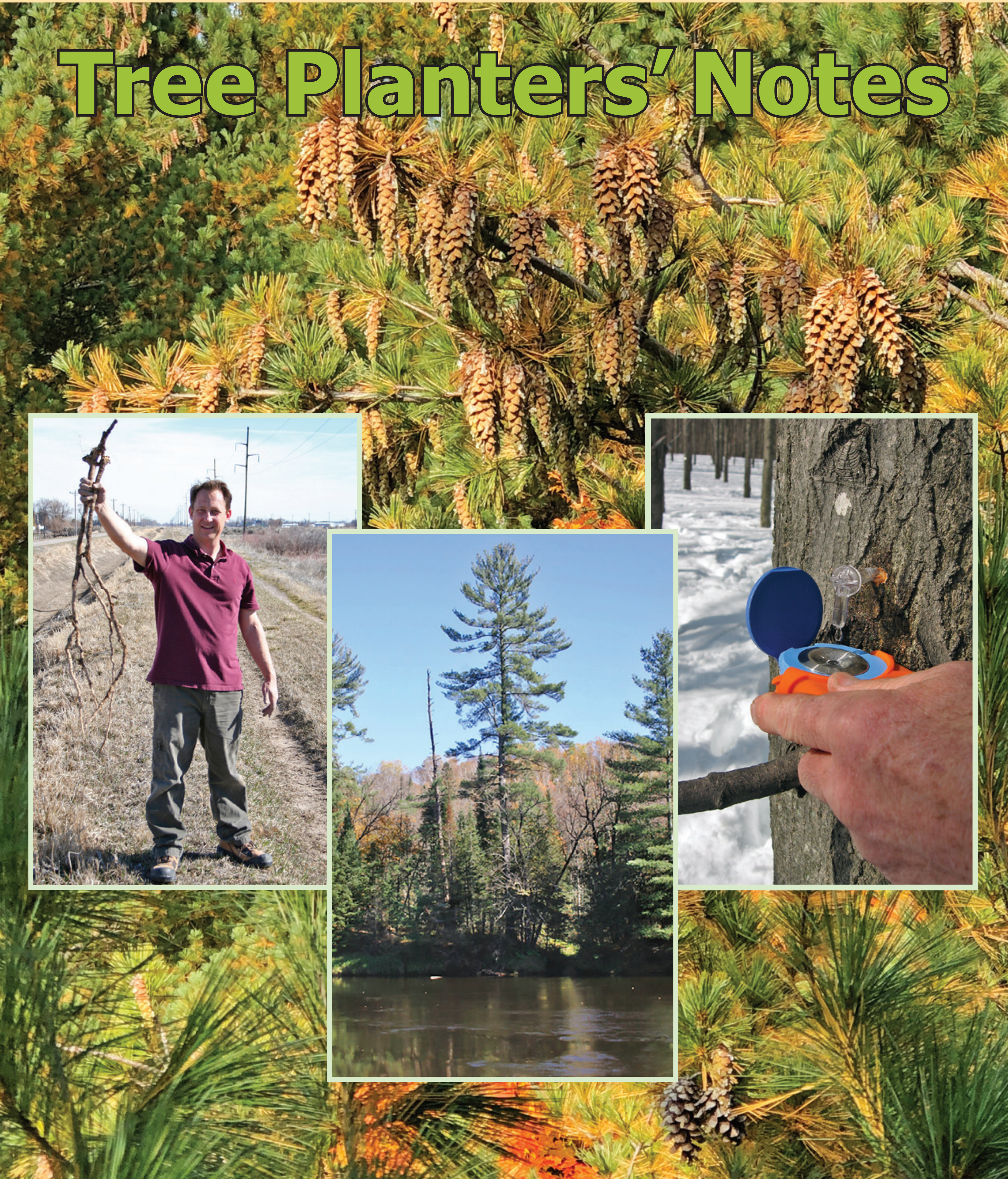
Forest Service
U.S. DEPARTMENT OF AGRICULTURE

Fall 2022 | Volume 65, No. 2

Tree Planters' Notes



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TPN is sponsored by the Cooperative Forestry Staff of the U.S. Department of Agriculture (USDA), Forest Service, State and Private Forestry Deputy Area, in Washington, DC. The Secretary of Agriculture has determined that the publication of this periodical is necessary in the transaction of public business required by law of this Department.

Editor: Diane L. Haase

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Printed on recycled paper.

Fall 2022

Dear TPN Reader,

Welcome to another issue of *Tree Planters' Notes* filled with a range of useful information to those who grow and plant trees for reforestation, restoration, and conservation.

This issue contains four more articles providing species-specific guidance for seed transfer within the Eastern United States: black spruce (p. 13), sugar maple (p. 21), black walnut (p. 29), and eastern white pine (p.37). Each article describes the species' distribution, growth habits, ecologic and economic importance, genetic characteristics, issues with pests and pathogens, and seed-transfer considerations. Other articles for seed-transfer guidance of eastern species were published in the Spring 2022 issue (red pine, yellow birch, and northern red oak) and the Fall 2021 issue (jack pine and white spruce).

In addition to the four articles on seed-transfer guidance, this issue contains seven other articles. DeWald et. al describe a tree improvement project to improve long-term sustainability of white oak (p. 4); Tilley et al. give results from studies on propagation and establishment of showy milkweed, a critical species for the monarch butterfly (p. 44); Cook discusses the use of biological control as part of an integrated pest management program along with results from trials to control black vine weevil (p. 54); South reviews manganese in bareroot pine nurseries with regard to deficiencies, toxicities, fertilization, and interactions with other factors (p. 60); Haase et al. give the annual report on production of tree seedings in the United States including quantities of bareroot, container, conifer, and hardwood seedlings along with estimated acres planted during fiscal year 2021 (p. 79); Windmuller-Campione et al. describe a study to evaluate restoration of floodplain forests using four species planted in three elevation zones (p. 87); and Tsedensodnom et al. present results from their study to develop nursery protocols for growing *Haloxylon ammodendron*, a drought-tolerant species widely used for restoration of Central Asia ecosystems (p. 98).

I'm sure each of you can find something useful in these pages that can be applied to your work. With increasing incidence of wildfires, floods, heatwaves, drought, and other climate-related concerns around the planet, tree planting is more important than ever. Keep up the good work!

Diane

Diane L. Haase

To plant trees is to give body and life
to one's dreams of a better world.

~ Russell Page

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Role of Tree Seedling Nurseries in the White Oak Genetics and Tree Improvement Project

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Abstract

White oak (*Quercus alba* L.) is a keystone species across the Eastern United States with high ecological and economic value. Various factors are converging to limit the species potential for long-term sustainability. To address the lack of successful white oak recruitment, a genetics and tree improvement program was developed and is being implemented by the University of Kentucky. The program has three phases (germplasm collection, genetic testing, and seed production). Tree seedling nurseries can contribute to each phase through production and deployment of improved white oak seedlings.

Introduction

White oak (*Quercus alba* L.) functions as a keystone species in the ecosystems in which it occurs throughout forests in the Eastern United States (figure 1) where it provides unique habitat for a broad array of bird and invertebrate communities (Tallamy and Shropshire 2009), its acorns provide a critical food source for over 100 vertebrate species (Brose et al. 2014), and it influences energy flow and nutrient cycling (Hutchinson et al. 2012). In addition to its ecological value, white oak has significant economic value (Bumgardner 2019) with strong demand for high-quality white oak products (Tripp 2015).

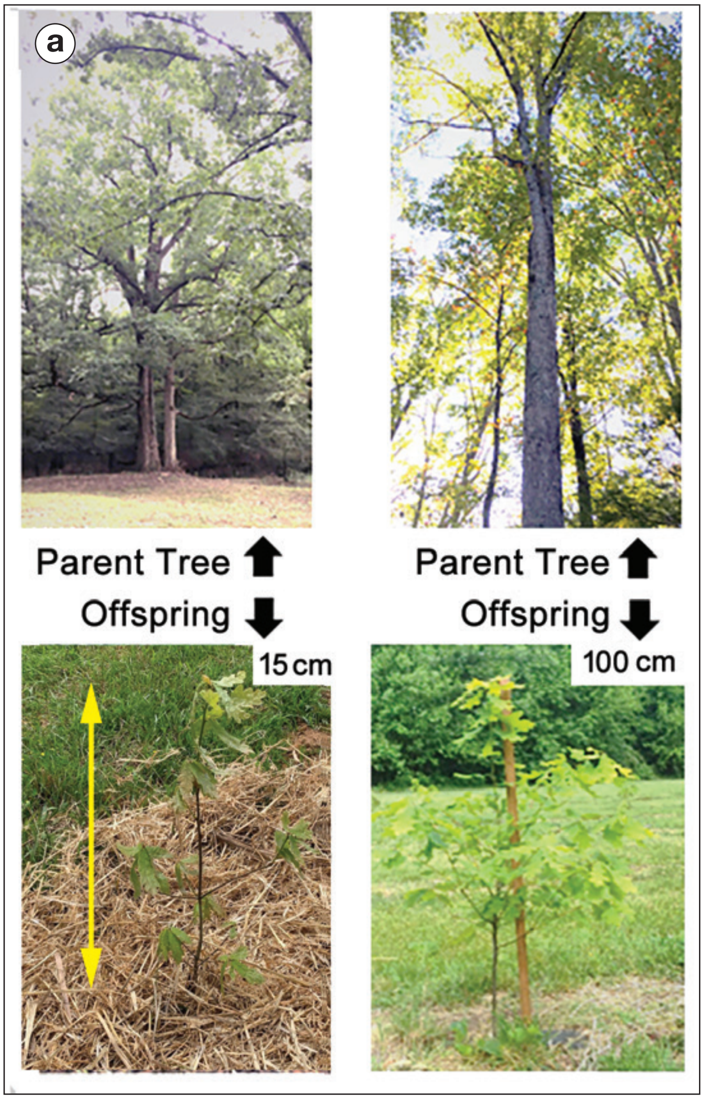
Despite its ecological and economic importance, long-term sustainability of white oak is uncertain. As overstory oaks are eliminated through natural mortality and harvesting, inadequate recruitment of competitive white oak seedlings results in stand compositional shifts toward more shade-tolerant species (Dey and Fan 2009). In these shaded conditions, the relatively poor competitiveness of white oak is due to slow aboveground juvenile growth, a preferential allocation of resources to the root system, and intermediate shade tolerance (Rebbeck et al. 2011).

In recognition of the lack of white oak recruitment and large-scale species compositional shifts, efforts to conserve and restore white oak ecosystems have been increasing (e.g., Hutchinson et al. 2012). In addition to a variety of management approaches that are being tested and implemented (e.g., Spetich 2020), organizations such as the White Oak Initiative (www.whiteoakinitiative.org) have been created to support the sustainable growth of the white oak resource (Fortuna 2021). Larger white oak seedlings

Figure 1. White oak's geographic range is the Eastern United States. (Source: USDA Forest Service, https://www.fs.fed.us/database/feis/pdfs/Little/quealb.pdf)

can improve the competitive status of oak regeneration relative to average-sized seedlings (Johnson et al. 2009) and can be planted to enrich advanced natural regeneration. This planting strategy might be especially critical when harvesting occurs in years of poor mast production, which is a regular occurrence with white oak (Greenberg and Parresol 2002). Development of high-quality white oak seedlings for artificial regeneration can be achieved through a combination of tree improvement and good nursery and planting practices (Sung et al. 2002). Not all trees that appear to be high quality in the forest will produce high-quality offspring. Seedlings from different parent trees can have very different growth rates when planted on the same site (figure 2a).

White oak genetic studies from the 1980s demonstrated significant genetic variation and high juvenile-mature correlations for height growth, indicating that genetic gains can be expected through selection at ages less than 15 years (Huang et al. 2016, O'Connor and Coggeshall 2011) (figure 2b). The collaborative White Oak Genetics and Tree Improvement Program (WOGTIP) was created at the University of Kentucky (UKY) to



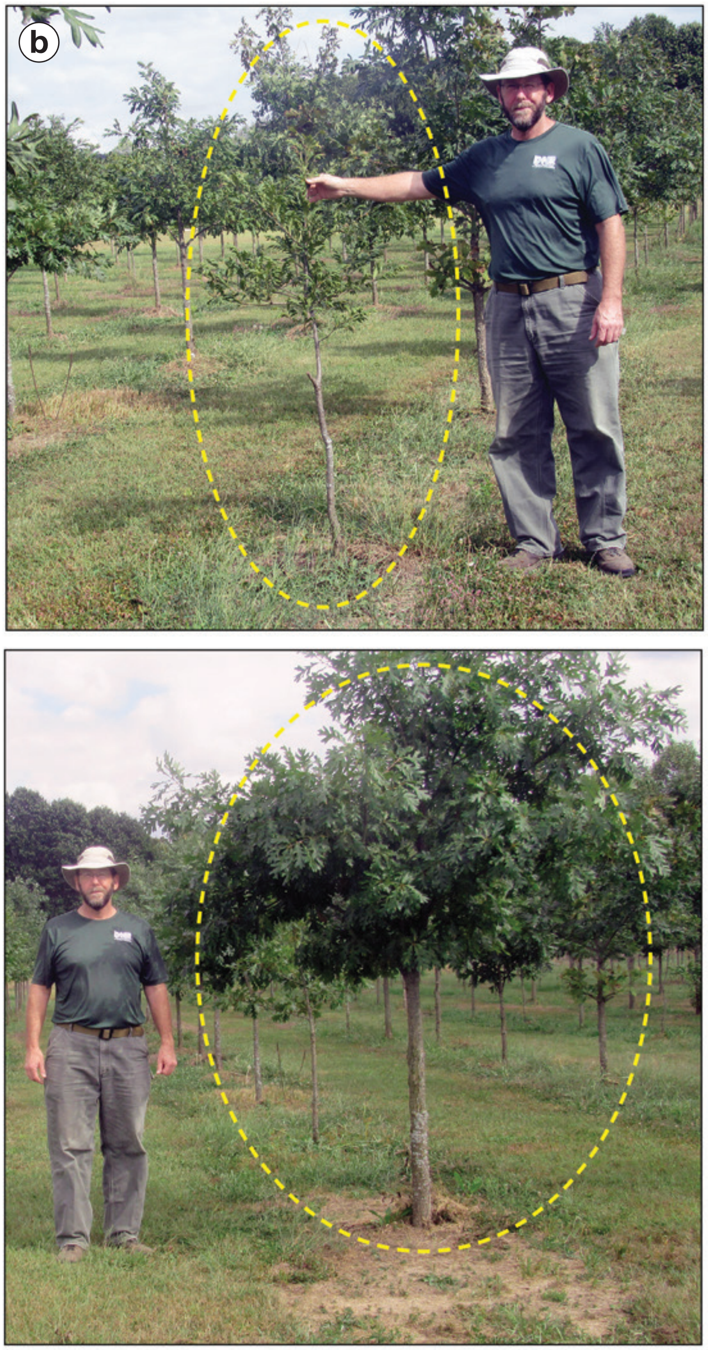


Figure 2. White oak has potential for growth improvement. (a) Seedling offspring from two high-quality white oak parents can vary significantly. The 1-0 seedlings were the same age and planted on the same site, yet they have very different growth rates. Similarly, (b) differences are evident in 10-year-old white oak trees grown from improved and unimproved acorns collected at the same time, grown in adjacent nursery beds, and outplanted as 1-0 seedlings on the same site (breeding and site set up by Phil O'Connor, Indiana Department of Natural Resources). The unimproved trees grew from a random sample of acorns sold to the nursery. The improved trees grew from acorns from controlled pollinations between two high-quality trees. (Photos by Laura E. DeWald, (a) 2021 and (b) 2019)

develop genetically improved seedlings to support multiple ongoing efforts focused on increasing success rates in white oak regeneration and recruitment over the long term. Specifically, the goals of WOGTIP are to develop a range-wide white oak tree improvement program that will collaborate widely and openly with industry (forest, wood, distilling); agencies and organizations (forestry, conservation, wildlife); and citizen scientists to quantify the levels and patterns of genetic variation as they may relate to important ecologic and economic traits, and to improve these traits for optimal seedling performance for recognized seed zones. A three-phase plan was developed to achieve the following goals of WOGTIP:

- Provide a sustainable supply of genetically improved white oak seedlings to meet current and future demands.
- Improve the ability to conserve and restore white oak in forests to achieve a variety of ecologic and economic goals across both regional and national scales.
- Provide genetic resources for future academic, operational, and industrial research and development.

Phase 1 - Collecting and Archiving Germplasm

Acorns are being collected from across the entire geographic range of white oak. Volunteers collect approximately 1 gal (3.8 L) of acorns from one tree per county (figure 3) in as many counties as possible where white oak occurs naturally. To date, over 500 collections have been made with at least one collection from every State within white oak's geographic range (figure 4). The eastern seed zones database (Pike et al. 2020) is being used to help identify gaps in the collections. Due to the natural periodicity of white oak mast production; spatial and temporal pressures from wildlife for acorns; and effects of weather on acorn yields, Phase I will require 3 to 5 years to complete.

To quantify effects of collection year within the genetic tests in Phase 2, each year's acorn collections will come from at least 20 percent of the same trees that were collected from in the previous year(s). Acorn-collecting volunteers include nonprofit groups, Federal and State natural resources agencies, woodland owners, citizen scientists, participants in programs such as the Master Naturalists, youth organizations such as 4-H, and college students in natural resources programs. Acorn collectors document their tree using the TreeSnap application for cell phones (treesnap.org), which automatically records the tree's GPS location. Because 50 to 90 percent of acorns can be infested with weevils (*Curculio glandium*) (Aldrich et al. 2003), volunteers conduct a float test to remove nonviable acorns from their collections. Volunteers document accession information specific to the seed tree. Shipping costs to send the acorns to UKY is funded through grants supporting WOGTIP. Seed collectors for tree seedling nurseries can also participate in the acorn collecting effort if they are willing to separate some of the white oak acorns they collect by parent tree. Nurseries can also help volunteer acorn collectors by recommending parent trees or areas where acorn production is consistent across years.


Figure 3. Volunteers collect enough acorns to fill a 1-gallon plastic bag and then ship the acorns to the University of Kentucky for the White Oak Genetics and Tree Improvement Program using prepaid priority mailing boxes. (Photo by Laura E. DeWald, 2019)

Annual acorn collecting began in 2019 and, as anticipated, acorn production has been highly variable. Late-spring frosts killed white oak flowers, heavy rains reduced pollen movement, late-summer droughts caused acorn development to abort, tropical storms denuded trees of acorn crops prior to maturity, and in 2020, Coronavirus COVID-19 policies negatively impacted participation by public employees. Despite these challenges, a total of 91 single-tree collections representing 9 States were sown in the nursery in 2019, and 112 collections representing 18 States were sown in 2020. The 2020 collections included the 20 percent recollections from 2019 trees needed for controls across years in the genetic tests.

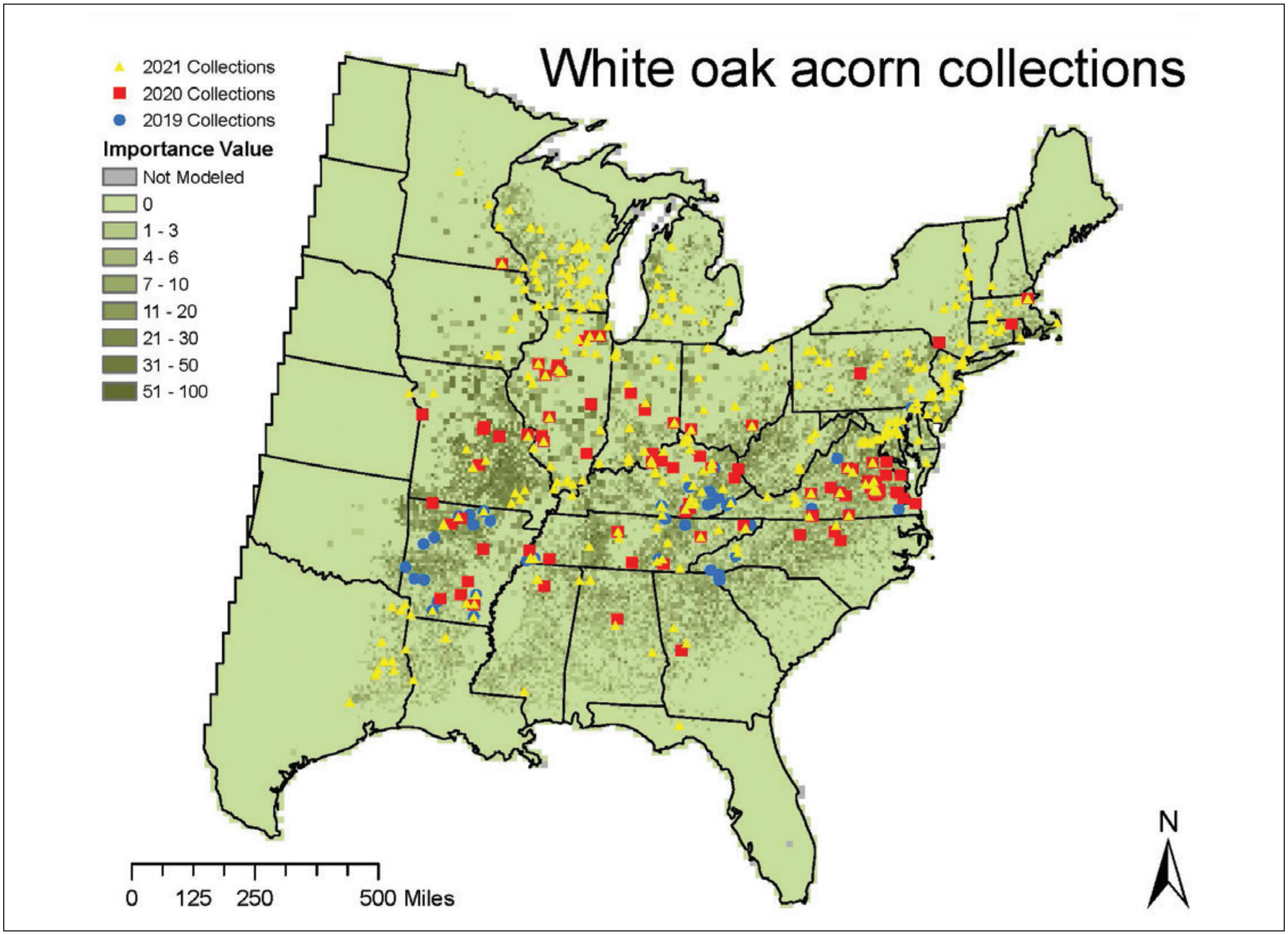


Figure 4. White oak acorns have been collected from multiple sites in the Eastern United States. The map also shows varying shades of green to indicate ecological importance of white oak in natural forests. Importance values are from the USDA Forest Service, Forest Inventory and Analysis database. (Source: USDA Forest Service, https://www.fs.fed.us/nrs/atlas/tree/v3/multi.php?spp=802)

At UKY, each acorn collection is weighed (figure 5). In addition, a random sample of 100 acorns per collection is weighed to estimate the number of acorns planted per collection. This weight data can also be used to quantify variations in acorn size. Since acorn size can affect initial seedling size, the data are also useful for comparing average seed weight with average 1-0 nursery seedling size for each seed lot. Mean seed source acorn weight in 2019 and 2020 ranged from 0.07 to 0.25 oz (2 to 7 g) and varied significantly ($p<0.001$) within and among seed sources.

