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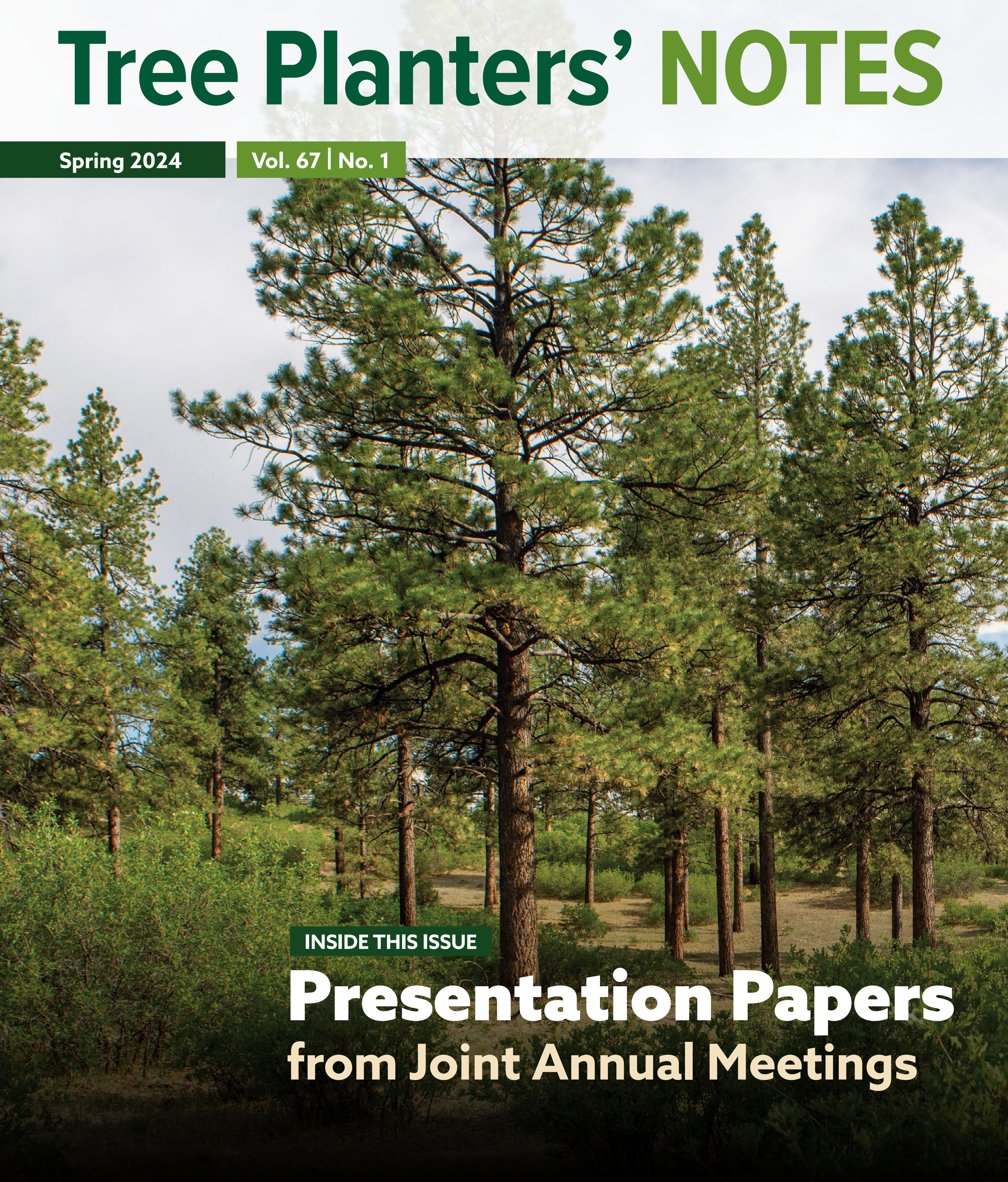

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Presentation Papers from Joint Annual Meetings

On the cover:
A stand of ponderosa pines on the San Juan National Forest, CO. Adobe Stock photo.

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Letter from the Editor

Dear TPN Reader,

This is my final issue as your editor. It has been a genuine pleasure working on this publication for the past 12 years. In total, I've edited 26 issues (including this one) containing 242 articles. When I took over in 2011, the journal had been languishing somewhat, with only nine issues published since 1997. Also, it had only been published in black and white. Since then, TPN has been published twice annually and is in full color. The photographs and other color graphics have truly given new depth and appeal to the articles. Many other changes and additions to TPN have occurred. The "Tree Planting State by State" series started in 2011 and has had 26 papers published thus far (and will continue beyond my retirement). Also, my colleague, Carrie Pike, facilitated a series of TPN papers on seed-transfer guidelines for tree species in the Eastern United States. These papers have been compiled into a U.S. Department of Agriculture, Forest Service, Agriculture Handbook (available soon, check the RNGR.net website for more information). Starting in 2014, papers from the annual meetings of the Western, Southern, and Northeastern Nursery Associations have been published in TPN. Incorporating the meeting papers into TPN eliminated the need for publishing separate proceedings and provided wider distribution for the papers.

> *"Acts of creation are ordinarily reserved for gods and poets, but humbler folk may circumvent this restriction if they know how. To plant a pine, for example, one need be neither god nor poet; one need only own a shovel."*
>
> *— Aldo Leopold*

During my years as your editor, I've had the opportunity to work with so many amazing people in the nursery, reforestation, and restoration communities. Some people had never published a paper before—especially many of those that were cajoled into writing for the "State by State" series. Even though some authors do not have strong writing skills or do not run a traditional research project, they have a worthwhile story to share. My approach as an editor has been to welcome all articles and work together to create a polished manuscript worthy of publication. Thus, no articles have been rejected since 2011 (except two that were completely out of the TPN scope). I believe this broad inclusion and editing support is important to uphold that which makes TPN unique. It is a completely applied journal and includes a wide range of technical and research articles that are easy to understand and readily applicable to on-the-ground nursery, reforestation, restoration, and conservation personnel. Many TPN articles have been cited in other journals or at professional meetings, workshops, and conferences. Tree Planters' Notes began in 1950, and I'm honored to have been a part of that 74-year legacy. And, I'm delighted to be handing the reins over to your new editor, Andrea Watts. She has degrees in English and forestry and a lot of writing and editing experience in the forestry world. She's excited for this opportunity, and I'm confident she will do an outstanding job of keeping this important resource available into the future. Contact information, guidelines to authors, and subscription options continue to be available online (https://rngr.net/publications/tpn).

Farewell and best wishes,

Diane

Diane L. Haase

Tree Planters' Notes (TPN) is published by the Forest Service, an agency of the U.S. Department of Agriculture. The purpose of Tree Planters' Notes is to benefit the nursery community by sharing information and raising awareness of issues related to nursery production and outplanting of trees, shrubs, and native plants for reforestation, conservation, and restoration.

TPN welcomes unsolicited manuscripts from readers on any subject related to nursery production. For editorial questions or to contribute an article, contact Editor Andrea Watts at andrea.watts@rngr.net. Tree Planters' Notes is available online **(https://rngr.net/publications/tpn)**.

TPN accepts both technical and research articles; each is reviewed by the editor. Please see the guidelines for authors for details about editorial policy, formatting, style, and submission **(www.rngr.net/publications/tpn/author_guidelines)**.

Note from the production staff: As mentioned in the "Letter from the Editor," the design of TPN has evolved over the years, and this year brings new changes. This issue presents a refresh of the layout. Additionally, minor updates to the TPN style and author guidelines will improve consistency across issues.

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State College, PA, July 17–20, 2023

Proceedings Papers Presented at Growing Growing Pains: Scaling Up the Reforestation Pipeline—Joint Annual Meeting of the Western Forest and Conservation Nursery Association and the Forest Nursery Association of British Columbia

Portland, OR, September 19–21, 2023

Figure 1. Stunted growth and short needles are two symptoms of zinc (Zn) deficiency in pine seedlings. The container on the right contains normal loblolly pine seedlings growing in a nutrient solution containing zinc chloride ($ZnCl_2$) (Lyle 1969). The seedlings on the left were grown in a nutrient solution that did not contain Zn. Deficient seedlings had short, thick, and twisted secondary needles. Photo by Jack May.

Land Leveling Can Cause Temporary Zinc-Deficiency in Pine Seedlings

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Abstract

Land leveling can cause zinc (Zn) deficiencies in corn (*Zea maize* L.) by removing topsoil and lowering the population of endomycorrhizal spores. Although Zn deficiencies on pine (*Pinus* spp.) seedlings are rare in established bareroot nurseries where ectomycorrhizal spores are airborne, a brief deficiency occurred after leveling "new ground" in Alabama. In July 1986, nonmycorrhizal loblolly pine (*Pinus taeda* L.) seedlings had purple cotyledons and short needles when planted on newly leveled ground. Plots of stunted seedlings were sprayed with a phosphorus (P) fertilizer, which increased height growth. The Zn deficiency lasted less than 7 months. In August, foliage on stunted seedlings in untreated plots ranged from 4 to 11 ppm Zn, but in November the level exceeded 90 ppm. The risk of a Zn or P deficiency in pine seedlings is low when short roots are ectomycorrhizal. When P and Zn deficiencies occurred on nonmycorrhizal loblolly pine seedlings, however, the Zn deficiency was overlooked since stunting and short needles are symptoms of both deficiencies.

Introduction

Although zinc (Zn) deficiencies in endomycorrhizal crops might be the most ubiquitous micronutrient deficiency worldwide (Alloway 2008, Swietlik 1999), Zn deficiencies in bareroot pine (*Pinus* spp.) seedlings are rare. Zn deficiencies have been reported on an 88 percent peat soil in New Zealand (Knight 1976) and at a nursery in Wisconsin (Tanaka et al. 1967). Although stunted pines at a Colorado nursery had foliage with 11 ppm Zn, stunted growth was likely due to alkaline soil with high soil calcium (Ca) (Landis 1988). Furthermore, pine seedlings with 9 ppm foliar Zn were classified as healthy (Knight 1976).

Zn-deficient pine seedlings can be grown in greenhouses under controlled conditions (Lyle 1969, Smith and Bayliss 1942), although Zn deficiency symptoms do not always appear (Hacskaylo et al. 1969). Two common symptoms on loblolly pine (*Pinus taeda* L.) are stunting and short needles (figure 1). In some species, Zn-deficient seedlings have a dark-green color (figure 2). Chlorotic needles are not a typical symptom of Zn deficiency in pines.

When preparing land for a new pine nursery, topsoil is often removed and stockpiled before land-leveling operations (Morby 1984). When leveling is completed,

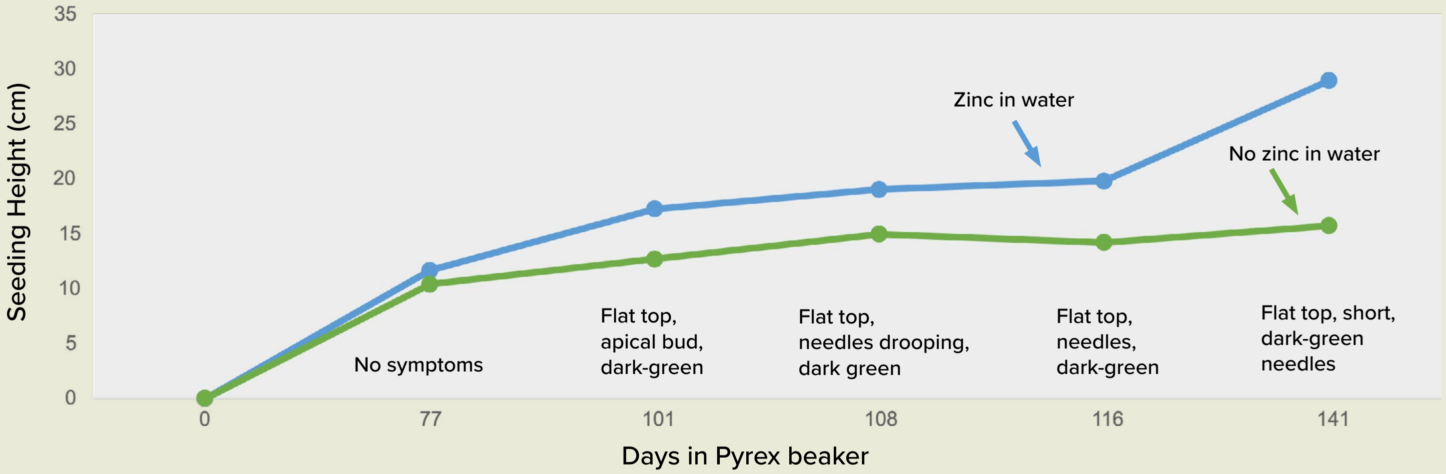

Figure 2. When growing in aerated water with no zinc (green line), Monterey pine seedlings show deficiency symptoms (stunting, dark-green needles, and short needles) between weeks 11 and 15. Adapted from Smith and Bayliss (1942).

topsoil is replaced, but the stockpiled soil may not be sufficient to cover all areas. Some spots may have 1 ppm Zn in soil (Grunes et al. 1961), while others may have more than 6 ppm (using the Mehlich 3 soil test). After land leveling, Zn deficiencies have occurred on several crops (Alloway 2008, Brye et al. 2004, Grunes et al. 1961, Shapiro 2019, Swietlik 1999, Viets et al. 1953). Land leveling combined with soil fumigation can deplete ectomycorrhizal spores and produce phosphorus (P) deficiencies (Trappe and Strand 1969), while land leveling alone can produce Zn deficiencies.

Determination of Zn Deficiency

Various methods are used to define Zn deficiency. The preferred way involves hypothesis testing with a fertilizer trial. For example, comparisons can be made among seedlings treated with zinc chloride ($ZnCl_2$), chelated Zn fertilizer, and untreated seedlings. If both Zn groups grow faster than the untreated group, then seedlings were likely Zn deficient. Another approach is to treat a group of seedlings with zinc sulfate ($ZnSO_4$) and assume that any growth response is due to the Zn supplement and not the sulfur (S) (i.e., seedlings were Zn, not S, deficient) (McKee 1976, Tanaka et al. 1967). A third method assumes Zn deficiencies can be determined simply by analyzing and comparing Zn levels in relation to foliage biomass. This math-based method is not scientific, but it is often used instead of hypothesis testing.

Seedlings with 9 ppm Zn in foliage can be considered normal (Knight 1976). This value is the threshold level used in this article. Defining deficient seedlings by comparing a foliar Zn test with a foliar distribution curve for Zn is not a valid method. When asymptomatic pines have 11 to 30 ppm Zn in foliage, they are not Zn deficient (Jokela et al. 1991, Knight 1976, Ruiter 1969, Stone 1968).

Zn Deficiency Symptoms

Zn deficiency symptoms can be produced in hydroponic systems when the water contains little or no Zn. Deficiency symptoms include stunting, short needles, rosette buds, and dark-green or bronze needles. When grown in water, Zn-deficient loblolly pine seedlings appear stunted with short needles (see figure 1), while Monterey pine (*Pinus radiata* D. Don) seedlings are stunted with short, dark-green needles (figure 2). When growing in over-limed peat, pine seedlings develop a rosette of buds in place of the usual single bud and may exhibit bronze foliage (figure 3). Stunting and rosette buds were observed in pine plantations in Australia (McGrath and Robson 1984).

Sometimes Zn deficiency in conifers remains undiagnosed, especially in the past prior to routine micronutrient analyses. For example, following land leveling, soil fumigation resulted in stunted, nonmycorrhizal Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) seedlings (Trappe and Strand 1969), but the Zn status was unknown.

At a nursery in Alabama, P-deficient pine seedlings (figure 4) were diagnosed in July 1986 while Zn deficiency symptoms were overlooked. Since stunting and short needles are also symptoms of P deficiency (Hacskaylo et al. 1969, Lyle 1969), researchers concentrated on improving growth by treating seedlings with phosphoric acid. Decades later, however, the data files were reexamined and the Zn deficiency was discovered.

Materials and Methods

A fertilizer trial was established in 1986 at the Union Camp Nursery near Inverness, AL (32°06′ N, 85°43′ W, altitude 140 m). The study tested the hypothesis that P fertilization does not affect growth of stunted pine seedlings. The climate for this area is warm and humid with a mean annual precipitation of 1,288 mm. Prior to expanding the nursery, the study area supported a 23-year-old pine plantation, and timber was harvested during the summer of 1984. Stump removal began in August after which the soil was leveled. On July 15, 1985, millet (*Panicurn ramosurn* L.) was sown as a cover crop. The soil was fumigated (March 15, 1986) with methyl bromide-chloropicrin (448 kg/ha). Before sowing loblolly pine seed, the soil received 224 kg/ha of triple superphosphate (TSP) and 112 kg/ha of potassium chloride (KCl). Seeds were treated prior to sowing with the fungicide triadimefon at 12.5 g of active ingredient per 10 kg of seed.

Seeds were sown with a vacuum precision machine on April 9, and then oxyfluorfen was applied at 0.56 kg ai/ha. Postemergence applications of oxyfluorfen at 0.56 kg ai/ha were applied on June 13 and August 15. To control emerged grasses, sethoxydim was applied on June 13 and July 9. Foliar applications of triadimefon (0.14 kg ai/ha) were applied on May 5, May 12, and June 5 to control fusiform rust, caused by *Cronartlum quercuum* (Berk.) Miyabe ex Shirae f. sp. *fusiforme* Birdsall and Snow. Ammonium nitrate was applied (100 kg/ha) on May 21 and July 8 and ammonium sulfate was applied (168 kg/ha) on June 12 and July 23. Rain in February (107 mm) and March (185 mm) was above normal, but rainfalls in April (18 mm), May (69 mm), and June (71 mm) were 98 mm, 34 mm, and 39 mm below normal, respectively (NOAA 1987).

Although germination was good, seedlings growing in the new, land-leveled ground showed signs of mosaic stunting in July (figure 4). On a few scattered areas, there were patches of normal, mycorrhizal seedlings. Stunted seedlings had purple cotyledons, though most primary needles were short and green (figure 5). This condition may occur when reinoculation with airborne ectomycorrhizal spores is delayed due to inadequate soil moisture in adjacent forests.

Figure 4. Stunted growth of loblolly pine seedlings was apparent during the first week of July 1986 in a recently land-leveled field at the Union Camp Nursery near Iverness, AL. Many seedlings were nonmycorrhizal, but a few patches of mycorrhizal seedlings were scattered throughout the field. Photo by David South, 1986.

Figure 3. Monterey pine seedlings from the Sweetwater Nursery in New Zealand showed a normal appearance (left) with 15 to 124 ppm foliar zinc (Zn) while stunted seedlings (to the right) had 1 to 5 ppm Zn (Knight 1976). Courtesy of Scion New Zealand, photo by H. Hemming, August 1974.

Since stunted seedlings lacked mycorrhiza, a P fertilization study was established on July 29, 1986. Two treatments (phosphoric acid fertilization and a control) were replicated five times on an area with uniformly stunted seedlings. Each plot was 1.2 m long by 1 m wide. The P treatment involved spraying a 3-percent solution (w/w) of phosphoric acid (H_3PO_4) at a rate of 18.3 g of P per m^2. Three weeks after treatment, seedlings were sampled for height, shoot dry weight, and root dry weight. Foliar samples were taken from each plot on August 18 (figure 6). On November 23, foliage and soil samples were collected for analysis at a laboratory in Memphis, TN.

Results

The phosphoric acid treatment increased growth and foliar P concentrations. Three weeks after treatment, acid-treated seedlings had 50 percent more mass and were 11 mm taller than untreated seedlings. By November, treated seedlings had twice as much mass and were 44 mm taller than untreated seedlings (South et al. 1988). Foliage of treated seedlings contained more P and sulfur (S) than nontreated seedlings in August, but this difference was

Figure 5. Stunted growth and short needles are two symptoms of phosphorus (P) deficiency in pine seedlings. This photo (July 29, 1986) compares stunted, nonmycorrhizal loblolly pine seedlings (left) with mycorrhizal seedlings (right). Stunted seedlings had a shoot dry mass of 173 mg while normal seedlings had a shoot dry mass of 576 mg (South et al. 1988). It is possible that P-deficient seedlings were also deficient in zinc (Zn). Foliar samples from five plots contained 5, 4, 7, 5, and 4 ppm Zn in August, and repeated samples collected in November contained 32, 25, 69, 73, and 34 ppm Zn, respectively. Photo by David South, 1986.

Figure 6. Stunted loblolly pine seedlings had short needles with purple cotyledons and 840 ppm foliar phosphorus. Seedlings on the right responded to a foliar-soil application of phosphoric acid (applied July 29). Photo by David South, 1986.

gone by November (table 1). Foliar Zn levels of 5 samples were below 9 ppm in August (4 to 7 ppm), but foliar samples from all 10 study plots ranged between 25 to 190 ppm by November. Soil samples collected in November indicated the acid treatment increased readily available P, manganese (Mn), and iron (Fe).

Discussion

Soil fumigation can kill mycorrhizal spores, but the risk of nonmycorrhizal roots increases on new ground that had topsoil removed prior to fumigation. Soil fumigated in the fall is typically reinoculated with airborne spores by April. For this reason, nursery managers should consider fumigating in the fall (Enebak et al. 1990, Hansen et al. 1990, Molina and Trappe 1984). During dry periods, production of ectomycorrhizal spores can be inadequate. At some nurseries, adding spores after fumigation increased the number of mycorrhizal roots (Marx et al. 1979, South 2018, Trappe and Strand 1969). At the Union Camp Nursery in 1986, natural inoculation with airborne spores was delayed due to low rainfall and apparently peaked between September and November. When soil fumigation delays mycorrhizal formation, seedlings can develop a P deficiency (South et al. 2018). In contrast, fumigation does not necessarily cause Zn deficiency. Under conditions of adequate available Zn, nonmycorrhizal pine roots can take up adequate Zn (Fomina et al. 2006, Hartley-Whitaker et al. 2000, Schier and McQuattie 1995). When Zn is inadequate due to land leveling, however, a temporary deficiency can occur on nonmycorrhizal seedlings before the fall equinox. Since P deficiency symptoms include stunting and purple needles, stunting due to a Zn deficiency was overlooked. Even without soil fumigation, land leveling can result in stunted, endomycorrhizal crops (Grunes et al. 1961, Swietlik 1999).

Several reasons could explain the ephemeral nature (<17 weeks) of the Zn deficiency. First, as roots grow, they uptake Zn from the soil solution. Second, after mycorrhizae develop (July to November), Zn uptake increases as mycelia spread throughout the soil. Third, since groundwater contains Zn, irrigation during the growing season adds Zn to seedbeds. For example, when water contains 0.04 ppm Zn, 500 mm of irrigation will provide 0.2 kg/ha of Zn.

When foliage samples are taken too late in the growing season, reasons for stunted pine seedlings may go unexplained. Since foliar samples in November had 2,100 ppm P, some might claim the mosaic stunting in July (see figure 4) was not caused by nonmycorrhizal seedlings. Likewise, others may say there was no proof Zn was inadequate in seedlings sampled in July. Although stunted Monterey pine seedlings had foliage with 2 to 5 ppm Zn (Knight 1976), this is not proof that loblolly pine seedlings with 4 or 5 ppm Zn were stunted due to a Zn deficiency. For example, loblolly pine tolerates low Zn levels better than shortleaf pine (*Pinus echinata* Mill.) (Wilson 1953). Treatment of stunted pine seedlings with $ZnCl_2$ (instead of phosphoric acid) would show if the stunted seedlings were deficient in Zn.

