index of injury = 10%) was established. The experiments described above were repeated again in 1992/3 with similar results (not shown). In both years, multiple regression statistical analysis did not detect a positive correlation between the index of injury measurements and Fv/Fm measurements in the extended crop.

The second finding of this study pertains to figure 3, which describes the ability of the photosynthetic efficiency measurement (Fv/Fm) to detect freezing damage to seedlings which are not freezing tolerant, that is, the extended crop in October. The Δ Fv/Fm measurements for the extended crop in October detect and illustrate the damage suffered by the needles following the freezing treatment to -30 °C (figure 3, open triangles). These values (about -0.5 Δ Fv/Fm) result from the difference between the high (0.7 to 0.8 Fv/Fm) measurements before the freezing treatment, and the low values (0 to 0.3 Fv/Fm) detected after thawing from freezing at -30 °C, that is, after damage sustained by the photosynthetic apparatus. As the extended crop increased its freezing tolerance through November, its pre-freezing test Fv/Fm values decreased gradually to about 0.4 due to dormancy onset and the post freezing test measurements gave values near 0.2, resulting in Δ Fv/Fm of about -0.2 through late November and December (open

triangles, figure 3). In contrast, the current crop had Δ Fv/Fm values near 0 throughout (dark triangles, figure 3), simply because the pre-freezing test values of 0.2 to 0.3 are subtracted from similar values after the -30 °C freezing treatment, indicating that the freezing tolerant current crop seedlings did not undergo a change in the Fv/Fm due to damage by freezing. These experiments were repeated in the 1992-1993 season with essentially the same results (data not shown).

Discussion

The lack of correlation between freezing tolerance and photosynthetic efficiency measured as Fv/Fm during the onset of dormancy in the extended crop appears to contradict suggestions in the literature, that variable chlorophyll *a* fluorescence may be a simple and fast indicator of seedling dormancy and freezing tolerance. Such a correlation clearly exists for the current crop (figure 2) and may exist for white spruce and Douglasfir seedlings produced outside, under natural conditions of a relatively mild coastal climate (Hawkins and Lister 1985, Vidaver and others 1989). The artificially extended greenhouse crop conditions in northwestern Ontario modify the onset of physiological seedling dormancy so as to make the fluorescence measurements of doubtful value as a measure of freezing tolerance. On the cellular level, the Fv/Fm parameter measures photosynthetic activity in the chloroplast and the index of injury measures the ability of the cytoplasm and the cell membrane to withstand low temperature and desiccation induced by extracellular ice. There is no known biological reason for the two cellular compartments to behave in a correlative fashion in respect to freezing tolerance. Öquist and Strand (1986) have shown no major changes in photosynthetic capacity of hardening Scots pine. However, a

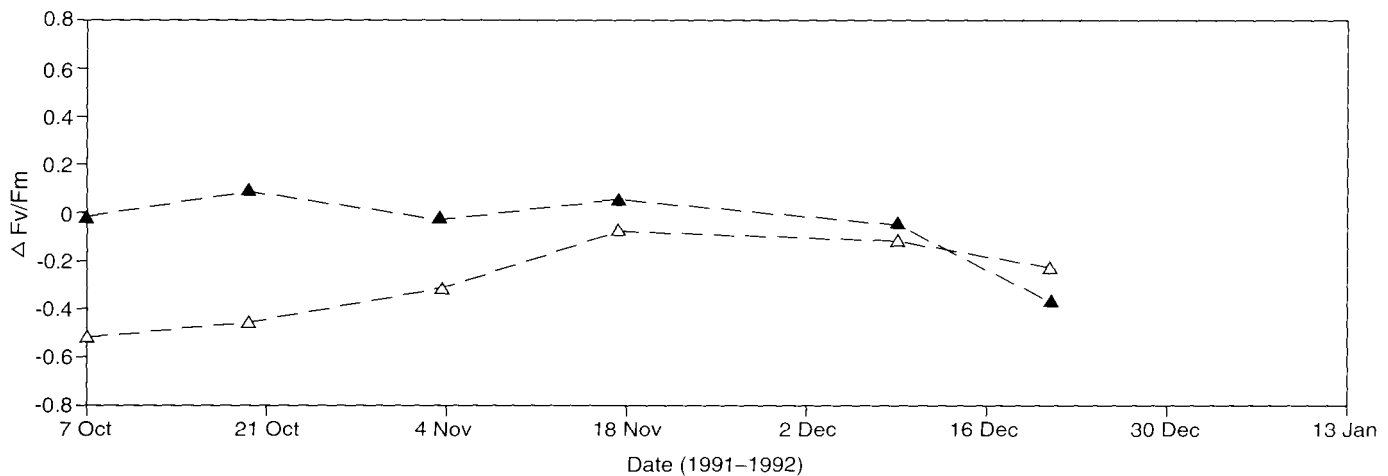


Figure 3—Damage sustained by the 1991-1992 crops in a freezing test to -30°C as measured by the difference (Δ Fv/Fm before and after the freezing test (dashed lines, triangles). Current crop (solid symbols), extended crop (open symbols).

detailed statistical analysis of chlorophyll fluorescence kinetics curves done by the same group (Sundblad and others 1990) suggested that a predictive correlation may exist between some features of the fluorescence kinetics curve and freezing tolerance in Scots pine. Our simple and readily obtained Fv/Fm measurement is not as revealing. Photosynthetic efficiency measured as Fv/Fm may be expected to decline not only due to the onset of dormancy as for the current crop in figure 2, but also due to direct damage to the photosynthetic apparatus of nondormant needles. This is the case following a damaging freezing treatment to non-hardy extended crop seedlings (figure 3). Extended crop seedlings in September had a high index of injury (20 to 40%, open squares, figure 2). Yet, these seedlings retained high photosynthetic efficiency (about 0.7, figure 2). However, following a freezing treatment at -30 °C, cell structure and photosynthetic apparatus of these seedlings was damaged, resulting in negative Fv/Fm (as calculated above). In contrast, the photosynthetic apparatus and cell integrity of the current crop at the same time of year are already protected by physiological dormancy onset, resulting in Fv/Fm values near 0.

A decline in Fv/Fm following damaging stress is well documented and has been used, among others, to assess frost sensitivity of wild and cultivated potato (Greaves and Wilson 1987); resistance of poplar clones to low and high temperature, as well as drought (Havaux and others 1988) and chilling tolerance of tomato hybrids (Walker and others 1990). **In this respect, variable chlorophyll *a* fluorescence will likely prove a simple, rapid method for the quantification of stress-induced damage to tree seedlings.** In the case of freezing tolerance studies, this approach does not appear to eliminate the use of expensive controlled freezing rate freezers. On the other hand, the chlorophyll *a* variable fluorescence measurements taken before a freezing test do not appear to be a reliable indication of the degree of physiological dormancy and freezing tolerance in seedlings grown under extended crop greenhouse conditions.

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