The Kentucky Division of Forestry is partnering with WOGTIP to grow seedlings for the project at its Morgan County tree seedling nursery near West Liberty, KY. Acorns are hand sown in furrows created by the hardwood planting machine, sprayed with a rodenticide to reduce crow predation, and covered with soil (figure 6). After sowing, a layer of mulch is applied to reduce losses due to cold temperatures and wildlife predation. Except for hand-sowing, standard nursery operating procedures are used (i.e., irrigation, weed control, fertilization, lifting, and cold storage) until outplanting as 1-0 seedlings.

In the nursery, the half-sibling family groups (seed sources) of acorns sown in 2019 and 2020 did not affect emergence timing in the spring but did affect percent emergence. Average emergence was 37 percent (range 0 to 80 percent) and 50 percent (range 0 to 95 percent) from the 2019 and 2020 acorn collections, respectively. Mast production across the Eastern United States was much higher in 2020 than in 2019. Acorn quality also appeared to be higher (larger size, fewer weevils) in 2020, which may explain the difference in average emergence between the 2 years.

County: Buncombe

Nearest Town: Asheville

TreeSnap Tree Identifier: Lab Powhatan 72

GPS coordinates of the tree: TreeSnap

NCBUNCFSEF-05

Figure 5. The weight of a random sample of 100 white oak acorns and the total weight of the acorn collection are used to determine the number of acorns planted from a parent tree. (Photo by Laura E. DeWald, 2019)

Similar to many tree seedlings nurseries, late-spring frosts at the Morgan County nursery can damage seedlings depending on their stage of development. Most white oak seedlings resprout from lateral buds at the root collar or along the base of stems, but this sprouting results in a high degree of forking and lateral branching. Thus, the nursery environment can affect assessment of genetic variation in seedling form at the time of outplanting. Continued assessment of the seedlings during Phase 2 could determine whether poor form at the time of planting can be outgrown if a seedling has strong apical dominance.

The same network of volunteers who collect acorns also collect scions from the same mother trees. Scions are being used to create two replicated, grafted clone banks to clonally replicate the parent trees (figure 7). Efforts are ongoing to propagate scions derived from all mother trees that contribute seeds to the WOGTIP. These clone banks will be used to create future clonal seed orchards for Phase 3.

Figure 6. (a) White oak acorns are planted by hand to keep seedling groups from each parent tree separate from each other in the nursery. (b) After planting, mulch is applied to protect seedlings from predators and from cold winter temperatures. (c) The beginning and end of each seedling group is delineated by colored wooden markers. (d) Seedling groups can be clearly seen in May from acorns planted the previous autumn. (Photos by Laura E. DeWald, 2019–2021)

Figure 7. (a) Using a shotgun, this private landowner collects white oak scion material for grafting. (b) Once collected, scions are grafted to clonally replicate the parent trees. (Photos by Laura E. DeWald, 2019–2021)

Grafting success is higher when scions are collected when the tree is fully dormant and when using scions collected from the upper crown where the branches get more sunlight, thus exhibiting greater annual growth. Meeting these criteria, however, can be problematic for most of the volunteers. As a result, most of the scion material collected to date has been of poor quality. Obtaining quality scion material suitable for grafting remains a significant challenge to WOGTIP. A network of volunteer arborists willing to climb or use a bucket truck and be paired with acorn collectors might be an effective way to get quality scion material. Personnel from tree seedling nurseries who have tree-climbing skills may be able to assist with scion collection. While not as desirable, material from the parent's best progeny could be an option when it is not possible to obtain scions directly from the parent tree.

Phase 2 – Provenance and Progeny Testing

At the time of lifting from the nursery (approximately 18 months following seed collection), seedling roots are dipped in a hydrophilic polymer to reduce desiccation and drought stress. The 1-0 bare-root seedlings are then placed in cold storage until hand- or machine-planting into provenance/progeny tests plots in late March and early April. Results from these tests will describe patterns of geographic variation and adaptation among seed sources. This data will provide information about climate change responses (i.e., provenance comparisons) and will evaluate parent trees for traits of interest to stakeholders (i.e., progeny comparisons).

A master test site was established at the Maker's Mark Distillery Star Hill Farm near Loretto, KY, and will include seedlings from the entire rangewide acorn collection. In addition, a network of smaller regional tests will be established to elucidate patterns of genetic variation and to quantify genetic by environment interactions on adaptive and commercially important traits. The geographic target for seed-source inclusion in these regional tests is 80 percent from one to two seed zones surrounding the site, 15 percent from three to five seed zones away from the site, and 5 percent from seed zones representing a larger movement south to north. Efforts are ongoing to identify locations and partners for establishment of the regional progeny test sites that will ideally be distributed across the range of white oak. Several collaborative groups including the USDA Forest Service, State agencies, and academic institutions are in the planning stages to install progeny tests in 2023 (pending success of acorn collecting in 2021).

Some of these regional tests can be established in collaboration with State nurseries and potentially located at nursery sites.

Regional tests will vary in size depending on the number of seed sources included, with most occupying 2.5 to 4 ac (1 to 2 ha). Approximately 20 seedlings per seed source (i.e., single mother tree collection in a single year) will be planted in single tree plots at 8- by 8-ft (2.4- by 2.4-m) spacing. This relatively close spacing will encourage competition among the trees and allow the regional tests to be thinned to become seed production areas (SPAs) during Phase 3. Seedlings to be planted on previously nonforested sites will be root-dip treated with an ectomycorrhizae solution at the time of planting (MycoApply Injector Ecto®, Mycorrhizal Applications, Grants Pass, OR). This product has a diversity of species that occur in white oak forests.

Data collection from the progeny/provenance tests and subsequent analyses will be organized by UKY. In addition to survival, traits measured at the time of planting and thereafter at 3- to 5-year intervals include height and form. Additional traits, such as phenology, which are strong indicators of adaptation and thus important for making decisions about migration under future climates, will be measured within the first few years of test establishment. Other traits of interest to stakeholders and partners may also be measured. Selection based on survival, growth, and phenology can be done within 7 to 15 years for white oak (Huang et al. 2016). Continuation of the regional tests beyond 15 years will be up to the partner. Most tests will likely be rogued (based on estimated genetic values) to transition to SPAs during Phase 3 to provide a supply of genetically improved white oak acorns of known origins for seedling production in the appropriate seed zones. The Maker's Mark site is intended to be maintained as a long-term repository of the rangewide collection.

Of the acorns collected in 2019, 63 of the 91 seed sources produced enough seedlings to be outplanted at the Maker's Mark site and 2 other small sites in 2021. Even though the best seedlings (based on root and shoot characteristics) within a seed source at the nursery were selected for planting, there was still significant ($p<0.001$) variation in height and root collar diameter within and among seed sources after accounting for variation due to acorn weight (figure 8). The variation in seedling morphology did not, however, show any obvious geographic patterns. Forking and numbers of lateral branches were counted on each seedling to quantify form. A seedling with "acceptable form" was defined as having no forks and <1 lateral branch per 3.9 in (10 cm) of height. On average, 71 percent (range 20 to 100 percent) of seedlings met this definition of acceptable form. Form varied significantly among and within seed sources ($p<0.001$). On an individual basis, seedlings that met our definition of acceptable form were taller ($p<0.01$). Therefore, despite selecting higher quality seedlings at the nursery level, there is still significant variation within and among seed sources in the Phase 2 progeny tests.

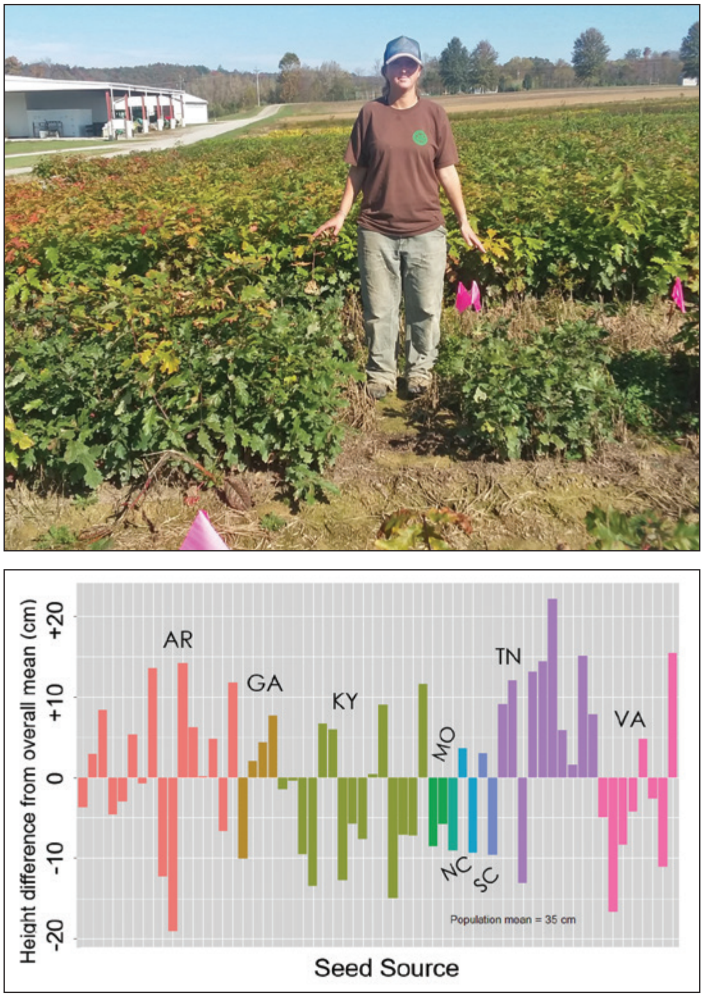


Figure 8. Genetic differences in white oak 1-0 seedling heights are evident in nursery trials. (a) The seed source on the left is from a tree in Kentucky and the seed source on the right is from North Carolina. (b) Nursery measurements in 2019 reveal height variation among seed sources. The two letter abbreviations are the State where the acorns originated for each color group. Bars with the same color represent seedlings from different trees within the State. (Photo by Laura E. DeWald, 2020)

Phase 3 – Selecting Parents, Seed Production, and Seedling Deployment

Phase 3 of the WOGTIP plan will be implemented after progeny tests are evaluated and analyzed (approximately 7 to 10 years after establishment). Scion material from more than 20 parent trees have already been grafted onto root stock (see Phase 1), and the grafted clones are being planted on one of the farms at UKY as part of a clone bank that will ultimately provide material for the grafted seed orchards. Pollen mixing among top performing and locally adapted parents within these orchards will ensure high levels of genetic diversity and will produce broadly adapted seeds for reforestation. Future breeding programs could employ controlled pollinations to target specific traits and growing areas. Grafted seed orchards are best established on State lands near or at existing nurseries to ensure the sites are maintained for reliable, high-quality seed production.

Mast production is highly variable in white oak and demand for improved seedlings will be high. Therefore, multiple SPAs of genetically improved trees are needed to supplement the planned grafted seed orchards. Two types of SPAs can be established. Most of the regional progeny tests will likely be rogued at 15 years (based on genetic information from the test) and transitioned to become seed orchards. New production areas can also be established on private and public lands using collaborative partnerships with private woodland owners and public agencies such as the USDA Forest Service and State natural resources agencies. These additional acorn production areas can be planted using seed sources also included in nearby regional tests and then subsequently rogued prior to acorn production to remove poor performing seed sources using progeny test results. Both types of SPAs should be able to supplement the seed supply derived from the grafted seed orchards to ensure a consistent annual supply of acorns to nurseries for producing genetically improved white oak seedlings.

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Acknowledgments

We acknowledge the contributions of the University of Kentucky Department of Forestry and Natural Resources, DendriFund, Brown-Forman Distillery, Inc., and Maker's Mark Distillery, Inc. for providing resources toward this project. The authors also acknowledge the numerous volunteers across the Eastern United States who helped collect white oak acorns for this project. Initial funding for this project was provided by University of Kentucky Department of Forestry and Natural Resources, Kentucky Agriculture Experiment Station, U.S. Department of Agriculture, Forest Service's Southern Research Station, and Kentucky Division of Forestry.

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

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Abstract

Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) is a dominant boreal tree species that is common across the northern Great Lakes and northern New England. This species competes best on lowland peat bogs and on upland sites. Black spruce regenerates naturally from seed rain from semi-serotinous cones or from seed released from cones in the duff layer. Interspecific crosses between black spruce and red spruce (*Picea rubens* Sarg.) occur commonly in areas where they are sympatric, primarily in Québec. Black spruce has high genetic variation and low population structure, but populations differentiate along latitudinal temperature gradients. Northern populations are likely to benefit from increased warming, while southern populations should be conserved and transferred northward as a strategy to retain favorable growth characteristics. Sources from 1.5 to 2.0° C mean annual temperature warmer than the planting site are considered suitable. In the Eastern United States, this would translate into a transfer distance of up to approximately 3˚ latitude, or 207 mi (333 km).

Introduction

Figure 1. Black spruce grows well in upland and lowland sites, such as this *Sphagnum* bog in northern Minnesota. (Photo by Jim Warren, USDA Forest Service, 2008)

Figure 2. Black spruce produces semi-serotinous cones which extends the window for seed dispersal. The current-year cones on black spruce (top) in this photo have not fully ripened; ripe cones are typically dark and lignified. (Photo by Carolyn Pike, 2010)

Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) is a relatively shade-tolerant tree species native to boreal and subarctic forests across North America. Black spruce can be considered both an early-successional species that regenerates after stand-replacing disturbances, and an important late-successional species that is able to survive as advanced regeneration in the understory. The species has a broad ecological amplitude, occurring both in lowland peat bogs (figure 1) and on upland sites, but charred organic matter is a preferred substrate (Jean et al. 2020). Trees can begin producing semi-serotinous cones as young as 10 years old (Viereck and Johnston 1990). The semi-serotinous nature of their cones permits natural regeneration from seed rain without fire (Johnstone et al. 2009) (figure 2). In addition, black spruce can regenerate from cones in the soil, although viability of seeds starts declining after 1 year (Fraser 1976). Natural regeneration by seed is common post-fire and may be supplemented through artificial regeneration with mechanical site preparation and subsequent planting (Hébert et al. 2014) or with limited site preparation and aerial seeding (Yuska 2022) (figure 3). Climatic warming, coupled with increased frequency of wildfire, may reduce the thickness of the soil organic layer, leading to black spruce's replacement by other conifer or hardwood tree species and/or increasing dominance of shrub species (Baltzer et al. 2021, Wilson et al. 2021). The Climate Change Atlas predicts that black spruce may lose habitat but will likely remain as a component of boreal forests in the Eastern United States because of its genetic diversity and ecological plasticity (Peters et al. 2020).

Black spruce is the progenitor to the more temperate red spruce (*Picea rubens* Sarg.) (Jaramillo-Correa and Bousquet 2003). Hybridization occurs naturally where red spruce and black spruce grow sympatrically in Québec (Perron and Bousquet 1997). Cytoplasmic gene capture (movement of organelles between species) may also have occurred in this sympatric region, further complicating the genetic history of black spruce and red spruce (Gérardi et al. 2010). Black spruce and white spruce (*Picea glauca* [Moench]) occupy similar transcontinental ranges across boreal forests but are genetically distinct and do not hybridize. Black spruce likely had five putative glacial refugia: two in the Central United States, one in the Pacific Northwest United States, one off the coast of Labrador, and one in Alaska (Gérardi et al. 2010, Jaramillo-Correa et al. 2004).

Genetics

Black spruce is comparable to other conifers in having high genetic variation and low population differentiation due to excessive migration of pollen and seed (to a lesser extent). In addition, black spruce can regenerate asexually through layering, a feature more common in subarctic and montane environments than

Figure 3. Black spruce often grows sympatrically with tamarack (*Larix laricina* [(Du Roi) K. Kochin]) as seen in this northern Minnesota forest (Photo by Carolyn Pike, 2004).

in boreal or sub-boreal forests. In areas where layering is common, genetic diversity remains high, a relic of previous warm climates where sexual reproduction was favored (Gamache et al. 2003).

High levels of genetic diversity in black spruce have been confirmed with allozymes (proteins that are phenotypically neutral) (Rajora and Pluhar 2003) and with nuclear and chloroplasts DNA. Chloroplast DNA, which is paternally inherited through pollen, revealed little structure among populations (a signal of high levels of pollen dispersal) (Gérardi et al. 2010) and was similar in magnitude to nuclear markers (Gamache et al. 2003). Lower levels of gene flow, through seeds, is evident in maternally inherited mitochondrial DNA but only in sub-Arctic populations (Gamache et al. 2003). Gamache et al. (2003) also reported finding rare alleles in populations residing along the northern range edges, a finding that was attributed to occasional long-distance dispersal events. Even along range edges in Newfoundland and Manitoba, low F_{ST} values (a ratio of genetic variation between sub-populations and the total population) were reported (0.059, 0.069, and 0.048 for Newfoundland, Manitoba uplands, and Manitoba lowlands, respectively) (O'Reilly et al. 1985, Yeh et al. 1986), indicating high rates of pollen and seed dispersal.

Seed-Transfer Considerations

Black spruce's importance to the pulp and paper industry has led to an extensive network of range-wide provenance tests (figure 4) to aid in tree improvement efforts. In eastern North America, genetic differences are expressed clinally, as opposed to ecotypically, with a pronounced latitudinal (north-south) trend (Morgenstern 1968, 1978; Morgenstern and Mullin 1990; Park and Fowler 1988; Pedlar et al. 2021). The species' excessive gene flow and genetic diversity generally preclude ecotypes from forming because unique gene assemblages are disrupted with nonlocal pollen or seed sources. Clinal variation is generally latitudinal, except in Maritimes where oceanic influences create a distinct east-west gradient. This north-south clinal variation is driven predominantly by adaptations to temperature gradients (Morgenstern 1978, Pedlar et al. 2021, Thomson et al. 2009, Yang et al. 2015). Across all these studies, moisture was a weak predictor of growth among black spruce provenances.

Survival and growth of black spruce is strongly impacted by synchrony of phenological traits, such as budbreak, with local conditions. Populations have adapted to spring temperatures by adjusting their heat requirements to synchronize budbreak with optimal conditions (i.e., northerly sources have a lower

Figure 4. This black spruce stand in northern Minnesota is one of a group of North American range-wide provenance trials planted with a similar set of families in the same year. This group of trials is valuable for measuring the effects of seed transfer and to study the association of genotype and phenotype in black spruce. (Photo by Carolyn Pike, 2004)

heat requirement compared with more southerly sources) (Johnsen et al. 1996, Usmani et al. 2020). As a result, southern sources will break bud earlier than northern sources at a common garden. Black spruce is resilient to freezing temperatures (-60° C [-76° F]) during endodormancy (the deepest form of winter dormancy) (Man et al. 2017). Black spruce is also relatively resilient to freezing temperatures during late winter and early spring, even after budbreak occurs (Man et al. 2021). Budset, which occurs in mid-summer (July) for black spruce, is relatively insensitive to temperature and likely predetermined genetically or affected by photoperiod (Usmani et al. 2020).

Transfer of black spruce seed from southern to northerly locales is recommended to ameliorate predicted adaptation lags when southern range-edge seed sources are growing in a climate that is warmer than optimal for the species (Pedlar et al. 2021, Thomson et al. 2009, Yang et al. 2015). Thomson and Parker (2009) showed that maximum height growth for a majority of provenances tested occurs at planting sites between 45 to 47° and 46 to 48° north latitude for eastern and western Ontario, respectively, north of the southern range edge. This optimal habitat will likely shift 2 to 4° northward with climate change, which is congruent with other predictions that suggest a habitat reduction is likely along southern range edges. Southern sources that are moved northward may experience delayed budbreak and budset (Johnsen et al. 1996). Southern range-edge sources are considered adequate for reforesting in central and northern parts of the range (Thomson et al. 2009), but conservation of these genotypes should be prioritized before they are extirpated. A generalized transfer recommendation of 2° latitude and 656 ft (200 m) in elevation was recommended for Canada to maximize yields (Morgenstern and Fowler 1969) and later refined to sources originating from sites that are 2.7 °F (1.5 °C) (Yang et al. 2015) to 4.0 °F (2.2 °C) warmer mean annual temperature (Pedlar et al. 2021). Black spruce can also tolerate transfers to drier (up to 18 in [455 mm] less mean annual precipitation) or cooler climates (up to 11 °F [6.1 °C] mean annual temperature) than climate origin before a reduction of 10 percent or more in height growth (Pedlar et al. 2020). Northward shifts of black spruce into subarctic zones are already evident through natural regeneration (Truchon-Savard et al. 2018), but artificial regeneration may be needed to bolster its presence on upland soils or on sites where soils have lost organic matter from fires (Baltzer et al. 2021). Seed transfer guidelines are summarized in Table 1.

Insects and diseases

Eastern dwarf mistletoe (*Arceuthobium pusillum* Peck), a native parasitic plant, is one of the main mortality agents of black spruce in the Lake States (figure 5). The plant's sticky seeds are released by catapulting, thereby facilitating their spread among trees, even trees of small stature (Baker and Knowles 2004). While other dwarf mistletoes only result in decreased growth, eastern dwarf mistletoe kills 75 percent of trees within 15 to 20 years (Baker and French 1980) (figure 6). Because eastern dwarf mistletoe can impact large and small stature trees, it can reduce black spruce regeneration and alter the light environment; species composition may shift to other early successional species, such as paper birch (*Betula papyrifera* Marsh.) and eastern larch (*Larix laricina* [Du Roi] K. Koch), in otherwise spruce-dominated forests (Skay et al. 2021).