Typically, ectomycorrhizal pine seedlings have foliage with more than 15 ppm Zn (Boyer and South 1985, Flinn et al. 1980, Jalkanen and Rikala 1995, Knight 1976). When soil contains less than 1 ppm Zn, nonmycorrhizal seedlings may become Zn deficient (i.e., <9 ppm foliar Zn). Nonmycorrhizal pines, with less than 5 ppm Zn in foliage, might outgrow the deficiency after short roots become mycorrhizal. There are no reports of Zn deficiencies for irrigated loblolly pine seedlings grown in "old ground."

Acknowledgments

Thanks to Mark Vedder for promptly notifying the Auburn University Southern Forest Nursery Management Cooperative about stunted seedlings at the Union Camp Nursery. I thank Chen Ding, John Mexal, and Diane Haase for reviews of earlier drafts of this manuscript. Thanks also go to Marléne Joubert at Scion for providing the image of Zn-deficient Monterey pine seedlings.

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Table 1. Effect of phosphoric acid (183 kg P/ha) on foliar and soil analysis of loblolly pine seedlings at the Union Camp Nursery

Table 1a. Foliar samples collected on August 18, 1986

Measured variable	N (%)	S (%)	P (%)	K (%)	Mg (%)	Ca (%)	B (ppm)	Zn (ppm)	Mn (ppm)	Cu (ppm)	Fe (ppm)	Na (ppm)	Al (ppm)
Acid	2.34	0.12	0.25	0.97	0.07	0.23	93	8.4	686	6	172	300	370
Control	2.32	0.09	0.08	1.02	0.11	0.28	86	7.2	728	8	232	320	590
P>F	0.629	0.007	0.001	0.085	0.001	0.019	0.77	0.07	0.043	0.57	0.038	0.37	0.001
LSD$_{05}$	0.11	0.01	0.04	0.06	0.01	0.04	64	1.3	39	6	54	55	71

Table 1b. Foliar samples collected on November 26, 1986

Measured variable	N (%)	S (%)	P (%)	K (%)	Mg (%)	Ca (%)	B (ppm)	Zn (ppm)	Mn (ppm)	Cu (ppm)	Fe (ppm)	Na (ppm)	Al (ppm)
Acid	1.86	0.088	0.21	0.45	0.126	0.30	38	103	1,140	5	281	240	534
Control	2.14	0.106	0.21	0.52	0.144	0.36	44	93	1,264	4	234	180	506
P>F	0.001	0.313	0.951	0.033	0.037	0.074	0.27	0.58	0.084	0.55	0.085	0.37	0.300
LSD$_{05}$	0.22	0.04	0.08	0.06	0.016	0.069	13	48	150	2	58	166	65

Table 1c. Soil samples collected on November 26, 1986

Measured variable	pH	S (%)	P (%)	K (%)	Mg (%)	Ca (%)	B (ppm)	Zn (ppm)	Mn (ppm)	Cu (ppm)	Fe (ppm)	Na (ppm)	OM (%)
Acid	5.1	4	73	20.6	27	98	0.6	5	15	1.7	34	10	1.5
Control	5.2	8	44	25.4	28	112	0.6	2	11	1.2	22	12	1.2
P>F	0.313	0.28	0.007	0.042	0.326	0.18	0.70	0.18	0.003	0.44	0.009	0.24	0.530
LSD$_{05}$	0.4	8	16	4.5	9	24	0.3	4	1.8	1.6	4	3	1.2

Foliar samples (from five control plots and five treated plots) were collected on August 18 and November 26, 1986. Soil samples were collected on November 26, 1986, using the Mehlich 3 soil test. The least significant difference (LSD) values are provided at the 0.05 level of probability. Foliar samples collected in August were below 8 ppm Zn from two treated plots and three untreated plots.

P>F = probability of a greater F value

Abbreviations
Al = aluminum
B = boron
Ca = calcium
Fe = iron
Mg = magnesium
Mn = manganese
N = nitrogen
Na = sodium
OM = organic matter
P = phosphorus
S = sulphur
Zn = zinc

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Figure 1. This loblolly pine tree growing in an unmanaged forest in North Carolina demonstrates the strong apical dominance of the species. Photo by K. Potter, USDA Forest Service, 2023.

Loblolly Pine: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Loblolly pine (*Pinus taeda* L.) is the most commercially valuable conifer in the United States. This native species is grown widely across the Southern and Central States. Genetic diversity of this species is high, and population structure is low with some east-west differentiation. Loblolly pine seeds and seedlings for planting are typically moved from a 5 °F (2.8 °C) warmer hardiness zone to a cooler zone to maximize growth potential. Fusiform rust (caused by *Cronartium quercuum* f.sp. *fusiforme*) can be a lethal pathogen to loblolly pine if not managed properly, while southern pine beetle (*Dendroctonus frontalis*) is a significant pest on older, more decadent stands. Loblolly pine is expected to perform well under climate change because of its high abundance, moderate shade tolerance, and broad adaptability.

Introduction

Loblolly pine (*Pinus taeda* L.) is a widely distributed, long-lived, intermediate shade-tolerant conifer with a broad ecological amplitude. The species has the highest commercial value of any tree species in the United States due in part to its fast growth, broad adaptability,

Figure 2. In wild stands, loblolly pine trees vary in height and diameter and often grow in stands mixed with hardwood trees, as seen in this stand in North Carolina. Photo by K. Potter, USDA Forest Service, 2023.

and strong apical dominance (figure 1). The growth and form characteristics of the species have been further enhanced by extensive breeding programs (Cumbie et al. 2012). For example, the program led by North Carolina State University is in its fourth breeding cycle and planning for a fifth cycle (Isik and McKeand 2019). The present value of efforts to breed improved loblolly pines and to deploy genetic gains to landowners is estimated to exceed $1.7 billion, reflecting an increase of $1,594 per acre ($3,937 per ha) across over 1 million acres (404,685 ha) of improved seedlings planted each year (McKeand et al. 2021). Loblolly pine forests comprise more than half of the standing pine volume in the Southern United States (Baker and Langdon 1990), and it is the most planted tree in the country (Abrahams 2023). The wood of loblolly pine is valued for construction because of its high density (Alden 1997) and concomitant high strength and stiffness. The species is also a prime candidate for carbon markets because of its high growth rates and preferred status as a plantation species across much of the region's coastal and piedmont forest sites (Huang et al. 2004).

Loblolly pine is native across the Southern United States, and it is grown successfully on other continents (Baker and Langdon 1990), including South America, Australia, Asia, and Africa (Schmidtling 2001). As with other southern pines, its natural distribution is limited in the north by lower winter temperatures and in the west by lower precipitation (Schmidtling 2003). In noncommercial stands, loblolly pine occurs on sites with higher soil moisture than other southern pines and may grow in pure or mixed stands with hardwoods that have relatively long intervals between fire events (figure 2) (Baker and Langdon 1990). In its northern range, loblolly pine occurs with shortleaf pine (*Pinus echinata* Mill.) as far north as New Jersey (Crocker et al. 2017), Maryland, and southern Illinois (Crocker et al. 2009). The rapid early growth of loblolly pine exceeds that of longleaf pine (*P. palustris* Mill.) on South Carolina sandhill plains at least until 19 years of age (Cram et al. 2010). Adult trees have thick bark and relatively high fire tolerance (USDA NRCS 2023), but seedlings are relatively intolerant of fire compared with shortleaf, longleaf, and slash (*P. elliottii* Engelm.) pines (Bradley et al. 2016, Pile et al. 2017). Seed germination is optimal on bare mineral soil (Edwards 1987).

Loblolly pine seedlings are grown in nurseries as both bareroot and containerized stock types (figure 3) (Grossnickle and South 2017, Porterfield 2006), performing best on mildly acidic nursery soils (South 2017). Young seedlings, whether in the nursery or

Figure 3. Most loblolly pine seedlings being planted across the Southern United States are grown as bareroot stock, but containerized seedlings are increasingly common. Photo by C. Pike, USDA Forest Service, 2018.

in the field, may be sensitive to winter cold snaps when temperatures drop below 25 °F (-4 °C) (Pickens and Crate 2018). Loblolly pine's range is predicted to shift northward as the climate warms over the next few decades because of its high abundance, fecundity, and adaptability (Iverson et al. 2004, Peters et al. 2020), while being limited by its current cold hardiness level (i.e., USDA plant hardiness zone, or approximately 0 to 10 °F [-17.8 to 12.2°C]) (Bannister and Neuner 2001). Shade tolerance of loblolly pine is greater than other southern pines, which is advantageous for its adaptability to climate change (Peters et al. 2020).

Genetics

Loblolly pine is a monoecious diploid species with high genetic variation typical of outcrossing, wind-pollinated tree species, despite a prior genetic bottleneck occurring during the last glacial period (Acosta et al. 2019). The species' postglacial period recovery of genetic diversity is in stark contrast to red pine (*Pinus resinosa* Aiton) that also experienced a bottleneck during the same glacial maximum but today harbors low genetic diversity (Echt et al. 1998). The fact that loblolly pine was able to recover from a dramatic reduction in population size and maintain high levels of genetic diversity is promising for its ability to respond to challenges like climate change and to adapt successfully to novel future conditions (Acosta et al. 2019). Loblolly pine's fast growth rate and wide adaptability have led to extensive selection and breeding efforts for coastal Atlantic, Piedmont, and western Gulf populations (Hooker et al. 2021, Sierra-Lucero et al. 2002). Similar to other *Pinus* species, most genetic variation for loblolly pine occurs within populations, rather than among populations as determined with protein (i.e., allozymes) (Hamrick et al. 1993) and DNA-based markers (Eckert et al. 2010, Lu et al. 2016). Evidence from allozymes, monoterpenes, and fusiform rust resistance suggest that loblolly pine existed in two refugia during the last glacial period: one in south Florida and/or the Caribbean and one in south Texas and/or northeast Mexico. These refugial populations likely migrated north during the Holocene and merged near the Mississippi River (Schmidtling et al. 1999).

Loblolly pine populations west of the Mississippi River are characterized with slower growth, but they have greater resistances to drought and fusiform rust (Wells and Wakeley 1966) than populations east of the river, which informs seed zone recommendations formulated by Schmidtling (2001). Specifically, the three seed zones are (1) east of the Mississippi River, (2) between the Mississippi River and east of the borders between Texas/Oklahoma and Louisiana/Arkansas, and (3) west of the borders between Texas/Oklahoma and Louisiana/Arkansas. Genetically improved seed from seed orchards (figures 4 and 5), including mass control-pollinated and control-pollinated full-sib, is the primary source of seed for reforestation (McKeand et al. 2021).

Loblolly pines have medium-sized cones (figure 6) compared with other *Pinus* species and wind-dispersed seeds (Krugman and Jenkinson 2008). Growth rates of hybrids with longleaf pine, known as Sonderegger pine (*P. x sondereggeri* H. H. Chapm.), are relatively high compared with the midparent (parental species' mean), but survival is higher for loblolly pine than the hybrid or the longleaf pine parent (Schoenike et al. 1975). Further work has shown no significant differences in height, diameter, volume, or fusiform rust severity between loblolly and

Figure 4. The wide spacing in loblolly pine seed orchards, as shown here in Georgia, is used to maximize seed production and to provide full access to crowns for cone collecting with a mechanical lift. Photo by C. Pike, 2018.

Figure 5. This seed orchard in Delaware is the most northerly seed orchard of loblolly pine in the United States. Seed orchards like this one may be used to increase seed production for planting in more northerly climates. Photo by R. Overton, USDA Forest Service, 2007.

Figure 6. Loblolly pine cones are medium-sized and typically release seeds while still on the tree. This habit requires that cones be handpicked before the seeds are released. Photo by C. Pike, USDA Forest Service, 2023.

Sonderegger pines (Henderson and Schoenike 1981). Loblolly pine also forms natural hybrids with pitch pine (*P. rigida* Mill.) in New Jersey, Maryland, and Delaware, and with pond pine (*P. serotina* Michx.) in New Jersey, Maryland, Delaware, and North Carolina (Baker and Langdon 1990). Hybridization occurs with shortleaf pine throughout the species' ranges, with higher rates west of the Mississippi River (Edwards and Hamrick 1995, Xu et al. 2008). The introgression between the species is thought to contribute to fusiform rust resistance of loblolly pine in this region (Florence and Hicks 1980).

Seed-Transfer Considerations

Seed-transfer recommendations for loblolly pine (and other southern pine species) are based largely on plant hardiness zones, or the average annual minimum temperatures (AAMT) for a locale, as supported by seed source study results (Schmidtling 2001). Winter temperatures are the best predictors of height growth in loblolly pine, including AAMT and number of frost-free days (Schmidtling 1994, 2001). Seedlings generally can be transferred from areas with AAMT within 5 °F (2.8 °C) of the planting location, although they can be moved as far as 10 °F (5.6 °C). The risk of cold damage increases for northward transfers, while growth decreases in southward transfers (Schmidtling 1994, 2003). Seeds from 150 mi (241 km) south of the planting site are generally favored because their growth exceeds local sources except in northern areas where local sources may be best (Schmidtling 2001).

Loblolly pine seed sources from the eastern seed zone (east of the Mississippi River) should not be planted in the western seed zones because of the risks posed by drought and fusiform rust. Western seed sources can be planted in the eastern seed zone, particularly for droughty sites and areas with high fusiform rust exposure, though these western sources will likely grow slower (Schmidtling 2003). Loblolly pine is also sensitive to photoperiod, with northerly populations being more sensitive than southerly populations (Perry et al. 1966). For this reason, movement from central to northern areas for assisted range expansion or assisted species migration (Williams and Dumroese 2014) should not exceed previously recommended maximum transfer distances, while transfers of less than 200 mi (322 km) are not likely to exhibit negative effects attributable to photoperiod alone. Loblolly pine is not recommended for planting in Illinois north of U.S. Route 40 (which runs near and parallel to Interstate 70 at roughly 39° N latitude) (Gilmore 1980) because of low minimum winter temperatures. In Maryland, local seed sources are recommended for planting (Little 1969), which is also consistent with Schmidtling (2001). Local sources should be favored along the edge of the northern range for assisted migration beyond the current range limit for assisted range expansion or assisted species migration. A summary of considerations for moving loblolly pine seed is contained in table 1.

Insects and Diseases

Loblolly pine generally outgrows longleaf and shortleaf pines but is more susceptible to pests, specifically southern pine beetle, fusiform rust (Moser et al. 2003), and pitch canker (caused by *Fusarium circinatum*). Breeding for resistance to fusiform rust (Carson and Carson 1989) has been occurring for decades with different deployment strategies (e.g., full-sib vs. half-sib families) depending on disease severity (Bridgwater et al. 2005). Western sources of loblolly pine have evolved a higher degree of resistance to fusiform rust compared with eastern sources.

Table 1. Summary of silvics, biology, and transfer considerations for loblolly pine

Loblolly pine *(Pinus taeda)*	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Average 18,000 seeds per pound (40,000/kg) (Krugman and Jenkinson 2008) • Cone/seed bearing may begin at 5 to 10 years; cone crops occur every 3 to 13 years (Krugman and Jenkinson 2008)
Insect and disease	• Insects: southern pine beetle • Diseases: fusiform rust, pitch canker, brown spot needle blight
Maximum transfer distances	• Intermediate tolerance to seed transfer (200–300 mi [322–483 km]) • Movement from warmer (5 °F [2.8 °C]) plant hardiness zones is typically practiced; movement from up to 10 °F (5.6 °C) warmer may also be tolerated • East to west transfer is not recommended, while west to east transfer might be acceptable for some sites provided that north-south transfer guidelines are followed
Palatability to browse	• Browse is rarely reported, but white-tailed deer in northern areas of the range are known to consume needles and may threaten seed sources that are moved northward
Range-expansion potential	• Expected to have generally favorable potential in a warmer climate because of broad ecological amplitude, high abundance, and good fire tolerance

Like other southern pines, decadent stands with low vigor may be preferentially attacked and negatively impacted by bark beetles. Brown spot needle blight (caused by *Lecanosticta acicola*) is a primary pathogen on needles of trees in *Pinus* species across the globe and a major concern for the southern pines grown in plantations (van der Nest et al. 2019).

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Red Spruce: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Red spruce (*Picea rubens* Sarg.) is a cool, temperate zone conifer that is widespread in the Northeastern United States and Canada and associated with fragmented, high-elevation mountainous areas of the Central and Southern Appalachians. The species prefers cool, moist climates with moderate summer temperatures and low exposure to drought stress. Red spruce is sensitive to cold stress, especially during midwinter thaws followed by abrupt return to subfreezing conditions. The species has low genetic diversity for an outcrossing, wind-pollinated conifer. Genetic data show an ongoing decline in effective population size exacerbated by more recent impacts of logging, fire, and acid rain. Red spruce naturally hybridizes with black spruce (*P. mariana* [Mill.] Britton, Sterns, & Poggenburg), which may provide a source of adaptive variation when reproductive barriers are overcome. Ongoing research suggests red spruce is vulnerable to climate change, especially where habitat fragmentation constrains natural opportunities for dispersal. Trait and genomic-based analyses of climate adaptation offer guidance for seed transfer and potential assisted migration within the species' range. Damage from insects and other pests is not widespread, but local outbreaks can cause damage to current-year growth and cone crops.

Introduction

Red spruce (*Picea rubens* Sarg.) is a shade-tolerant, coniferous tree that prefers cool, moist sites throughout mid to high elevations in the Appalachian Mountains and along coastal areas of Maine and the Canadian Maritime Provinces. Its geographic distribution shows a strong inverse latitude-elevation relationship, with red spruce occurring at its highest elevations in the Central and Southern Appalachians of West Virginia, Virginia, North Carolina, and Tennessee (most common above 3,300 ft [1,000 m]), more moderate elevations in the Adirondacks and Northern Appalachians of New York and New England (most common between 2,500 to 4,000 ft [750 to 1,200 m]), and near sea level in the northern Maritime forests (Cogbill and White 1991).

Red spruce is associated with a variety of forest types but is probably best known as a codominant member of high-elevation spruce/fir forests where it occurs with balsam fir (*Abies balsamea* [L.] Mill.) or Fraser fir (*A. fraseri* [Pursh] Poir.) in the northern or southern part of its range, respectively (figure 1). At lower mountain elevations, red spruce is a common component of mixed conifer-northern hardwood forests, where it commonly occurs with sugar maple (*Acer saccharum* Marshall), eastern hemlock (*Tsuga canadensis* [L.] Carrière), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) (Verrico et al. 2020). In high-latitude coastal areas of its range in Maine and Maritime Canada, red spruce is a dominant member of a cool, maritime-influenced conifer forest community. Elsewhere in the interior of its range, red spruce sometimes occurs in “frost pocket” wetland or bog sites in association with red maple (*Acer rubrum* L.), tamarack (*Larix laricina* [Du Roi] K. Koch), eastern hemlock, and with its closely related black spruce (*P. mariana* [Mill.] Britton, Sterns, & Poggenburg). In the Central and Southern Appalachian regions, red spruce is a foundational species that provides critical high-elevation, cool, shady habitat for a variety of regionally rare or endemic wildlife species (Byers et al. 2010) (figure 2).

Figure 2. This red spruce forest in Spruce Knob, WV, shows structural diversity and recruitment from the understory. Cool, moist conditions at higher elevations (>4,000 ft [1,219 m]) in the Central Appalachians support the development of mature red spruce communities. Photo by Stephen R. Keller, 2013.

Historically, red spruce was probably more widespread throughout both the northern and southern extents of its range and occupied additional areas with warmer climates than its current distribution (Cogbill 2000, Van Gundy et al. 2012). Logging, fire, and atmospheric pollution (acid rain) have severely impacted red spruce and reduced its distribution and abundance, particular in lower elevation northern hardwood forests (Foster and D’Amato 2015, Koo et al. 2015, Siccama et al. 1982). In recent years, red spruce has been rebounding in growth and seedling recruitment at lower elevations, including recolonizing downslope in montane forests, suggesting a slow recovery from the legacies of land use and pollution (Foster and D’Amato 2015, Kosiba et al. 2018, Verrico et al. 2020, Wason et al. 2017).

Figure 1. This montane red spruce forest in northern Vermont is typical of forest types between 2,500 and 3,500 ft (762 and 1,067 m) in elevation. Photo by Stephen R. Keller, 2019.

Although associated with high-elevation or high-latitude areas in the Appalachian Mountains, red spruce is not a boreal species but rather a cool-temperate zone species (Dumais and Prévost 2007, White and Cogbill 1992). Red spruce appears to be limited by midsummer (July) temperatures (Cogbill and White 1991, Hamburg and Cogbill 1988), being sensitive to conditions of high temperatures during the growing season when adequate moisture is unavailable through precipitation, humidity, or cloud immersion (Day 2000, Hamburg and Cogbill 1988, Keller et al. in press, Lachmuth et al. 2023). Red spruce is also sensitive to cold temperatures during the fall and spring transition seasons (Yetter et al. 2021) and achieves only moderate cold tolerance in midwinter, incurring damage from temperatures below -40 °F (-40 °C) unlike true boreal spruce species in the northeast such as white spruce (*Picea glauca* Moench) and black spruce (DeHayes et al. 2001, Strimbeck et al. 2007). Winter injury to red spruce can also occur at less extreme temperatures when a midwinter warm period is followed by an abrupt return to cold. During these times, red spruce will temporarily deharden and resume photosynthesis, resulting in susceptibility of current-year foliage to rapid transitions back to subfreezing temperatures (Schaberg 2000).

Red spruce seedling recruitment is best under partial shade. Photoinhibition damages seedlings exposed to full sunlight (Dumais and Prévost 2007, 2016). Due to its shade tolerance and slow growth habit, red spruce can persist in the understory for decades but requires canopy release to achieve its full growth potential (Rentch et al. 2016). Dominant canopy trees can persist for centuries as a late-successional species in the forest community. Red spruce can grow on a variety of substrates, from poorly drained bogs to exposed upland sites with shallow soils, but it commonly occurs on moist, slightly acidic soils with a well-developed humus layer (Spodosols).

During the last ice age, red spruce retreated to a southern refugium located in the unglaciated areas of the Carolinas and stretching westward toward the Mississippi River Valley, from which it recolonized northward after the glaciers retreated (Keller et al. in press, Lachmuth et al. 2023, Lindbladh et al. 2003, Watts 1979). After glaciation, red spruce may have retreated to a northern coastal refugium near the Canadian Maritimes during the mid-Holocene warm period, approximately 5,000 to 8,000 years ago, after which it is thought to have recolonized inland (Schauffler and Jacobson 2002).

Red spruce is most closely related to black spruce, from which it speciated during the Pleistocene glacial period, and with which it still overlaps geographically in areas from Pennsylvania northward (Jaramillo-Correa and Bousquet 2003). Red spruce and black spruce are known to hybridize naturally throughout their areas of sympatry (Capblancq et al. 2020, De Lafontaine et al. 2015, Jaramillo-Correa and Bousquet 2003, Perron and Bousquet 1997), and artificial hybrids are also possible through controlled crosses (Major et al. 2003, 2005). Despite overlapping ranges in the north, neither red spruce nor black spruce are closely related to white spruce, the latter of which shows closer phylogenetic relationships to western spruces (e.g., *Picea engelmanii* Parry ex Engelm. and *P. sitchensis* [Bong.] Carr.) (Feng et al. 2019, Lockwood et al. 2013).

Genetics

Red spruce is a diploid species (2n=24) with a very large genome (genome size of the closely related black spruce is ca. 18.3 Gbp [Lo et al. 2023]). Red spruce is also monoecious, producing separate male and female cones (figure 3) and has a wind-pollinated, outcrossing mating system. Based on the mating system and compared with other similar conifers (including black spruce), red spruce would be expected to have high genetic diversity and low population structure, but it does not meet these classic expectations (table 1). On the contrary, multiple genetic studies using a variety of marker types have shown red spruce to have quite low levels of genetic diversity compared with similar conifer tree species (Capblancq et al. 2020, Hawley and DeHayes 1994, Keller and Trott 2017, Perron et al. 2000). Low levels of diversity correspond to a bottlenecked effective population size (N_e) in red spruce that shows evidence of long-term decline over thousands of years, pre-dating more recent anthropogenic impacts (Capblancq et al. 2020, Jaramillo-Correa et al. 2015, Keller and Trott 2017).

Some of this initial reduction in N_e is attributable to the speciation event with black spruce, in which red spruce is

Figure 3. Reproductive structures in red spruce include male (left) and female (right) strobili. Photos by Brittany M. Verrico, 2017.

Table 1. Summary of silvics, biology, and transfer considerations for red spruce

Red spruce *(Picea rubens)*	
Genetics	• Genetic diversity: low compared with other outcrossing conifers; long-term history of diversity decline • Genetic structure: three geographically distinct regions of genetic ancestry are the northern, midlatitude, and southern parts of the range; F_{ST} between regions = 0.02–0.03 • Gene flow: historically high within regions, though may be reduced due to habitat fragmentation and land use; gene flow between regions appears limited
Cone and seed traits	• Abundant cone crops every 3 to 8 years • Nonserotinous cones averaging 150,000 cleaned seeds/pound (330,000 seeds/kg) • Seeds disperse in late summer/early fall from cones produced that year • Seeds possess no physiological dormancy
Insect and disease	• Impacts on red spruce from insect pests and other diseases are generally low • Reductions in growth and vitality can arise during local outbreaks of spruce budworm, spruce coneworm, yellowheaded spruce sawfly, and eastern dwarf mistletoe • Eastern spruce gall adelgid is an introduced species that alters growth form of current-year shoots
Palatability to browse	• Low; not a preferred browse by deer or moose
Maximum transfer distances	• Intermediate tolerance to seed transfer (200–300 mi [322–483 km]) • Transfer to colder climates (more than 1.8 °F [2 °C] colder than the source) often results in cold damage and reduced growth • Transfer into warmer climates (5.4 to 9 °F [3 to 5 °C]) warmer than source) may be tolerable but must be evaluated with consideration to temperature seasonality (warmer winters may benefit red spruce while warmer summers do not) and transpirational demand • Southern range-edge populations may be at risk for extirpation due to climate conditions near current thresholds, low genetic diversity, and habitat fragmentation
Range-expansion potential	• Regional stands in New England, northern New York, and eastern Canada are likely to expand northward but will still be constrained by long-range dispersal capacity • Opportunity for infilling in areas of former range where land-use change and other anthropogenic disturbances eliminated spruce during the last two centuries, especially at lower elevations • Regional populations in mid-Atlantic and Central and Southern Appalachians have limited range-expansion potential due to fragmentation and lack of continuous suitable climate habitats

thought to have diverged as a small, isolated subpopulation of black spruce during the Pleistocene glacial period and captured just a subset of its progenitor's genetic diversity (Jaramillo-Correa and Bousquet 2003, Perron et al. 2000). The trend toward declining N_e in red spruce has continued after its divergence with black spruce, with more recent bottlenecks dated to the mid to late Holocene (Capblancq et al. 2020, Jaramillo-Correa et al. 2015, Keller and Trott 2017). Low genetic diversity in red spruce has been associated with reduced seedling vigor under greenhouse conditions, particularly for seedlings originating from the southern part of its range (Capblancq et al. 2021).

At a landscape scale, red spruce shows genetic population structure between three geographically separated ancestry groups: the northern core of the range (New York, New England, and Canada), the southern fragmented range edge (Maryland south to North Carolina and Tennessee), and the margin or transition zone between the core and edge (bog sites in central and northern Pennsylvania) (figure 4). These three ancestry groups diverged ca. 8,000 years ago after glacial retreat and, while genetically distinct, there are only modest levels of divergence at nuclear loci, with F_{ST} (the proportion of genetic variance contained in a subpopulation relative to the total) of 0.02 to 0.03 (Bashalkhanov et al. 2013, Capblancq et al. 2020). Gene flow still occurs between regions but at a very low rate of 1 migrant exchanged every 4 to 20 generations, equating to an approximate maximum migration frequency between regions of 1 individual per 100 years (Capblancq et al. 2020).

At a more local scale within regions, population differentiation in the nuclear genome among populations is typically quite low ($F_{ST} < 0.01$) consistent with its wind-pollinated mating system (Keller and Trott 2017, Verrico 2021). Cytoplasmic genomes (mitochondria and chloroplast) show limited haplotype variability in red spruce

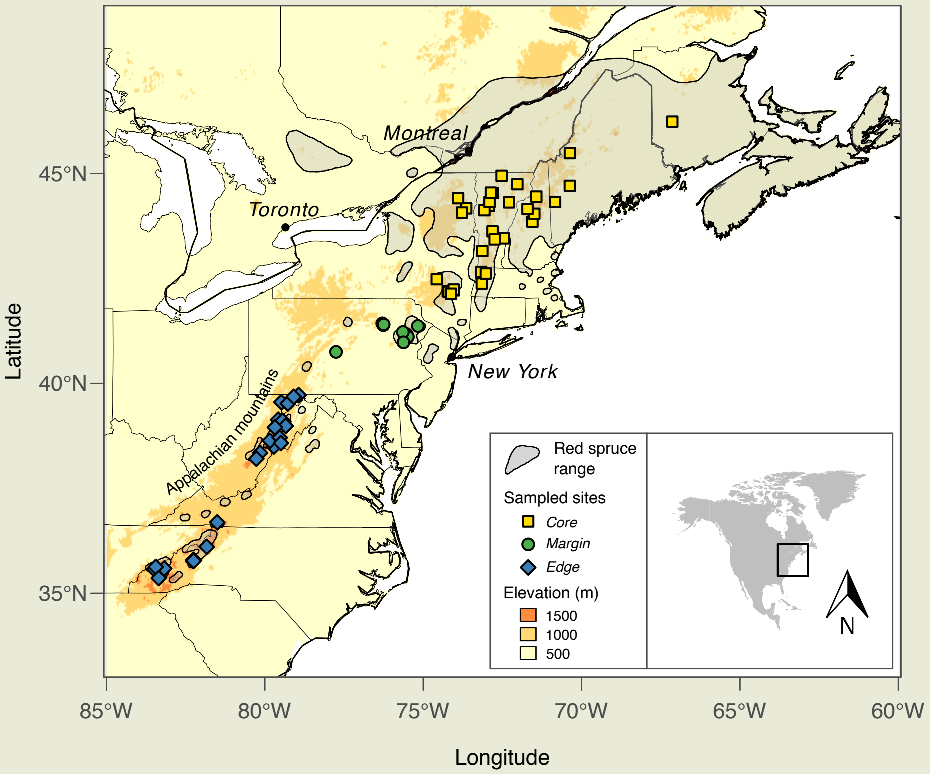

Figure 4. Range-wide structure of genetic ancestry in red spruce. Symbols denote the 65 populations (N=340 individuals total) sampled for exome-capture genomic sequencing by Capblancq et al. (2020). Colors denote genetic ancestry clusters based on principal component analysis of single-nucleotide polymorphisms (SNPs), which separated samples genetically into three regional clusters: a southern range edge (blue), a midlatitude margin (green), and a northern range core (yellow).

relative to black spruce, and a trend for greater population structure in mitochondrial DNA (dispersed through seed) than chloroplast DNA (dispersed through pollen), consistent with higher levels of gene flow through pollen (Gérardi et al. 2010, Jaramillo-Correa and Bousquet 2003).

Red spruce exhibits patterns of local adaptation to climate at both local and regional scales. At the trait level, common garden estimates of genetic variation in budbreak and budset shows clinal patterns of trait variation along climatic gradients of elevation and latitude (Butnor et al. 2019, Prakash et al. 2022, Verrico 2021). Evidence also indicates that plasticity in budbreak timing shows locally adapted genetic variation in response to gradients in climate seasonality (Prakash et al. 2022). At the molecular level, clinal adaptation in stress response genes is evident along seasonal gradients of temperature and precipitation, as well as historic air pollution (Bashalkhanov et al. 2013, Capblancq et al. 2023).

As noted previously, red spruce and black spruce are capable of hybridization. Naturally occurring hybrid genotypes occur in the northern part of the red spruce range (Capblancq et al. 2020, de Lafontaine et al. 2015, Perron and Bousquet 1997). Areas of advanced introgression between red spruce and black spruce can also be found in wetlands and bogs of Pennyslvania. Natural hybrid genotypes with a mix of red spruce and black spruce genetic ancestry show positive heterosis for growth in common garden experiments (Prakash et al. 2022). In contrast, controlled crosses between red spruce and black spruce suggest reduced seed viability and slightly negative heterosis for growth among surviving first-generation hybrids (Major et al. 2003, 2005). The reduced seed set along with the ecological (habitat) separation is probably sufficient to keep the two species distinct, even in the face of occasional hybridization.

Molecular studies shed further light by showing that the barriers to hybridization vary considerably across the genome with some gene loci forming strong isolating barriers, while other loci are highly permeable to introgression (de Lafontaine et al. 2015). Further, genomic studies show that backcrossing of hybrids with red spruce occurs more frequently than backcrossing to black spruce, suggesting introgression is directional and occurs more easily toward red spruce (de Lafontaine and Bousquet 2017). Ongoing studies of natural advanced generation backcrosses suggests that introgression introduces adaptive variation into red spruce (which is otherwise low in genetic diversity), which may facilitate its adaptation along climatic gradients (Prakash and Keller, unpublished data). Synthesizing across these studies indicates that hybridization between red spruce and black spruce (1) is relatively common in the north, (2) is likely selected against in the first generation as a result of reduced seed viability, (3) backcrosses preferentially with red spruce in cases where hybrids survive to maturity, and (4) may increase adaptive potential in red spruce populations due to introgression of genetic diversity from advanced generation backcrossing.

Seed-Transfer Considerations

While not grown commercially, red spruce is the focus of active restoration and reforestation efforts for conservation of biodiversity, especially in the southern portions of the range where logging and fire have severely reduced its former range (Adams and Stephenson 1989). Consideration of seed sourcing and transfer guidance for red spruce comes from a variety of sources, including climate models, provenance trials, progeny tests, and genomic analyses. Climate-based species distribution models generally predict a severe contraction of red spruce's range by the end of this century (Beane and Rentch 2015, Koo et al. 2014, Lachmuth et al. 2023) with overall decreases in importance values over much of its existing range (Peters et al. 2020). These forecasts raise awareness that seed sourcing for reforestation and restoration should take into consideration both current and future climates (Walter et al. 2017).

Several provenance trials exist for red spruce (Morgenstern et al. 1981, Wilkinson 1990) that offer insight into the response of red spruce growth to climate transfer distance (TD = test site climate – seed source climate). A recent study of trials in Maritime Canada showed that growth (height and diameter at breast height [DBH]) measured on adult trees responded most to TD based on temperature variables and less so to precipitation (Li et al. 2020). In these trials, growth response of warm-climate provenances was negatively affected by seed transfer into colder test sites (negative TD); conversely, cold provenances benefited slightly from transfer into warmer test sites, up to 5.4 °F (3.0 °C) warmer than the source climate. These responses were strongest for climate variables associated with growing season length (frost-free period and growing degree days), pointing to risk of cold damage and thus slower growth upon transfer to colder climates. It is important to note that all the test sites and most of the source provenances in Li et al. (2020) were northerly (eastern Canada), so the data do not necessarily capture the response of midlatitude and southern provenances to warming above their baseline.

A recent test evaluated red spruce progeny from 340 mothers sampled from 65 provenances across the range and grown in raised beds at 3 test sites stratified by latitude (Vermont, Maryland, and North Carolina) (Prakash et al. 2022). The three test sites were generally warmer than the climate at the seed sources (Prakash et al. 2022), producing a range of TD values (based on mean annual temperature) from 7.2° F (4 °C) colder to 22 °F (12 °C) warmer than the source climate. Seedlings showed a decrease in first-year height increment growth with increasingly warmer TDs (figure 5). In their second year, growth declined under both the coolest and warmest TDs, but was resilient to, or even slightly benefited from, moderate warming (5.4 to 9 °F [3 to 5 °C]). A related analysis that considered the influence of a broader set of 11 climate variables, including different aspects of seasonal temperature as well as precipitation and humidity-related variables, found a consistent reduction in seedling height growth with increasing transfer distance away from the source climate (Capblancq et al. 2023, Lachmuth et al. 2023).

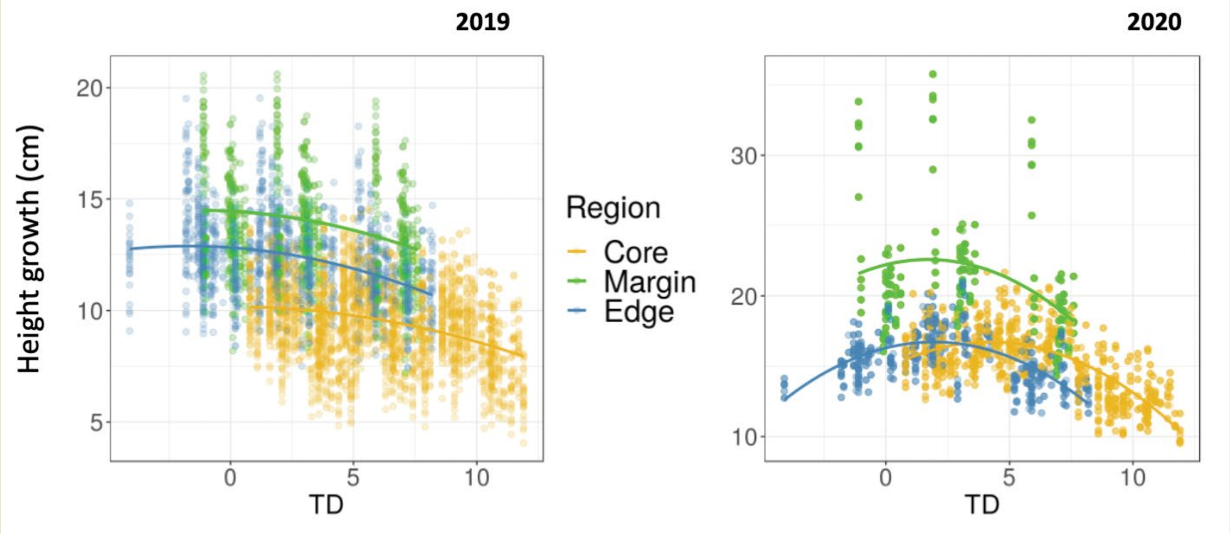

Figure 5. Red spruce seedling height growth after 1 year (2019) and 2 years (2020) postplanting into outdoor raised bed common gardens varied by climate transfer distance (TD = test site − source) based on mean annual temperature (°C) and regional genetic ancestry groups (core, margin, and edge) assigned based on genomic data (see also figure 4). Height growth data were reanalyzed from Prakash et al. (2022).

The entire set of findings on red spruce transfer indicate that red spruce has a negative growth response to seed transfer toward sites that are both warmer and drier (e.g., higher evaporative demand) than its source climate, and that simple proxies of temperature or geographic distance alone are likely insufficient to properly evaluate the transfer impact. If based solely on mean annual temperature, it appears that red spruce can tolerate, or even benefit from, moderate warming (figure 5) likely reflecting its sensitivity to frost damage (Li et al. 2020). Best practice would thus be seed transfers into areas where current and future climate will most closely match the historic source climate, considering the combined effects of both growing season temperature and precipitation/humidity, while also being mindful to avoid risk of frost damage under colder transfers. This practice meshes well with dendrochronology studies in red spruce, which show an overall growth benefit from warmer winters (i.e., less cold damage) alongside negative growth impacts of warmer and drier conditions during the growing season (Kosiba et al. 2018, 2013; Yetter et al. 2021). Ongoing work is aimed at integrating knowledge of local adaptation from quantitative genetics (St. Clair et al. 2022) and population genomics (Lachmuth et al. 2023a, 2023b) into multivariate climate transfer models to help predict optimal seed sources and recipient sites for planting under current and future climate. These genetically informed approaches are under continued development and are available as online tools to provide an additional resource for making seed-transfer decisions (https://fitzlab.shinyapps.io/spruceApp/ and https://seedlotselectiontool.org/sst/).

Insects and Diseases

Red spruce is the target of a few pests but none that have achieved high levels of impact across broad landscapes. Perhaps the most damaging insect pest is the spruce budworm (*Choristoneura fumiferana* Clemens), a native insect that damages buds and current-year shoots of red spruce, especially when growing sympatrically with balsam fir. An important seed pest in some areas is the spruce coneworm (*Dioryctria reniculelloides* Mutuura & Munroe), whose larvae tunnel into developing seed cones and consume the seeds; this can sometimes have considerable local impact on the seed crop (figure 6). In some areas, yellowheaded spruce sawfly (*Pikonema alaskensis* Rohwer) larvae will feed on new needle growth and cause high impacts locally. The eastern spruce gall adelgid (*Adelges abietis* L.) is an introduced pest from Europe that primarily attacks Norway spruce but is occasional on red spruce, with its nymphs feeding at the base of current-year twigs and creating pineapple-shaped galls. The parasitic plant eastern dwarf mistletoe (*Arceuthobium pusillum* Peck) primarily infects black spruce but can also be common on white spruce and red spruce (in its northern range), producing the characteristic "witches' broom" growth form, reducing growth, increasing susceptibility to other stressors, and in some cases causing mortality (Baker et al. 2006).

Figure 6. These red spruce cones in northern Vermont show damage incurred by spruce cone worm (*Dioryctria reniculelloides*). Note the small entrance holes visible on the cones and the brown discoloration indicating seed predation. Photo by Stephen R. Keller, 2017.

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Figure 1. The two black cherry trees in this photo are in a mesic hardwood forest in southeast Wisconsin dominated by sugar maple. These trees show the black cherry's dark, scaly bark and long, branchless boles in a heavily shaded environment. The tree on the left has scalier/shaggier bark than typical black cherry. Photo by Nicholas LaBonte, USDA Forest Service, 2023.

Black Cherry: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Black cherry (*Prunus serotina* Ehrh.) is a shade-intolerant hardwood tree that is found occasionally to frequently in a variety of hardwood forest types across the Eastern United States and extreme southeastern Canada, as well as parts of Mexico. Valued for its colorful, dense, and highly workable wood, black cherry is also a notable source of soft mast for wildlife. Black cherry regenerates readily on disturbed sites when adequate seed crops are present. In the heart of its commercial range, however, well-documented regeneration problems occur due to complex and unique circumstances. Black cherry has high genetic diversity due to high levels of seed dispersal and pollen flow, while population structure is low. Common garden studies revealed that black cherry is somewhat more sensitive to seed transfer than some other hardwoods with similarly expansive ranges and high genetic diversity. Seed-transfer distances of 200 to 300 miles (322 to 483 km) from south to north, or approximately 3 degrees latitude northward, is considered a safe recommendation to maximize growth. Black cherry is affected by a variety of native damaging insects and fungal diseases that reduce its economic value. Under climate change, black cherry is likely to expand its range northward but may suffer from increased stress and insect attacks in parts of its range.

Introduction

Black cherry (*Prunus serotina* Ehrh.) is a medium-to-large, early-successional hardwood tree that grows on a variety of well-drained soils throughout the Eastern United States, usually as a minor component of mixed hardwood forests. It grows best on well-draining, rich, loamy, or sandy soils (Marquis 1990), although it is often found in old field environments with degraded, rocky, sandy, or clay soil. On suboptimal sites, black cherry rarely attains commercial size or form. The species is considered shade intolerant;

although its seedlings can persist for years in shade and respond to release (Auclair and Cottam 1971), they are not competitive with more shade-tolerant species in partially shaded growing conditions (Marquis 1979). A mature black cherry's very dark, scaly, "burnt potato chip" bark is distinctive (figure 1). Black cherry produces racemes of small, mildly fragrant white flowers in late spring or early summer (figure 2) that mature into small, dark purple drupes in early fall (figure 3). Leaves and twigs have a distinctive bitter almond or cherry scent due to cyanogenic glycosides, including amygdalin (Telichowska et al. 2020).

Black cherry is sympatric with several other native *Prunus* species in different parts of its range along with commonly cultivated *Prunus* species (e.g., peach, plum, cherry, and apricot) introduced from Europe and Asia. It is only distantly related to the sympatric native pin cherry (*Prunus pensylvanica* L. f.) and the widely planted domestic stone fruits (Shi et al. 2013). Hybridization has not been documented with these species or the more closely related sympatric chokecherry (*Prunus virginiana* L.), which is a thicket-forming shrub.

Black cherry's glacial refugia are not entirely clear. Its broad current distribution in Mexico indicates that it was able to migrate south quite effectively as the climate cooled (Guzman et al. 2018, McVaugh et al. 1952), and it still occurs near a site in Texas where seed remains have been found in Pleistocene packrat middens (Van Devender 1979). Analysis of chloroplast DNA in its northern range hints at several refugia east and west of the Appalachian Mountains (Pairon et al. 2010). Its persistence in likely Pleistocene refugia indicates its potential to adapt to climate changes and migrate to nearby suitable habitats if necessary, although the Climate Change Tree Atlas identifies insects and diseases as potential complicating threats in the future (Peters et al. 2020).

Figure 2. Black cherry flowers can proliferate across eastern forests in the spring. Photo by Richard Gardner, bugwood.org.

Figure 3. Black cherry fruits (left) are a favored food source for birds in the Eastern United States. The leaves of black cherry (right) are relatively small in stature, but crowns produce dense shade during the active growing season. Photos by Franklin Bonner, USDA Forest Service (retired), 2010, and Steve Katovich, USDA Forest Service, 2019.

Black cherry will likely be able to expand its range in some areas given current evidence and its large native range, adaptability, and dispersal ability (Segura et al. 2018). In the areas where it is most abundant, however, black cherry may struggle to benefit from climate change due to other factors that are currently causing it to diminish in importance. In its core commercial range on the Allegheny Plateau, black cherry is a dominant canopy species (up to 50 percent of basal area in some areas) and produces large veneer logs and sawlogs more consistently in this area than anywhere else in its native range. Black cherry reproductive success has declined dramatically in these areas, however, due to plant/disease feedbacks at high densities and changes in nitrogen deposition rather than climate stress (Royo et al. 2021).

Genetics

Black cherry is a monoecious tetraploid (2n = 4x = 32) with a relatively small genome of 490 Mb (Jung et al. 2019). Its nectar-producing flowers are visited by a variety of generalist insects (McLaughlin et al. 2022), and ground-dwelling Andrenid miner bees seem to be the most important pollinators. Black cherry is primarily outcrossing and can generally be considered self-incompatible (Gordillo-Romero et al. 2020). Its fleshy fruits are eaten and dispersed in the digestive tracts of a variety of animals, and it is likely that birds are an effective means of long-distance seed dispersal. Black cherry apparently does not hybridize readily with its closest relatives, so hybridization is not a concern for seed movement considerations.