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

Black spruce, *Picea mariana* (Mill.)	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Serotinous to partially serotinous cones, 335,000 to 664,000 seeds per pound (739,000 to 1,464,100 seeds per kg)
Insect and disease	• Budworm, mistletoe
Palatability to browse	• Low; generally not preferred by white-tailed deer
Recommended transfer distances	• Southern range-edge populations should be prioritized for conservation and moved northward • Transfer distances up to 3° northward (70 to 200 mi [113 to 322 km]) are likely safe • Sources with mean annual temperature up to 2.7 to 4.0 °F (1.5 to 2.2 °C) warmer than the designated planting site
Range-expansion potential	• Likely to expand northward • May lose habitat from excess fires and loss of soil organic matter

Figure 5. Dwarf mistletoe, a parasitic plant, can devastate black spruce stands in northern Minnesota. These photos illustrate the growth form on black spruce twigs. (Photos by Ella Gray, University of Minnesota, 2021)

Figure 6. This black spruce stand shows the typical damage incurred by dwarf mistletoe in northern Minnesota including witches' brooms where the mistletoe proliferates, dead crowns, and fallen dead trees. (Photo by Raychel Skay, University of Minnesota, 2021)

Spruce budworm (*Choristoneura fumiferana* [Clem]) is the most important defoliator of spruce species across North America. Spruce budworm is more likely to cause severe defoliation in mixed stands of balsam fir (*Abies balsamea* (L.) Mill) and black spruce compared with pure stands of black spruce because balsam fir is a preferred host (Lavoie et al. 2021). In the Lake States, white spruce is generally favored as a host for spruce budworm because of its early budbreak relative to black spruce (Nealis and Régnière 2004). In New England, spruce budworm prefers red spruce over black spruce as a host (Fraver et al. 2007), especially in introgressed regions of Québec (Manley and Fowler 1969). Yellow-headed spruce sawfly (*Pikonema alaskensis* [Rohwer]) defoliates spruce species when trees are less than 10 to 12 years old, but usually prefers white spruce over black spruce in the Lake States (Katovich et al. 1995). Stigmina needle cast (*Stigmina lautii*) and Rhizosphaera needle cast (*Rhizosphaera kalkhoffii*) can damage black spruce foliage (Juzwik 1993). Black spruce cones may be afflicted with spruce cone rust (*Chrysomyxa pirolata* Wint.) which can reduce seed yields considerably (Singh and Carew 1990). In Alaska, spruce bud rust (*Chrysomyxa woroninii* Tranz.) has been reported on black spruce and white spruce (McBeath 1984), but it is not a common pathogen in the Eastern United States.

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Sugar Maple: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Sugar maple (*Acer saccharum* Marsh.) is a shade-tolerant hardwood tree native to forests across eastern North America. Genetic diversity of this species is high due to high levels of seed dispersal and pollen flow. Population structure is moderate along range edges where populations are isolated and gene flow may be limited. Sugar maple may hybridize with southern maple (*A. floridanum* [Chapm.] Pax), but hybridization events are considered rare. Common garden studies revealed relatively weak clines for growth traits and strong variation in phenological traits, although few common gardens exist. Seed transfer distances up to 200 mi (322 km), or roughly 2 degrees latitude northward, are considered a safe recommendation to avoid phenological mismatches. Widespread decline reported in New England and the Lake States has been attributed to insects and diseases on mature trees. Pear thrips, defoliators, *Eutypella*, and *Armillaria* fungi may impact seedlings and mature trees. Sugar maple is likely to expand northward with climate change, but southern populations may be subject to inbreeding from increased isolation among discontinuous stands.

Introduction

Sugar maple (*Acer saccharum* Marsh.) is a late-successional, shade-tolerant (Canham 1988), broad-leaved tree species, native to the United States and Canada. The bark is dark gray and exhibits different morphotypes ranging from flat plates, to raised shells, to elongated protrusions (Sajdak 1968). The species is renown for its colorful fall foliage that can vary from yellow to red (figure 1). Sugar maple occurs across eastern North America with disjunct populations in the tropics, occurring at high elevations as far south as Guatemala (Vargas-Rodriguez

Figure 1. Maple leaves vary from yellow to orange in the fall, creating a patchwork of colors that is a major attraction to tourists across the Northern United States. (Photo by Carolyn Pike, 2021)

et al. 2015). Sugar maple is believed to have had one southern glacial refugium that spread north and westward at the end of the last ice age (Miller and Parker 2009). A study that incorporated disjunct sugar maple populations, however, found that multiple glacial refugia may better explain the current geographic range in temperate and tropical forests (Vargas-Rodriguez et al. 2015).

Sugar maple has a broad ecological amplitude and can grow in northern hardwood (figure 2) and southern boreal forests on a variety of soil types and substrates (Barras and Kellman 1998) but grows best on well-drained loams (Godman et al. 1990). The species has high shade tolerance and is sympatric with basswood (*Tilia americana* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), and black cherry (*Prunus serotina* Ehrh.). In addition, its roots exude a leachate that has some allelopathic properties that may enhance its competitive ability in northern hardwood forests (Tubbs 1973). Sugar maple regeneration is most common from seed, which can successfully establish on a wide range of substrates, such as rotten wood, bare soil, and leaf litter (Caspersen and Saprunoff 2005). Artificial regeneration is relatively uncommon because of the species' propensity to regenerate naturally in the understory (figure 3).

Sugar maple is projected to adapt well to climate change because of its shade tolerance; ability to shift northward; plasticity (Peters et al. 2020, Prasad et al. 2020); and capacity to inhabit a wider climatic range than it currently occupies (Putnam and Reich 2017). Populations within the current southern range of sugar maple have not yet shown evidence

Figure 2. This mature stand of sugar maple in Wisconsin was recently thinned to allow light to reach the forest floor. (Photo by Christel Kern, USDA Forest Service, 2021)

Figure 3. Sugar maple is highly shade-tolerant and regenerates readily in full and partial shade of the understory. (Photo by Carolyn Pike, 2021)

of range contraction (Hart et al. 2014). Optimum temperatures for sugar maple germination may be higher than current norms, so the species should not be limited by germination temperature in the future (McCarragher et al. 2011). Wide-ranging dendrochronological studies failed to correlate radial growth with any single climate factor and concluded that the species is highly plastic, which bodes well for its ability to adapt to novel climates (Copenheaver et al. 2020).

Sugar production from sugar maple trees (figure 4) is, and has always been, a major food source for tribes (Chamberlain 1891) and an important commodity to rural economies across the species' range. Sugar production is likely to be impacted by climate change, leading to concerns about the sustainability of this resource (Oswald et al. 2018, Rapp et al. 2020). The zone of optimum production may shift north from the 43rd to the 45th parallel (Rapp et al. 2020), or syrup yield may remain relatively stable across a broad latitudinal and temperature gradient (Houle and Duchesne 2020). Researchers agree that the annual sap-collection season will begin and end earlier due to earlier freeze/thaw cycles (Rapp et al. 2020, Skinner et al. 2010). More information on this taxon can be found in Godman et al. (1990) and Nesom and Moore (2006).

Genetics

Sugar maple, a monoecious diploid (Kriebel 1957), is self-compatible, although selfing rarely produces viable seed (Gabriel 1967). Pollen, shed in the spring, is both wind- and insect-dispersed (Gabriel and Garrett 1984) and capable of long-distance dispersal (Khodwekar et al. 2015). The species is also highly dichogamic with male and female organs maturing at different time intervals: on some trees, males

Figure 4. Maple syrup is a major industry for residents of northern States and an important food source for tribes. In this image, a maple tap is testing for sugar content, in the early spring at a sugar maple forest in Michigan. (Photo by Paul Bloese, 2014)

mature before females (protandry), while on other trees, females mature before males (protogyny) (Gabriel 1968). This flowering asynchrony among trees within a stand may lower local gene flow or genetic diversity since not all combinations of outcrosses are likely (Gabriel 1968). Seeds are medium-sized double samaras, averaging 15,540 seeds per lb (7,030 per kg) and are dispersed in the fall (Zasada and Strong 2008). Usually, only one of the paired samaras contains a viable seed (Godman et al. 1990).

The taxonomy of sugar maple is not yet settled. Black maple (*Acer nigrum* F. Michx.), the closest relative to sugar maple (Jackson et al. 2020), is sometimes considered a subspecies (*Acer saccharum* ssp. *nigrum*) and may hybridize with sugar maple in the Central United States where their ranges overlap (Gabriel 1973, Skepner and Krane 1998). Florida maple (*Acer floridanum* [Chapm.] Pax or *Acer barbatum* Mich.), also known as southern maple, has relatively disjunct populations and is sometimes considered a subspecies (*Acer saccharum* var. *floridanum* [Chapm.] Small & A. Heller). Kriebel (1975) recognized sugar maple as a single species with multiple forms—saccharum, nigrum, and floridanum—which correspond to the species *A. saccharum*, *A. nigrum*, and *A. floridanum*. Despite its complicated taxonomy, hybridization of sugar maple with black maple or Florida maple is not known to widely occur.

The amount of genetic diversity and gene flow varies across the geographic range of sugar maple. Low to moderate genetic diversity is reported in tropical populations where stands are disjunct and isolated (Vargas-Rodriguez et al. 2015). Where sugar maple stands are contiguous, genetic diversity is high and rare alleles are uncommon (Foré et al. 1992, Foré and Hickey 1992, Graignic et al. 2016, Gunter et al. 2000, Khodwekar et al. 2015). Genetic diversity of southern populations in eastern Tennessee may exceed northern populations in Wisconsin (Gunter et al. 2000) due to the presence of rare alleles in the southern populations. Because sugar maple populations along the southern range edge are relatively isolated, rare alleles that evolve are not as readily dispersed to other populations. This low dispersal results in inflated estimates of genetic diversity, which may be an artifact of reduced gene flow or prior hybridization with *A. floridanum* or *A. nigrum*.

Across most of its range, even where populations are relatively continuous, moderate levels of spatial genetic structure have been reported for sugar maple, likely from occasional inbreeding and limited seed dispersal (Geburek 1993; Geburek and Knowles 1992; Perry and Knowles 1988, 1991; Young et al. 1993). Sugar maple's opportunistic nature may also explain this phenomenon. Sugar maple proliferates in the understory of uneven-aged stands resulting in cohorts that are uniquely positioned to take advantage of light gaps or other resource pulses. These cohorts contribute seeds during years when gaps or other favorable conditions are randomly created, resulting in their disproportionate representation. These synchronous cohorts are shaped by a combination of random events and natural selection (Mulcahy 1975).

Seed-Transfer Considerations

Sugar maple growth traits such as height, stem diameter, and leaf tannin content generally exhibit weak clinal (provenance) variation, as observed in both common gardens (Baldwin et al. 1987) and natural stands (Gunter et al. 2000). Conversely, phenological traits often follow predictable geographic patterns. For example, timing of fall coloration exhibited strong latitudinal trends, with sources from northern latitudes (from cooler climates) exhibiting coloration earlier than southern sources (from warmer climates). Similarly, northern sources tend to leaf out earlier in the spring and senesce earlier in the fall than southern sources (Kriebel 1957, Kriebel and Wang 1962, Putnam and Reich 2017, Ren et al. 2020). In common garden studies, sugar maple trees originating from northerly regions (relative to a common garden) are prone to damage from early spring frosts, while trees from southerly sources are more prone to damage from fall frosts (Kriebel 1975). Drought resistance is generally higher in sugar maple trees that originate from dry climates relative to seed sources from cool, moist climates. Sun scorch and leaf injury following extreme summer heat were more severe on northern genotypes than southern genotypes in a common garden trial (Kriebel 1975). Sun scorch also exhibited east-west clines in which sources from Ohio had more leaf damage than sources from Illinois.

Kriebel (1975) defined three ecotypes of sugar maple corresponding to northern, central, and southern populations based on a variety of phenological traits (table 1). For these reasons, Kriebel (1975) defined a local seed source as one that originated within 100 mi (161 km) from the planting site. No other studies have assessed sugar maple seed-transfer distances empirically, so this recommendation may not apply to other parts of its range. Given that sugar maple is likely to expand its range northward with climate change (Caspersen and Saprunoff 2005) and is highly plastic (Guo et al. 2020), it is likely tolerant to seed-transfer distance up to 200 mi (322 km) in the Northern United States. Seed transfer guidelines are summarized in Table 2.

Table 1. A summary of traits for major subgroups of sugar maple based on Kriebel (1957).

Sugar maple population	Drought resistance	Susceptibility to leaf damage during summer	Cold resistance	Apical dominance
Northern	low	high	high	strong
Central	high	moderate	high	strong
Southern	high	high	low	weak

Insect and Diseases

Insects and diseases that impact growth and survival of mature sugar maple have been extensively studied, especially across New England. Defoliators are the most common insects that affect sugar maple, including native species such as forest tent caterpillar (*Malacosoma disstria* Hbn.) (Gross 1991), which affects sugar maple in New England and, to a lesser degree, across the Lake States (Minnesota and Wisconsin). The Bruce spanworm (*Operophtora bruceata* [Hulst]) and saddled prominent (*Heterocampa guttivitta* [Walker]), both native caterpillars, also feed on sugar maple (Houston et al. 1990). Pear thrips (*Taeniothrips inconsequens* [Uzel]) (Gardescu 2003) is the most important nonnative defoliator of sugar maple as its feeding can also introduce anthracnose fungi (*Discula campestris* [Pass.] Arx) (Brownbridge et al. 1999, Stanosz 1993). Sugar maple is not considered a primary host for the nonnative spongy moth (formerly gypsy moth) (*Lymantria dispar* L.) (Barbosa and Greenblatt 1979). Seedlings may also be defoliated by caterpillars in the Tortricidae including (*Clepsis melaleucana* Walker) (a native generalist caterpillar) and by European slugs (*Arion subfuscus* Draparnaud). Herbivory from a

Table 2. Summary of silvics, biology, and transfer considerations for sugar maple.

Sugar maple, *Acer saccharum* (Marsh.)	
Genetics	• Genetic diversity: high • Gene flow (pollen): high • Gene flow (seed): moderate to high
Cone and seed traits	• Medium-sized, winged seeds • 7,070 to 20,110 cleaned seeds per pound (3,200 to 9,100 per kg)
Insect and disease	• Forest tent caterpillar, pear thrips, sugar maple borer, and Asian longhorned beetle • Armillaria, anthracnose, and Eutypella canker
Palatability to browse	• Moderately palatable to deer browse
Maximum transfer distances	• Seed-transfer distances have not been tested across its range • Based on common garden studies, 100 to 200 mi (161 to 322 km) is the longest recommended seed-transfer distance
Range-expansion potential	• Northward potential is high • No evidence of southern range-edge contraction • Southern range-edge populations may become more disjunct and isolated

variety of other insects such as leafhoppers (*Typhlocyba* spp.) was reported as well (Gardescu 2003). Sugar maple borer (*Glycobius speciosus* [Say]) significantly impacts wood quality on mature trees with low vigor, especially after defoliation events (Wink and Allen 2003). Sugar maple is a preferred host of Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky), a large beetle native to Asia that travels on firewood and on pallets used for international shipping (APHIS 2022).

Mature trees and seedlings can be impacted by native *Armillaria calvescens* Bérubé & Dessureault (Bauce and Allen 1992), anthracnose (*Glomerella cingulate* (Stoneman) Spauld. & H. Schrenk), and leaf spot fungi such as *Cristulariella depraedans* (Cooke) Hohn (Gardescu 2003). Cankers caused by *Eutypella parasitica* Davidson and Lorenz usually occur on the lower bole (Kessler and Hatfield 1972, Kliejunas and Kuntz 1974). Other factors contributing to decline episodes in sugar maple stands include drought coupled with prior defoliation events (Horsley et al. 2002, Payette et al. 1996), climatic factors (Bauce and Allen 1991), and nutrient stress in New England (Bal et al. 2015) and Pennsylvania (Bailey et al. 2004).

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Acknowledgments

The authors thank Christel Kern (USDA Forest Service, Northern Research Station) for providing images and Steve Katovich (USDA Forest Service, Forest Health Protection) for providing insight on forest health issues.

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

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Abstract

Black walnut (*Juglans nigra* L.) is a shade-intolerant hardwood tree common in riparian forests across the Central United States. Commercial values for top-quality black walnut logs are the highest for any tree in North America. Production of juglone from walnuts may have phytotoxic effects on neighboring plant communities. Genetic diversity of this species is high due to seed dispersal and pollen flow characteristics,while population structure is low. Common garden studies revealed relatively weak clines for growth traits but strong latitudinal gradients for cold tolerance. Seed transfer distances of 200 mi (322 km) from south to north, or roughly 2 degrees latitude northward, is considered a safe recommendation to maintain growth. At the northern edge of the species' range, such as Minnesota, local sources are best. Leaf anthracnose is an important pest, and thousand cankers disease can be a concern, especially in drought-prone areas. Black walnut is likely to expand northward with climate change, but its migration may require human assistance, and such expansion may be limited by soil conditions, site availability, deer browse, or drought.

Introduction

Black walnut (*Juglans nigra* L.) is a highly valued, long-lived, early successional hardwood tree species that grows in riparian areas (bottomlands) across much of the Central and Southern United States into upstate New York and New England, spanning plant hardiness zones 3 through 9 (U.S. Department of Agriculture, Agricultural Research Services 2012). While it is classified as a shade-intolerant species, saplings can survive under light to medium shade, although growth under these conditions is not suited for commercial production (Carpenter 1974). Black walnut grows best on well-draining sandy or silt loams (Losche 1973) and may also grow on mineland soils or spoils if nutrition and drainage are adequate (Ashby 1996). On optimal sites, black walnut exhibits rapid growth, but is notoriously sensitive to site and soil conditions. On sub-par sites, black walnut grows slowly, and mortality is high. Natural regeneration is severely impacted by heavy grass competition, especially fescue (*Festuca* spp.) (Krajicek 1975). Therefore, both careful site selection and control of competing grass vegetation is critical for black walnut plantings to be successful (Smith 1983), especially for those grown for timber (figure 1).

Black walnut's darkly colored bark and deep fissures distinguish it from the lighter gray bark plates of butternut (*Juglans cinerea* L.) (Farlee et al. 2010).

Figure 1. A plantation of black walnut managed for future timber requires intensive care to ensure that it will thrive. (Photo by M. Coggeshall, USDA Forest Service, 2005)

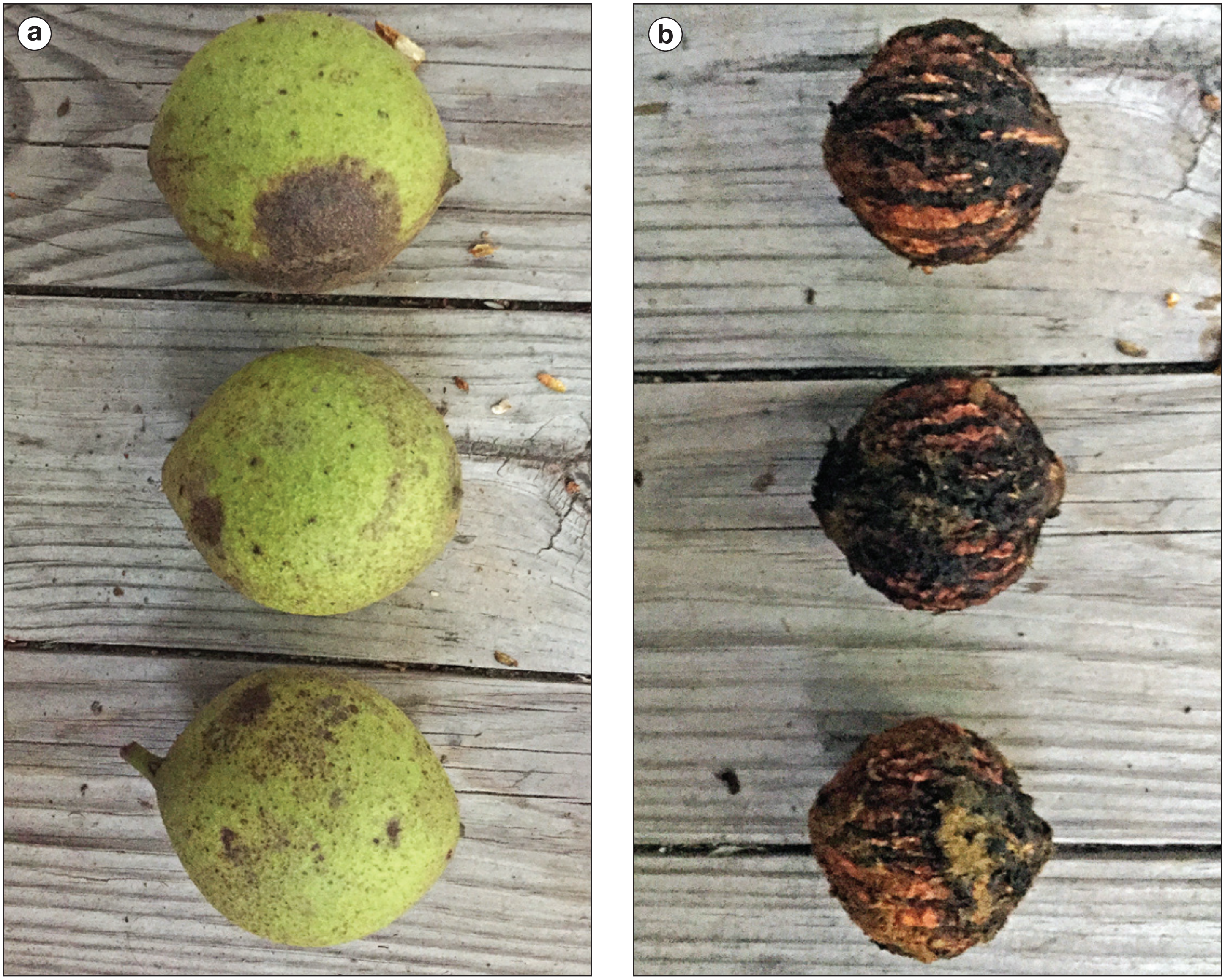

Figure 2. Three black walnuts are shown (a) before and (b) after the husk is removed. (Photos by Aziz Ebrahimi, Purdue University, 2021)

In addition, black walnut's fruits are generally round-shaped and hairless (figure 2) in contrast to the oblong, hairy, and sticky fruits of butternut (Farlee et al. 2010). Black walnut is valued for veneer (figure 3), with board-foot values frequently exceeding those for black cherry (*Prunus serotina* Ehr.) and nearly double those for oak (*Quercus* spp.), which, in many years, is the second most valuable hardwood in the central hardwood region (Settle and Gonso 2020). Black walnut is also cultivated for its edible nuts (Coggeshall 2011, Reid et al. 2009) (figure 4).