Studies of genetic structure in black cherry revealed weak differentiation among populations with relatively low F_{ST} (a measure of population differentiation) estimates using 8 nuclear microsatellite loci: 0.06 for trees sampled within the native range of black cherry and 0.09 for invasive populations in Europe (Pairon et al. 2010). A smaller study with five microsatellite markers found high heterozygosity (0.7 to 0.8) and slightly lower allelic richness (30 to 40 vs. 40 to 50 unique alleles observed) in western range limit compared with core range populations (Beck et al. 2014), which indicates high genetic diversity on the black cherry genome. A large study using 12 microsatellite markers and DNA from herbarium specimens found limited isolation by distance, indicative of high gene flow and limited genetic structure (Konrade et al. 2018). A microsatellite marker study of black cherry in South America, where it is introduced and naturalized, also showed high heterozygosity and low population differentiation (Guadalupe et al. 2015), although Ecuadorian populations likely only contain a subset of the genetic diversity found in native Mexican populations based on chloroplast haplotype analysis (Downey et al. 2000).

Seed-Transfer Considerations

A meta-analysis of common garden studies of five major hardwood species in the Northeastern United States found that black cherry was more sensitive to climatic variables than other species tested (red oak [*Quercus rubra* L.], black walnut [*Juglans nigra* L.], yellow birch [*Betula alleghaniensis* Britton], and red maple [*Acer rubrum* L.]), especially for mean coldest month and warmest month temperatures (Leites et al. 2019). This finding indicates that black cherry seed should not be moved as far north as some other native hardwoods for assisted migration because of heightened sensitivity to both cold winter and hot summer temperatures. The distinct morphology of black cherry subspecies from dramatically different climates (Guzman et al. 2018) indicates that locally adapted genetic strains of this species have developed despite pervasive gene flow. Local adaptation is probably less pronounced in the relatively homogenous Northeastern United States versus the arid-to-tropical, mountainous extreme south and west of black cherry's sprawling native range, but investigators have observed adaptive differences in black cherry from high and low elevations in the Appalachian Mountains (Barnett and Farmer 1980).

Table 1. Summary of silvics, biology, and transfer considerations for black cherry

Black cherry *(Prunus serotina)*	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Fleshy fruit with single seed • About 2,000 cleaned seeds per pound (4,000 per kilogram) • Can be stored in freezer or refrigerator 3 to 5 years if dried to 4 to 6 percent moisture
Insect and disease	• Eastern tent caterpillar and cherry scallop shell moth are major defoliators; peachtree borer and peach bark beetle attack stems • Vulnerable to generalist decay fungi; black knot fungus causes defects
Palatability to browse	• Not a preferred browse species, but browsing can be a problem when pressure is high and preferred species are absent
Maximum transfer distances	• Relatively sensitive to seed transfer: distances less than 200 mi (322 km) are safe • Use caution with transfers greater than 250 mi (402 km)
Range-expansion potential	• Black cherry is likely to expand in some areas due to excellent seed dispersal and decline in other areas where it is currently abundant due to stress from insects, diseases, and drought

In earlier studies, black cherry has showed strong site by provenance interactions and poor performance of sources that had been moved more than 5 degrees latitude north or south of the planting site (Carter et al. 1983, Genys and Cech 1975), which indicate a level of local adaptation. Sources from locations south of the planting site within 210 mi (338 km, or 3 degrees latitude) are generally strong performers (e.g., Walters 1985), although some sources from 350 miles (563 km, or 5 degrees latitude) south of the planting site may perform well. Sources from 200 to 250 miles (322 to 402 km)—3 degrees of latitude—south of the planting site will likely be the best performers at a given location, but moving sources farther than this is risky. Collections from parent trees with superior phenotypes do not necessarily exhibit significantly better performance than collections from average parent trees (Pitcher 1982).

Insects and Diseases

Many native insects and diseases affect black cherry. The species is a preferred food source of the eastern tent caterpillar (*Malacosoma americanum* F.), which can cause defoliation, reduced growth, and occasionally mortality due to repeated attacks (Marquis 1990). Cherry scallop shell moth (*Rheumaptera prunivorata* F.) can also cause defoliation. Black cherry is vulnerable to several stem borers that can damage the wood and leave distinctive pitch spots on the outer bark (Kulman 1964), including the peach bark beetle (*Phloeotribus liminaris* Harris), lesser peachtree borer (*Synathedon pictipes* Grote & Robinson), and cambium miner (*Phytobia pruni* Gross).

The most recognizable fungal disease of black cherry is black knot, caused by *Apiosporina morbosa* Schwein., which causes large, woody black swellings on stems and can destroy the timber value of trees. Leucostoma canker (*Cytospora leucostoma* [Pers.] Sacc.) is a fungus that causes cankers and branch mortality, often in association with cambium miner feeding (Gross 1967). Several species of generalist wood decay fungi, including *Armillaria mellea* (Vahl) P.Kumm. and *Laetiporus sulphureus* (Bull.) Murrill, attack the wood of mature black cherry trees. Due to its typical canopy position and somewhat weak branch structure, black cherry is often damaged by storms (figure 4). These injuries provide infection courts for decay fungi (Campbell and Davidson 1940, Downs 1938), although most wounds can be compartmentalized. Increased frequency of severe storms and ice storms in a changing climate could increase economic losses of black cherry due to these opportunistic native fungi.

White-tailed deer (*Odocoileus virginianus* Zimmermann) do not prefer black cherry as browse compared with many commonly co-occurring species (Sample et al. 2023), which allows black cherry to regenerate well (relative to other hardwoods) in areas with heavy browse pressure. Browsing can be a serious problem, however, in areas with high pressure where preferred trees are uncommon. Although the defensive hydrocyanic acid-producing compounds in the leaves are highly poisonous to cattle (Smeathers et al. 1973) and other livestock, deer and rabbits are either not as vulnerable to harm from these compounds or do not consume enough at one time to be harmed.

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Figure 4. This large black cherry is growing in southwestern Michigan in a forest with deep, sandy soils. The forest is dominated by American beech (*Fagus grandifolia* Ehrh.), northern red oak (*Quercus rubra* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carrière). This tree, growing among others with storm damage, demonstrates crown form and canopy position typical of good-quality stands in most of black cherry's range. Photo by N. LaBonte, USDA Forest Service, 2023.

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Figure 1. A climate-adapted forest planting site was established in a forest canopy gap in Pennsylvania State University's Stone Valley Experimental Forest overlying sandstone bedrock. Photo by Denise Alving, 2021.

Preliminary Takeaways From a Small-Scale, Climate-Adapted Experimental Forest Setup

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Abstract

Climate change and climate adaptation are at the forefront of many current forest management conversations. This article describes the process of designing, planting, and monitoring a climate-adapted forest on small plots in Pennsylvania State University's Stone Valley Experimental Forest and the Pennsylvania Department of Conservation and Natural Resources' Rothrock State Forest. Plots were established on contrasting shale and sandstone geologies due to their anticipated influence on seedling survival and growth for novel species and extant species under future climate conditions. Publicly available tools and resources, including the Climate Change Response Framework, Climate Change Tree Atlas, and Eastern Seed Zone Forum, were used to select management strategies, species for the study, and seedling sources. This paper was presented

at the Joint Annual Meeting of the Northeast Forest and Conservation Nursery Association and the Southern Forest Nursery Association (State College, PA, July 17–20, 2023).

Introduction

The climate is changing. For example, temperatures in Pennsylvania are expected to rise up to 8 °F (4.5 °C) on average by the end of the century. This rise in temperature will be paired with a change in precipitation patterns. During the fall, winter, and spring, precipitation is projected to rise up to 7 to 12 percent (Butler-Leopold et al. 2018, Frankson et al. 2017, Union of Concerned Scientists 2008). During the summer, when temperatures are expected to increase the most, precipitation is expected to remain consistent, resulting in hotter and drier conditions.

Pennsylvania currently sits at the intersection of two major forest types: the northern hardwoods (dominated by maple [*Acer* spp.], beech [*Fagus* spp.], and birch [*Betula* spp.] trees), and the oak-hickory forests to the south (*Quercus* spp. and *Carya* spp.). Changing temperature and precipitation patterns will likely result in stress and eventually mortality of more cold-adapted tree species and populations, while those with higher tolerance for hot, dry conditions will begin to find their footing in the region. This shift may result in the oak-hickory forests moving farther north in the State and northern hardwoods also retreating north.

Researchers and forest managers are considering strategies to mediate the loss of northern hardwoods, maintain oak-hickory forests, and facilitate establishment of novel species expected to thrive under future conditions. Underground conditions may provide some direction. Analysis of 565 forest inventory plots across the Valley and Ridge province of Pennsylvania showed that chestnut oak (*Quercus prinus* L.) stored more carbon in plots overlying sandstone bedrock, while northern red oak (*Q. rubra* L.) stored more carbon in plots overlying shale bedrock (Reed and Kaye 2020). These differences in carbon storage can be attributed to differential species growth over the two bedrocks. Soils derived from shale bedrock typically have higher nutrient availability and water retention compared to soils derived from sandstone (Hoagland et al. 2017, Jin et al. 2010). Hence, shale bedrock facilitates higher growth rates than sandstone bedrock for species that can take advantage of the available resources. These differences lead to tree species that can tolerate poorer sites (e.g., chestnut oak) and grow well over sandstone but are outcompeted by other tree species (e.g., northern red oak) on more nutrient-rich shale sites. Understanding characteristics of sites where species have good growth allows for targeted tree planting to mitigate climate stress and can support the establishment of new species. This article describes an ongoing project to explore the climate adaptation potential of specific tree species in the context of site conditions due to bedrock.

Materials and Methods

Site Selection and Plot Establishment

This project was established on a site in Pennsylvania State University's Stone Valley Experimental Forest (Huntingdon County, PA) and on a site in Pennsylvania Department of Conservation and Natural Resources (DCNR)'s Rothrock State Forest (Huntingdon and Mifflin Counties, PA).
The first step in establishing a forest management plan is understanding the land area to be managed. Tree seedlings establish in areas where there is sufficient light to provide energy for germination and growth, such as canopy gaps (Muscolo et al. 2014). In Stone Valley Experimental Forest, plots were established in four gaps (two overlying shale and two overlying sandstone geology, identified using U.S. Geological Survey maps of Pennsylvania) where natural disturbances, including windthrow, insect damage, and fire, had opened areas of higher light infiltration (figure 1). Each rectangular plot (25 by 10 m [82 by 33 ft) was planted with seedlings spaced in a 1 by 1 m (3.3 by 3.3 ft) grid. In the Rothrock State Forest, rectangular plots (30 by 10 m [98 by 33 ft] and 30 by 15 m [98 by 49 ft]) were established in two open area harvest sites—one on shale and one on sandstone bedrock (figure 2).

There are distinct advantages and disadvantages to planting in large harvested areas as compared with natural

Figure 2. A climate-adapted forest planting site was established in a harvest site in Pennsylvania's Rothrock State Forest overlying sandstone bedrock. Photo by Denise Alving, 2021.

canopy gaps. Seedlings in the harvested areas in Rothrock State Forest had full direct sunlight. While the higher light intensity allowed these seedlings to easily reach heights up to 1.5 m (5 ft) in the first 2 years, they were competing with rapidly resprouting maple and birch seedlings, as well as dense blueberry (*Vaccinium* spp.) bushes (figure 3). On the other hand, seedlings planted in the canopy gaps in the Stone Valley Experimental Forest were growing in partial shade with minimal competing vegetation, with the tallest individuals reaching only 0.9 m (3 ft).

Management Goals and Strategies

Once project sites were selected, the next step was identifying management goals and strategies for these sites. The U.S. Department of Agriculture (USDA) Forest Service's Northern Institute for Applied Climate Science developed the Climate Change Response Framework (https://forestadaptation.org/) based on a growing number of climate-adapted forest field experiments. The framework identifies 10 forest management strategies that are described online (https://adaptationworkbook.org, Swanston et al. 2016). These strategies focus on (1) protecting organisms and habitats at risk of loss, (2) maintaining and expanding the ranges of current species and habitats expected to be successful under future climates, and (3) assisted migration.

Figure 3. This planted oak tree at one of the climate-adapted forest plots on a harvest site reached nearly 1.5 m (5 ft) in height after 2 years. Photo by Alina Iwanowicz, Pennsylvania State University, 2022.

Assisted migration is an ecological management strategy to intentionally plant species predicted to be adapted to future climate conditions into niches likely to be left empty by decline of current native species (Kawecki and Ebert 2004, Lunt et al. 2013, Millar et al. 2007). This experiment included three management strategies: (1) mitigate loss to three native species that are considered at risk; (2) maintain and expand the ranges of two species projected to thrive under future climate conditions; and (3) introduce four southern species with assisted migration.

Species Selection

Climate-adapted forest plantings should incorporate not only species that will grow onsite now but also those that will thrive under future conditions. Predicting species tolerances using only current species distributions can be challenging; however, tools are available that allow land managers to make informed decisions about species selection. The Forest Service's Climate Change Tree Atlas (https://www.fs.usda.gov/nrs/atlas/tree/) is a climate envelope model that projects potential future suitable habitats for 125 tree species across the Eastern United States. The model calculates a current importance value for a given species in a given location using stem density and basal area measurements collected and analyzed at fixed time intervals from the Forest Service's Forest Inventory and Analysis Program plots across the United States. Importance values range from 0 (if the species is completely absent) to 200 (if the stand only has one species growing). Potential future changes in habitat suitability of species were estimated based on 38 soil, topography, and climate variables using 3 different global circulation models across low and high greenhouse gas emission scenarios to project future suitable habitats for each tree species (Iverson et al. 2008, Prasad et al. 2014). These habitat projections are at a 1 by 1 degree resolution.

For the two sites in Pennsylvania, a species with an importance value >1 in Huntingdon County, PA, was considered present. If a species was estimated to stay the same or increase under a high-emission scenario by the end of the century, it was designated a climate winner. If a species was estimated to decrease by >1 under the high-emission scenario, it was designated a climate loser. Any species with a current importance value <1 that increased >1 under a high-emission scenario in the model was considered a new arrival (figure 4). Nine species were selected: four new arrivals, two climate winners, and three climate losers (table 1). Climate losers were included in the study because of their current high regional importance values and potential future decline. Many of these species provide key ecosystem services, and mitigating population loss will allow for these services to continue with minimal disruptions.

Seed Sourcing

Seed source for each seedling species selected was based on the geographic origin of the seedlings and the availability of seedlings from nurseries. Many tree

Figure 4. Sweetgum is considered a "new arrival" species in central Pennsylvania. It is a mesophytic species whose current natural range extends through southeast Pennsylvania. Higher temperatures and changing precipitation patterns may allow this species to become a dominant species in central Pennsylvania by the end of the century. Photo by Denise Alving.

species occur across large latitudinal and altitudinal gradients throughout the United States, with local populations adapted to local climate and having the highest growth rate compared with individuals sourced from populations adapted to warmer or cooler climates. Differences in phenology and adaptation to local seasonal extremes may explain these patterns (Leites et al. 2019).

The USDA divided the United States into hardiness zones based on the minimum temperature reached within a zone during the coldest part of the year. These hardiness zones were used to identify seedling source populations that share the same hardiness zone as the project sites. To source seedlings for novel species adapted to future climate that are typically found in a hardiness zone with a minimum winter temperature tolerance of up to 5.5 °C (10 °F) warmer than the planting area, the Eastern Seed Zone Forum (http://www.easternseedzones.com/) was used. This tool delineates estimated future seed zones based on existing eco-physiological and plant hardiness zone delineations, among other factors (Pike et al. 2020). The predicted plant hardiness zone in Pennsylvania by the end of the century is 7. Distribution maps show that the closest points in plant hardiness zone 7A are currently in northern Virginia and New Jersey. This information was used to select species for the new arrival category (table 1).

Seedlings came from two types of nurseries: (1) local commercial nurseries, including Musser Forests (Indiana, PA) and the Aquatic Resource Restoration Company (Glen Rock, PA) and (2) State nurseries, including the New Jersey State Nursery (Jackson, NJ) and Virginia State Nursery (Crimora, VA). Many of the seedlings sourced for the initial planting were donated by the Keystone 10 Million Tree project (K10), a nonprofit organization whose goal is to plant 10 million trees in Maryland, Pennsylvania, and Delaware before 2025. The K10 organization covered the costs of purchasing and shipping seedlings from local nurseries and loaned planting supplies. All seedlings were 1- to 3-year-old bareroot, primarily because of availability, cost, and ease of shipping.

Planting Schedules and Considerations

Initial planting of 1,700 study trees in Stone Valley Experimental Forest and Rothrock State Forest was completed from May 7 to June 15, 2021, just after the average day of the last frost in Pennsylvania but before periods of heat and drought in July. Student volunteers used best practices for planting bareroot seedlings in the spring as outlined by Penn State Extension (Jackson 2023). Care was taken to be consistent with planting standards and that planting holes were deep enough to avoid compressing roots or leaving root collars exposed. Additional plantings were done in 2022 and 2023 to replace individuals that died in previous seasons. Seedlings will remain in place for the foreseeable future.

Seedling Maintenance

Once planted, seedlings are vulnerable to damage by defoliators and browsers, with spongy moth (*Lymantria dispar* L.) and voles (*Microtus arvalis* Pallas) being the most common at the project sites. To avoid damage, tree tubes were used early in the growing season. The tubes were held in place with a stake, topped with a mesh sleeve, and sunk about 8 cm (3 in) into the ground (figure 5). Tree tubes provide seedlings structural stability and protect them from insects and rodents. Removal of competing vegetation, especially at higher densities, was also easier with tree tubes protecting the base of seedlings. Late in the first season it was evident that tree tubes retained significant

Figure 5. Tree tubes were installed initially to protect seedlings from animal and insect damage. Each 1.5-m (5-ft) tube was zip-tied to a wooden stake that was hammered into the ground to discourage rodent damage. Photo by Cathryn Pugh, Pennsylvania State University.

Table 1. Tree species planted in study sites

Species	Scientific name	Years planted	Producer	No. Planted	Price per seedling	Cost
New arrival species						
Sweetgum	*Liquidambar stryaciflua*	2021	Keystone 10 Million Tree Project	200	Donated	Donated
		2023	Musser Forests	125	$1.57	$196.25
Shortleaf pine	*Pinus echinata*	2021	New Jersey State Nursery	200	Donated	Donated
		2022	Virginia State Nursery	200	Donated	Donated
		2023	Virginia State Nursery	50	Donated	Donated
Loblolly pine	*Pinus taeda*	2021	New Jersey State Nursery	200	Donated	Donated
		2022	Virginia State Nursery	180	Donated	Donated
		2023	Virginia State Nursery	110	Donated	Donated
Southern red oak	*Quercus falcata*	2021	Virginia State Nursery	250	$0.70	$175
Climate winner species						
White oak	*Quercus alba*	2021	Keystone 10 Million Tree Project	200	Donated	Donated
Black oak	*Quercus velutina*	2021	Keystone 10 Million Tree Project	200	Donated	Donated
		2023	Musser Forests	100	$1.49	$149
Climate loser species						
Red maple	*Acer rubrum*	2021	Keystone 10 Million Tree Project	200	Donated	Donated
		2022	Musser Forests	100	$1.40	$140
		2023	Musser Forests	100	$1.40	$140
Sugar maple	*Acer saccharum*	2021	Keystone 10 Million Tree Project	200	Donated	Donated
		2022	Aquatic Resource Restoration Company	110	$0.70	$77
Northern red oak	*Quercus rubra*	2021	Keystone 10 Million Tree Project	200	Donated	Donated
		2022	Musser Forests	100	$1.07	$107
			Total # planted:	**3,025**	**Total cost:**	**$984.25**

Each species was designated as a **new arrival**, **climate winner**, or **climate loser** based on future climate projections. Many seedlings were donated, resulting in lower costs for the project.

moisture, which increased the susceptibility of the seedlings to mold and rot, especially pine seedlings. Thus, tree tubes were removed late in the first season and deer fencing surrounding the whole plot was installed (figure 6).

The deer fence excludes browsing from large mammals, including white-tailed deer (*Odocoileus virginianus* Zimmermann) and black bears (*Ursus americanus* Pallas), but does not exclude small mammals and insects. The deer fencing alone does provide some benefits over the tree tubes, including more light reaching the seedlings, more air circulation to prevent mold and fungus growth, and more space for seedlings' lateral branching. Future plantings could use a combination of seedling protection methods, such as opting to keep the deer fencing as a large-scale preventative and using shorter tree tubes to prevent small mammal access to stem base and roots while still allowing for air circulation around leaves. Some biological controls, such as spraying oak and maple leaves with *Bacillus thuringiensis* in 2022 for spongy moth, were moderately effective at mediating insect damage.

Monitoring and Measurement

Following initial planting and a 2-week adjustment period, baseline measurements were taken at each site. Height from ground to tallest woody point on stem, diameter at base, and survival were recorded for each planted tree. Thereafter, height, diameter, and survival were measured each year in November (end of growing season) and in

Figure 6. Deer fence was established around the climate-adapted forest plots. In this photo, both deer fencing and tree tubes are protecting the seedlings; later in the season, however, tree tubes were removed due to concerns about moisture and fungal damage. Photo by Denise Alving, 2021.

the following April (start of the new growing season). The biannual measurement allows for an account of mortality associated with conditions in the previous season and an assessment of height and diameter growth. Every May, a portion of seedlings that died were replaced with new seedlings of the same original age. From May to September, competing vegetation at each site was managed by hand clipping, specifically targeting grasses, forbs, and volunteer seedlings that shade out the study trees. In addition to these semi-annual measurements and management efforts, soil cores were taken from each of the six plots for chemical content and texture analysis. Also, leaf samples were collected in 2021 for genetic sampling from two of the plots in Stone Valley Experimental Forest and flash-frozen for RNA extraction and gene expression studies. Stomatal conductance, leaf mass to area ratio, and water use efficiency were being measured in the 2023 and 2024 growing seasons to compare seedling physiology between bedrocks and climate adaptation strategy.

Preliminary Findings

Data collection and analysis for the project are ongoing, with survivorship and growth measured thus far for the first 2 years of the experiment. While definitive patterns of survival, growth, and gene expression by bedrock and climate adaptation strategy will take several years to emerge, some general trends have emerged.

First, survival of seedlings planting in 2021 is highest for northern red oak and sweetgum and lowest for loblolly pine and shortleaf pine. Of surviving individuals, loblolly pine and shortleaf pine seedlings have the highest relative growth, while sweetgum has the lowest. Trends have also emerged between the two bedrocks. Overall, survival is higher for loblolly pine, northern red oak, southern red oak, and black oak planted over sandstone bedrock. Relative growth of sweetgum was higher for those planted over sandstone bedrock as compared with those over shale bedrock. These initial results are surprising because the anticipation was for seedling growth and survival to be higher over shale bedrock due to its greater water and nutrient availability compared with sandstone bedrock. Future analyses will evaluate soils, seedling genetic expression, and physiology to explain seedling growth and survival rates of the different species.

Discussion and Future Directions for the Project

This experiment is entering its fourth year in 2024. Continued collection of survival and growth data will be useful to identify long-term patterns among species and bedrocks. Continued analysis of gene expression data, as well as collection and analysis of physiological data, will lead to an increased understanding of the changes in plant biological processes across sites with different bedrock and their effects on survival and growth. The initial intensive data collection and analysis stage is expected to continue through early 2025, after which the project will transition into a long-term maintenance phase. Annual site maintenance and measurements of survival and growth will continue through the Forest Dynamics Lab at Penn State and in collaboration with land managers from the Stone Valley Experimental Forest and Pennsylvania's DCNR. The plots will continue to be available for new student research projects and educational opportunities within the university and local audiences. These sites are also registered with the Climate Change Response Framework with the goal of making the climate-adapted forest site design and research outcomes available to a wider audience seeking to apply this knowledge to their land management.