Black walnut is sympatric with other riparian, mesophytic hardwoods such as yellow poplar (*Liriodendron tulipifera* L.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), basswood (*Tilia americana* L.), beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marshall), oaks, and hickories (*Carya* spp.) (Williams 1990).

Black walnuts are notable for the production of juglone, a chemical that has allelopathic properties that can inhibit the growth of some neighboring plants, such as crimson clover (*Trifolium incarnatum* L.) and the nonnative amur honeysuckle (*Lonicera maackii* Maxim.) (Rietveld 1983). Phytoxicity on native trees is reported for white birch (*Betula papyrifera* Marshall) (Gabriel 1975) and, to a lesser extent, on eastern white pine (*Pinus strobus* L.), with such effects amplified on sites with poor drainage and lower plant vigor (Rietveld 1983). Juglone can inhibit growth of conifer seedlings, but in small quantities it can stimulate their growth (Funk et al. 1979).

Figure 3. This veneer of black walnut is a good representation of a highly valued timber product from this species. (Photo by M. Coggeshall, USDA Forest Service, 2009)

Figure 5. The immature catkins (male flowers) of black walnut will dry prior to opening and releasing pollen. (Photo by M. Coggeshall, USDA Forest Service, 2003)

The phylogeny of the genus *Juglans*, which includes both butternuts and walnuts, is complex because it traverses multiple continents and is divided into three sections based on origin, but not present locality. For example, black walnut occurs in the Rhysocaryon section which includes all New World walnuts, while butternut is part of the Cardiocaryon section, which is otherwise entirely Asian (Aradhya et al. 2006a, b; Aradhya et al. 2007). Although they co-occur, butternut and black walnut cannot hybridize because of their distinct phylogeny. One glacial refugium, in the lower Mississippi Valley, is supported by the genetics of extant trees, with no evidence of postglacial bottlenecks (Victory et al. 2006). Black walnut is likely to persist in its present range owing to its high genetic variation and its ability to produce and disperse seeds. Its shade and drought intolerance, however, may limit its growth or survival on sites where such conditions predominate (Morin et al. 2007).

Figure 4. This large bag of black walnuts was collected from a seed orchard. Black walnuts are best picked from the ground rather than directly from the tree. (Photo by M. Coggeshall, USDA Forest Service, 2004)

Genetics

Black walnut is a monoecious diploid, with outcrossing enforced by pronounced dichogamy (i.e., female and male flowers are produced at different times on a tree). Cultivars and clones may be distinguished by their consistent timing of peak male (figure 5) and female bloom (figure 6) (Ebrahimi et al. 2018, Pang et al. 2021), which has implications for breeders and may lead to Wahlund effects, or nonrandom breeding within stands or orchards (Robichaud et al. 2006). Black walnut is characterized by especially high genetic variation and low population structure based on nuclear microsatellites, with F_{ST} values (a ratio of genetic variation between subpopulations and the total population) near 0.017 (Victory et al. 2006). Despite the fruit's large size (figure 7), seeds and pollen are readily dispersed. Few detectable differences in fruit size occur among populations. One study showed that nuts from northern provenances had lower fresh weight than nuts from southern provenances, but no association was found between nut size and fresh weight or seedling vigor (Funk and Polak 1978).

Figure 6. After pollination, the female flowers of black walnut will develop into a nut inside an outer husk. (Photo by Keija Pang, Purdue University, 2011)

The success of black walnut seed and pollen dispersal may be attributed to several factors including small mammals (mainly squirrels), hydrochory (i.e., nuts can float and move long distances on rivers), and high levels of wind-dispersed pollen movement. Genetic diversity of neutral alleles is lower in northern populations compared with southern populations, but these latitudinal-based differences account for less than 10 percent of genetic variation (Victory et al. 2006).

Black walnut's high commercial value has led to decades of research on genetics and genetic improvement for artificial reforestation with this species (Beineke and Masters 1973, Mckenna and Coggeshall 2018, Mckenna and O'Connor 2014, Michler et al. 2004). Beineke (1972) speculated that inbreeding from high-grading could be a cause for concern, but merchantable value was not associated with rare alleles that would be lost by thin-from-above practices (Robichaud et al. 2010). Efforts to improve stem form (straightness for log quality), heartwood color, and growth continue today at the Hardwood Tree Improvement and Regeneration Center at Purdue University (West Lafayette, IN).

Figure 7. This abundant black walnut fruit crop is maturing on a grafted tree in a seed orchard. (Photo by M. Coggeshall, USDA Forest Service, 2003)

Seed-Transfer Considerations

A series of provenance trials highlighted clinal variation in black walnut, especially for variation between extreme sites (Bey 1976). Cold tolerance, which is a limiting factor for seed transfer, also varies clinally and latitudinally, with 40 percent of height growth attributed to latitude alone (Williams et al. 1974). Cessation of late-season growth is more differentiated than budbreak timing in the spring. Bey et al. (1971) found that southern sources started growing 3 days earlier and continued for 2 weeks longer than northern sources. Leaf fall is also strongly associated with latitude.

Optimal seed-transfer distances depend, in part, on the location of the planting site relative to the range edge. Populations along the southern range edge may experience insufficient chilling hours to break bud dormancy (Morin et al. 2007), especially if northern sources are moved south two or more USDA Hardiness Zones (e.g., from zone 5 to zone 7) (U.S. Department of Agriculture, Agricultural Research Service 2012). Published seed-transfer zones for black walnut have not been widely implemented (Deneke et al. 1980), but sources from up to 200 mi (322 km) south of the planting site are recommended for production forestry, except in extreme northern sites where local sources are best (Bey et al. 1971, Bey 1980, Bresnan et al. 1994, Clausen 1983, Rink and Van Sambeek 1988, Wendel and Dorn 1985). The improvement in growth attained by planting southerly sources may be due to an extended growing season because southern sources flush earlier and drop leaves later than northern (or local) sources when moved northward (Bey et al. 1971). For restoration, managers may consider combining local sources with sources from as far as 200 mi (322 km) south of the planting site to ensure that seedlings have sufficient cold tolerance to survive and thrive on the site. See table 1 for a summary of seed-transfer considerations.

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

	Black walnut, *Juglans nigra*
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Large, hard, recalcitrant seeds can be freezer stored for 2 to 3 years; seeds can be sown with husk intact (Rink 1988) • 11 to 100 cleaned seeds per pound (25 to 220 per kg) (Bonner 2008)
Insect and disease	• Anthracnose (leaf disease) • Thousand cankers disease (vectored by walnut twig beetle) may become problematic with increasing drought • Shoot borers and ambrosia beetles can cause dieback and degrade form, especially in stressed trees
Palatability to browse	• Browse and antler rub slow growth and degrade value where white-tailed deer pressure is high
Maximum transfer distances	• 200 to 300 mi (322 to 483 km) from south to north is recommended to maximize growth • Local sources are recommended for reforesting along the northern range edge
Range-expansion potential	• Likely to migrate northward, but may be limited by soil and moisture conditions • Phytotoxicity of juglone may affect understory or adjacent plant communities

Black walnut exhibits sensitivity to local climate. Average July temperature and length of growing season were strongly correlated with height growth of 15-year-old trees, compared with other factors such as January temperature and annual precipitation (Smith 1983). Cold temperatures during the active growing season are more important than nadir winter temperatures because fully dormant tissues across provenances are cold hardy to extreme temperatures (George et al. 1977). Rainfall is an important determinant of height growth during periods of active growth (Bey et al. 1971), whereas temperatures of air and soil are more important for determining diameter growth (Bey et al. 1971). In provenance trials, mean annual temperature of the seed source also explained strong clines in tree heights (Leites et al. 2019).

Insects and Diseases

Black walnut has many minor pests and pathogens that feed on foliage, roots, fruit, and stems. These pests can reduce commercial value, but few currently pose major health risks. Several summaries of insect and disease pests have been published and are recommended for more detailed information (Katovich 2004, Mielke and Ostry 2004, Miller 1973).

Insect pests include shoot borers such as *Acrobasis demotella* Grote, which can reduce the dominance of the apical stem and degrade commercial value, but generally do not threaten survival (Katovich 2004). Other shoot borers (e.g., *A. caryivorella* Ragonot and *A. juglandis* LeBaron) feed on black walnut buds, emerging shoots, and leaves, but are usually less common than *A. demotella* (Miller 1973). Ambrosia beetles (*Xylosandrus germanus* [Blandford]), can attack healthy or declining trees causing dieback and sprouting from the tree's base (Katovich 2004). The shoot moth (*Gwendolina concitatricana* Heinrich) can injure or kill terminal buds, reducing commercial value. Walnuts are a favored food source for numerous other insects such as curculios, weevils (e.g., *Conotrachelus retentus* Say) and husk flies (*Rhagoletis suavis* Loew) (Miller 1973), which can become problematic in seed orchards. Lepidopterans may be commonly found on walnuts (Nixon and McPherson 1977), but usually pose few threats to tree health except for walnut caterpillar (*Datana integerrima* Grote & Robinson), which can become locally abundant in certain years and degrade tree vigor (Farris et al. 1982).

Anthracnose (*Gnomonia leptostyla* [Fr.] Ces. & De Not.), the most important foliar disease of black walnut, causes leaves to drop prematurely on susceptible trees, but its association with reduced growth is still not solidly established. Walnut bunch disease, or walnut witches'-broom, believed to be incited by a mycoplasma like organism (Chen et al. 1992), is less common than anthracnose but can lead to stunted crowns and mortality (Berry 1973). *Phytophthera citricola* Sawada, *Cyclindrocladium* species, *Pythium* species, and *Fusarium episphaeria* (Tode) W.C. Snyder & H.N. Hansen, are root pathogens generally associated with mortality of black walnut seedlings growing in nurseries. These root pathogens can be difficult to control even with fumigation (Berry 1973). Thousand canker disease (*Geosmithia morbida* M.Kolařík, E.Freeland, C.Utley, & Tisserat) vectored by walnut twig beetle (*Pityophthorus juglandis* Blackman) (Grant et al. 2011, Sitz et al. 2021) may pose a threat in the future in areas that experience persistent drought such as parts of the Western United States where black walnut is not native (Tisserat et al. 2011).

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Acknowledgments

The authors thank Steve Katovich (USDA Forest Service, State and Private Forestry, Forest Health and Protection) for reviewing the manuscript and to Mark Coggeshall (USDA Forest Service, Northern Research Station, emeritus), Keija Pang, (former Ph.D. student, Purdue University), and Aziz Ebrahami (Purdue University) for providing images.

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

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Abstract

Eastern white pine (*Pinus strobus* L.) is an iconic component of cool-temperate, mixed broadleaf/conifer forests and southern boreal forests in eastern North America. This species has moderate shade tolerance and broader site preferences than most northeastern North American conifers. Genetic diversity of eastern white pine is high at the species and population levels, as expected given its life-history characteristics (i.e., a wind pollinated, obligate outcrosser with a long lifespan). Seeds sourced from far south of the planting site tended to perform best in progeny tests, suggesting long-distance seed transfer is possible. Sources from the southern Appalachians, however, experienced cold damage at northern test sites. Transfer distances of 200 mi (322 km) northward are considered safe for assisted migration, although longer transfers may be safe if they do not cross the floristic tension zone between the boreal and temperate forest. There are no known population-level differences for resistance to common insects or diseases or resistance to herbivory, but assisted migration is best avoided in areas with severe white pine blister rust where local sources selected for blister-rust resistance will remain optimal.

Introduction

Eastern white pine (*Pinus strobus* L.) is a large, long-lived coniferous tree, occurring naturally on a wide range of sites in northeastern North America. Its native range includes nearly the entire Appalachian Mountain system from far northern Georgia through New England to Newfoundland; southern Québec and Ontario; the Cumberland and Allegheny plateaus; most of the Great Lakes Basin; and the upper Mississippi River watershed in Minnesota and Wisconsin. In scattered locations in southern Wisconsin, Iowa, Illinois, Indiana, and Kentucky, stands of native eastern white pine occur outside the main range boundary on suitable sites, usually in areas where eroded sandstone is close to the surface (McIntosh 1948). Eastern white pine is an ecological keystone species; large, long-lived white pines add habitat elements and structural complexity (figure 1) that critically support large wildlife species like

Figure 1. Eastern white pine is a large, long-lived tree species. This photo in a northern Minnesota mixed-species forest shows typical crown outline and great height of eastern white pine. (Photo by Steve Katovitch, USDA Forest Service, 2018)

osprey, bald eagle, and black bear (Latremouille et al. 2008, Rogers and Lindquist 1992).

Eastern white pine was heavily logged from colonial times (in New England) until the early 1900s (in the western Great Lakes), which reduced its abundance and eliminated most large, old specimens. The lumber is light and easily worked but strong for its weight, which made it prized for shipmasts, construction lumber, flooring, siding, and many other uses (Peattie 1948). Eastern white pine may be considered a cultural keystone species for Indigenous societies, who use parts of the tree medicinally and recognize its importance to other beings, including bald eagles and fur-bearing mammals (Uprety et al. 2013). Eastern white pine also has symbolic significance to Native peoples as an especially majestic and distinctive tree (e.g., Uprety et al. 2013) and as a "tree of peace" to the Iroquois (Schroeder 1992).

Eastern white pine occurs on a broad range of sites in boreal and broadleaf forest ecosystems (Abrams 2001, Wendel and Smith 1990). In general, this species grows best on well-drained sites with ample fertility but competes best on sites with average to below average fertility. In the warmest parts of its range, eastern white pine occurs as groves or scattered trees within a matrix of dry-mesic to mesic hardwood or hemlock/hardwood forest types, often in areas with steep topography (figure 2). The trees may form a supercanopy where scattered individuals exceed the height of surrounding hardwoods. White pine does not form single-species stands naturally but may dominate extensive areas in the northern part of its range on well-drained, rocky or sandy loam soils. A good surviving example of this occurrence is the Menominee tribal forest in northeastern Wisconsin, which escaped clearcutting during the cutover era. On drier sites, especially on outwash plains, eastern white pine is a component of mixed stands with red pine (*Pinus resinosa* Aiton) and/or jack pine (*P. banksiana* Lamb.), although it does not occur on the driest sands. In the northernmost parts of its range, eastern white pine is an element of boreal forests dominated by aspen (*Populus* spp.), birch (*Betula* spp.), fir (*Abies* spp.), and spruce (*Picea* spp.) (e.g., Engelmark et al. 2000). Finally, despite its overall preference for drier sites, eastern white pine frequently occupies less saturated microsites within conifer swamps and may even be a dominant species in some wet forests (e.g., the Pinhook Bog in northern Indiana).


Figure 2. Eastern white pine can be found growing with hardwoods, such as this sandy upland site in northern Indiana. (Photo by Nick LaBonte, 2022)

Eastern white pine is more shade tolerant than red pine and jack pine, which allows it to persist in canopy gaps and somewhat sunny microsites such as steep slopes or rock outcrops in hardwood-dominated forests. Seeds germinate best with access to mineral soil. Eastern white pine is less resistant to fire damage than red pine when mature, and it does not have serotinous cones like jack pine, so it is adversely affected by high-intensity fires. While individual trees may be injured or killed by fire, occasional fire had an overall positive effect on maintaining the dominance of eastern white pine (often alongside red pine) in the "pineries" of the Great Lakes region by eliminating hardwood and shrub competition and maintaining ideal seedbed conditions (Heinselman 1973).

Like all pines, eastern white pine produces seed cones on a 2-year cycle. The first-year cones are relatively easy to see from the ground and may be used for advance forecasting and seed collection planning during the period between the hardening-off of new shoots

Figure 3. Eastern white pine cones require 2 years to mature. These first-year cones are at the start of their second growing season. (Photo by Nick LaBonte, 2022)

in their first fall and the initiation of new growth in the spring (figure 3). When cones mature in their second year, cone scales open and disperse mature, winged seeds rapidly, usually in late August or early September (figure 4). Because of the short window between eastern white pine seed maturity and dispersal and the great height of seed-bearing wild trees, managed seed-production plantings are an especially important tool for maintaining a supply of seed (figure 5). Eastern white pine is a preferred browse species (Wendel et al. 1990) and may be damaged by white-tailed deer, moose, and hare. Protection during winter using bud-capping or other strategies may be needed for successful establishment. Fencing may be effective over small areas.

Figure 4. Eastern white pine can produce heavy cone crops as seen here on the Superior National Forest in Minnesota. (Photo by Ryan Pennesi, USDA Forest Service, 2020)

Figure 5. Seed orchards are important for production of eastern white pine seed, such as this grafted eastern white pine at the USDA Forest Service, Oconto River Seed Orchard, northern Wisconsin. (Photo by Paul Berrang, USDA Forest Service, 2003)

Genetics

Eastern white pine is closely related to western white pine (*Pinus monticola* Douglas ex D. Don), limber pine (*P. flexilis* James), and the five-needled pines of Mexico and will form hybrids with these relatives when in close proximity (Critchfield 1986), but there are no natural range overlaps that provide opportunities for hybridization in the wild. The most recent common ancestor of eastern white pine and its western relatives probably lived 15 to 20 million years ago (Jin et al. 2021). Eastern white pine is documented in the southern Appalachians during the last glacial maximum along with many of its present-day associates (Jackson et al. 2000); this population was probably the sole glacial refugium for the species (Nadeau et al. 2015). Large-scale genetic differences across the native range of eastern white pine likely originated as different sets of lineages became postglacial colonizers east and west of the Appalachians. These genetic lineages are most obvious in chloroplast DNA (Zinck and Rajora 2016) but can be identified in the nuclear genome as well (Nadeau et al. 2015, Rajora et al. 2016). As a result of this recolonization process, the eastern white pine lineage in the western Great Lakes States is distinct from the northeast and southern parts of the species' range (Zinck and Rajora 2016).

Eastern white pine retains high levels of genetic variation, genetic diversity, and heterozygosity throughout its range, even in isolated populations (Rajora et al. 1998). Most genetic variation is distributed within populations while a small, but significant, amount is distributed among populations ($F_{ST} = 0.06$ to 0.10 based on microsatellite and allozyme estimates) (Nadeau et al. 2015, Rajora et al. 2016). Genetic differentiation is more substantial when a larger part of the range is sampled (Zinck and Rajora 2016). Eastern white pine is an outcrossing species and suffers from inbreeding depression when self-pollinated (Johnson 1945, Patton and Riker 1958). Overall genetic diversity remains high despite intensive harvesting from 1850 to 1910, suggesting that the species did not experience a genetic bottleneck. The effect of harvesting on genetic variation in eastern white pine is unclear. Recent research indicates harvesting may have a neutral effect, reduce inbreeding (Marquardt et al. 2007), or have a negative effect on local genetic diversity (Buchert et al. 1997).

Seed-Transfer Considerations

There is extensive literature on eastern white pine provenance testing, and the results of the many studies tell a consistent, but complex, story about the deployment of eastern white pine seed. In general, a few seed sources outrank others in height growth in a wide variety of locations, and local sources may not display the most rapid growth. In the Lower Peninsula of Michigan, seed sources from the western and central Lower Peninsula grew faster than sources from the Upper Peninsula or the Lake Huron side of the Lower Peninsula (Wright et al. 1969). In the Northeastern United States, seed sources from the southern Appalachians had the greatest height after 10 years as far north as Pennsylvania, but New York and Pennsylvania sources did better farther north in Massachusetts and Maine (Garrett et al. 1973). In Iowa and Ohio, sources from lower Michigan, Tennessee, and Georgia were the best performers after 16 years of growth (Funk 1979). Michigan provenances also performed well in Maryland (Genys 1983). In Québec, Northeastern United States, Michigan, and southern Ontario sources performed well, although some provenances from these areas were not top performers (Beaulieu et al. 1996). The tendency of some lower Michigan provenances to grow rapidly extends as far as Germany (Stephan 2004).

In northern locations such as the upper Great Lakes, southern seed sources of eastern white pine are vulnerable to cold damage, but sources may move hundreds of miles north before a cold-hardiness penalty to survival and growth is observed (Lu et al. 2003). In multiple genetic trials, sources from south of the planting site were the best performers (Fowler and Heimburger 1968, Funk 1971, King and Nienstaedt 1968). Synthesizing climate models and eastern white pine provenance tests, Joyce and Rehfeldt (2013) illustrated potential seed movement zones under different warming scenarios. In general, their acceptable movement distance was longest in the Appalachian Mountains and somewhat shorter (~200 mi [322 km]) near eastern white pine's range limit in the western Great Lakes where a strong climatic gradient creates a floristic tension zone between the boreal and temperate forests. Summer warmth (degree days) and mean minimum temperature are both predictive of performance of eastern white pine seed sources in rangewide tests (Joyce and Rehfeldt 2013), which indicates that obtaining seed from up to several hundred miles south of the planting site is a good practice. Summer moisture stress, snowfall, and vulnerability to storm and cold damage in spring and fall are all likely to influence eastern white pine radial growth (Chhin et al. 2018). Eastern white pine's shade tolerance and ability to grow on a range of sites enhances its adaptability to climate change according to the Climate Change Tree Atlas (Peters et al. 2020). The ability to establish and grow on a wide range of sites may allow eastern white pine to migrate more effectively than similar species like red pine or jack pine that are dependent on specific site conditions for recruitment. In addition, eastern white pine's high genetic diversity and large native range give it evolutionary tools, in the form of genetic variation and adaptive potential, that make it more likely to thrive in a changing climate than most other Northeastern North American conifers.

In summary, white pine seed can be transferred over large distances without negative impacts on survival and growth with a few caveats (table 1). Sources from south of the planting site are likely to perform as well or better than local sources, and sources more than 200 mi (322 km) from the planting site are susceptible to cold damage if they are brought north of the ecological tension zone. Broadly speaking, transfer within the boreal and mixed-broadleaf biomes is acceptable, but transfer between the two, near the tension zone, should be limited to 200 mi (322 km).

Insect and Disease

Eastern white pine is affected by numerous native and nonnative pathogens and insects which have contributed to reducing its ecological and economic value in the post-cutover era (Wendel and Smith 1990). White pine blister rust, introduced in the early 1900s, is a damaging, nonnative disease that spends part of its lifecycle on gooseberry and currant shrubs in the genus *Ribes*, where it causes minor foliar symptoms, and completes reproduction on five-needle pines as a parasite of live tissue. In susceptible pines, infections cause needle and twig dieback and necrotic bark cankers that can be large enough to girdle branches (figure 6) or kill young trees outright. These cankers produce characteristic bright orange fruiting structures in spring. Risk of pine infection is highest in areas where *Ribes* species are abundant with cool, humid conditions prevalent in late summer and early fall (Ostry et al., 2010).