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Scaling Up Nursery Production for Agroforestry

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Abstract

The agricultural industry will become increasingly vulnerable in the coming decades as the impacts of climate change intensify, putting farmer livelihoods and food security at risk. To mitigate the impacts of increased drought, flooding, and unpredictable climatic regimes, scaling up methods of sustainable agricultural production is critical. Agroforestry—the integration of perennial trees, shrubs, and herbaceous plants into productive agricultural landscapes—is rooted in traditions of Indigenous land stewardship and subsistence farming. Agroforestry has the potential to store greater amounts of carbon than annual cropping systems, improve soil and water health, increase on-farm biodiversity, and reduce nutrient inputs and outputs. In temperate regions, scaling up agroforestry is challenged by barriers to farmer adoption, including lack of technical service assistance, economic pressure toward large-scale, monoculture cropping systems, and limited supply of appropriate planting stock. Despite these barriers, agroforestry is of great interest among farmers and agricultural support organizations, evidenced by the ample representation of agroforestry-related projects funded through the U.S. Department of Agriculture's Partnerships for Climate-Smart Commodities program. This article addresses the limited supply of planting stock for agroforestry and emphasizes the importance of coordinating efforts between agroforestry and reforestation, especially within the nursery industry. This paper was presented at the Joint Annual Meeting of the Northeast Forest and Conservation Nursery Association and the Southern Forest Nursery Association (State College, PA, July 17–20, 2023).

Introduction

In the coming decades, ecological disruptions will intensify, requiring increased development of new and transformative climate adaptation and mitigation strategies (Anderson et al. 2020, Diaz et al. 2019, Lobell and Gourdji 2012). Building a more sustainable and just global food system will necessitate multifaceted, varied methods of adaptation and mitigation (Wezel et al. 2009). Agriculture faces the specific challenge of making revolutionary changes to the way we grow food while also maintaining a dependable food supply and mitigating carbon emissions.

In North America, vulnerabilities are compounded by decades of intensive agricultural practices that degrade soils and water resources, reduce biodiversity, and rely heavily on the production of monoculture crops (Kramer et al. 2019). Dominant agricultural practices rely heavily on annual cropping systems, which often underutilize strategies that could potentially store greater amounts of carbon in soil, improve the health and diversity of ecosystems, and reduce nutrient inputs and outputs (Chenyang et al. 2020, Lal et al. 2007). In addition, agriculture accounts for approximately 18 percent of global greenhouse gas emissions (figure 1), fueling an interest in agricultural practices that store, rather than emit, greenhouse gases (Ritchie and Roser 2023). No single solution exists to these challenges, but approaches exist that can minimize negative outcomes while supporting productive agricultural systems.

Agroforestry is an approach to climate change mitigation and adaptation that involves integrating trees, shrubs, and herbaceous perennial plants into agriculture (figure 2). By intentionally combining trees and shrubs with crops or livestock, agroforestry can offer economic, environmental, social, and cultural benefits to farmers looking to diversify their farm offerings (Gold and Garrett 2009). Aligned with principles of agroecology and regenerative agriculture, agroforestry is a contemporary term for methods of producing food, fiber, fuel, and medicine that are rooted in Indigenous knowledge and have been practiced for thousands of years (Elevitch et al. 2018, Miller and Nair 2006, Rossier and Lake 2014, Wezel et al. 2009).

Implementing agroforestry practices on productive agricultural landscapes can increase soil organic carbon stocks, improve food security and crop yields, increase biodiversity, provide wildlife and pollinator habitat, and mitigate acute effects of climate change, such as heat stress, drought, and flooding (Cardinael et al. 2021, Chenyang et al. 2020, Schoeneberger et al. 2012). As a method of carbon sequestration, agroforestry has the potential to store carbon aboveground and belowground in plant biomass and soil carbon at greater rates than

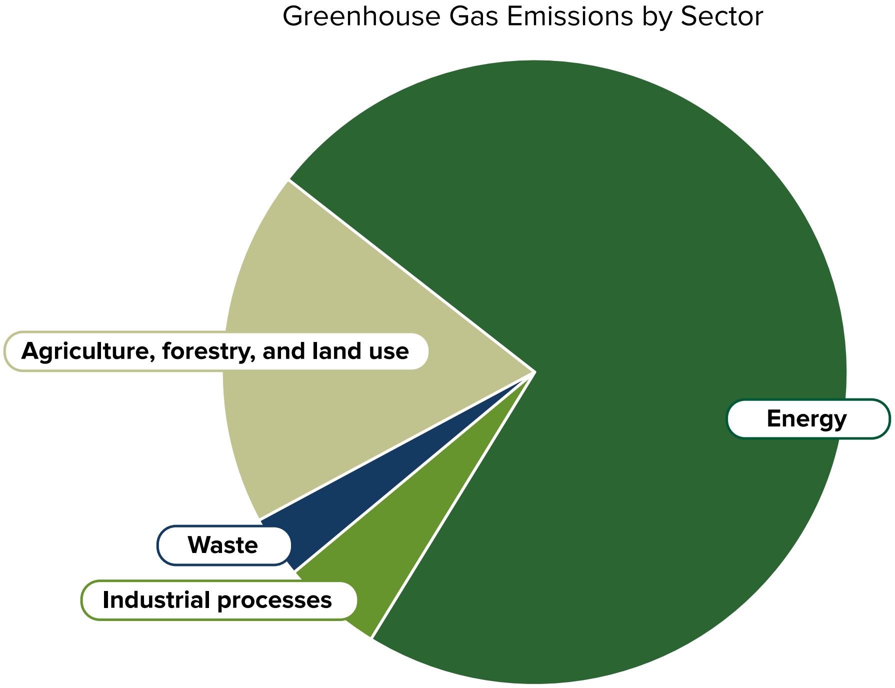


Figure 1. Agriculture, forestry, and land use sectors (beige) account for 18.4 percent of greenhouse gas emissions (not including associated transportation, food processing, packaging, and refrigeration). Electricity, heat, and transportation (dark green), industry (light green), and waste (blue) account for 73.2, 5.2, and 3.2 percent of emissions, respectively. Source: Richie (2020).

climate mitigation strategies used in annual cropping systems, such as cover cropping and no-till (Chenyang et al. 2020). In addition to the important ecological benefits it confers, agroforestry competes economically with conventional farming when the long-term environmental benefits and the cost of negative externalities associated with agriculture are integrated into economic models (Thiesmeier and Zander 2023).

Currently, agroforestry is commonly practiced in tropical regions, where using perennial cropping systems is part of longstanding agricultural traditions (Miller and Nair 2006, Smith 2010). In contrast, modern agricultural production in temperate regions of North America is currently dominated by annual row crop systems. Consequently, agricultural financing programs, crop insurance, education, economic markets for crops, and Federal support programs are shaped

Figure 2. Early silvopasture establishment necessitates protection from both livestock and wildlife. A combination of tree tubes and portable electric fencing can be used to protect tree seedlings (left). The tree tubes protect the tree from rodent girdling and deer rubbing and encourage vertical growth, allowing the tree to get above browse height sooner. Integrating livestock can be an economically viable method of vegetation management during the establishment phase as seen here with Katahdin sheep grazing alongside apple (*Malus* spp.) seedlings (center). Katahdin sheep utilize the shade from naturally established conifer trees intentionally left by the farmer (right). Photos by Alex Caskey, Barred Owl Brook Farm.

to fit large-scale, annual crop production (Carlisle et al. 2022). To scale up agroforestry adoption, current systems of agricultural advising, financing, and market development must be adapted to accommodate perennial crops and diversified farming systems (Valdivia et al. 2012).

This article outlines specific challenges associated with scaling up agroforestry at different stages of the "plant material pipeline," with a focus on the role of plant nurseries. Access to consistent, well-adapted, diverse sources of planting material is not a unique issue; scaling up efforts along the reforestation pipeline are also challenged by limited nursery capacity (Fargione et al. 2021). To better understand the interface between plant production for agroforestry and reforestation, it is important to consider the specialized knowledge, partners, industries, and supply chains of each. Greater collaboration between concerned parties is necessary at every stage of plant production, including ensuring seed supply, producing healthy plants, and generating demand for a diverse range of species. As agroforestry and reforestation scale up, it is mutually beneficial to identify areas where needs overlap and to prioritize collaboration.

A Brief History of Agroforestry

Agroforestry is not a new concept; Indigenous knowledge-holders have been familiar with the practice of combining trees and crops to provide food and ecological benefits for centuries in both tropical and temperate ecosystems (Steppler and Nair 1987). Currently, agroforestry is more widely practiced in tropical and subtropical ecosystems and is less widespread in temperate regions. Even a low level of adoption in temperate zones is impactful. Despite the variability in carbon sequestration estimates, which are influenced by factors such as site characteristics, species composition, system age, management practices, and climate, agroforestry systems have a carbon sequestration potential ranging from 0.12 Pg carbon per year to 0.31 Pg carbon per year (petagram = 10^{15} g) (Terasaki Hart et al. 2023). This potential is comparable to other prominent natural climate solutions, such as reforestation, which has an estimated sequestration potential of 0.27 Pg carbon per year. The U.S. Department of Agriculture (USDA) defines five agroforestry practices: windbreaks and hedgerows, riparian buffer zones, forest farming, silvopasture, and alley cropping or intercropping. To fully conceptualize the versatility of agroforestry, it is helpful to describe the principles that underlie these practices.

Agroforestry is guided by the goal of creating an agroecological system that is mutually beneficial for crops, livestock, the surrounding environment, and the people and cultures who steward the land. Gold and Garrett (2009) describe four key criteria to distinguish agroforestry systems from other land use practices. The first defining principle is that the system must be *intentionally* designed, established, and managed. Secondly, the different elements of the system, including crops, livestock, and trees or shrubs, are *integrated* both structurally and functionally. Integrating physical forms and biological functions creates beneficial relationships between elements of the system. Third, agroforestry systems are *intensively* managed to maintain the functions that the system was designed to fulfill. And fourth, the system cultivates *interactive* relationships among the different components. For example, rows of apple trees planted in an orchard are not considered an agroforestry system; but if livestock were integrated and intensively managed in an interactive manner between orchard rows, that system could be considered agroforestry.

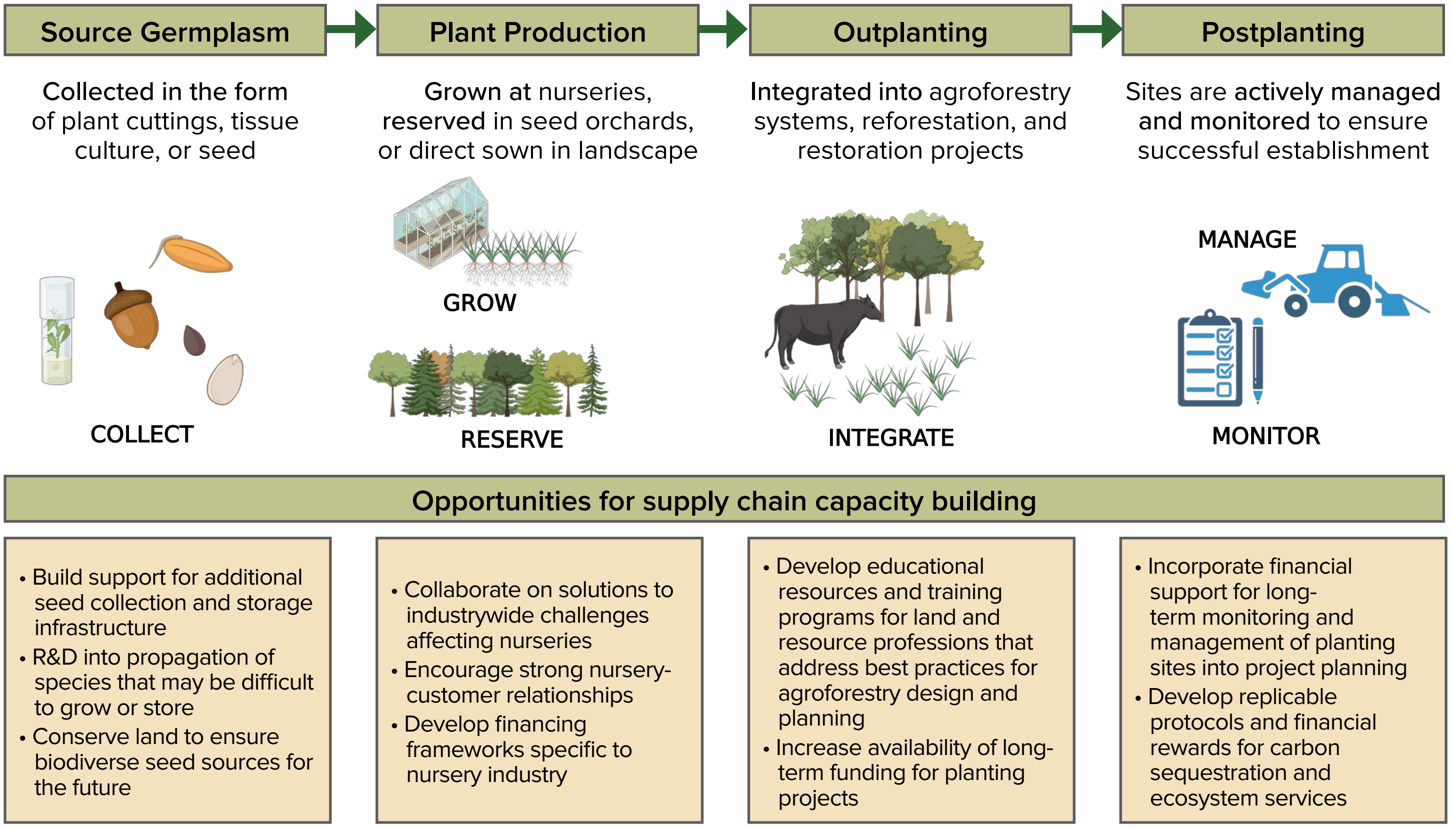
Agroforestry creates a working landscape that provides both economic and environmental benefits to agricultural producers (Van Der Wolf et al. 2019). Goals may vary widely between different agroforestry systems, making it difficult to measure success or provide a simple guide to establishment (Jose 2009). Similar to ecosystem restoration and reforestation, agroforestry can be implemented on marginal farmland, in pastures, or areas that provide multiple ecosystem services such as riparian zones or sensitive ecosystems. For example, an area seasonally inundated with water may not be appropriate for vegetable production but could be suitable for creating a hedgerow of harvestable crops such as elderberry (*Sambucus* spp.) or hazelnut (*Corylus* spp.). Or, depending on the farmer's goals, this same area could be used to establish a riparian buffer to reduce nutrient runoff or to plant living fences to keep livestock out of streams. Agroforestry can also be integrated into annual cropping systems, though there is potential for reduced yields if competitive interactions are not intentionally managed (Reynolds et al. 2007). To ensure beneficial impacts, the integration of perennial crops must be designed to fit into the local context, which includes accommodating local environmental conditions, farmer priorities, and relevant local markets (Brown et al. 2018).

Scaling Up: The Agroforestry Plant Material Pipeline and Associated Barriers

Scaling up agroforestry in the United States is limited by a range of factors, including a shortage of professional consulting agroforesters and technical support staff, costs associated with establishment and management of plantings, and insufficient knowledge of tree crop management among landowners and farmers (Kronenburg et al. 2023, Stanek & Lovell 2020). A growing interest in implementing agroforestry practices in agricultural systems exists, demonstrated by an increasing number of organizations advocating for policy development, increased financial and educational resources, and improved coordination among agroforesters, farmers, nurseries, and researchers. Through the Partnership for Climate-Smart Commodities program, USDA has placed greater emphasis on promotion of agroforestry practices by distributing approximately $802 million in the program's first year to support 39 projects that include an element of agroforestry. Though not specific to agroforestry, the Inflation Reduction Act of 2022 pledged $18 billion toward climate-smart agricultural practices, enacted through conservation programs such as the Environmental Quality Incentives Program, Conservation Stewardship Program, and Conservation Reserve Program. While this support has generated huge opportunities, these programs are often criticized for their inflexibility and must be adapted to support multifunctional agricultural systems (Stanek and Lovell 2020).

Limited access to appropriate plant material is one of the primary barriers to scaling up agroforestry, which is a familiar logistical barrier to conservation professionals across the United States who must procure a wide variety of plant materials for use in restoration and reforestation plantings (Fargione et al. 2021, Jalonen et al. 2018). Current nursery production levels are inadequate to meet expanded reforestation goals, which estimate 128 million acres of land available for increased tree cover (Chizmar et al. 2022, Fargione et al. 2021, McCormick et al. 2021, Piñeiro et al. 2020, Sow et al. 2018, White et al. 2018). Similar to the challenges faced by reforestation projects, which use many of the same plant species as riparian buffer, windbreak, or hedgerow plantings, procuring plant material that is both appropriately adapted to regional conditions and can be purchased in the specific quantities and varieties necessary for a desired planting can be a significant hurdle for agroforestry adopters. As reforestation and agroforestry efforts are scaled up, nurseries will need to dramatically increase production to meet the projected demand for trees, shrubs, and herbaceous perennials (Cardinael et al. 2021, Chenyang et al. 2020, Fargione et al. 2021).

To better understand the barriers in the plant material pipeline, it is helpful to describe the four stages of the pipeline (figure 3). The pipeline begins by (1) sourcing germplasm—gathering appropriate propagative material; (2) plant production—the collected germplasm is used to grow


Source Germplasm → **Plant Production** → **Outplanting** → **Postplanting**

Source Germplasm: Collected in the form of plant cuttings, tissue culture, or seed

Plant Production: Grown at nurseries, reserved in seed orchards, or direct sown in landscape

Outplanting: Integrated into agroforestry systems, reforestation, and restoration projects

Postplanting: Sites are actively managed and monitored to ensure successful establishment

Opportunities for supply chain capacity building

Source Germplasm:
- Build support for additional seed collection and storage infrastructure
- R&D into propagation of species that may be difficult to grow or store
- Conserve land to ensure biodiverse seed sources for the future

Plant Production:
- Collaborate on solutions to industrywide challenges affecting nurseries
- Encourage strong nursery-customer relationships
- Develop financing frameworks specific to nursery industry

Outplanting:
- Develop educational resources and training programs for land and resource professions that address best practices for agroforestry design and planning
- Increase availability of long-term funding for planting projects

Postplanting:
- Incorporate financial support for long-term monitoring and management of planting sites into project planning
- Develop replicable protocols and financial rewards for carbon sequestration and ecosystem services

Figure 3. At each stage of plant material flow within agroforestry, reforestation, and restoration projects, opportunities exist for collaboration across these disciplines. These opportunities are not exhaustive but offer a starting point for future conversations.

plants at a nursery or is seeded directly onto a landscape to be conserved or used as a seed orchard; (3) outplanting—species are selected based on project goals, local landscape, and availability and then established in the landscape; and (4) postplanting—plants are monitored and maintained to ensure successful establishment and production and to help producers access markets for their products (from carbon credits to fruit and nut crops). These four stages are described in more detail in subsequent sections.

The process of species selection weaves itself into every stage of the plant material pipeline. The diversity of plant material needed for agroforestry presents a unique challenge for scaling up production. For example, a crop-oriented system may require specific cultivars that can produce a commercially viable fruit or nut crop. On the other hand, an agroforestry system oriented towards improving water quality and wildlife habitat may require native species from regionally sourced seed. Most nurseries can grow a wide range of plants, but it often requires sourcing young plant material from other nurseries. In addition, based on the plant material being grown, the inputs, equipment, and knowledge needed to grow specific plants can vary. For this reason, it is important to communicate project needs to regional nurseries far in advance to give growers adequate time to source and grow plant material.

When sourcing germplasm, propagative material may be collected by the nurseries, independent contractors who specialize in seed collection, or via federally funded programs like Seeds of Success. These collectors often make choices about where seed is collected from and what plant genetics will be represented based on specific project objectives (Harrison et al. 2023). Nurseries make decisions about what species to grow based on customer demands. The Target Plant Concept (TPC) (Dumroese et al. 2016, Rose et al. 1990) emphasizes the importance of feedback and communication in a nursery-client partnership to guide choices for species selection and stock specifications and to improve plant performance in outplanting sites. The TPC, though developed for forest restoration, can be applied to agroforestry as well.

Selection of species, genetic sources, and stock types are as diverse as the environments where agroforestry or reforestation are implemented, and decisions made by those who supply and purchase plants can have huge impacts on long-term ecosystem health (White et al. 2018). For reforestation, restoration, and agroforestry projects, plant selection should be based on site conditions and planting goals (Jalonen et al. 2018). Careful consideration of impacts on native plant communities and potential for invasiveness must also be factored into selections. Due to the specific needs of each project and site, it can be challenging to form lists or guides that detail the appropriate species to use in agroforestry and reforestation. To help better inform efforts to scale up production and adoption, there is currently a list of popular species for agroforestry in development by the National Agroforestry Center, a program run jointly by USDA's Forest Service and Natural Resources Conservation Service in Lincoln, NE. Additionally, a list of potential agroforestry species was developed for the State of Vermont through Vermont Farm-to-Plate, which may be useful to growers in plant hardiness zones 3, 4, and 5 (Toensmeier 2023).

Sourcing Germplasm

Plant material may be generated from (a) stem or root cuttings, (b) tissue culture, or (c) seed (figures 4 and 5). Some species used in agroforestry systems may need to be clonally propagated or improved for commercial agricultural production. For example, if the goal of the agroforestry system is to produce a fruit crop such as pears (*Pyrus* spp.) or black currant (*Ribes nigrum* L.), the parent plant is often a cultivated variety that reliably produces a consistent, robust crop. To clonally propagate (through tissue culture, grafting, cuttings, or carefully controlled

Figure 4. Northern pecan (*Carya illinoinensis* [Wangenh.] K. Koch) seeds beginning to sprout (left). This variety of pecan was selected for its short growing season, cold hardiness, and culinary attributes. These unique characteristics come at a cost of $2.20/seed to the nursery grower. Seed collection and sourcing are important for agroforestry; here (right), workers collect black walnuts (*Juglans nigra* L.) from mature, naturally established trees on a farm in Parks, AR. Photos by Alex Caskey, Barred Owl Brook Farm.

Figure 5. Cuttings, such as willow (*Salix* spp.) (left), and grafted plants, such as honey locust (*Gleditsia triacanthos* L.) (center) and mulberry (*Morus* spp.) (right), grown at Barred Owl Brook Farm in Westport, NY, are common propagative material for agroforestry plants. Photos by Alex Caskey, Barred Owl Brook Farm.

seed production) and breed plants that can be used for food production, the equipment, material supply chain, skill set, and labor needs differ from growing plants from seed. For example, hazelnuts can be propagated clonally through stooling, but there are production limits to this approach. Producing large numbers of clonal plants for commercial use requires the establishment of breeding programs, variety trials, and access to facilities such as tissue culture labs for clonal propagation.

While the development of improved plant varieties is a unique challenge, a robust, genetically diverse seed supply is a vital aspect of the plant supply for agroforestry, especially for practices like hedgerow or riparian buffer establishment. For production-oriented agroforestry systems, the conservation and use of landrace varieties, which have high levels of genetic diversity, play a crucial role in developing resilient crops that can adapt to a wide variety of environmental conditions (Martín et al. 2017). Presently, insufficient native seed is available to satisfy current and projected demand (Harrison et al. 2023). This bottleneck is exacerbated by the increasing loss of areas used for seed production due to urban development and other disturbances such as wildfires (Harrison et al. 2023, Jalonen et al. 2018). Due to the specialized skills, knowledge, and equipment associated with tasks like seed cleaning, tissue culturing, and plant breeding, a single nursery will often focus on filling a specific demand category. As agroforestry and reforestation are scaled up, it is vital to support a wide variety of nurseries, both big and small, to facilitate a diverse plant supply.

Plant Production

Propagative material may be grown at a nursery facility, in a seed orchard, or sown directly into the landscape (figure 6). Not all plant material is grown to be sold. A subset of

Figure 6. Chestnut (*Castanea* spp.) burr (left) and hybrid chestnut seedlings (right), shown here at the East Hill Tree Farm nursery in Plainfield, VT, is an example of a plant being produced for agroforestry. Photos by Nicko Rubin, East Hill Tree Farm.

Figure 7. Improved willow (*Salix* spp.) and poplar (*Populus* spp.) trees were planted at Barred Owl Brook Farm (Westport, NY) to establish living fence posts that will restrict livestock access to the adjacent drainage channel (left). The trees will also provide shade and tree fodder for sheep in addition to myriad ecological benefits for wildlife (right). Photos by Alex Caskey, Barred Owl Brook Farm.

propagated plants may be conserved to be used as a future source of propagative material (Harrison et al. 2023). No national studies, quantitative or qualitative, have assessed the extent of nursery production for agroforestry systems. However, nearly any woody perennial can be used in an agroforestry system, assuming it provides food, fiber, fuel, or ecosystem services in the landscape. Consequently, many nurseries are already growing, or equipped to grow, appropriate species for agroforestry (Gold and Garrett 2009). For example, in the Northeast United States, elderberry is often grown for berry production, landscaping, and riparian restoration projects, and can benefit farmers who may want to establish an alley cropping system that produces a fruit that can be harvested and sold.

Studies evaluating nursery production of perennial trees and shrubs can give us broad insights into the ability of nurseries to produce plants for agroforestry. Forest and conservation nurseries in the United States produced 1.27 billion tree seedlings specifically for reforestation and conservation plantings (Haase et al. 2020). A portion of those seedlings were likely used to establish windbreaks, riparian buffers, or silvopasture or intercropping systems. Reforestation, restoration, and agroforestry plantings often rely on the same State, Tribal, Federal, and private nurseries to supply plant material and are equally affected by industrywide challenges. Enhancing nursery production for multiple purposes and connecting producers to demand can foster progress toward the protection of both natural and agriculturally productive ecosystems.

When asked about constraints to expansion, workforce and uncertainty about demand were reported as the most ubiquitous challenges facing nurseries. After labor, market risks and financing were the most common limitations (Fargione et al. 2021). NurseryMag's 2022 "State of the Industry" report corroborates this, with nurseries reporting that labor issues (65 percent of participants reported), increased expenses (63 percent), and the economy (67 percent) as their biggest challenges (NurseryMag 2022). While these surveys can give broad insights into challenges faced by the nursery industry, there is a need to generate more indepth information about specific barriers.

Outplanting

After plants have been propagated, they must be integrated into agroforestry, restoration, or reforestation plantings (figure 7). The success of outplanting in an agroforestry system is dependent on many of the same factors as those in a reforestation project: compatibility of plant species and the specific environment, use of proper planting techniques, and appropriate care and monitoring after they establish. In addition to these challenges, planning an agroforestry system can be a complex endeavor, and successful outplanting requires specialized knowledge about agroforestry system design. Careful and knowledgeable planning must be done to manage interactions between trees, shrubs, crops, and groundcovers. Successful outplanting requires careful consideration of root interactions, allelopathy, nutrient cycling, water requirements, ecosystem services, and potential complementary or competitive relationships among species. A shortage of knowledgeable technical service providers and land use professionals, who may not be familiar with agroforestry practices and have limited opportunities for agroforestry training, can have a negative effect on outplanting success (Stanek and Lovell 2020, Workman et al. 2003).

Based on the goals and design, successful plant establishment in an agroforestry system may require more intensive management than restoration and reforestation projects. For example, irrigation systems, tree tubes, and deer fencing may need to be installed to protect the landowner's investments. Agroforestry plantings may also require additional materials, such as mulch, fertilizer, and compost, that raise the cost associated with the project. Procuring plants can be a challenge, especially when there are limited local sources of plant material or a project uses specific cultivars from a variety of specialized nurseries. While conservation-oriented plantings often rely on large amounts of low-cost plants, this contrasts with many agroforestry plantings, where plants may have been selected for improved genetics and often come at a higher cost per plant.

Postplanting

For an agroforestry system, the work has only just begun once roots are in the ground. One of the key principles defining agroforestry systems is that they must be intensively managed. Short funding timelines and lack of planning can often result in low survival rates in reforestation and restoration plantings. In an agroforestry system, where plants may be used for agricultural production, growers must be able to financially support themselves until the system begins producing a crop, which could take 5 to 7 years for some fruit and nut trees.

Establishing agroforestry systems involves entering a long-term relationship with the management and evolution of that system. As the plants grow, the system will need to be maintained and adjusted to adapt to changes in light, water, and maintenance needs. This maintenance may include pest and weed control, nutrient management, pruning and thinning, and water management. The intensity of management may range based on the system. For example, a riparian buffer zone may only require periodic removal of invasive species, while an alley cropping system with both annual and perennial crops will require frequent management typical in agriculture.

Beyond maintenance considerations, the long-term success of agroforestry systems requires access to developed markets for agroforestry products, monitoring of environmental benefits and potential carbon sequestration, and access to continuing education and training for landowners and technical service providers. For systems that do not produce a crop, it is vital to provide landowners with incentives to maintain plantings on their land, which may include payment for ecosystem services or carbon sequestration. A significant knowledge gap in the carbon sequestration potential of both reforestation and agroforestry exists currently (Terasaki Hart et al. 2023).

Conclusion

The challenges associated with obtaining well-adapted sources of plant material is documented in literature surrounding reforestation but less well-documented for agroforestry. Preliminary research indicates that barriers to scaling up are similar for reforestation and agroforestry, and that expanding access to planting stock would be beneficial for both communities. Both communities are affected by the need for diverse, regionally adapted planting stock as well as the overarching challenges of finding skilled laborers, high market risk, and poor financing opportunities (Fargione et al. 2021, Haase and Davis 2017, NurseryMag 2022). While plant production for agroforestry and reforestation differ in significant ways, they both engage with similar players, notably the nursery industry. Moreover, they share the common goals of sequestering carbon and improving ecosystem resilience at a time when the health and resilience of the planet's forests and agricultural systems are threatened by a rapidly changing climate. While pursuing the restoration of natural and agro-ecosystems amid significant ecological change, it is beneficial to collaboratively develop frameworks to incentivize reforestation and agroforestry plantings and to support the growers that make these projects possible.

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Cold Case: Making the Case for Applied Modeling of Cold Hardiness in Seedling Production and Regeneration

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Abstract

Climate change creates unprecedented challenges for seedling production and reforestation. Developing new tools is necessary to understand seedling physiology and phenology under novel environmental conditions. A process-oriented cold hardiness model that can accurately predict daily cold hardiness is a tool that can inform nursery cultural decisions, planting, and seed source selection, especially in cases of assisted migration. This model can provide daily estimates of cold hardiness status and biologically interpretable parameters that reveal population-specific characteristics with low error and high efficiency. This paper was presented at Growing Pains: Scaling up the Reforestation Pipeline—Joint Annual Meeting of the Western Forest and Conservation Nursery Association and the Forest Nursery Association of British Columbia (Portland, OR, September 19–21, 2023).

Introduction

The future success of seedling production and reforestation faces many challenges. An overarching theme to these challenges is the impacts of climate change and modern forest management practices. These factors disrupt the natural cycles of plants that have evolved over millennia. One such cycle is plant phenology, the timing of recurring life events that are commonly associated with seasonal changes such as budburst in spring, flowering and fruiting in summer, and leaf senescence in fall. Phenology has been observed and recorded for much of recent history, with cherry blossom records dating back to the 800s (Piao et al. 2019). Growing degree days (GDD) may be the first occurrence of phenological modeling, originating in the 1700s, and is still commonly used by growers, agronomists, entomologists, and pathologists (Piao et al. 2019). The concept of GDD can be thought of as a type of “thermal time” and is still applied to nursery crop production and reforestation (Bradford 2002, Ferguson et al. 2011, Kaya et al. 2021).

Tracking thermal time in GDD and chill hours is common in nurseries. These empirical methods are based on historical research and serve as a guide for growers. This practice has sufficed for many decades across many different production systems, but the future, under climate change, will demand a more thorough understanding of seedling phenology and physiological mechanisms to create tools capable of mitigating unprecedented challenges.

In addition to climate change, increasing seedling demand due to postwildfire reforestation efforts also creates challenges in seedling production and regeneration. On Federal land in the United States, forest loss to wildfires in recent decades has resulted in a backlog of reforestation demand. The 2021 Repairing Existing Public Land by Adding Necessary Trees (REPLANT) Act aims to reforest 1.2 billion trees in response to this backlog (Stabenow 2021). This heavy demand pressure for seedlings strains nursery production, challenges infrastructure capacity, and disrupts typical growing and planting practices, all of which create novel risks to seedling cold hardiness

(Fargione et al. 2021, Grossnickle and MacDonald 2021). In response to climate change, assisted migration (seed source movement) is likely to soon become the standard in reforestation. Though the intention is moving populations or species to new regions where they are better adapted, assisted migration creates the risk of maladaptation, or a mismatch between evolved traits and the local environment (Malmqvist et al. 2018). Understanding how populations will handle future heat and drought and how they will tolerate current environments, including cold weather extremes, will be important to prevent maladaptation and ensure reforestation success.

Cold hardiness is a phenological characteristic of plants that is driven in part by temperature and is thus susceptible to effects of climate change. Cold hardiness—the ability of a plant tissue to survive low temperature exposure—can be characterized into three phases during the dormant season of temperate woody plants (Bigras et al. 2001). First, acclimation occurs during fall into winter when plants gradually become cold hardier. Second, peak hardiness (or maximum hardiness) occurs during winter and is when plants show the greatest resistance to cold stress. Third, deacclimation occurs when plants rapidly and irreversibly lose cold hardiness and progress toward budburst and vegetative growth resumption. Though the phenology of cold hardiness and dormancy overlap, and both respond to temperature, they occur via separate mechanisms within plant tissues and follow different seasonal patterns.

Dormancy phenology also progresses through a series of stages driven by environmental conditions. In conifer seedlings, drought-induced dormancy may occur in summer or early fall. At this stage, the plant is in a state of ecodormancy, also called quiescence (Haase 2011), and dormancy can be released (i.e., growth can resume) if the environment becomes favorable. A species-specific combination of photoperiod and chilling temperatures contributes to the progression into endodormancy in the late fall and early winter, which cannot be released by environmental conditions directly but is controlled by internal physiology (Lang et al. 1987). This physiological dormancy must be released through the accumulation of chilling temperature exposure (i.e., a chilling requirement). When chilling requirements have been met, endodormancy progresses into ecodormancy during which forcing temperatures contribute to budburst and cold hardiness deacclimation (Bailey and Harrington 2006), which are highly correlated throughout late winter into spring (Aitken and Adams 1997).

Mismatched phenology (when plant response and environmental cues become asynchronous) can impact seedling success, especially in terms of growth and hardiness. Temperature changes related to climate change have modified the timing and duration of phenological stages during dormancy, with reductions in chilling being the most important driver across temperate tree species (Ettinger et al. 2020). Accumulation of chilling temperatures is important to release endodormancy, control the efficacy of forcing temperatures for budburst, and regulate the rate of cold hardiness deacclimation (Bigras et al. 2001, Harrington and Gould 2015). Seasonality is predicted to change more in the future with longer summers and shorter winters, springs, and autumns. These changes will further disrupt dormancy phenology and reduce chilling accumulation (Wang et al. 2021). As budburst and shoot elongation occur, woody plants are the least cold hardy. Thus, a mismatch in the timing of budburst and seasonal climate can result in negative outcomes such as increased cold damage due to early deacclimation (Arora and Taulavuori 2016, Wisniewski et al. 2018) or delayed budburst due to lower exposure to chilling (Ettinger et al. 2020, Hsu et al. 2023). Climate change in the Pacific Northwest is anticipated to result in increases in precipitation as rain rather than snow (Mote et al. 2016). This change can affect seedling production systems. For example, the seedling lifting window will shift due to soil saturation, early warming, and late freezes, resulting in catastrophic damage to nursery crops or planted seedlings.

Empirical methods, like GDD, are likely to be inadequate in the future when environmental conditions fall outside of historical observations. However, models based on the understanding of biological processes can be more effective when applied to novel conditions, such as those caused by climate change (Cuddington et al. 2013). Fortunately, seedling production and reforestation efforts can be improved through implementing new technologies. New computing abilities and data collection techniques allow for the increased use of modeling tools in nursery production and reforestation practices (MacKenzie and Mahony 2021, Pasala and Pandey 2020).

This article describes a process-oriented cold hardiness model trained and tested with historical published Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) data. This example is meant to demonstrate how a model can be used for daily, real-time predictions of phenology status. This case uses cold hardiness in units of estimated lethal temperature to 50 percent of a population (LT_{50}). Applied use of this model to provide predictions on a daily time scale can be useful in frost protection decision making and characterization of specific seed lots. Real-time knowledge of seed lot hardiness status can be used to inform decisions about culturing, lifting, storage requirements, planting timing, and planting site.

Methods

Cold hardiness observational data were extracted from published literature. Criteria for data selection were the inclusion of multiple dates of cold hardiness observations for a seed source replicated over one or more dormancy seasons. Of the data sources reviewed, only one had multiple seasons of cold hardiness data for two seed sources (Timmis et al. 1994). Data were extracted from three additional data sources, which are described in a separate publication (Stuke et al. 2024). Data extraction from figures was performed with the ImageJ 'Figure Calibration' plugin (Miller 2011, Schneider et al. 2012). Cold hardiness from second-year bareroot Douglas-fir seedlings grown in Olympia, WA, was determined using artificial freeze tests and calculation of the LT_{50} based on visual damage expression (Timmis et al. 1994). Daily minimum and maximum temperatures for the closest weather station were acquired from climate data online (NOAA 2022) from October 1 through May 1 and included three dormancy seasons (starting in October 1974, 1976, and 1977). For the two seed sources tested (table 1), elevation was estimated based on the coordinates of the collection site (USGS 2022). Seed sources were identified as high and low elevation, and both were tested during all three full dormancy seasons.

Table 1. Modeling Data

Seed source ID	No. of data points	Seed source lat. (°N)	Seed source long. (°W)	Seed source elevation (m)
High	29	46.11	122.54	630 (2,067 ft)
Low	24	46.93	123.81	100 (328 ft)

The data set consists of 53 data points from 2 seed sources, both grown at the same nursery site in Olympia, WA, (46.9° N, 123.08° W) over a series of 3 dormancy seasons in the 1970s (1974–1975; 1976–1977: 1977–1978).

Modeling

The model used in this project was modified from a grape (*Vitis* spp.) cold hardiness extension testing program (Ferguson et al. 2011, 2014). This model was selected because it is used for real-time predictions of cold hardiness for dozens of grape cultivars and only requires daily minimum and maximum temperature as the input variables. The model has reliably predicted grape bud cold hardiness across many cultivars over many years (Ferguson et al. 2014). Though grapes and conifers differ in many ways, the model has several applicable features for many species, such as the use of daily average temperature for cold hardiness prediction, testing with many years of climate data from a broad geographic range, biologically interpretable parameters, inclusion of chilling and forcing temperature accumulation requirements, and parameters specific to the acclimation and deacclimation periods of cold hardiness phenology. These aspects make the model a strong candidate for use in tree seedling operational decisions.

This cold hardiness model uses a set of biologically interpretable parameters for each seed source tested (table 2). Parameters specific to each seed source are determined using an automated model calibration process built into Cropbox: a declarative crop modeling framework (Yun and Kim 2023). To prevent overfitting, 70 percent of data points from each seed lot were randomly selected as a training dataset (used for calibration) and the remaining 30 percent were used as a testing dataset for model validation.

The general operation of the model is that chilling units are accumulated until the chilling requirement is met. Thereafter, forcing units are accumulated until the upper limit of cold hardiness is met or the end of the modeling

Table 2. Parameters and variables used in the cold hardiness model

Symbol	Description	Range
DD_c	Chilling degree-days	
DD_f	Forcing degree-days	
H_c	Cold hardiness	-40 to 0 °C (-40 to 32 °F)
$H_{c,ll}$	Lower limit cold hardiness temperature	-25 to -15 °C (-13 to 5 °F)
$H_{c,ul}$	Upper limit cold hardiness temperature	-5 to 0 °C (23 to 32 °F)
$H_{c,0}$	Initial cold hardiness value	-7 to 0 °C (19.4 to 32 °F)
$T_{th,a}$	Threshold temperature of acclimation	0 to 10 °C (32 to 50 °F)
$T_{th,d}$	Threshold temperature of deacclimation	0 to 15 °C (32 to 50 °F)
k_a	Acclimation rate	0 to 1
k_d	Deacclimation rate	0 to 1
R_f	Forcing requirement	100 to 500 DD_f
R_c	Chilling requirement	-500 to -100 DD_c

Adapted from Ferguson et al. (2011, 2014). Manually input range limits, based on biological assumptions, are included for model parameters.

period is reached, whichever occurs first (figure 1). A series of equations determines the daily change in cold hardiness based on daily temperature inputs (figure 2), which can estimate LT_{50} daily. Model performance was determined using goodness of fit metrics, which compare model predictions with observed LT_{50} values. The model's equations and assumptions are published in Stuke et al. (2024).

Results

The parameters used in the model (table 2) result in different responses for the different seed lots produced at the same time and location. Estimates for the high- and low-elevation seed lots have some notable differences (table 3). The parameters have easily interpretable meanings and can reveal characteristics about how different populations respond to certain climate conditions. For example, the high seed lot had a lower temperature threshold for deacclimation and a lower chilling requirement compared with the low seed lot (table 3). This difference suggests that the high seed lot is very sensitive to warming and may be more vulnerable to early deacclimation, which may create issues when producing this seed lot in warmer regions or in cases of early warming, especially if late frost occurs.

The two seed sources primarily differed in the shoulder seasons (fall and spring), with the low seed source acclimating and deacclimating later than the high seed source (figure 3). The model fits the general pattern of cold hardiness observational data, but in the 1976–1977 and 1977–1978 dormancy seasons, peak cold hardiness estimates did not achieve low enough LT_{50} values. This

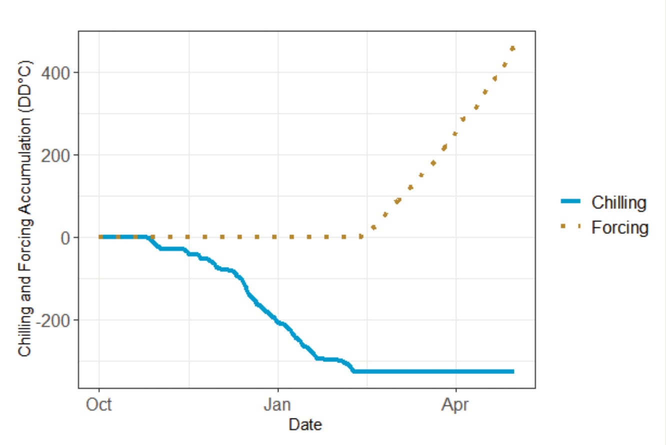

Figure 1. The model described in this paper operates by accumulating chilling during acclimation and forcing during deacclimation after a chilling requirement is met.

Table 3. Parameter estimates for high and low seed sources

Parameter	High	Low
$T_{th,a}$	7.3 °C (45 °F)	7.9 °C (46 °F)
$T_{th,d}$	**0.07 °C (32 °F)**	**1.3 °C (34 °F)**
R_c	**-338 DD_c**	**-788 DD_c**
R_f	173 DD_f	422 DD_f
$H_{c,ll}$	-24 °C (-11 °F)	-24 °C (-11 °F)
$H_{c,ul}$	-0.6 °C (33 °F)	-3.8 °C (25 °F)
$H_{c,0}$	-5.6 °C (22 °F)	-4.7 °C (24 °F)
k_a	0.7	0.5
k_d	0.09	0.1

Parameter estimates from Timmis et al. (1994) indicate phenological differences in the high and low seed sources. Biologically meaningful differences are bolded and include chilling requirement (R_c) and the temperature threshold for deaclimation ($T_{th,d}$). Parameters were determined during model training using 70 percent of datapoints for each seed source. Parameter definitions are listed in table 2. Chilling degree days are given in negative values.

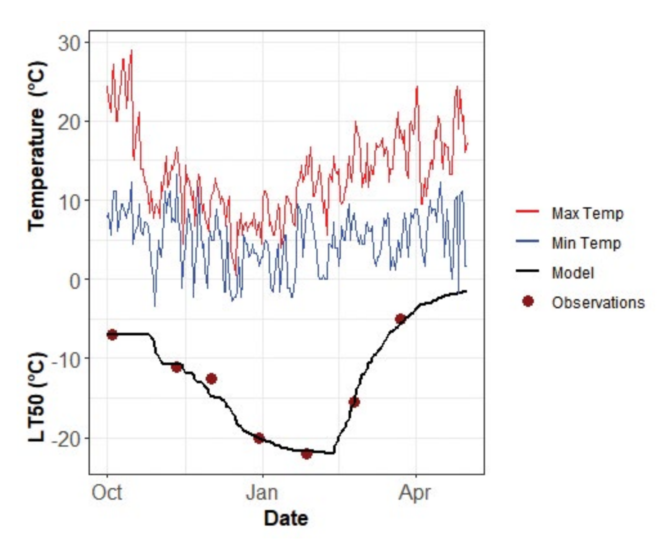

Figure 2. The model used here functions on daily temperature inputs and produces estimates of cold hardiness, which can be specific to populations based on parameter values selected during the model training process. The model operates on a daily time interval, so that estimates of cold hardiness can be updated after weather data from the previous day are available. This input method also allows the opportunity for predictions of future cold hardiness by using historical averages to project weather patterns.

result may be attributed to a minimum limit of -25 °C (-13 °F) assigned to $H_{c,ll}$ parameter fitting, which should be a consideration for adjustment in future model runs (Stuke et al. 2024).

Model residuals (figure 4) and goodness of fit statistics (table 4) demonstrate quantitatively how the model performed. For this dataset, the model had a good fit, with a slightly better fit for the low seed source than for the high seed source. This difference may be due to the low seed source having more data points, which may have improved the model calibration process. The regression of residuals shows that the model performed very close to the 1:1 line (figure 4) with a slope of 0.95, where a slope of 1.0 and complete overlap with the 1:1 line would indicate a perfect fit. Root-mean-square error (RMSE, the average difference between the model's predicted values and the actual values) ranges from 2.03 to 2.7 °C (35.66 to 36.86 °F), which demonstrates how accurate the model is on average. Modifying the parameter range for the lower limit of cold hardiness to include the low temperature LT_{50} in 1976 and 1977 may reduce the RMSE, since these are the largest error sources in the model fit.