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

Eastern white pine, ***Pinus strobus*** **L.**	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Cones not serotinous, 0 to 73 winged seeds per cone • Most seeds release in late August to early September • 26,500 seeds per pound (58,400 seeds per kg)
Insect and disease	• Major pests: white pine blister rust and white pine weevil • Others: heterobasidion root disease, armillaria root rot, white pine cone borer, white pine sawfly
Palatability to browse	• A preferred food of white-tailed deer in winter over much of its range; also targeted by rabbit, hare, and moose • White pine may be heavily browsed
Maximum transfer distances	• Seed sources originating up to 200 mi (322 km) south of the planting site will likely perform as well or better than local sources; longer distance transfer possible in certain areas (see text) • Unique gene pool in western Great Lakes; seed transfer southward not recommended
Range-expansion potential	• Likely to expand northward; may lose habitat in southern part of range • Shade tolerance and broad site preferences may create opportunities for persistence and even localized population expansion

Eastern white pine harbors naturally occurring resistance to white pine blister rust. Thus, an effective disease response can be passed from parent trees to offspring (Pike et al. 2018). While it was initially thought that the species was uniformly susceptible, refinements to resistance screening protocols revealed that blister rust resistance could be improved through breeding in eastern white pine, even though it does not possess major gene resistance as found in some western North American white pines (King et al. 2010, Merrill et al. 1986). Prevailing weather conditions and local climate are only conducive enough to blister rust spread and development to limit eastern white pine establishment in localized areas of eastern North America, such as the Lake Superior shoreline in Minnesota and Wisconsin, but improved blister-rust resistant lines are suitable for planting in high-risk areas if they are available.

Root rots caused by *Armillaria mellea* and *Heterobasidion annosum* can also damage eastern white pine (Costanza et al. 2018), especially in areas where hardwood (*Armillaria*) and conifer (*Heterobasidion*) stumps are present near young eastern white pines. The dyer's

Figure 6. Eastern white pine shows branch flagging due to white pine blister rust as seen in this stand on the Superior National Forest in Minnesota. (Photo credit: Paul Berrang, USDA Forest Service, 2007)

polypore (*Phaeolus schweinitzii*) is a native fungus that causes a destructive, brown butt rot in mature eastern white pine (Wendel and Smith 1990).

The most damaging insect to affect eastern white pine is the white pine weevil (*Pissodes strobi*), which can result in multiple leaders and a rounded crown, especially in low-density, open-grown areas (Wendel and Smith 1990). Adults typically fly less than 35 ft (10.7 m) above the ground and seek out robust terminal leaders associated with fast-growing trees. The adult lays eggs near the terminal shoot where subsequent feeding by larvae kills the terminal, resulting in decreased growth, multiple leaders, and rounded crown (Ostry et al., 2010). Trees taller than 35 ft (10.7 m) or those with decreased leader diameter due to shaded or partially shaded conditions typically are not impacted. Other impactful insect pests include several additional species that attack shoots and twigs: European pine shoot moth (*Rhyacionia buoliana*), eastern pine shoot borer (*Eucosma gloriosa*), and white pine aphid (*Cinara strobi*); defoliating sawflies (*Neodiprion pinetum* and *Diprion similis*); insects that attack wood and vascular tissue, including Zimmerman pine moth (*Dioryctria zimmermani*) and pine root collar weevil (*Hylobius radices*); and the white pine cone borer (*Eucopina tocullionana*), a moth that specifically attacks developing cones and can devastate seed crops, thereby negatively affecting natural regeneration and cone crops in seed orchards (Costanza et al. 2018, Goulding et al. 1988). In addition to these biological agents, eastern white pine is susceptible to ozone damage, although this is a problem localized to areas near major cities and is not a concern in most of the native range (Costonis and Sinclair 1969).

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Establishment and Management of Showy Milkweed in Idaho's Snake River Plain

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Abstract

Milkweed (*Asclepias*) species are necessary for monarch butterflies (*Danaus plexippus* L.) to complete their lifecycle. Strategies to boost monarch populations include establishing and maintaining milkweed stands throughout their range. The Aberdeen Plant Materials Center conducted a series of studies to investigate methods to establish new milkweed populations and to manage existing milkweed populations for optimum monarch habitat. In the first study, milkweed rhizomes were sorted into various size classes and planted into greenhouse conditions to determine the viability of each class. All size classes showed at least some viability, indicating that wild-collected rhizomes may be an effective means of stand establishment. In the second study, four planting treatments, including spring and fall seeding, greenhouse transplants, and rhizomes, were evaluated in a field planting to compare establishment levels. All treatments showed good establishment ranging from 27 to 79 percent. Finally, we compared plant response to 2 years of three management strategies (mowing, burning, and a nontreated control). Management strategies did not result in significant differences in milkweed stem densities.

Introduction

Milkweeds (*Asclepias* spp.) are highly valuable species in western North American riparian and wetland ecosystems, offering a pollen and nectar source that is used by numerous native insects. Milkweeds are valuable in attracting beneficial insects in agricultural systems (Fiedler et al. 2008, James et al. 2016). As such, members of the genus are desirable for conservation and promotion of native pollinators (Borders and Lee-Mäder 2014, Landis and Dumroese 2015, Waterbury and Potter 2018). Despite their value, milkweed populations are in notable decline due to increased chemical use and agricultural and urban expansion. Perhaps of greatest importance is milkweed's critical role as the larval food source for monarch butterflies (*Danaus plexippus* L.).

The monarch butterfly is a widely recognized and iconic species in North and Central America. Western monarch populations winter in Mexico and southern California and then migrate north through California and several western States through the spring and summer. Despite once being abundant on the landscape, populations have been in steady decline for decades. For example, Thanksgiving counts conducted by volunteers of the Xerces Society on the California coast have indicated dramatic reductions in recent years (Pelton 2017, Xerces Society 2020). The species has been petitioned for listing as an endangered species under the Endangered Species Act. That listing was deemed warranted yet precluded by higher priority actions (USDI Fish and Wildlife Service 2020). Reasons cited for declining monarch numbers include habitat loss in several key areas of its migration, such as forest loss in the monarch winter range in Mexico and habitat loss along the California coast due to urbanization. Changes in the landscape have also reduced key host plant species throughout the monarch summer range (Flockhart et al. 2015, Halsch et al. 2020, Pleasants and Oberhauser 2013).

Monarch butterflies are entirely dependent on milkweed species for reproduction and completing the summer stretch of their migration. Adult females lay eggs strictly on milkweed plants, which the caterpillars then feed upon (figure 1). The chemicals within the plant tissues are taken up by the caterpillars

Figure 1. Monarch butterflies lay their eggs exclusively on milkweed. The caterpillars then feed on the plant tissue, such as the two in this photo feeding on showy milkweed in southern Idaho. (Photo by Derek Tilley, 2016)

making them unpalatable to birds and other predators. Milkweed species also provide a critical nectar and energy source for the adult monarch's late-summer migration (Alonso-Mejia et al. 1997). Many efforts are currently underway to reintroduce milkweed species for monarch recovery and to support general pollinator habitat (Tilley et al. 2018).

Idaho's Snake River Plain (figure 2) has recently been recognized as an important waypoint in the lifecycle of the western monarch (Dumroese et al. 2016). Numerous monarchs pass through this corridor in summer after leaving the Pacific coast in the spring. Showy milkweed (*Asclepias speciosa* Torr.) (figure 3), the most widespread milkweed species in the region, was once common in semiarid uplands, wetlands, flood plains, and meadows below 1,830 m (6,000 ft) elevation throughout much of the Snake River Plain and Northern Basin and Range ecoregions (Welsh et al. 2003). In the Intermountain West, however, showy milkweed populations are increasingly limited to creek sides, canals, and disturbed areas that may or may not be sprayed with chemicals or mowed regularly. Creation of new milkweed habitat and conservation of patches already on the landscape, therefore, are key to monarch preservation in the Western United States.

Showy milkweed is a native, herbaceous perennial that readily grows from widespread rhizomes, producing stems averaging 45 to 150 cm (1.5 to 5 ft) tall in summer. The gray-green leaves are opposite, 10 to 18 cm (4 to 7 in) long, oval, and covered in velvety hairs. The stems and foliage exude the namesake's milky latex sap when cut. Rose-purple flowers are situated in loose clusters at the top of

Figure 2. The Snake River Plain ecoregion in southern Idaho (Omernik and Griffith 2014) is an important corridor in the western monarch butterfly summer migration. The field experiment described in this paper is located in Aberdeen, ID, indicated by the blue star. (Source: U.S. Environmental Protection Agency, 2021)

Figure 3. Showy milkweed is widespread in the Snake River Plain and can be found growing in wet meadows and on streambanks and canals throughout the region. (Photo by Derek Tilley, 2018)

the stems. Showy milkweed flowers bloom from May to September and resemble crowns, with the corolla (petals) reflexed and hoods above the corolla. The fruit is a large pod, 8 to 13 cm (3 to 5 in) long, which splits down one side in fall to release reddish-brown, flat seeds. Each seed has a tuft of white, silky hairs (coma) that allows it to be dispersed by wind.

Establishment of showy milkweed in pollinator seed mixtures and other conservation plantings has been discouraging (Bullard et al. 2020). As a result of limited establishment success from seeding, alternative establishment methods are being explored. Greenhouse grown transplants, for example, can be a useful means of establishment. While more expensive than seed, transplants often have higher percent establishment and are more reliable than seeding. For example, Bullard et al. (2020) observed significantly higher establishment from late-spring transplants than fall-seeded showy milkweed in central California.

Showy milkweed produces large, fleshy rhizomes that may be a useful means of vegetative propagation (Tilley et al. 2018, Welsh et al. 2003). Large clonal stands are common in sandy soils. In heavier soils, the plants produce large-crowned taproots from which multiple stems arise. These rhizomes can reach over 1.2 m (4 ft) in length (figure 4) and could potentially be divided into numerous smaller sections, which could then be used for greenhouse or field establishment. Rhizomes might also offer the advantage of being planted deeper into the soil and therefore being less susceptible to drying periods that limit establishment from seed. Establishment from rhizomes could further be valuable in establishing mature plants quickly. Bullard et al. (2020) observed significantly greater establishment of fall-planted rhizomes compared with fall seeding of showy milkweed in California's Central Valley. They also found that plants grown from rhizomes were significantly taller than seeded materials after the second year of growth.

Maintaining and promoting milkweed stands may require specialized management strategies. The effects of various management treatments on stand persistence are unknown. Weed management recommendations in milkweed habitat typically include mowing late in the fall when monarchs have left the region (Borders and Lee-Mäder 2014) or early in the

Figure 4. Showy milkweed produces large, fleshy rhizomes that can offer a means of vegetative propagation. (Photo by Nathaniel Tilley, NRCS Earth Team, 2017)

spring before plants have come out of winter dormancy (Tilley et al., 2018). Early spring canal burning is a common practice throughout the Snake River Plain. This practice may be beneficial because burning often occurs before milkweeds have begun to emerge. Showy milkweed germinates and resprouts at warmer temperatures and thus later in the spring than many of its cohabitants (Borders and Lee-Mäder 2014). Heat transfer from burning and changes in species composition and density from mowing may, however, negatively affect milkweed rhizomes and seedlings.

Due to concerns regarding habitat loss in the western migration route of monarch butterflies, we conducted greenhouse and field trials to investigate establishment and management strategies for native milkweed.

Materials and Methods

In 2016 and 2017, the U.S. Department of Agriculture (USDA), Natural Resources Conservation Service (NRCS), Aberdeen Plant Materials Center (IDPMC; Aberdeen, ID) initiated multiple studies to examine establishment and management techniques for installing and supporting milkweed stands for monarch butterfly habitat.

Rhizome Viability

In the first study, we evaluated the viability of showy milkweed rhizomes for use in establishing new stands. On March 17, 2017, we dug rhizomes from a native stand near Rupert, ID, and cut them into segments that fell into two categories: root crowns (a thickened, but not elongated, area where the stem joins the root) and elongated spreading rhizomes. Crown segments were divided into small (< 25 mm diameter) and large (> 25 mm diameter) sizes. Elongated rhizomes were divided into six sizes (diameter by length): 3 by 100 mm, 6 by 50 mm, 13 by 50 mm, 13 by 100 mm, 20 by 25 mm, and 20 by 100 mm (1 in = 25 mm; figure 5). We then planted these into 30- by 45- by 8-cm (12- by 18- by 3-in) greenhouse flats filled with a peat and perlite growing medium (Sunshine Mix # 4, Sungro Horticulture, Inc., Agawam, MA) to a depth of approximately 25 mm (1 in). The flats were watered daily for 20 min and allowed to grow for 4 weeks. The medium was then washed away and the number of live, sprouted plants was recorded. Plants were considered sprouted if new roots or shoots longer than 2 mm were observed.

Figure 5. Wildland-harvested showy milkweed rhizomes and root crowns were cut and divided into size classes to compare viability for use in propagation. (Photo by Derek Tilley, 2017)

The rhizome viability evaluation was not replicated or subjected to any statistical evaluation, but the percentage of rhizomes that produced plants are presented in the results section. This information was used to make decisions on rhizome cutting size for use in the field-establishment study.

Field Establishment

In the second study, we examined showy milkweed field establishment in a drained, constructed wetland pond located at IDPMC. Our trial compared four planting treatments: fall seeding, spring seeding, rhizome transplants, and greenhouse plugs grown from seed. The establishment trial was set up as a randomized complete block with six replications. The soil at the field site is classified as a Declo silt loam, and average natural precipitation in the area is 230 mm (9 in) (USDA Natural Resources Conservation Service 2021).

The seed bed was prepared with multiple passes of mechanical tillage in the summer of 2016 followed by a pass with a packer to firm the seed bed. Each plot contained four 7.6-m (25-ft) long rows with 1-m (3.3-ft) spacing between rows. The fall and spring seeding occurred on November 9, 2016 and April 5, 2017, respectively. Seed was collected from a natural population in Rupert, ID in 2016 and cleaned following the methods described in Tilley (2016) to an approximately 95 percent purity and 85 percent viability. Both planting times were seeded using a hand-pushed belt seeder (Almaco, Nevada, IA) set to a depth of approximately 12 mm (0.5 in) with a seeding rate of 81 pure live seeds (PLS) per linear m (25 PLS/ft) at a spacing of approximately 13 mm (0.5 in). Rhizomes were harvested from the same stand in Rupert, ID, on March 17, 2017, and stored in wet burlap sacks in a dark, cold environment averaging 10 to 13 °C (50 to 55 °F) with 10 to 30 percent relative humidity. Rhizomes averaging approximately 13 mm (0.5 in) in diameter were cut into approximately 7.5- cm (3-in) long sections and planted at 0.6-m (24-in) spacing on April 20, 2017, to a depth of approximately 2.5 cm (1 in). For greenhouse transplants, we sowed five seeds into 164-ml (10-in^3) Ray Leach SC-10 Cone-tainers™ on February 24, 2017, using the same growing medium and greenhouse conditions described for the viability assessment. The transplants were thinned as needed to one plant per pot and installed in the field after 88 days of growth on May 23 at 0.5-m (20-in) spacing. At the time of planting, the greenhouse transplants were 5 to 10 cm (2 to 4 in) tall. Effective plants/m (ft) of row for each treatment were: seeds = 81 (25), rhizomes = 1.6 (0.5), and transplants = 2 (0.6).

The study site was sprinkler irrigated once weekly for approximately 12 h or 7.5 cm (3 in) of applied water to encourage growth and to approximate conditions typically associated with local milkweed habitat in wet meadows and canal banks. Nontarget species observed in the planting area included Kentucky bluegrass (*Poa pratensis* L.), crown vetch (*Coronilla varia* L.), Canada goldenrod (*Solidago canadensis* L.), yellow salsify (*Tragopogon dubius* Scop.), and various ruderal weeds. We did not apply any weed-control treatments during the study period as we wanted the site to revegetate naturally and develop typical competition levels.

The plots were evaluated for percent establishment and average plant height in the first and second growing seasons (July 13, 2017 and May 30, 2018, respectively). Because of mortality and recruitment from seed and rhizomatous spread, we did not do any further evaluation after 2018. Percent establishment was determined by counting the number of plants in a randomly located 1-m (3.3-ft) section of the middle two rows encompassing an area of 2 m^2 (21.5 ft^2). Because different numbers of propagules were used for each treatment, counts were converted to percent establishment for comparison using the following equation: [(plants/m)/(propagules/m)] x 100. For average height, we randomly measured four plants within the randomly selected evaluation area.

Stand Management

In 2020, we established new plots within the test area to measure the effect of management treatments on milkweed stands. We established 60-m^2 (646-ft^2) (4 by 15 m [13.1 by 49.2 ft]) plots in a randomized complete block design with four replications. Each management plot incorporated equal areas of the four establishment methods and thus were expected to possess similar plant densities and age groups. The management trial consisted of two active treatments (mowing and burning) and a passive, nontreated control. Mowing treatments were done using a push mower with the blade set at 10 cm (4 in) off the ground. The burning treatments were conducted by spreading a 5 cm (2 in) deep layer of dry straw evenly throughout the plot and igniting it with a propane torch (figure 6). We measured fire temperatures at the soil surface with a high temperature, K-type thermocouple (Minnesota Measurement Instruments, St. Paul, MN) and with a handheld infrared thermometer (Etekcity, Anaheim, CA). Average temperatures generally ranged from 400 to 500 °C (752 to 932 °F) with some flareups exceeding 1,000 °C (1,832 °F). Mowing and burning treatments were done each spring in mid-March, consistent with common management practices on Idaho canals. We conducted management treatments for 2 years (2020 and 2021). The plots were evaluated in July 2021 using five, 1-m^2 (10.8-ft^2) frames placed randomly in the plot. Because plants are rhizomatous and a single plant could produce multiple stems, we counted stem density rather than whole plants (Cracroft et al. 2020). Sums were averaged for mean stems/m^2.

Experimental Analysis

All analyses were conducted using Statistix 10 Analytical Software (Tallahassee, FL). Data for all experiments were tested for normality and homogeneity of variances to determine the appropriate test analyses. Percent establishment data for 2017 and 2018 and the plant height data for 2018 were normally distributed and met the assumptions needed for an analysis of variance (ANOVA). We therefore used the one-way ANOVA procedure followed by the least significant difference means separation at $P<0.05$ level of significance. Establishment density measurements for 2017

Figure 6. The field experiment evaluated 3 management treatments, including burning as shown in this photo, applied for 2 years on established showy milkweed stands. (Photo by Derek Tilley, 2021)

and 2018 and plant height data for 2017 did not meet the assumptions of normality. For those data, we used a Kruskal-Wallis nonparametric analysis followed by Dunn's Test to separate mean ranks with a significance level of $P<0.05$. Stem density data from the 2021 management study were not normally distributed and were log transformed prior to analysis using the one-way ANOVA as described above. Means were back transformed for presentation.

Results and Discussion

Rhizome Viability

We saw excellent sprouting from the larger rhizome sections, including both sizes of crown sections and the large 20- by 100-mm segments (figure 7). Longer sections produced more viable sprouts than shorter sections of the same diameter, but segments as short as 25 mm still had sprouting from 80 percent of segments (table 1). Small-diameter rhizomes (3 and 6 mm) had the lowest sprouting percentages but were above 50 percent viability. Several uncounted rhizomes exhibited early signs of sprouting at the time of measurement, indicating that we might have recorded higher sprouting percentages if we had postponed the evaluation. These results indicate that practically all portions of harvested rhizomes have potential for use in field plantings.

Table 1. Rhizome crowns and larger segments tended to have the highest viability after 4 weeks.

Initial size (diameter by length in mm)	Total segments planted	Viability (% sprouting)
3 by 100	24	50
6 by 50	30	70
13 by 50	20	67
13 by 100	20	85
20 by 25	14	80
20 by 100	10	100
Crowns < 25	15	100
Crowns >25	4	100

1 in = 25 mm

Figure 7. Showy milkweed rhizome sections of all sizes showed excellent viability. This photo shows sprouts emerging from a 13- by 100-mm-rhizome section after 4 weeks in the greenhouse. (Photo by Derek Tilley, 2017)

Field Establishment

Seeding treatments had more propagules/m and resulted in significantly greater plant establishment densities in the first 2 years of establishment than transplanting greenhouse-grown materials or planting rhizome sections (figure 8). Because of this higher density, spring-seeded plots had 25 times more plants than the rhizome plots and 45 times more than the greenhouse transplants during the establishment year. These differences persisted during the second year. Spring seeding tended to result in more plants than fall seeding for both seasons, though this difference was nonsignificant (figure 8). Plant density of greenhouse transplants increased from 0.9 to 1.7 plants/m of row (0.3 to 0.5 plants/ft) over the two seasons, suggesting these more mature plants had begun to spread vegetatively in the second year of growth.

Final plant density was largely determined by initial planted propagule spacing and density. If more plants per area are desired, a higher planting rate can be successfully adopted. Even with fewer plants resulting from rhizomes, the number of established plants may be sufficient to develop healthy stands, especially considering the clonal nature of the species. The observed trend in rhizome mortality from the first to second growing season, however, is surprising and cause for concern.

Because of differences in initial propagule density, plant density may not fully explain the differences between planting methods. For example, young plants from the seeding treatments are likely to experience higher competition and be more susceptible to environmental stressors such as drought. More mature transplants and plants developed from healthy rhizomes may be more resilient and thus be an economical alternative for establishing milkweed populations. Percent establishment may be a valuable measure for determining the optimum planting method.

Despite having the lowest plant density in 2017, nearly 80 percent of rhizomes produced plants in 2017. By 2018, however, rhizome mortality reduced percent establishment significantly (figure 9). Establishment from seeding treatments were 27 to 54 percent from the fall- and spring-seeded treatments, respectively, in the first growing season (figure 10) which is higher than

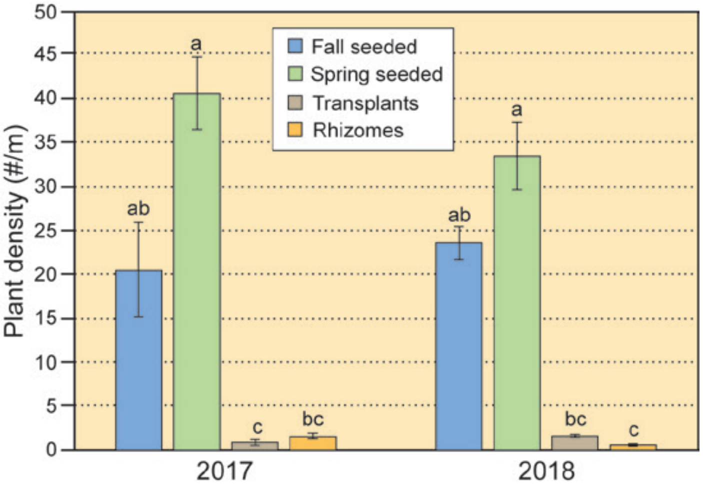

Figure 8. Fall and spring seeding treatments had significantly higher showy milkweed plant density after 1 and 2 growing seasons compared with greenhouse transplants or rhizomes, although initial planting density was also much higher for seeded plots. Error bars are ±1 standard error. Within each year, bars with different letters were significantly different at P<0.05.