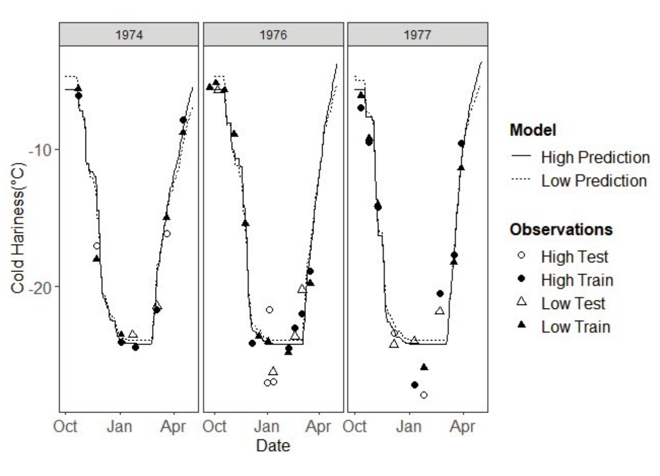

Figure 3. Model fits are shown here by lines, and observed cold hardiness is indicated by points. The difference between an observation and the modeled value at any timestep indicates a model residual, which can be used to calculate error. Training data are used for model calibration and testing data are used for model evaluation. Training data included 70 percent of data points and testing data included the remaining 30 percent. This separation reduces bias and the likelihood of overfitting.

Table 4. Model validation statistics for high and low seed sources

Statistic	High	Low	Combined
MAE	2.43	1.67	2.0
RMSE	2.7	2.03	2.35
d	0.91	0.97	0.95
n	7	9	16

Model validation statistics summarizing goodness of fit using model residuals for the Timmis et al. (1994) data demonstrate good model fits for both seed sources but a better fit for the low seed source. Seed sources were modeled separately, and statistics are provided for each seed source, including mean absolute error (MAE; the average of the absolute values of model residuals), root-mean-square error (RMSE; the magnitude of error), index of agreement (d; an indicator of model efficiency on a scale of -1 to 1), and number of data points (n) for each seed source.

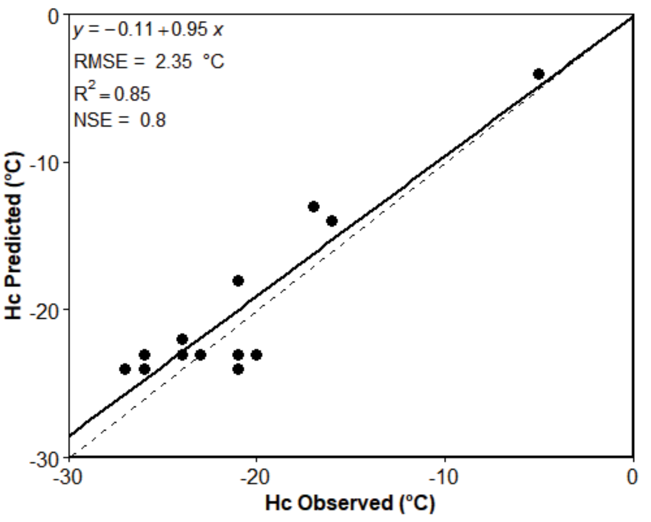

Figure 4. The relationship between observed and predicted cold hardiness values shows low error, indicating good model performance. Points show model residuals (observed and predicted value for each data point). Dotted lines show a 1:1 relationship between observations and predictions and the solid line shows the linear regression between observations and predictions. The linear regression equation, root-mean-square error (RMSE), R^2 (the coefficient of determination), and Nash–Sutcliffe model efficiency (NSE) for each scenario are listed in the plot. Only datapoints from the testing subset are shown (30 percent of all datapoints).

Discussion

Knowing the daily estimated cold hardiness for seedlings in production can be valuable in determining minimum requirements for frost protection. Though it is a critical component of cold damage prevention in the nursery, irrigation-based frost protection of bareroot and outdoor grown container stock can have many disadvantages. Irrigation-based frost protection works by applying water to seedlings during cold weather events to provide insulation in the form of ice and warming by latent heat through the exothermic reaction that occurs when water freezes (Rose and Haase 1996). The physical weight of ice can cause mechanical damage to seedlings, reducing overall yield. Application of irrigation can oversaturate soils creating standing water and exclude equipment from accessing bareroot seedlings, thereby delaying lifting (figure 5). Lifting can also be delayed in container crops that are frost protected if blocks remain frozen. Nutrients can be lost through leaching of soil or soilless media and directly from foliage. Irrigation equipment can be damaged if pipes freeze during frost protection (figure 5). Additionally, frost protection can reduce chilling accumulation if seedling temperature is not kept below the threshold of physiologically active chilling temperatures. Though knowing cold hardiness status is key to making frost protection decisions, accurate temperature monitoring and site-specific weather predictions across nursery zones are critical.

In addition to the daily estimated LT_{50}, the calibrated model can be used to characterize and rank different plant populations by their sensitivity to specific weather conditions. For example, a comparison between chilling requirements and deacclimation rates can be used to determine which populations are more likely to deacclimate earlier during warming events (table 3). This knowledge can be used to prioritize interventions and select appropriate populations for reforestation, especially in cases of assisted migration. Knowing the status of chilling requirement in relation to accumulated chilling can also be helpful in determining if additional storage is required to artificially induce hardening (Omi et al. 1991).

This model currently runs on calendar date and does not include a photoperiod component. For Douglas-fir seedlings that do not experience photoperiod manipulation (i.e., blackout or artificial lighting), natural daylength is minimally impactful on cold hardiness acclimation and deacclimation (Stuke et al. 2024). For nursery operations using blackout to induce budset, consideration of when to start the modeling period is important. The rapid change of photoperiod that blackout induces can trigger a stress response in seedlings that alters natural phenology and may have unique cellular and physiological consequences (Wallin et al. 2017). The impact of blackout on cold hardiness phenology is an area that requires more research to adequately model.

Seedling production and reforestation is critical to establishing forests that will grow into the future. Fargione et al. (2021) estimated that the economics to establish 26 million hectares (64.25 million acres) in the contiguous United States vary widely but could be $33 billion or higher during the next 15 years, depending on planting targets and capacities (Fargione et al. 2021). The REPLANT Act further demonstrates investment in reforestation through the allocation of $123 million in Federal funds annually (Stabenow 2021). If phenological issues affect seedling survival on even a fraction of reforested acreage, large costs will occur. The impact of cold damage on seedlings is likely underestimated because of the delay in expression of visual damage. Cold damage

Figure 5. Ice accumulates over bareroot seedlings due to irrigation-based frost protection (left). Though this practice is necessary to protect vulnerable seedlings, it can have many negative impacts as well, such as ice formation on irrigation equipment (right). Accurate estimation of cold hardiness can help in frost protection decision making. Photos courtesy of Washington Department of Natural Resources, Webster Nursery, Olympia, WA.

decreases seedling quality and increases disease even in nonlethal cases (Reich and Kamp 1993).

As the demands of reforestation and assisted migration place extra pressure on seedling production systems and forest regeneration, and climate change creates atypical weather patterns and extremes, understanding and predicting seedling responses to unprecedented seasonal conditions will be more important than ever. This model integrates seedling phenology and physiology in a seedling production context to guide future planting and population selection for reforestation.

Conclusion

Though the model described in this article is not yet ready for nursery and reforestation operations without parameterization for specific populations, it provides the foundation for a tool that can be further developed with additional data. Modern modeling resources cannot replace intuitive and experienced growers and foresters, but they can be leveraged to assist in decision making and risk prevention. These tools will be critical for nursery production and forest regeneration as novel difficulties and unprecedented weather extremes increase in frequency due to climate change. Building strong collaborations among nurseries, foresters, and researchers will be crucial to overcome future demands and challenges.

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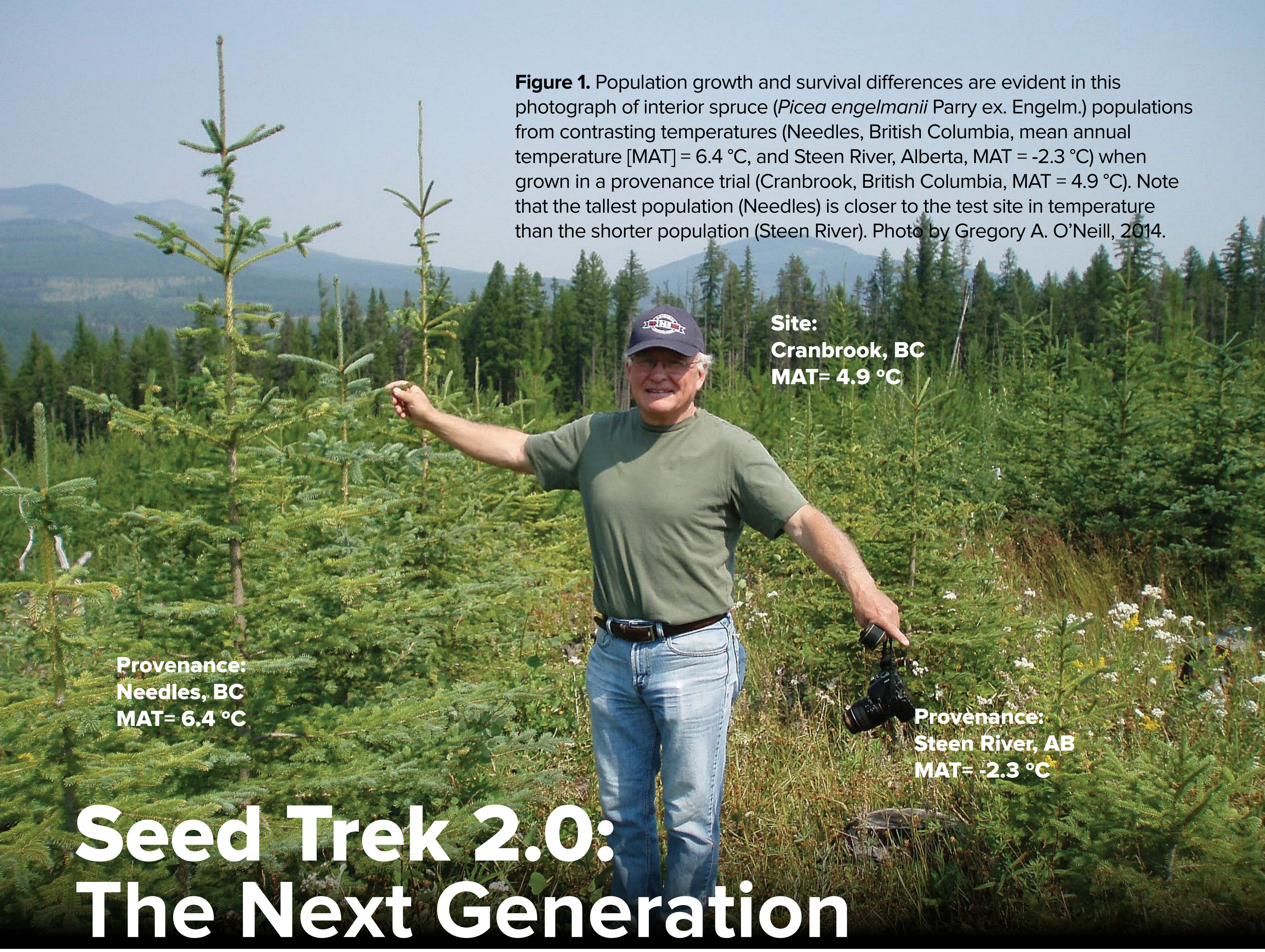

Figure 1. Population growth and survival differences are evident in this photograph of interior spruce (*Picea engelmanii* Parry ex. Engelm.) populations from contrasting temperatures (Needles, British Columbia, mean annual temperature [MAT] = 6.4 °C, and Steen River, Alberta, MAT = -2.3 °C) when grown in a provenance trial (Cranbrook, British Columbia, MAT = 4.9 °C). Note that the tallest population (Needles) is closer to the test site in temperature than the shorter population (Steen River). Photo by Gregory A. O'Neill, 2014.

Seed Trek 2.0: The Next Generation of Seed-Transfer Systems

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Abstract

The intention of this article is to make a case for foresters to "boldly go where no forester has gone before," thereby deconstructing the 100-year-old paradigm of planting with local seed sources (Thrupp 1927). Using the concepts of safe seed-transfer distance and migration distance, foresters can incorporate assisted migration into a climate-based seed-transfer system that matches a seed lot's historical climate with the planting site's future climate. Methods proposed here are low risk, low cost, easily implemented, transparent, and can help ensure that plantations are established with seed sources that will be well-adapted throughout the life of the plantation. This paper was presented at Growing Pains: Scaling up the Reforestation Pipeline—Joint Annual Meeting of the Western Forest and Conservation Nursery Association and the Forest Nursery Association of British Columbia (Portland, OR, September 19–21, 2023).

Historical Seed-Sourcing Methods

In the days before replanting seedlings after harvest was common practice in North America, the forest immediately surrounding a logged area or the seedbed laying dormant in the soil was relied upon to naturally provide the next generation of trees. In addition to being the cheapest option for reforestation, reliance on natural regeneration also built on the assumption that "local is best," i.e., the trees growing in a particular area are best adapted to the climate, pests, and soils of that area.

As the scale of industrial logging accelerated throughout the 20th century, foresters were forced to acknowledge that their timber base was ultimately finite, and that rotational forestry and sustained yield harvest were required to manage timber resources in the long term. This recognition led to increasing criticism of the slow and inconsistent regeneration provided by nature and a shift to plantation forestry. Planting seedlings after harvest is now ubiquitous throughout the United States and Canada and is legally required in many jurisdictions.

These widespread replanting programs necessitated efficient seed-collection programs, which ultimately led to a new question in reforestation: "If local is best, then how 'local' is local?" For many important timber species, seed zones were established to ensure that seedlings would be similarly adapted to the areas where they were planted. Seed-zone boundaries were often drawn along major geographic barriers or latitudes to group regions based on similar temperature and precipitation regimes. This system is referred to as geographic-based seed transfer, whereby the physical location of seed collection dictates the broader area in which it can be replanted.

To further inform and refine these seed zones, forestry researchers established provenance tests in which seed sources from various locations are planted side by side in recently harvested areas (figure 1). With many of these experiments replicated in multiple environments across or even outside a species' range, growth and survival data can be used to identify regions where trees will grow similarly, how far seed can be moved before trees start to become maladapted (figure 2), and whether certain regions produce particularly vigorous trees.

Climate Change Impacts on Forests

Numerous reports have already linked large-scale forest disturbance with climate change during the 20th and 21st centuries (Seidl et al. 2017). Collectively, these reports indicate that climate change is already impacting forests (as opposed to something that might impact forests in the future). The mountain pine beetle epidemic that devastated lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests of western Canada (Sambaraju et al. 2012), powdery mildew infection of oaks (*Quercus* spp.) in Europe (Marçais and Desprez-Loustau 2014), mortality of savanna parkland tree species in the African Sahel (Maranz 2009), and declines of aspen (*Populus* spp.) in western North America (Worrall et al. 2013), yellow cypress (*Callitropsis nootkatensis* [D. Don] Oerst. Ex D.P. Little) in Alaska (Hennon et al. 2006), and Scots pine (*Pinus sylvestris* L.) in Switzerland (Rebetez and Dobbertin 2004) are just a handful of species that have been impacted, at least in part, by climate change.

Provenance tests have emerged serendipitously as climate change laboratories (Carter 1996, Mátyás 1994). By testing populations from a range of source climates across a range of plantation climates, provenance tests show the real, on-the-ground impacts of climate change and seed transfer on tree growth and survival (figure 2). When these tests are conducted for many years, they sample the range of climatic extremes present at a plantation while integrating

Figure 2. Climate change impacts on tree growth and form can be assessed in provenance trials when the same populations are planted in differing climates. In these photographs, the same lodgepole pine (*Pinus contorta* Douglas ex Loudon) population from a cold northern British Columbia provenance was planted at a site with the same mean annual temperature (MAT) as its source (-1.3 °C) (left) and at a site with a MAT of 2.9 °C (i.e., 4.2 °C warmer MAT than the provenance climate) (right). Growth and form are excellent when populations are planted in a climate similar to that of their origin but are poor when planted in climates considerably warmer than that of the population origin. Photos by Gregory A. O'Neill, 2010.

diverse effects of biotic and abiotic stressors. Provenance tests reveal that, in the short term, a small amount of climate change may benefit growth rates. In the long term, however, productivity of naturally regenerated forests or plantations established with local seed sources is expected to decline substantially. For example, in central British Columbia, productivity of natural stands of lodgepole pine, the Province's primary lumber species, is expected to decline 30 to 60 percent (relative to 1975 productivity levels) by 2085 due to climate change (O'Neill et al. 2008).

Climate is changing too quickly for populations to follow their optimal climate through natural migration (Ash et al. 2017, Lenoir et al. 2020) or for natural selection to allow them to thrive under new climates (Davis and Shaw 2001, Rehfeldt et al. 2002) (figure 3). This rapid change creates an evolutionary lag, in which trees' annual life cycles become desynchronized from seasonal environmental cues and the pests they have evolved to tolerate. Together, these factors can contribute to reduced tree and stand productivity and increased pest damage. Many large shifts in climate have occurred in the geologic past, but forests survived. The unprecedented rate of current warming, however, requires innovative forest management strategies to avoid large-scale disturbance. Fortunately, foresters are positioned to respond proactively to climate change.

Figure 3. The rate of climate change is vastly outpacing the rate at which trees can migrate from one generation to the next, thereby creating an evolutionary lag that predisposes trees to poor growth and health. In this comic sketch, the tree's "climate home" is speeding northward much faster than the tree can keep pace. Image courtesy of Peter Strother, artist.

Rationale for Assisted Migration

To the extent that tree populations are locally adapted to biotic or abiotic disturbance agents, it may be possible to mitigate future disturbances through forestry-assisted migration—the establishment of plantations with seed sources from climates slightly warmer than that of the plantation. Forestry-assisted migration, as discussed in North America (Pedlar et al. 2012), includes both assisted population migration (movement of populations within the species' current natural distribution) and assisted range expansion (movement of populations slightly outside the species' current natural distribution). Exotic translocation (movement of populations to locations far outside the species' natural distribution where they are not expected to establish naturally in the foreseeable future) is not commonly considered within the rubric of forestry-assisted migration (Ste-Marie et al. 2011).

Plant biologists have migrated plant hardiness zones to facilitate selection of horticultural species and cultivars appropriate for a changed climate (McKenney et al. 2014) (figure 4). In agriculture, retrospective analyses of productivity and crop area for maize, wheat, and rice—three of the world's most important agricultural crops—show a poleward shift in their use, a response thought to have substantially moderated climate change impacts to these crops (Sloat et al. 2020). Forestry is usually a longer term proposition than horticulture or agriculture, and fewer interventions are available to protect forest plantations compared with horticulture plantings. Thus, a more considered approach to assisted migration is warranted in forestry.

Safe Seed-Transfer Distance and Migration Distance

When discussing forestry-assisted migration, two key concepts must be distinguished—safe seed-transfer distance (SSTD, a.k.a. critical seed-transfer distance) (Ukrainetz et al. 2011) and migration distance (O'Neill et al. 2017). SSTDs are the climate or geographic distances seed may be moved to provide some operational flexibility in the seed source selection process without displaying unacceptable declines in productivity. Migration distance is the climatic difference between a seed source and a plantation that seed should be migrated to optimize adaptation through the life of a plantation (Ukrainetz et al. 2011).

SSTDs are derived from trends relating population transfer distance to population growth, survival, or health traits using provenance test data (Raymond and Lindgren 1990) and are used to help determine seed-zone sizes and seed-transfer limits (figure 5). As the number of planted tree species vastly exceeds the number of species with

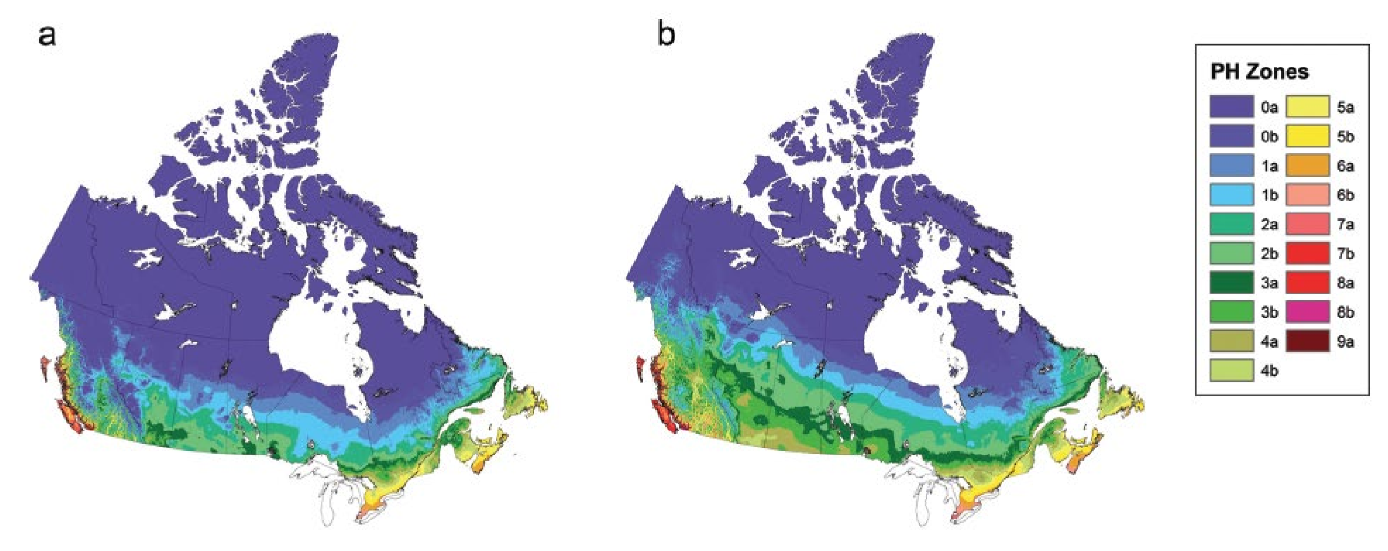

Figure 4. Canadian plant hardiness (PH) zone maps for 1931–1960 (a) and 1981–2010 (b) show substantial northward movement of plant hardiness zones. Source: McKenney et al. (2014).

good, long-term provenance tests, seed-transfer systems are often developed using SSTD estimates inferred from other species or from local practitioners. Therefore, in the absence of provenance test data, SSTDs for climatic variables can be inferred from the maximum climatic range present within existing geographic seed zones, assuming that maladaptation is rare for plantations within those zones. Climatic SSTDs used in British Columbia's climate-based seed-transfer (CBST) system are approximately +/- 3 °C mean annual temperature, +/- 4 °C mean coldest month temperature, +/- 3 °C continentality (difference between the temperatures of the warmest and coldest months), and +/- 40 percent of mean annual precipitation or mean summer precipitation, although these values differ slightly among species. Switching from a geographic-based seed-transfer system to a CBST system and incorporating assisted migration into a seed-transfer system does not alter maximum SSTDs. Consequently, the establishment of new provenance tests is not necessary when converting to a climate-based system if existing SSTDs in geographic-based systems result in acceptable plantation growth and health.