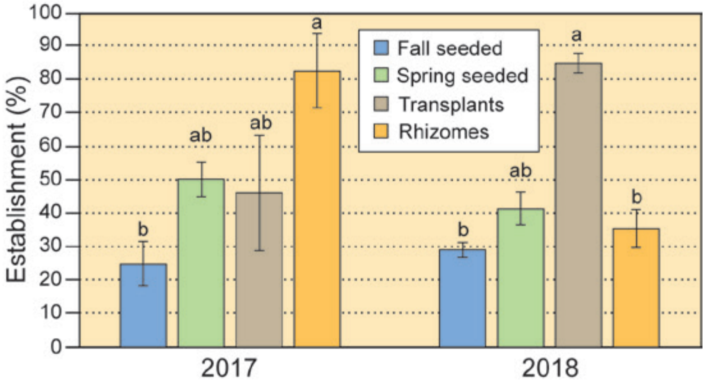

Figure 9. In the first growing season after planting, showy milkweed rhizomes produced the highest percent establishment compared with the other planting methods. By the second season, transplanted plants had the highest percent establishment. Error bars are ±1 standard error. Within each year, bars with different letters were significantly different at P<0.05.

Figure 10. Seeded rows averaged 21 and 41 showy milkweed plants/m^2 (6.5 and 12.6 plants/ft^2) from fall or spring seedings, respectively, in the first growing season. (Photo by Derek Tilley, 2018)

reported previously (Bullard et al. 2020). In the second season, transplanted greenhouse plants had significantly more establishment than all other treatments.

Milkweed establishment for all treatments was likely aided by site treatment (i.e., reduction of competition prior to establishment) and irrigation. Although showy milkweed is often found in semiarid sites, it may be worthwhile to target areas with higher soil moisture, such as depressions or areas with a shallow water table for milkweed establishment rather than spreading seed across an entire project, especially if seed or stock materials are limited.

Average height of plants from rhizomes was significantly taller in both seasons that it was for those germinated from seeds (figure 11). Our results differ from those observed in the San Joaquin Valley of California (Bullard et al. 2020), where fall seeded and fall transplants of showy milkweed were similar in height to rhizome-grown plants at the end of two growing seasons. This difference could be due to variations in growing degree days between the two locations.

Some of the rhizome-grown plants produced flowers in 2018 (figure 12), while none of the plants from the other planting methods produced flowers during the study. Establishing more mature plants via rhizomes may be a means of more quickly providing a nectar source for monarchs and other pollinators than direct seeding or using young greenhouse-grown plants. Flower and seed production from rhizome-established plants could also be beneficial in promoting stand spread via seed dispersal.

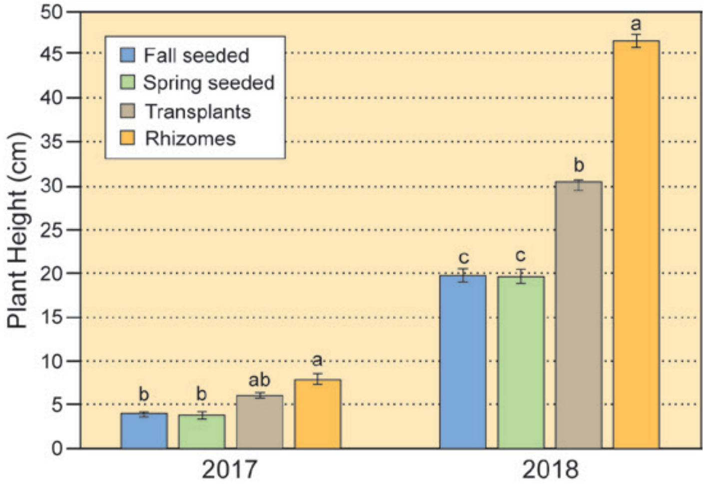

Figure 11. Showy milkweed plants that emerged from rhizomes were significantly taller than plants established with seeding or greenhouse transplants. Error bars are ±1 standard error. Within each year, bars with different letters were significantly different at $P<0.05$.

Response to Management

An outbreak of cobalt blue milkweed beetles (*Chrysochus cobaltinus* LeConte) decimated showy milkweed plants in 2020 at the study site (figure 13). These insects are commonly observed on Idaho milkweeds,

Figure 12. Some of the showy milkweed plants produced from rhizomes had flower buds after 2 growing seasons, whereas those planted from seed or greenhouse transplants did not produce any flowers during the 2-year field experiment. (Photo by Derek Tilley, 2018)

preferring showy milkweed, but rarely cause issues. The larvae feed on milkweed roots and the adults feed on the foliage. These beetles tend to balloon in dense stands of milkweed, peaking over a 2- to 4-year period, and can wipe out entire stands. Occasionally, outbreaks are so bad that hand removal may be necessary (Vaughan 2020). In 2021, cobalt blue milkweed beetle numbers had returned to acceptable levels and did not require treatment.

The burn and control treatments had about twice the plant density as the mowing treatment, though this difference was not statistically significant (figure 14). Flash burning of aboveground grass and thatch is common in southern Idaho canal systems. Apparently, this practice does not transfer heat far enough into the soil to harm the deep-sitting rhizomes and rootstocks of showy milkweed despite reaching surface temperatures in excess of 1,000 °C (1,832 °F). Burning treatments completely clear the area of aboveground cover and increase sunlight capture by milkweed after emergence. Conversely, mowing treatments could promote vegetative spread and cover of sod-forming grasses, such as Kentucky bluegrass, thus reducing light interception by milkweed.

Figure 13. An infestation of cobalt blue milkweed beetles significantly damaged mature showy milkweed plants at the field experiment site in 2020. (Photo by Derek Tilley, 2020)

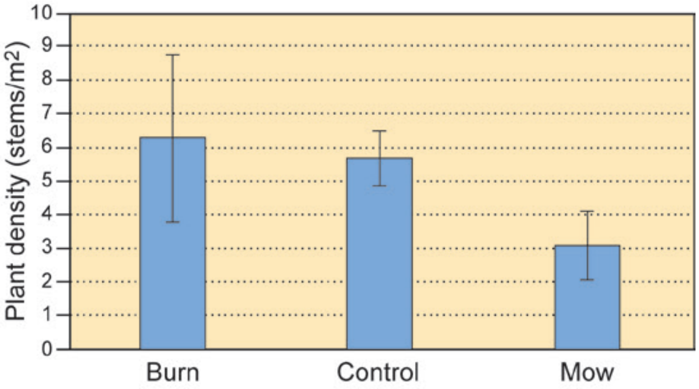

Figure 14. Showy milkweed plant density did not differ statistically among burning, mowing, and nontreated control management treatments applied for 2 years, though there tended to be fewer plants in the mowing treatment. Error bars are ±1 standard error.

Conclusion

Showy milkweed can be established in the field through a variety of methods that can be tailored for a given project. Wildland-collected rhizomes are highly viable and can be cut into small sections to establish new plants on field sites. A small number of rhizomes could easily yield several dozen plants at minimal cost or effort. For larger plantings, direct seeding in the spring or fall can generate milkweed stands under the right conditions. Irrigation or targeting areas of increased moisture may increase establishment success. Greenhouse-grown transplants and plants from rhizomes establish more quickly, produce larger plants, and have earlier flowering compared with plants from seed in the first two growing seasons. Effects of mowing and burning treatments on stem density are inconclusive. Current recommendations (Borders and Lee-Mäder 2014, Tilley et al. 2018) may be adequate.

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Incorporating the Use of Biological Control Organisms Into Integrated Pest Management Tactics in Forest Nurseries

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Abstract

Integrated pest management uses multiple techniques to control pest organisms. Incorporating the use of biological control agents against economically important insect pests that occur in nursery production sites, such as lygus bug and black vine weevil, can be beneficial. Typical biological control agents include parasitic wasps and flies, invertebrate predators, and entomopathogenic nematodes and fungi. Two tests were conducted to determine the usefulness of entomopathogenic organisms against black vine weevil larvae. In the first test, virtually all larvae in nematode-treated soil and 50 percent of those in fungal-treated soil died within 16 days. In the second test, 85 percent of the tested larvae survived for 14 days in the control treatment, while only 5 percent survived in the nematode treatment. The high levels of mortality demonstrate the potential of using biological control as part of an integrated approach to pest management of nursery pests.

Introduction

Pest management strategies in forest nurseries usually involve implementing suppression (reactive) or prevention (proactive) practices. Suppression practices are aimed at regulating populations of pest species that cause economically intolerable levels of crop damage. Prevention practices are aimed at maintaining pest damage below economically intolerable levels.

Integrated Pest Management (IPM) considers the entire ecosystem that is being managed and constitutes a broad-based approach to reduce or maintain pest populations below a level at which they cause economic damage. IPM requires that potential pest species be monitored regularly and uses strategies that are both suppressive and preventive.

As the name implies, IPM does not rely on any single pest-management technique, but instead can integrate a combination of techniques (i.e., mechanical, biological, and chemical) against a pest (any organism that interferes with our intended goal) to manage and maintain its population level below where it causes economic damage (this does not necessarily imply zero damage). Mechanical management techniques include using barriers or traps or manually removing the pest to protect a crop. Biological techniques include using microorganisms (i.e., bacteria, fungi, and viruses), invertebrate predators (e.g., ladybird beetles and lacewings), and/or insect parasitoids (e.g., parasitic flies and wasps). Chemical techniques include applications of pesticides (insecticides, fungicides, and herbicides) using foliar, granular, or drench products. Given the potential to use a combination of management techniques, individual IPM strategies can be developed for specific crop systems and conditions and may range from simple to complex, but all require that the pest species be monitored through time.

Some major tenets of IPM are:.

- There is no silver bullet. IPM does not depend on a one-size-fits-all strategy, but instead requires that the manager tailors the practices to fit the overall goal.
- It is important to treat the causes, not just the symptoms. Pest outbreaks do not simply happen; there is usually a root cause. By addressing the cause, the manager can lessen the time and effort required to control a pest outbreak.

- Pest presence does not always mean there is a pest problem. If a pest species is found at low density, it may not be causing economically important damage.
- If you kill the natural enemies, you inherit their work. In other words, if pest management tactics cause mortality to biological enemies of the pest, then the manager must also eliminate the pests that would have been killed by the natural enemies.
- Pest management strategies can be “just in time” or “just in case.” IPM depends upon monitoring pest populations (sampling and forecasting) to allow the manager to determine and schedule appropriate treatments.

In this article, I have included a review of two insect pests: tarnished plant bug and black vine weevil. Both have common biological enemies that growers may be able to incorporate into their IPM practices. To further understand this, I conducted two biocontrol trials with black vine weevil which are also described in this article.

Tarnished Plant Bug, *Lygus hesperus* Knight (Hemiptera: Miridae)

Lygus hesperus is native to Western North America, including both the Western United States and southwestern Canada. This insect is one of the most important true bug pests present in both horticultural and agricultural crops where it feeds on numerous economically important host species (Scott 2012). Feeding damage typically occurs on reproductive structures and terminal buds, causing stem lesions, distorted needles, and multiple tops. This damage results in decreased plant health and quality. Widespread damage by *L. hesperus* occurs on nursery crops throughout the United States and Southern Canada (South 1991), with damage occurring on both hardwood and conifer species (Sapio et al. 1982, Schowalter et al. 1986). Common nursery hosts include Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), true fir (*Abies* spp.), pine (*Pinus* spp.), spruce (*Picea* spp.), and hybrid poplar (*Populus* spp.).

Lygus hesperus spend the winter as adults (figure 1), often in plant debris and transplant beds (South 2012). After hatching, the insect's development is temperature dependent and it goes through multiple nymphal instars before reaching the adult stage (Cooper and Spurgeon 2012). The adults can be active fliers but spend much of their time on their host plants (Blackmer et al. 2004). Both adults and nymphs feed on plant juices using piercing/sucking mouthparts. In the Northern States there are three to four generations per year, and damage to 1-0 conifer seedlings usually occurs from June to September (South 2012). Populations can be monitored by examining nearby weedy species, using visual damage of the nursery crop, and confirming the identification by catching and examining individual specimens (South 2012).

Figure 1. The tarnished plant bug (*Lygus hesperus*) (adult pictured) is an important pest in nursery crops. (Photo by USDA Agricultural Research Service)

While more important in traditional agriculture, multiple biocontrol options are available against *Lygus hesperus*. These biocontrol agents include naturally occurring parasitoids such as the wasps *Anaphes iole* Girault (Hymenoptera: Mymaridae) and *Peristenus relictusis* Loan (Hymenoptera: Braconidae) that use *L. hesperus* eggs as hosts (Haye et al. 2007, Zhu and Williams 2002). Naturally occurring predators can also be biocontrol agents such as bigeyed bugs (*Geocoris* spp. [Hemiptera: Geocoridae]), damsel bugs (*Nabis* spp. [Hemiptera: Nabidae]), minute pirate bugs (*Orius tristicolor* White [Hemiptera: Anthocoridae]), and several species of spiders that feed on *L. hesperus* during its nymphal stages (Zalom et al. 2018). Similar to the parasitoids, predators are more important mortality agents in traditional agricultural settings than in nurseries.

Black Vine Weevil, *Otiorhynchus sulcatus* Fabricus (Coleoptera: Curculionidae)

Otiorhynchus sulcatus is native to Europe and was introduced into North America in the early 1900s (Drooz 1985). The adult weevil (figure 2) is matte

Figure 2. Black vine weevils (*Otiorhynchus sulcatus*) (adult pictured) feed on more than 100 host plants. (Photo by USDA Agricultural Research Service)

black in color, approximately 9 to 12 mm long, and consists entirely of females that reproduce parthenogenetically (without mating) (Moorhouse et al. 1992). The front wings (elytra) of adult black vine weevil are fused, making them incapable of flight and limiting the distance they are capable of dispersing (Maier 1978).

Black vine weevils feed on over 100 host species with the adults feeding nocturnally on foliage and leaving a distinct notching pattern (Warner 1975). Most of the damage to plants occurs from larval root feeding (Nielsen and Dunlap 1981). The weevils primarily overwinter as mature larvae (for up to several months), but some adults may also survive the winter (Moorhouse et al. 1992). Larvae are creamy white, legless grubs and appear curved in appearance. Larvae inhabit the soil where they feed on small roots, but as they mature, they can feed on larger roots and girdle seedlings (Moorhouse et al. 1992). Common nursery hosts include yew (*Taxus* spp.), spruce, rhododendron (*Rhododendron* spp.), hemlock (*Tsuga* spp.), and grape (*Vitis* spp.) (Drooz 1985). These insects have also been found in containers in which Douglas-fir and oak (*Quercus* spp.) were growing (personal observations).

Because adult black vine weevils are strongly nocturnal in their movements, direct observation is not adequate to assess weevil presence. Assessment must include a variety of boards, cardboard, pitfall traps, and sticky bands (Smith-Fiola 2001). In addition, foliage can be examined for adult feeding.

Multiple insecticides are registered for use against black vine weevil (Frank et al. 2020). In addition, several predators are natural enemies of black vine weevil (Moorhouse et al. 1992). Entomopathogenic nematodes and fungi are frequently used to control the soil-inhabiting larvae in nurseries (Bruck 2005, Klingen et al. 2015).

Biocontrol Trials

Two trials at the Franklin H. Pitkin Forest Nursery (Moscow, ID) were conducted to test the effects of nematode and fungal applications on black vine weevil larvae. The objectives were to confirm the presence of black vine weevil, evaluate biocontrol potential in a nursery greenhouse setting, and generate data on the efficacy of biocontrol treatments on black vine weevil.

Methods

In mid-February 2019, weevil larvae were collected from infested containers containing Douglas-fir or oak seedlings. These larvae were transported to the University of Idaho's forest entomology lab and maintained for 24 h at 20 °C in 500-ml-plastic containers filled with dampened potting mix used at the nursery. The next day, larvae were transferred into pots (2 larvae in each of 36 pots). Larvae were covered with approximately 2.5 cm of potting mix. Containers were maintained at 24 °C in the laboratory with a 12:12 h (light:dark) regimen throughout the trial period.

Three treatments were each randomly assigned to 12 containers: (1) control (no organisms added), (2) nematode application (one mealworm infected with the nematode *Heterorhabditis bacteriophora* placed just beneath the medium surface) (figure 3), or (3) fungal application (*Isaria fumosorosea* was suspended in water and applied to the medium surface at 1.6 ml/L).

Larvae were examined 4, 8, 12, and 16 days after treatment (using four, two, two, and four containers, respectively, from each treatment) to determine if they were alive and appeared healthy. At each sampling time, larvae from each container were removed, separated from one another, touched with a dull probe to determine if they would respond to touch, and then maintained individually in small petri dishes with damp potting mix to determine if (and

Figure 3. Mealworm larvae infected with *Heterorhabditis bacteriophora* were used in the nematode treatments to test biological control of black vine weevils. (Photo by Stephen Cook)

when) they were infected with one of the entomopathogens. All larvae were alive when transferred and subsequently classified as dead when they did not respond to touch during the examinations or showed signs of infection as described below.

Dead larvae were dissected to determine if nematodes were present in the cadaver. Larvae that showed obvious infection with one of the entomopathogens were counted as infected and discarded. Larvae infected by nematodes turn reddish in color prior to death, while larvae infected with fungus turn a brownish color prior to death (figure 4). Larvae that had successfully pupated were counted as healthy since they had completed development. Because a large percentage of individuals had pupated, the trial concluded before eclosion to the adult stage and emergence from the containers occurred. Because of the limited replication, no statistical tests were conducted.

The second experiment was conducted in February and March 2020 to provide a statistically defensible study on larval mortality caused by the nematode. Black vine weevil larvae were collected from the Franklin H. Pitkin Forest Nursery and handled in the same fashion as described for the first trial. Four larvae were randomly assigned to each of 10 pots. Two treatments (five pots each) were included: (1) control and (2) the same nematode treatment used in the first trial. Larvae were removed from the pots after 10 days to determine overall survival and nematode infection. A students-t-test was conducted using the Statistix 10 software package (Analytical Software 2013) to compare survival of the larvae between the two treatments.

Figure 4. These (right) healthy, (middle) fungus-infected, and (left) nematode-infected black vine weevil larvae were removed from potting soil 12 days following treatment. (Photo by Stephen Cook)

Results

In the first trial, larval survival declined over time, especially for those in the nematode or fungal treatments (figure 5). No black vine weevil larvae in the nematode-treated containers survived to pupate, while 75 and 50 percent of larvae had pupated in the control and fungal-treated containers, respectively. The nematode treatment caused mortality faster than the fungal treatment. This result may be because nematodes were introduced in infected mealworms, and thus the density and timing of dispersal may have given them an advantage over the fungus treatment in a short-term trial. Commercially available nematodes are typically applied suspended in a water solution which may disperse more slowly and be at lower density than used in this trial. Although not analyzed statistically, this trial indicated that both biocontrol treatments were effective.

In the second trial, larvae in the control treatment had higher survival than those in the nematode treatment ($t = 7.16$; 8 df; $[P > t] = 0.0001$) (figure 6). Some of the larvae in the control treatment died, but none were determined to be infected with nematodes.

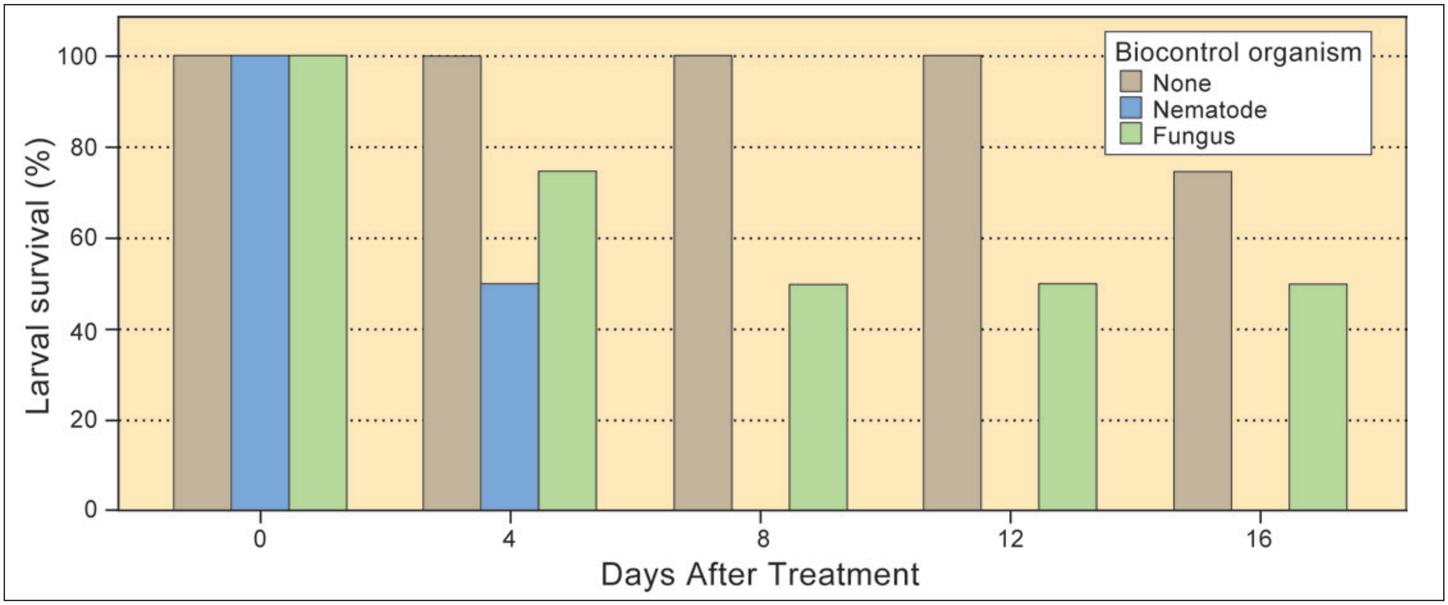

Figure 5. Larval survival varied by treatment during a 16-day assessment period for the biocontrol trial conducted in 2019.

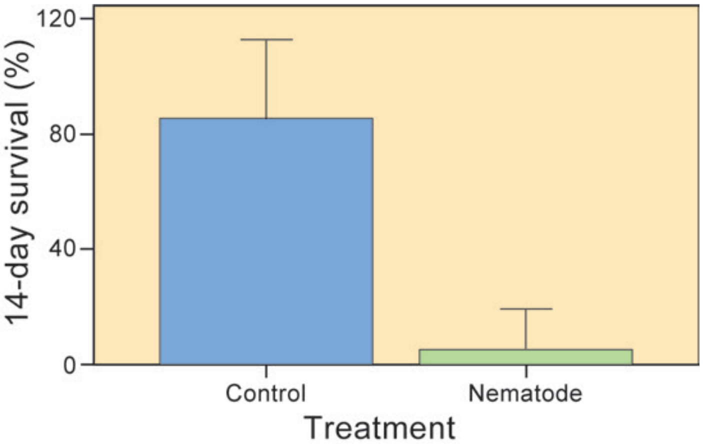

Figure 6. In the 2020 trial, larval survival for those in the control treatment was significantly greater than those in the nematode treatment based on Students' t-test comparisons (t = 7.16; 8 df; [P > t] = 0.0001).

Conclusions

IPM is a broad-based approach to management of an entire system. A combination of techniques including biological control are typical in a nursery IPM program. Some pest species, such as *Lygus hesperus,* have a large complex of natural enemies that prey upon them. For other pests, such as black vine weevil, natural enemies, such as entomopathogenic nematodes and fungi, can be effective treatments against infestation. These natural enemies can penetrate the soil mix to attack and kill root-feeding larvae. Results from the current trials further demonstrate that nematodes, such as *Heterorhabditis bacteriophora*, and fungi, such as *Isaria fumosorosea*, can be used in an IPM system to kill black vine weevil larvae. Both the nematode and the fungus are commercially available entomopathogens that infect soil invertebrates and pose no threat to plant material.

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Acknowledgments

I would like to thank the University of Idaho's Pitkin Forest Nursery for bringing the infestation to my attention and furnishing the potting mixture and weevil larvae used for the experimental trials. The work was supported in part by the University of Idaho's Agricultural Experiment Station Hatch project (I002810) and the USDA-NIFA Critical Agricultural Research and Extension Program project, "Integrating plant physiology, insect management and extension strategies to improve survival of nursery stock."

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Manganese Fertilization in Bareroot Pine Nurseries

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Abstract

Manganese (Mn) deficiencies in bareroot pine seedlings are rare when nursery soil is below pH 6.5, but they can occur when soil pH is above 6.5 and calcium (Ca) is above 6,000 ppm. Growth can be reduced when needles contain less than 20 ppm Mn. A simple way to avoid a Mn deficiency is to not sow pine on calcareous soils. When avoiding calcareous soils is not possible, treating seedlings with $MnSO_4$ (manganese sulfate) might prevent development of visual symptoms. Use of Mn fertilization in bareroot pine nurseries is currently infrequent because soils typically provide sufficient Mn to seedlings, and several nurseries located on calcareous soils have ceased operation. Mn toxicity does not occur at nurseries with low cation exchange capacity, but when soil Mn is greater than 300 ppm, low soil oxygen (especially after extended rainfall) may increase soil Mn to toxic levels. To avoid Mn toxicity, managers can sow seed on sandy soils with Mn levels below 200 ppm and apply lime to keep soil above pH 5.0. This article gives an overview of publications and observations regarding the use of Mn in bareroot pine nurseries and associated products, challenges, and misconceptions.

Introduction

Manganese (Mn) is a commonly applied micronutrient in the United States, and its use on agronomic crops can exceed 15,000 tonnes annually (Mortvedt 1991). In Australia, about 32 tonnes of Mn were applied to *Eucalyptus* plantations in 2003 (May et al. 2009). In comparison, reforestation nurseries in the United States likely purchased less than 300 kg total of Mn in 2020. Although fertilizers are generally not applied to seedlings at many container nurseries in developing countries (Hubbel et al. 2018), Mn fertilizer is typically added to potting media in developed countries (Donald 1991, Landis et al. 1989). Assuming 0.15 mg/container, the total amount of Mn used to grow 320 million container seedlings (Haase et al. 2021) might be 50 kg. For bareroot pines, less than 250 kg of Mn might be applied to grow 893 million seedlings.

At many bareroot nurseries, $MnSO_4$ is not applied (Donald 1991, van den Driessche 1984) because the soil contains enough Mn to keep foliage above 40 ppm (table 1). For example, a sandy soil with 4 ppm Mn can grow pine seedlings with 500 to 700 ppm Mn in foliage (van Lear and Smith 1972) (figure 1). When soil Mn drops below 5 ppm, $MnSO_4$ may be applied before sowing (Davey 1991, South and Davey 1983), or it may be applied to hardwood seedlings after leaves become chlorotic (Altland 2006). Although Mn deficiency symptoms can be relatively easy to identify for some angiosperms, symptoms might be overlooked on pine seedlings growing in calcareous soils since iron (Fe) and Mn deficiencies appear similar (Alejandro et al. 2020, Stone 1968).

Details about the role of Mn in plants and the role of soil pH in Mn solubility have been reviewed previously (Alejandro et al. 2020, Broadley et al. 2012, Eaton 2015, Landis 1998, Mortvedt 1991). Mn moves to the top of trees in the xylem, but movement in the phloem is limited (Ducic and Polle 2005, Kluthcouski and Nelson 1979, Loneragan 1988). Despite the importance of Mn for photosynthesis (Safford 1975), there are only a few published trials where Mn was tested in bareroot pine nurseries. Due to a lack of research, several misconceptions regarding Mn have emerged. For this reason, a literature review was undertaken for this article to establish what is known about Mn fertilization practices in bareroot pine nurseries. Although many questions remain unanswered, a summary of some practical information and observations are provided.

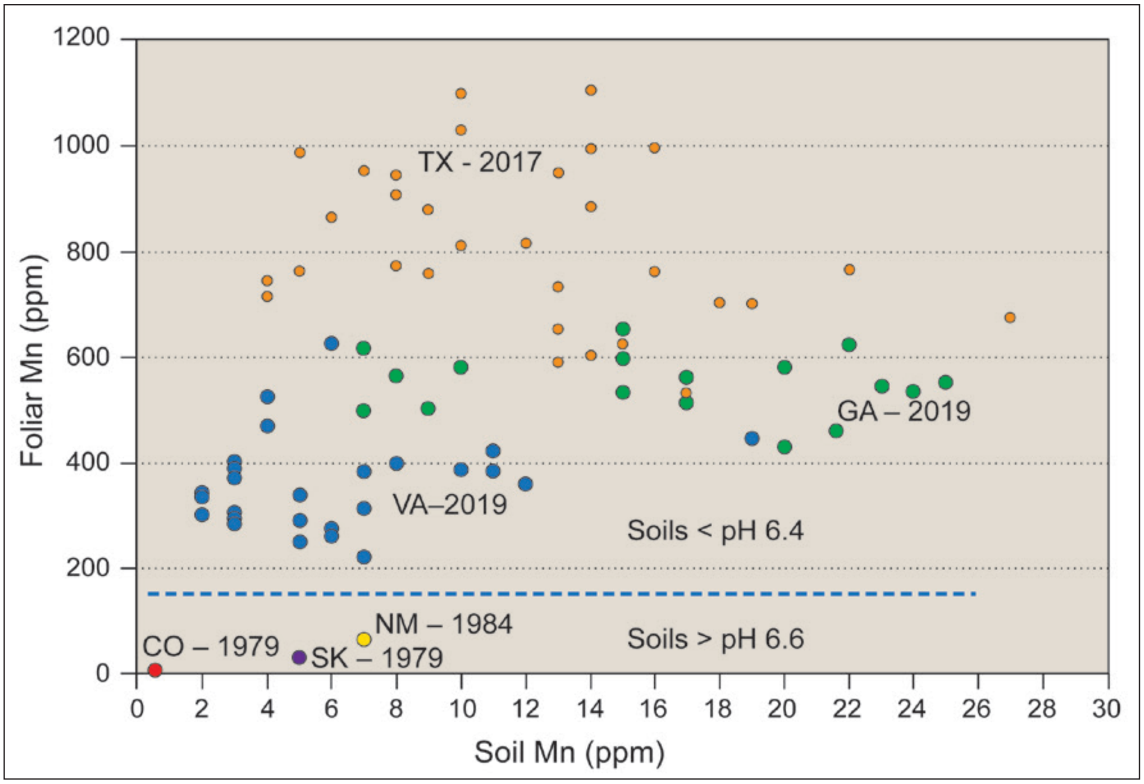

Figure 1. Foliar Mn values varied for bareroot pine seedlings sampled from nurseries in Colorado (CO), Georgia (GA), New Mexico (NM), Texas (TX), Saskatchewan (SK), and Virginia (VA). Soils sampled after 2016 were extracted using the Mehlich 3 procedure. Nursery soils with pH > 6.6 (CO, NM, SK) had foliar values less than 70 ppm Mn, while more acid soils had foliar concentrations greater than 200 ppm Mn (GA, TX, VA). Data points obtained from personal files and from publications by Carter (1980), Landis (1988), Mexal and Fisher (1987), Solan et al. (1979), and South et al. (2017).

[Abbreviations: AN = ammonium nitrate. B = boron. Ca = calcium. CEC = cation exchange capacity. Cl = chlorine. Cu = copper. EDTA = ethylenediaminetetraacetic acid. DTPA = Diethylenetriamine pentaacetic acid. Fe = iron. HCL = hydrogen chloride. K = potassium. LSD_{05} = Least significant difference. Mg = magnesium. Mn = manganese. $MnCl_2$ = manganese chloride. MnO = manganese oxide. $MnSO_4$ = manganese sulfate +1 H_2O. N = nitrogen. Na_2HPO_4 = sodium phosphate. P = phosphorus. ppm = parts per million. Pt = *Pisolithus tinctorius*. r = Pearson's correlation coefficient. S = sulfur. TSP = triple superphosphate. Tt = *Thelephora terrestris*. Zn = zinc. Except where noted, soil pH was measured in water. See table 1 for species scientific names.]

Manganese in Soils

Mn availability in bareroot nurseries is determined mainly by soil pH. In general, Mn deficiencies occur in basic soils while a few very acid soils (pH<5) may produce toxic levels during periods of low soil oxygen. When growing in calcareous soils, stunted pine seedlings may have low foliar Mn (< 10 ppm) which is a diagnostic deficiency symptom (Horak 2008, Landis 1988, Ruiter 1983, Will 1990). Although Mn is plentiful in basic soils (unavailable plus extractable), the oxidized forms are biologically inactive (Altland 2006). In acid soils, however, Mn typically occurs as Mn^{++} and, therefore, foliar values below 100 ppm Mn are rare when soil pH is below 6.5 (figure 1). Even so, some acid soils (pH 3.9) may contain 0.1 ppm Mn (Mehlich 3) (Vogel and Jokela 2011).

Various soil factors influence the amount of extractable Mn. In low CEC soils, rainfall can lower extractable Mn, but in fine textured soil, saturated conditions can increase Mn levels. Since available Mn is positively related to the proportion of silt and clay in nursery soils (South and Davey 1983), a deficiency is unlikely in acid soils with less than 85 percent sand. Even in soils with less than 0.5 ppm Mn (Mehlich 3), foliar levels in needles can be >130 ppm Mn (Vogel and Jokela 2011). Mahler (2004) stated that Mn deficiencies do not occur in acid soils. Although organic matter can reduce leaching of cations, soil organic matter may be negatively correlated with soil Mn (r = -0.35; r = -0.40; r = -0.16; NCSFNC 1991, Smiley et al. 1986, South et al. 2018, respectively). Adding 67,000 kg/ha of peat to a nursery soil might temporarily increase soil Mn by 3 to 5 ppm (McGrath et al. 1988, Mexal and Fisher 1987, Munson 1982). When sandy soils with low CEC are limed, the uptake of Mn by pine seedlings declines (Marx 1990) (figure 2).

Table 1. Scientific and common names of selected species and the reported range of foliar manganese (Mn). Seedlings were grown in soil except for one hydroponic study included as a comparison (Goslin 1959).

Species	Common Name	Mean (ppm)	Min (ppm)	Max (ppm)	Reference
Bareroot nurseries					
Acer rubrum L.	Red maple	--	70	285	Altland 2006
Picea abies (L.) Karst.	Norway spruce	50	28	1,986	Benzian and Smith 1973
Pinus banksiana Lamb.	Jack pine	414	350	495	Iyer et al. 1971
P. contorta Douglas ex Loudon	Lodgepole pine	284	80	703	Landis 1976
P. echinate Mill.	Shortleaf pine	412	60	560	Bryson 1980
P. elliottii Engelm.	Slash pine	224	95	486	Munson 1982
P. nigra Melville	Corsican pine	56	--	--	Benzian and Smith 1973
P. ponderosa Lawson & C. Lawson	Ponderosa pine	110	50	600	Baer 1984
P. ponderosa Lawson & C. Lawson	Ponderosa pine	13	6	20	Landis 1988
P. radiata D. Don	Monterey pine	188	70	350	Flinn et al. 1980
P. radiata D. Don	Monterey pine	176	32	487	Knight 1978
P. radiata D. Don	Monterey pine	437	100	1,500	Hopmans and Flinn 1983
P. radiata D. Don	Monterey pine	100	38	216	Richardson and Perkins 1985
P. resinosa Aiton	Red pine	182	102	268	Iyer et al. 1971
P. resinosa Aiton	Red pine	339	295	371	Iyer and Wilde 1974
P. strobus L.	Eastern white pine	157	92	255	Iyer et al. 2002
P. sylvestris L.	Scots pine	558	322	901	Raitio 1983
P. sylvestris L.	Scots pine	369	45	735	Januszek et al. 2014
P. taeda L.	Loblolly pine	308	196	404	Danielson 1966
P. taeda L.	Loblolly pine	518	85	1,350	Boyer and South 1985
P. taeda L.	Loblolly pine	486	135	1,677	Starkey and Enebak 2012
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir	523	250	860	Krueger 1967
Greenhouse nurseries					
Pinus caribaea Morelet	Caribbean pine	480	350	703	Hart and Widdowson 1981
P. elliottii Engelm.	Slash pine	595	184	2,950	Van Lear and Smith 1972
P. occidentalis Swartz	Hispaniola pine	347	54	1,138	Hubbel 2015
P. ponderosa Lawson & C. Lawson	Ponderosa pine	192	66	374	Majid 1984
P. sylvestris L.	Scots pine	667	88	1,604	Goslin 1959
Field sites					
Pinus elliottii Engelm.	Slash pine	296	251	315	Vogel and Jokela 2011
P. elliottii Engelm.	Slash pine	76	21	284	Grey 1988
P. patula Schiede ex Schltdl. & Cham.	Mexican weeping pine	1,308	276	2,790	Schutz 1990
P. pinaster Aiton	Maritime pine	55	18	90	Trichet et al. 2018
P. radiata D. Don	Monterey pine	109	1	593	Grey 1988
P. radiata D. Don	Monterey pine	258	139	431	Hans 2013
P. rigida Mill.	Pitch pine	1,268	649	1,911	Berry 1982
P. sylvestris L.	Scots pine	727	209	1,202	Steinbeck 1965
P. sylvestris L.	Scots pine	476	120	1,740	Innes 1995
P. taeda L.	Loblolly pine	222	51	409	Sypert 2006

Most nursery soils contain less than 200 ppm Mn (South and Davey 1983, Tanaka et al. 1967), and about half contain less than 35 ppm Mn (figure 3). One field (pH 6.7) contained 0.56 ppm extractable Mn (Solan et al. 1979). A tentative maximum value of 200 ppm Mn has been proposed for bareroot seedbeds (Davey 1991). Increasing soil pH may decrease soil solution Mn (figure 4), which can decrease foliar Mn concentration (Marx 1990, Plass 1969, Wright et al. 1999, Xu et al. 2020). In contrast, available Mn increases when soil becomes saturated for an extended period (Levan et al. 1986, Slaton and Iyer 1974, Stone 1968). When the soil (pH 4.5) at nursery 19 (figure 3) remained saturated, the Mn level exceeded 800 ppm in one field (data not shown). The combination of low soil pH, low soil oxygen, and high soil Mn can result in stunted and chlorotic pine seedlings.

Soil Testing

To estimate the amount of soil Mn available to plants, soil laboratories use different extraction methods. Tests that extract all Mn (available plus unavailable) are not useful for making fertilizer recommendations. A Mehlich 3 test might extract only 12 percent of the total Mn (Michopoulos et al. 2021) and a Mehlich 1 test would extract even less of the total (Mylavarapu et al. 2002, Sistani 1995). Nursery soils (pH 4.5 to 6.1) can range from 1 to 278 ppm Mn with Mehlich 1 or 2 to 500 ppm with Mehlich 3 (figure 2). When testing the same soil, reports may indicate 8 ppm (Mehlich 1) or 15 ppm (Mehlich 3). Therefore, when using a 5 ppm Mn value to trigger fertilization, nursery managers relying on Mehlich 3 tests will fertilize less frequently than those relying on Mehlich 1 tests. When using Mehlich 1, 4 ppm Mn is considered adequate for growing pines and other species (Horneck et al. 2011, Roberds et al. 1976, Tanaka et al. 1967).

Laboratories using Mehlich 3 may produce similar results (Tucker and Hight 1990), but occasionally there are large differences among laboratories (table 2). As a result, managers who use laboratory Z would spend more money on Mn fertilization than mangers who receive reports from laboratory Y (table 2).

Manganese in Foliage

Some nursery managers apply Mn to soil and then monitor foliar nutrients as part of a quality-control program. Typically, nursery managers compare foliar Mn values with ranges deemed adequate in published nursery manuals. Unfortunately, many of these ranges are not based on research trials in bareroot pine nurseries (table 3). When an upper value of 250 ppm Mn is used for all tree species (Landis 1997, Römheld 2012), then many pine samples listed in table 1 would be considered above adequate.

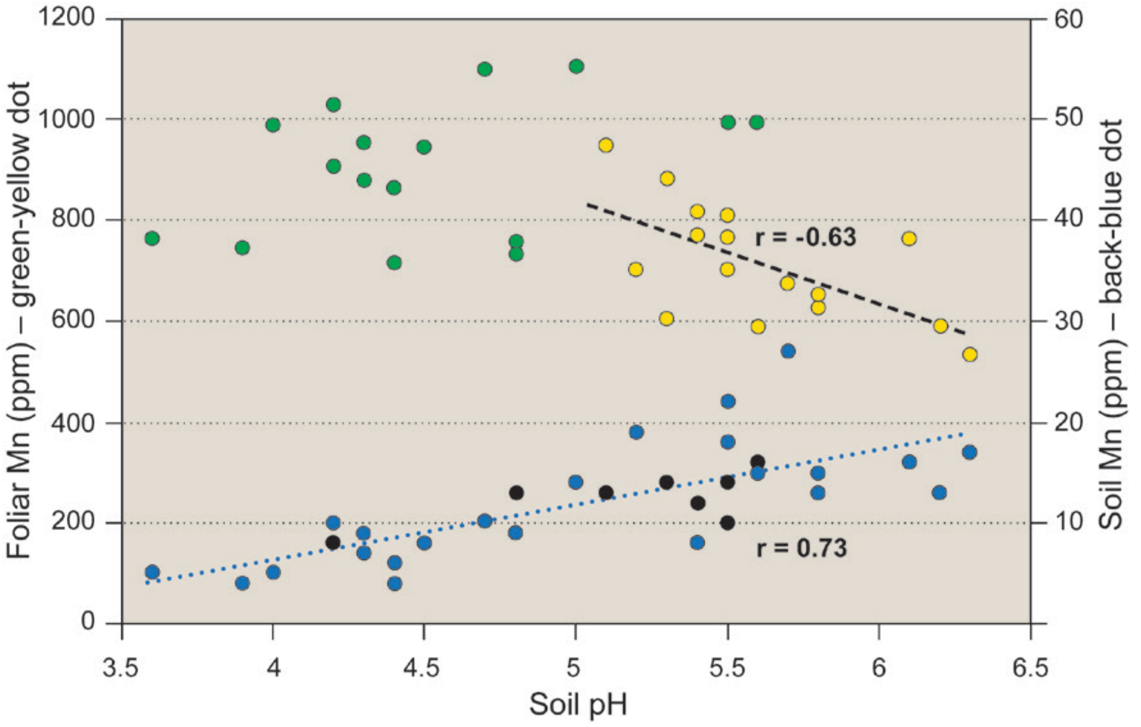

Figure 2. At a sandy nursery soil in Texas with less than 30 ppm Mn (Mehlich 3), Mn concentrations in loblolly pine (*Pinus taeda* L.) foliage declined after dolomitic lime was applied before sowing (South et al. 2017). As a result, there was a negative relationship (black line) between soil pH and foliar Mn for 16 lime plots (yellow dots). Green dots represent foliage from seedlings growing in plots not treated with lime. There was a positive relationship (blue line) between soil pH and soil Mn (blue dots). Sulfur was applied to 12 plots below pH 5.1 and black dots represent control plots that were not treated with lime or sulfur.

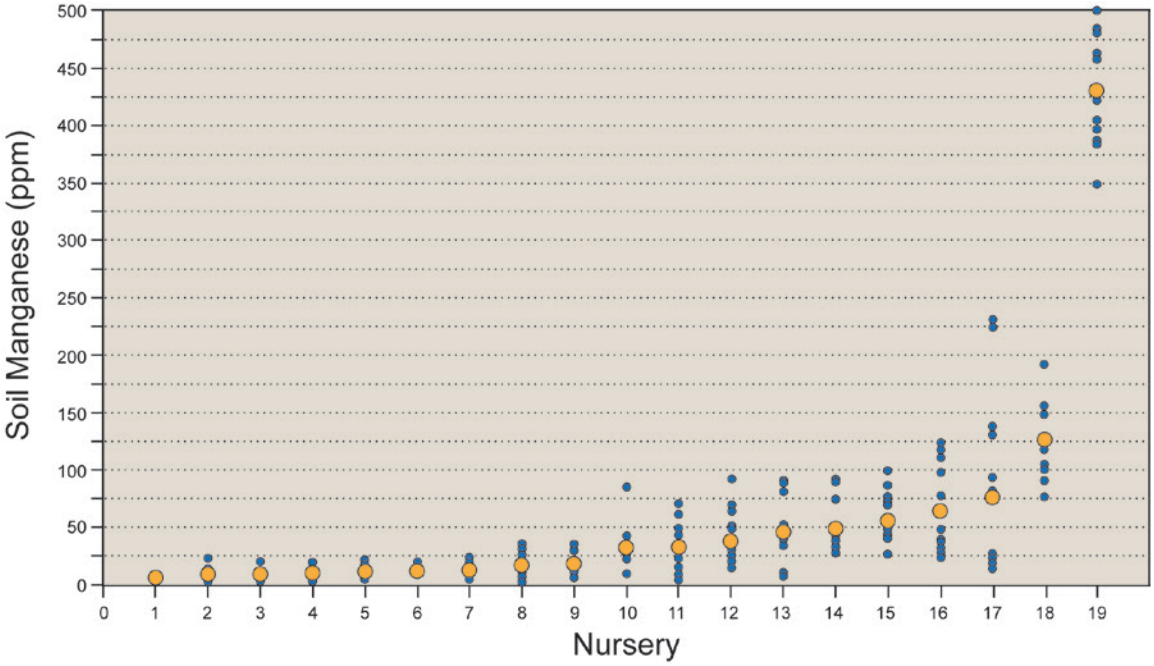

Figure 3. Soil Mn (Mehlich 3) from 19 southern nurseries in the United States varies from 2 to 500 ppm (excluding nursery 19 outlier, mean for the other 18 nurseries was 35 ppm). Each nursery is represented by a mean (orange dot) of about 15 soil samples. After receiving soil tests, Mn fertilizer was applied in March to 11 fields at 5 nurseries (i.e., 11 out of 282).