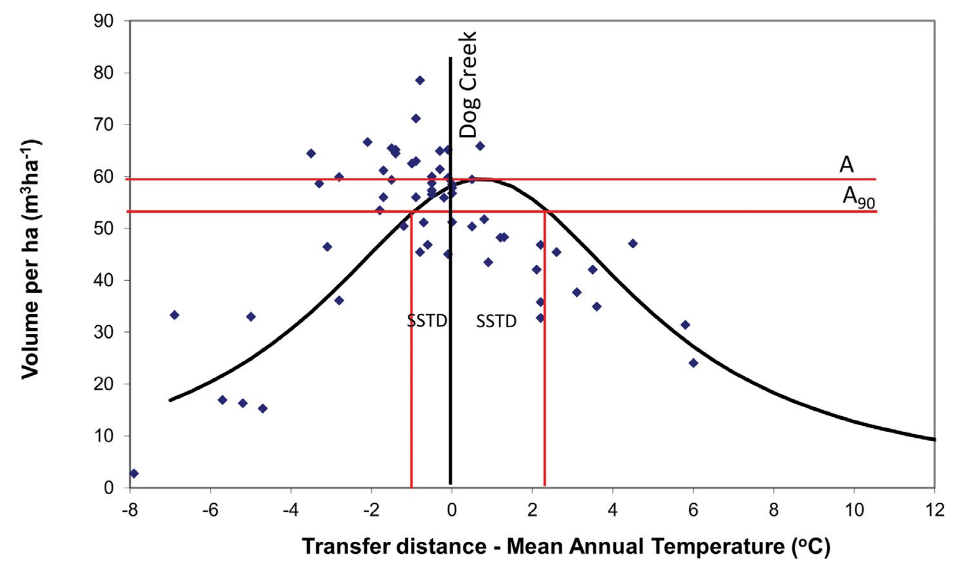

Figure 5. Calculation of safe seed-transfer distance (SSTD) is illustrated in this transfer function from a lodgepole pine (*Pinus contorta* Douglas ex Loudon) provenance trial at Dog Creek, British Columbia. A peaked function is fitted to relate population mean growth (volume per ha) as a function of population climate-transfer distance (the site climate minus the population climate; mean annual temperature transfer in this figure). Upper and lower SSTDs are obtained by interpreting the transfer distance at 90 percent of the maximum fitted value.

While evidence mounts in support of forestry-assisted migration (Nigh 2014, Pedlar et al. 2012, Williams and Dumroese 2013), there has been little discussion regarding migration distance. Migration distances that are too long can predispose plantations to frost damage or new pests, whereas migration distances that are too short may be ineffective at helping plantations escape drought and heat damage in the hot and dry parts of planted species' ranges (Mátyás 2010). Given the relative stability of climate in the millennium prior to the Anthropocene and the rapid rate of anthropogenic climate change, it may be assumed that populations best adapted to the present climate of a plantation are more likely to be found where a plantation's current climate existed a century ago, rather than locally. Even if populations selected for reforestation are optimally adapted to the present climate of a plantation they will likely be substantially maladapted at harvest. Furthermore, populations optimally adapted to the climate at harvest may not perform well during establishment when trees are most sensitive. Weighing the risk of maladaptation during seedling establishment versus the risk of maladaptation as a stand approaches maturity, British Columbia elected to use a migration distance that matches seed source climate during the period 1931 to 1960 (i.e., prior to significant Anthropogenic climate change) with the climate expected for the plantation at a quarter of the rotation age (approximately 15 years after planting in British Columbia) (O'Neill et al. 2017, Ukrainetz et al. 2011) (figure 6).

Devising a Climate-Based Seed-Transfer System

While fixed-zone, geographic-based seed-transfer systems around the world are straightforward (seed must stay within its zone of origin), they do not lend themselves to assisted migration, and SSTDs based on geography may over- or under-transfer seed, as geography is only a surrogate for climatic adaptation of plants. Therefore, converting to a climate-based system could facilitate adoption of assisted population and assisted range expansion and capitalizes upon widely available climate models (Wang et al. 2016). In CBST, seed sources suitable for use at a plantation are identified by first predicting the climate of the plantation in the future (e.g., 15 years) based on a specified migration distance. For all the climate variables determined to be relevant for adaptation, seed sources that are within the SSTD above or below this new climate can be examined (figure 7). If a seed source is within the SSTD for all variables, it can be used for reforestation. This system can also be used to determine how broadly a particular seed source can be planted. Including a minimum of four SSTD variables is recommended, with at least one being a precipitation-related variable.

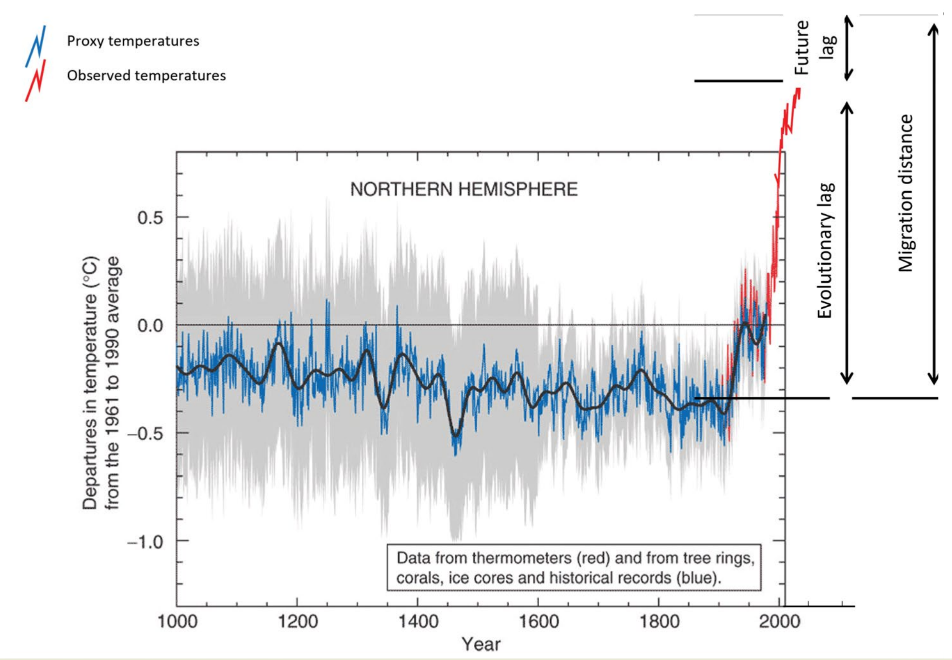

Figure 6. Migration distance is the climate distance seed is moved to account for climate change during the Anthropocene (evolutionary lag) and during the first fourth of a plantation's lifespan (future lag). Here, migration distance is illustrated for mean annual temperature (MAT) in this line chart of MAT (expressed as the annual deviation from the 1961 to 1990 MAT) for the Northern Hemisphere over the 20th century. Evolutionary lag is the difference in MAT between current and historical MAT (where historical is the most recent period when adaptation lag is presumed to be least). Future lag is the difference in MAT between current and future MAT. Migration distances are calculated for each SSTD variable. Climate deviations are from Houghton et al. (2001).

Additional Criteria

Provenance tests generally consist of a handful of plantations located within the species' natural distribution, so they are not useful in determining the climatic limits of a species' range, now or in the future. Consequently, prior to choosing a seed source, species' future climate niche distribution models are needed to confirm that a plantation's future climate is within the intended species' fundamental future climate niche, thus ensuring the intended species is appropriate for current and future climates at the plantation.

Species' future climatic niche distributions are particularly important when planting beyond the species' cold limit (to ensure that the species' climate niche will include the plantation shortly after planting) or at the trailing (warm) edge (to ensure that the species' climate niche will continue to include the plantation throughout most of the rotation). Species selection for future climates must also continue to adhere to species' edaphic (soil nutrient and moisture) requirements (Mackenzie and Mahony 2021).

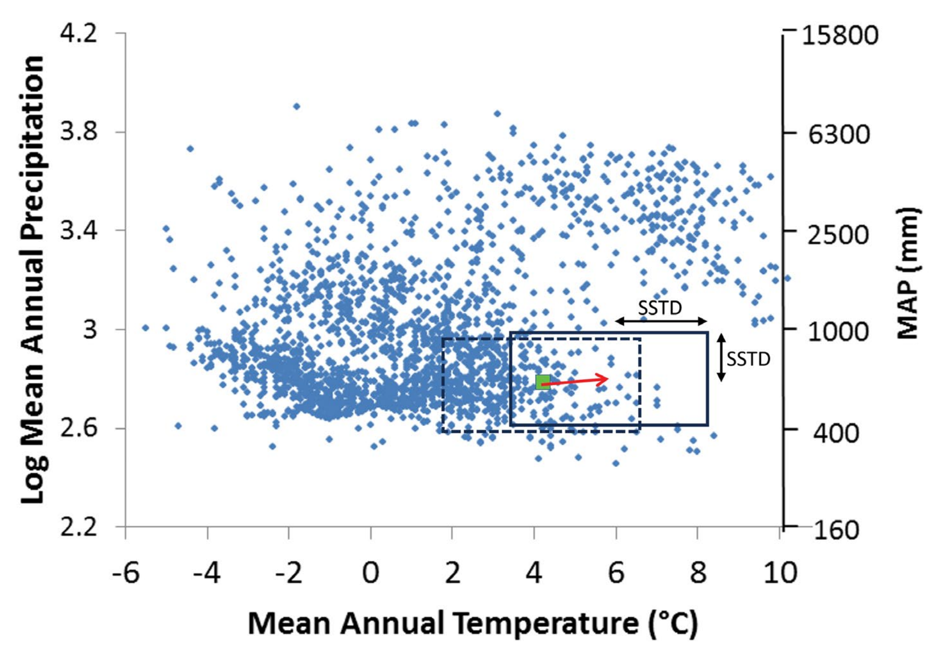

Figure 7. This two-climate variable schematic illustration shows the climates where seed can be obtained for a reforestation site using a climate-based seed-transfer (CBST) system. The migration distance (red arrow) is added to the climate of the reforestation site (green square) to identify the climate of the focal point at the head of the arrow. The seed procurement area (solid black box), where seed suitable for a reforestation site can be obtained, is defined by the safe seed-transfer distance (SSTD) on either side of the focal point. Without assisted migration, the seed procurement area is shown as the dashed black box centered on the plantation climate.

Risks

Assisted migration implemented without a CBST tool in place can pose risks. Seed sources transferred beyond their safe transfer distances can fail due to maladaptation. Alternatively, species introduced intentionally (e.g., cane toads in Australia and kudzu in the United States) or unintentionally (e.g., spotted knapweed, zebra mussels, blister rust, and Dutch elm disease in North America) (https://www.invasivespeciescentre.ca/) can become invasive, wreaking havoc on the recipient ecosystem by disrupting or displacing local species, particularly when an introduced species reproduces readily and escapes controls imposed by other organisms in its native habitat. The risk of a species failing or becoming invasive is negligible in forestry-assisted migration when a CBST system is in place to constrain the procurement of seed sources to within common SSTDs and migration distances. Likewise, the risk of acquiring a hitchhiking pest that becomes invasive is also minimal in forestry-assisted migration because climate migration distances used in CBST are associated with short geographic transfer distances, usually in the order of 200 to 300 m upward elevation transfer or 200 to 400 km poleward transfer, and do not require transcontinental or intercontinental transfers that are commonly associated with species invasions (Mueller and Hellmann 2008). Considering risks associated with species invasion, abundant provenance testing confirms that restoring seed sources into their historical climates of last century entails considerably less risk than planting local seed sources that will experience climates 4 °C warmer than their historical climate by the time of harvest.

Other Climate Change Adaptation Strategies

Assisted migration as a climate change adaptation strategy in forestry is low cost (seed from a location slightly warmer than the plantation compared with local seed are generally comparable in cost), low risk, easily implemented, and transparent. However, other valuable climate change adaptation strategies also warrant consideration. Genetic diversification may also mitigate climate change impacts to forests by buffering some of the uncertainty in climate and pest predictions. Planting multiple (climatically appropriate) seed sources from slightly different climates in each plantation (Looney et al. 2023) or employing a wider range of reforestation species (Mason et al. 2012) could help ensure that a harvestable crop is achieved should extreme climate events or pest outbreaks result in significant mortality.

In genetic-selection programs, selecting or breeding for pest resistance or testing and selecting for wide climate tolerance are proactive strategies to address potential pest and climate disturbances. Greater use of silviculture methods that provide more overstory and structural diversity (Gustafson et al. 2020), careful attention to matching stock type to plantation environment (Christiansen et al. 2023), careful microsite planting, and use of nurse plants (Carbajal-Navarro et al. 2019) can also reduce mortality risks at establishment.

Next Steps

As assisted migration shifts seed procurement to slightly warmer climates, some operators may find that suitable seed sources are unavailable locally (O'Neill and Gómez-Pineda 2021), forcing them to search for seed lots in neighboring jurisdictions. Seed lot owners may be unwilling to sell seed if they also have concerns regarding obtaining seed from their neighbors. To reverse this cycle of stagnation, seed lot databases from across jurisdictions should be shared, to provide wider markets for seed collectors and producers, an economy of scale for seed marketing, and, importantly, facilitation of the use of nonlocal seed lot databases, thereby assisting the migration of climatically suitable seed sources (Williams and Dumroese 2013). As stated by Erickson and Halford (2020), "A [common] seed zone framework greatly facilitates seed use planning and creates opportunities for sharing and exchange of plant material among landowners and seed banking programs and partners." By expanding the scale, seed demand can be aggregated, supporting investments in expanded databases and a willingness to supply a wider market for the next generation of forests.

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Exciting Updates to the National Reforestation and Restoration Directory and the Addition of a New Marketplace

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Abstract

The Reforestation, Nurseries, and Genetic Resources (RNGR) program is a leading source of technical information for nurseries and land managers who are engaged in tree propagation and planting, as well as native plant restoration and conservation. One popular RNGR resource is its online national directory of forest and conservation nurseries. The current increased interest in tree planting efforts and production of restoration plant materials signaled a need to improve the offerings and functionality of the directory. The nursery database has been updated to meet the growing demands for information, products, and services related to the entire reforestation and restoration supply chain, from seed to outplanting. Additionally, a marketplace has been added to provide a location for communitywide classified ads for available and needed supplies and services. This paper was presented at Growing Pains: Scaling up the Reforestation Pipeline—Joint Annual Meeting of the Western Forest and Conservation Nursery Association and the Forest Nursery Association of British Columbia (Portland, OR, September 19–21, 2023).

The Reforestation, Nurseries, and Genetic Resources Online Platform

The Reforestation, Nurseries, and Genetic Resources (RNGR) program of the U.S. Department of Agriculture's Forest Service, in collaboration with Southern Regional Extension Forestry, hosts a website (https://rngr.net/) that provides up-to-date technical information for nurseries and land managers to improve the production and planting of trees and other native plants for reforestation, restoration, and conservation. In addition to sharing publications, webinars, and other resources, the website has hosted a nursery and seed directory that helps users connect with more than 1,100 businesses across the United States and Canada that provide seed supplies and nursery propagation services.

In recent years, it has become increasingly clear that landscapes across the globe need increased reforestation and restoration plant materials to mitigate disturbances, respond to climate change, and provide ecosystem services. To support this, efforts are underway to increase tree planting and native species restoration in the United States and Canada. These efforts will require a transformation across the supply chain in both the public and private sectors. As customers in a greater number of geographies seek to reforest and restore tree cover, it is critical to increase information flow and ensure that it is easily accessible. Thus, the RNGR nursery and seed directory has been expanded to provide a more informative aggregation platform where clients can quickly find businesses specialized in supplies, equipment, and services to support seed collection, nursery propagation, outplanting, and other aspects of reforestation and restoration. The updated platform expands on the information available for each directory listing, broadens the scope to include supporting businesses, and adds the "Branch Out Marketplace" where participants can share or find available products and services.

The new RNGR platform will continue to host the nursery and seed directory but will have an expanded scope and search functionality. The expanded directory is intended to be a comprehensive tool that incorporates all businesses providing relevant services or equipment for all aspects of plant production and outplanting, such as seed collection,

RNGR REFORESTATION, NURSERIES, & GENETIC RESOURCES

Search

Home | Directory & Marketplace | Publications | Resources | Seed Lab | Tribal | Tropical | About | Admin

Home → Directory & Marketplace → Directory

Directory

Marketplace

NATIONAL REFORESTATION & RESTORATION DIRECTORY

The directory is your online source for finding businesses that support the propagation of forest and native plant materials in the US and Canada. You can search the directory by name, state, product, or business type.

SEARCH THE DIRECTORY

Offering Category: Products or Services: Operating Area:

Search

Add a new directory entry

RNGR.N… EFFORT… XTENSION FORESTRY AND IS A COLLOBORATIVE

Southern Regional Extension Forestry

RNGR REFORESTATION, NURSERIES, & GENETIC RESOURCES

Search

Home | Directory & Marketplace | Publications | Resources | Seed Lab | Tribal | Tropical | About | Admin

Home → Directory & Marketplace → Directory

Directory

Marketplace

NATIONAL REFORESTATION & RESTORATION DIRECTORY

The directory is your online source for finding businesses that support the propagation of forest and native plant materials in the US and Canada. You can search the directory by name, state, product, or business type.

SEARCH THE DIRECTORY

Offering Category: Nursery
Products or Services: Services
Operating Area: Georgia

Search

Add a new directory entry

Search Results

23 results matched your search criteria: **State** = GA

- ATL Urban Farms
- ATS Partners LLC
- ArborGen - Bellville SuperTree Nursery
- ArborGen - Georgia SuperTree Nursery
- Bell Brothers Inc
- Carters Nursery | Bowater Forest Products Division
- Clifton Forest & Appraisal Service Inc
- Eco Gardens
- Flint River Nursery
- Garden Delights LLC | Lazy K Nursery Inc
- IFCO Seedlings
- International Forest Company
- John Deere Landscapes
- Meeks' Farm & Nursery Inc
- Native Forest Nursery
- Nearly Native Nursery
- Plum Creek Timber Company - Jesup Nursery
- Randy's Perennials & Water Gardens
- Rock Spring Restorations
- Rutland Forest Nursery
- Southern Roots Tree Nursery
- The Testing Nursery
- Transplant Nursery

Nursery type

☐ **Federal** *federal government except Bureau of Indian Affairs*
☐ **Forest Industry** *company engaged in forestry*
☐ **Not-for-Profit** *non-profit, non-business entities*
☐ **Private** *not Government*
☐ **State** *state/province/insular/university operation*
☐ **Tribal** *American Indian/First Nation including Bureau of Indian Affairs*

Production capacity

○ Less than 100,000
○ 100,000 – 1,000,000
○ 1,000,000 – 5,000,000
○ More than 5,000,000

RNGR.NET IS SPONSORED BY THE USDA FOREST SERVICE AND SOUTHERN REGIONAL EXTENSION FORESTRY AND IS A COLLOBORATIVE EFFORT BETWEEN THESE TWO AGENCIES.

Southern Regional Extension Forestry

Figure 1. The updated Reforestation and Restoration Directory (https://rngr.net/) has improved search functionality, including intuitive search boxes to facilitate keyword searches by project area, product, or service (top). The search returns listings and a map of businesses that meet the search terms (left).

processing, and storage; nursery propagation and storage; site preparation and outplanting; and postplanting services (figure 1). Previously, the directory provided basic contact information; now, participating businesses can provide a more detailed description of their services and products, thereby facilitating keyword searches. In a future phase, the RNGR program will engage with the urban forestry community to understand how it might be useful to urban greening efforts. Currently, however, the directory and marketplace focus only on native species.

In addition to the updated and improved directory, the Branch Out Marketplace will further support reforestation and restoration efforts (figure 2). Similar to existing and familiar platforms such as Craigslist and Facebook Marketplace, Branch Out will create a community of users that offer time-limited goods and services. For example, nurseries could advertise excess stock, planting crews could seek new contracts for a given location, and used equipment could be sold, traded, or given away. Listings in the marketplace will be free but limited to 90 days. This new resource is intended to increase direct communication among restoration, reforestation, and conservation businesses and clients, and contribute to greater supply chain efficiency.

Join the Reforestation, Nurseries, and Genetic Resources Community

The updated and expanded directory and new marketplace require your direct participation to provide their intended benefit! If you are new to the industry or were not previously listed in the directory, you can easily add your business and start using the RNGR platform at https://rngr.net/participate. You will be prompted to enter information about your business and the products or services it provides for forestry, conservation, and/or restoration. RNGR staff will verify the data provided by each business, thereby ensuring that the directory is accurate and up to date. For those businesses already listed in the directory, you will need to update your business listing with more detailed information so that your business can be keyword searchable.

BRANCH OUT MARKETPLACE

The marketplace is a resource for sharing and finding currently available products and services. This resource helps to match existing inventory of seed, seedlings, supplies, equipment, labor with customers. Register here to add a new listing or to search the listings.

Storage

New posting 3
Southeast
Expires in 25 days
Interdum et malesuada fames ac ante ipsum primis in faucibus. Nullam consequat ultricies tristique. Fusce finibus erat eu turpis ullamcorper semper. Vivamus volutpat elementum augue ut facilisis. Praesent feugiat, ex eu efficitur dignissim,

Deployment

Seed Deployment services available
Expires in 28 days
For the next 90 days only!

Collection training

New posting
Expires in 55 days
Interdum et malesuada fames ac ante ipsum primis in faucibus. Nullam consequat ultricies tristique. Fusce finibus erat eu turpis ullamcorper semper. Vivamus volutpat elementum augue ut facilisis. Praesent feugiat, ex eu efficitur dignissim, odio velit elementum tortor, quis

Collection training

Detail Test 22
Midwest
Expires in 68 days
Sold as is.
No refunds

-- FIN --

Disclaimer: *Inclusion of your business information on this website is not an endorsement or recommendation of a specific supplier, commercial product or service, trademark, or otherwise.*

Figure 2. The new Branch Out Marketplace offers a platform where reforestation and restoration businesses can offer or seek available time-limited products and services.

All businesses in the directory will be able to post time-limited classified ads in the Branch Out Marketplace by entering specific information about the product or service offered. Thus, potential consumers can best match their needs. For example, sellers of nursery overstock will be asked to provide information about the seed source to enable clients to make informed decisions.

Growing Forward

Increased risks associated with extreme weather events, international and national tree planting commitments, and a growing interest in carbon offset markets are driving an increase in demand for tree planting and native plant restoration across the United States and Canada. Uncertain market demand has limited investment in critical nodes along the reforestation and restoration supply chain, resulting in some areas with insufficient or poor infrastructure, a dearth of skilled labor, and insufficient access to funding for capital improvements. Amid these growing pains and increasing demands, the updated RNGR directory and marketplace helps to remove the guesswork by creating a place for businesses to connect with clients. Please join this endeavor and contribute to its success. This is version 1.0—anticipate minor issues and be patient as improvements are made. Opportunities to improve will arise, and your input and feedback are encouraged and welcome as this platform evolves. Finally, remember that the RNGR website also hosts numerous other resources related to seedling production and outplanting, including publications, webinars, current event listings, and job and educational opportunities.

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Upcoming Nursery Conferences and Meetings

2024 Joint Annual Meeting: Southern and Northeastern Forest and Conservation Nursery Associations

July 22–25, Little Rock, AR

https://westernforestry.org/upcoming-conferences/2024-joint-annual-meeting-southern-and-northeastern-forest-and-conservation-nursery-associations

2024 ICSGA & WFCNA Western Nursery Meeting

September 4–5, Wenatchee, WA

https://westernforestry.org/upcoming-conferences/icsga-wfcna-western-nursery-meeting

2024 Intertribal Nursery Council Conference

September 10–12, Grande Ronde, OR

https://westernforestry.org/upcoming-conferences/2024-intertribal-nursery-council-conference

Forest Nursery Association of British Columbia Conference

September 11–13, Vernon, BC

https://www.fnabc.com/copy-of-2022-fnabc-agm

Hawai‘i Native Plant Growers’ Meeting

February 5–6, 2025, Big Island, Hawai‘i

https://westernforestry.org/upcoming-conferences/hawai%ca%bbi-native-plant-growers-meeting