Although laboratories may list a normal range for Mn based on survey data, that range is not synonymous with an adequate range and may not reflect foliar values determined from a fertilizer response curve. As a result, normal ranges vary by country, region, and species. One laboratory might list a normal range of 100 to 250 ppm Mn for pine based on greenhouse tests with soybean [*Glycine max* (L.) Merr.] (Ohki 1976), while another may list a range of 75 to 500 ppm.

Although Powers (1974) reported an adequate Mn range of 100 to 5,000 ppm for all tree species, this range is not valid for pine. The upper limit of 5,000 ppm likely originated from mature stands of Norway spruce in Germany with 5,210 ppm Mn in foliage (Stone 1968). Even an upper limit of 3,000 ppm Mn is too high for some pine species (Schutz 1990, van Lear and Smith 1972). A more appropriate upper limit might be 1,700 ppm Mn, since visual toxicity symptoms have been observed when loblolly pine foliage reached 1,895 ppm Mn. Although some suggest Mn is toxic when foliage exceeds 700 ppm (Adams and Walker 1975, de Lanuza 1966, Lafond and Laflamme 1970), millions of pine seedlings have been produced with greater concentrations in foliage. At three nurseries (table 2) and in one greenhouse trial (Kavvadias and Miller 1999), Mn in pine foliage exceeded 1,300 ppm. In a greenhouse, growth of slash pine was greater at 795 ppm foliar Mn than at 642 ppm foliar Mn (figure 5).

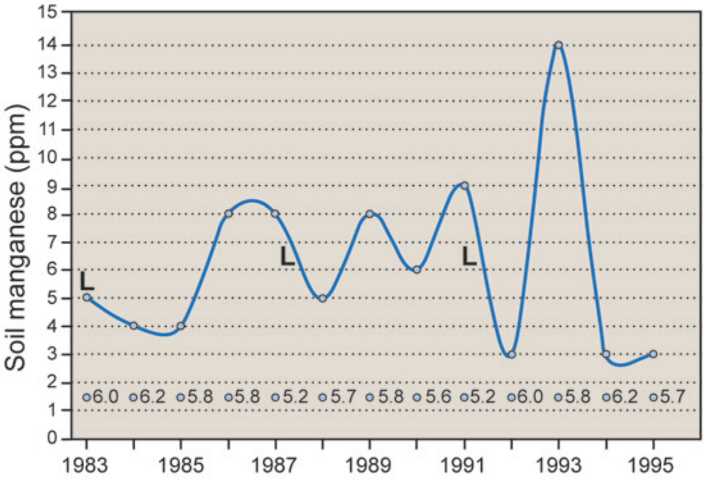

Figure 4. Soil Mn and pH varies by year for Field I-2 at the Westvaco Nursery in South Carolina. This field produced cover crops from 1983 to early 1995, and soil Mn (Mehlich 1, in November) varied from 3 to 14 ppm. Dolomitic limestone (indicated by the black L in the figure) was applied in the spring of 1983 (2,240 kg/ha), 1988 (2,240 kg/ha), and 1992 (1,456 kg/ha). Liming increased soil pH and temporarily decreased soil Mn. An application of FRIT 287 (28 kg/ha on March 23, 1995), provided 7.8 kg/ha of Mn.

The lower number in the adequate Mn range could be as low as 30 ppm (Carter et al. 2021) or 20 ppm (Albaugh et al. 2010, Horak 2008, Jokela 2004, Will 1978). For example, Hubbel (2015) suggested that pine seedling growth may have been inhibited because foliar Mn (54 to 85 ppm) was below the adequate range published for conifer needles (Landis 1997, Timmer 1991). Hubbel's container-grown seedlings with 54 ppm Mn were, however, taller than seedlings in the same trial with 384 ppm Mn in foliage. Thus, it will likely be a waste of Mn and money to fertilize pine nursery stock when foliar Mn levels drop to 50 ppm. At lower levels, however, Mn fertilization may be beneficial. Calcareous nurseries in Colorado and New Mexico (Landis

Table 2. Examples of Mn soil test results (ppm - Mehlich 3) using actual soil laboratories. Laboratories X and Z indicate a low level for soil A, while laboratory Y indicated Mn was at a very high level. Laboratory X ranks 38 ppm Mn as a medium level, while 160 ppm Mn was considered to be within the optimum range.

Sample	Laboratory X	Laboratory Y	Laboratory Z
	Mn ppm	Mn ppm	Mn ppm
Soil A	🟨 11	🟦 32	🟨 3.5
Soil B	🟨 13	🟧 15	🟨 7.9
Soil C	🟧 38	🟦 43	🟧 8.0

🟨 Low 🟧 Medium 🟦 Very High

1988) may have benefitted from a 20-ppm trigger for applying foliar Mn.

Manganese Deficiency

"In plants, Mn deficiency often occurs as a latent disorder, without clear visual symptoms. Thus, the magnitude to which Mn deficiency affects crop yield is difficult to quantify" (Alejandro et al. 2020). The Mn deficiency range for pine needles is 1 to 22 ppm (de Lanuza 1966, Landis 1988, Lange 1969, Ruiter 1983, Trichet et al. 2018). In hydroponics, stunting is observed before obvious symptoms appear (Ingestad 1958, Stone 1968). When visual deficiency symptoms occur on stunted pines, the needles have a pale green color (Brown 1955, de Lanuza 1966, Kavvadias and Miller 1999, Lyle 1969, Majid 1984). When stunted Scots pine were grown in hydroponics without Mn, however, there were no diagnostic visual characteristics (Goslin 1959). Since Mn deficiency symptoms on pines are elusive (i.e., few or no photos), most descriptions found in nursery manuals describe symptoms found on hardwoods.

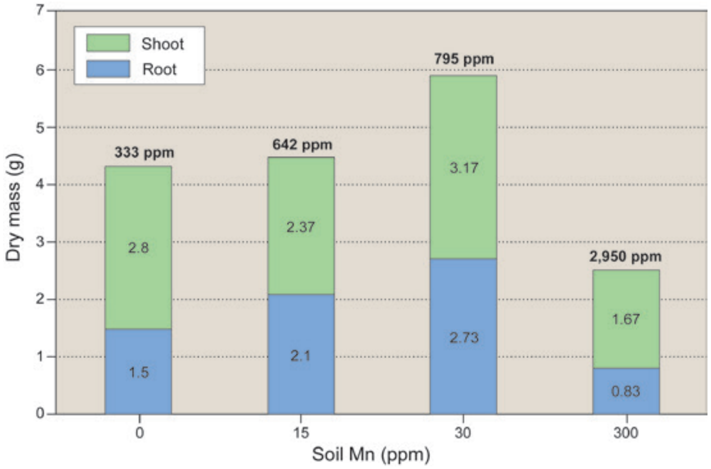

Figure 5. The effect of manganese sulfate concentrations (0, 15, 30 and 300 ppm Mn) on root and shoot dry mass of slash pine (*Pinus elliottii* Engelm.) seedlings in a greenhouse (van Lear and Smith 1972). The Lakeland sand initially contained 0.4 ppm Mn and each pot was treated twice with 100 ml of Mn solution over a 3-month growing period. Foliar Mn concentrations (age 6 months) are listed above each bar.

Sometimes stunted seedlings occur in alkaline soils, and the reason for poor growth is unknown. The best way to test for Mn deficiency is to establish fertilizer rate trials using $MnCl_2$ and $MnSO_4$ (Ingestad 1958). If both sources increase growth, then the deficiency was not due to low sulfur. Tests of $MnSO_4$ did not improve growth of conifers in U.K. nurseries (Benzian 1965), and only a few Mn trials have been installed at nurseries in North America (table 3). In several plantation trials, deficiencies were alleviated after applying 30 to 40 kg/ha of $MnSO_4$.

Although pictures are available of Mn-deficient pines in plantations (Davis et al. 2015, Lange 1969, Trichet et al. 2018, Will 1985) and greenhouses (de Lanuza 1966, Hernández-Gil 1989, Goslin 1959) (figure 6), photographs from bareroot nurseries (pH > 6.5) might not exist. When Mn was applied at high rates, seedling yield increased by more than 13 percent at two nurseries

Figure 6. Stunted growth is a symptom of Mn deficiency. The container on the right contains loblolly pine (*Pinus taeda* L.) seedlings (normal color Munsell 7.5 GY 5/6) growing in a nutrient solution containing $MnCl_2$ (Lyle 1969). The seedlings on the left were grown in a nutrient solution that did not contain Mn (foliage color 7.5 GY 7/8 or 6/6). In some cases, deficient seedlings produced no secondary needles. (Photo by Jack May, 1965)

Table 3. Pine response to manganese sulfate ($MnSO_4$; MS) varied in nursery, greenhouse, and field trials where seedlings were grown in soil. Using rates applied in tests before 1966, the cost (2022 USD) to apply nursery treatments would exceed $1,980/ha, while the cost to apply field rates would be less than $400/ha. See table 1 for species' scientific names.

Treatment	Pine common name	Response variable	% response	Reference
Bareroot nursery trials				
381 kg MS/ha	Ponderosa	Number of seedlings	+ 100	Stoeckeler and Slabaugh 1965
268 kg MS/ha	Ponderosa	Number of seedlings	+ 14	Wahlenberg 1930
224 kg MS/ha	Slash	Height	+ 10	Steinbeck 1962
224 kg MS/ha	Loblolly	Chlorosis	0	Shoulders and Czabator 1965
224 kg MS/ha	Slash	Height	- 6	Steinbeck 1962
292 kg MS/ha	Shortleaf	Dry mass	- 7	Auten 1945
Greenhouse nursery trials				
30 mg Mn/L	Slash	Dry mass	+ 37	Van Lear and Smith 1972
55 mg Mn/L	White	Dry mass	0	St.Clair and Lynch 2005
5 mg Mn/L	Slash	Dry mass	- 13	Van Lear and Smith 1972
5 g MS/pot	Mexican weeping	Dry mass	- 22	Buchler 2002
448 kg MS/ha	Red	Dry mass	- 47	Slaton and Iyer 1974
Field trials				
40 kg MS/ha	Monterey	Volume	+ 465	Donald et al. 1987
40 kg MS/ha	Monterey	Height	+ 123	Grey and de Ronde 1988
40 kg MS/ha	Monterey	Volume	+ 106	de Ronde et al. 1988
18 kg MS/ha	Monterey	Height	+ 63	Lange 1969
30 kg MS/ha	Slash	Volume	+ 22	Jokela et al. 1991
45 kg MS/ha	Slash	Height	+ 6	Pritchett 1960
23 kg Mn/ha	Loblolly	Height	0	Sypert 2006
6.6 kg Mn/ha	Loblolly	Volume	0	Vogel and Jokela 2011

(table 3). Since Mn is an active ingredient in some fungicides, high rates of $MnSO_4$ may have reduced the activity of damping-off fungi. No significant height increase occurred after Mn fertilization at nurseries in Indiana and Georgia (Auten 1945, Steinbeck 1965).

Manganese Toxicity

Toxicity of an element can be estimated by establishing a rate study and measuring germination or seedling biomass over time (Juárez-Mirón 2021, Morrison and Armson 1968, Radwan et al. 1979, van Lear and Smith 1972). Toxicity occurs when seedling dry mass is reduced by 10 percent (Ohki 1985) or when a 5- to 9-percent reduction is statistically significant ($\alpha = 0.1$). For example, in a greenhouse trial using saturated soil with low soil oxygen (Slaton and Iyer 1974), two applications of $MnSO_4$ (224 kg/ha/application) reduced shoot mass of red pine by 13 to 45 percent. In another trial, a rate equivalent to 1,866 kg/ha of $MnSO_4$ reduced dry mass by 58 percent (figure 5). Since pines are more tolerant of Mn than other species (Ingestad 1958, Schöne 1992, St. Clair and Lynch 2005), however, it may be difficult to demonstrate a growth reduction when applying less than 200 kg/ha of $MnSO_4$ to well-aerated soils (table 3). In one trial, toxicity occurred when soil was treated with 300 ppm Mn (figure 5).

In other research, toxicity might be declared when Pearson's correlation between Mn and seedling height is negative. For example, negative correlations have been reported between pine heights and foliar Mn (Adams and Walker 1975, Espinoza 2009, Madgwick 1964, South et al. 2018, Steinbeck 1965). Since faster growth reduces foliar Mn concentrations due to carbohydrate dilution, however, these correlations may have little or nothing to do with Mn toxicity.

Although 30 ppm of B or Cu is more toxic to pine seedlings than 30 ppm of Mn (van Lear and Smith 1972), nursery soils typically contain less than 5 ppm of B or Cu. In contrast, some nursery soils contain more than 200 ppm Mn (figure 3), and extended rainfall events can increase exchangeable Mn to toxic levels (Nelson 1977, Siman et al. 1974, Stone 1968). In fact, it may take only 3 days of saturated soil to increase Mn by more than 100 ppm (Graven et al. 1965).

Low soil oxygen has resulted in Mn toxicity at several bareroot nurseries where soil pH was below 5.0. For example, in December 1972, rainfall totaled more than 60 cm at the Wind River Nursery in Washington (Johnson 1975) and Mn toxicity was observed on 2-0 Douglas-fir (Youngberg 1980, 1984). Mn toxicity also occurred on loblolly pine at the Stuart Nursery in Louisiana where rainfall from July through October 1959 was the fifth wettest for the county (Shoulders and Czabater 1965). Similarly, the Camden (figure 7) and Lucky Peak Nurseries in Idaho experienced the fourth wettest October in 2009 and 1975, respectively. Toxicity symptoms also occurred on spruce (Landis 1990). Saturated soil and inadequate aeration stunted 2-0 ponderosa pine seedlings growing in pH 5.5 soil at the Lucky Peak Nursery (Morby et al. 1978), but since micronutrient analysis of pine needles did not include Mn, a Mn toxicity could not be confirmed.

In general, pines with less than 1,500 ppm foliar Mn are not injured, but levels above 1,800 ppm may be toxic. When a pine plantation in South Africa was established on a high Mn soil with low soil pH, toxicity occurred when foliage reached 2,790 ppm Mn (Schutz 1990). In Germany, a diseased Douglas-fir

Figure 7. Chlorotic loblolly pine (*Pinus taeda* L.) seedlings resulted from high soil Mn in a Lenoir soil series. Total rainfall for Wilcox County, AL, in December 2009 was 28.9 cm and, by January 2010, soil Mn ranged from 348 to 414 ppm (pH 4.8 to 5.1). By mid-summer, seedlings in this field were chlorotic, but seedlings in an adjacent field (pH 5.1) were green. Chlorotic needles analyzed in August contained foliar levels of Mn (1,895 ppm), Ca (2,200 ppm), Fe (86 ppm), B (79 ppm), Cu (8 ppm) and Zn (62 ppm). Three foliar applications of Fe did not reduce chlorosis but an application of 1,120 kg of dolomitic lime (before sowing on an adjacent block) produced green seedlings. In some places, chlorotic pine seedlings had dead terminals with resin exudation which are symptoms of a Ca deficiency (Lyle 1969). A Ca deficiency can be induced by high soil Mn (El-Jaoual and Cox 1998, Langheinrich et al. 1992). (Photo by David South, August 8, 2010)

plantation (47 years old) with chlorotic needles had foliar Mn levels that exceeded 7,000 ppm, which likely interfered with Fe metabolism (Kaus and Wild 1998). When growing in perlite, pine seedlings can be injured when foliage contains 3,100 to 4,335 ppm Mn (Kavvadias and Miller 1999, Morrison and Armson 1968). In a study with Mn- and Zn-contaminated soil, pine growth was reduced by 50 percent when foliage contained 3,000 ppm Mn (Beyer et al. 2013).

If needed, managers can apply dolomitic lime to reduce the risk of Mn toxicity (Hopmans and Flinn 1983, Lasota et al. 2021, Phares 1964, Shoulders and Czabator 1965). At one nursery, adding 2,240 kg of dolomite temporarily reduced soil Mn levels by about 1 to 3 ppm (figure 4).

Excessive application of Mn could be toxic if it interferes with Fe uptake (Kaus and Wild 1998, Lafond and Laflamme 1970, Morrison and Armson 1968). Therefore, some laboratories calculate a foliar Fe/Mn ratio and provide expected ratios from 0.3 to 1.0. Actual ratios for bareroot loblolly pine ranged from 0.11 to 4.8 (median = 0.8) when foliage was sampled in July (Starkey and Enebak 2012). In one greenhouse trial (van Lear and Smith 1972), the best growth of slash pine seedlings occurred when the Fe/Mn ratio was 0.04 (i.e., 33/795). Thus, suggestions that the desired Fe/Mn ratio for pine seedlings should range from 1.3 to 1.7 are not true (Barrick and Nobel 1993, Boyer and South 1985, South 2021). For bareroot jack pine (Morrison and Armson 1968) and loblolly pine (Sypert 2006), the foliar Mn concentration is more operationally meaningful than the foliar Fe/Mn ratio.

Although high concentrations of $MnCl_2$ reduce germination of red maple and Norway spruce (Mai and Williams 2019. Rîşca et al. 2011), limited data exist regarding the effect of $MnSO_4$ on germination of pine seed. A trial at the Vallonia Nursery in Indiana (pH 6) found no significant effect on shortleaf pine when soil was treated with 67 kg/ha of Mn (Auten 1945). Similar results were reported for other pines (Morrison and Armson 1968, Stoeckeler and Slabaugh 1965, Wahlenberg 1930).

Manganese Loss in Soils

Depending on species, soil type, cultural practices, and seedling size, a million bareroot pine seedlings may contain 0.6 to 1.5 kg of Mn (Boyer and South 1985, Donald and Young 1982, Flinn et al. 1980, Knight 1978). As a result, harvesting 1.5 million seedlings might lower soil Mn by about 1 ppm, and irrigation might lower it by another 0.5 ppm (Trichet et al. 2018). Over time, leaching, weeding, and harvesting soybean crops might lower extractable Mn by about 3.7 ppm/year (Hickman 2002).

Due to soil pH dynamics, excessive rainfall, irrigation, differences in laboratory procedures, and removal of nutrients at harvest, soil Mn levels can vary from month to month (Danielson 1966, Kazda and Zvacek 1989, Munson 1982, Sparrow and Uren 1987, Trichet et al. 2018) and year to year (figure 4). For example, when irrigation water contains 0.02 ppm Mn, 1,000 mm of irrigation will add 0.2 kg/ha of Mn to the soil. Likewise, when pines are treated with 13.4 kg/ha of the fungicide mancozeb (Marx et al. 1984), about 2.3 kg/ha of Mn is applied over the top of seedlings. Small amounts of Mn in fertilizers and dolomite (Dillard et al. 1982, Fan et al. 2012, Lasota et al. 2021, Weber 1964) also contribute to increasing soil Mn levels. These factors might explain why the average Mn level (35 ppm Mehlich 3) for 18 nursery soils was 8 ppm higher than the average for soil in 39 nonfertilized pine plantations (NCSFNC 1991).

Ectomycorrhiza Effects on Manganese

Nonmycorrhizal pine roots can take up a sufficient amount of Mn so seedlings do not become deficient (Hobbie et al. 2009, Shoulders 1972). For example, stunted, nonmycorrhizal loblolly pine seedlings exhibited P deficiency symptoms (South et al. 1988) and yet had more than 600 ppm Mn in shoots. In fact, even higher foliar Mn concentrations were observed for nonmycorrhizal pine seedlings in North Carolina (South et al. 2018).

In greenhouse trials, pine seedlings inoculated with Pt had more growth and higher foliar Mn concentrations compared with noninoculated seedlings (Miller and Rudolph 1986, Mitchell et al. 1990). On a coal spoil in Alabama (pH 3.4), young pines with Pt had 1,290 ppm foliar Mn compared with 1,808 ppm Mn for seedlings with naturally inoculated Tt (Berry 1982). The Pt inoculated seedlings grew faster than seedlings with natural Tt, however, suggesting that the lower foliar Mn concentrations were likely due to carbohydrate dilution.

Fumigation Effects on Manganese

According to Foy (1984), Mn toxicity is “frequently induced or intensified by N fertilization, which lowers soil pH, fumigation with steam or methyl bromide, air drying, or flooding (Nelson 1977, Kluthcouski and Nelson 1979).” Although fumigation of seedbeds will increase foliar Mn of pine, Mn toxicity induced by either methyl bromide or chloropicrin fumigation has not been recorded in southern pine nurseries. For example, Mn toxicity did not occur after treating nursery soil with methyl bromide followed by fertilization with more than 100 kg/ha of N (Fraedrich and Dwinell 2003, Marx et al. 1984, Marx 1990, Munson 1982, South et al. 2018). Although fumigation with methyl bromide increased foliar Mn in loblolly pine needles to more than 800 ppm (Fraedrich and Dwinell 2003), shoot mass increased by more than 90 percent. When compared with soil fumigation, too much irrigation (producing anaerobic soil) is more likely to induce chlorotic seedlings (Grasmanis and Leeper 1966, Korstian et al. 1921).

Fertilizer Effects on Manganese in Pine Seedlings

Manganese Fertilization

Only a few fertilizer tests with Mn were conducted in bareroot nurseries before 1966 (table 3). Prior to 1980, Mn fertilization was rarely conducted in operational bareroot pine nurseries. As a precautionary measure, 2 kg/ha of Mn (33.6 kg/ha of Frit 503) was applied before sowing pines at a few southern pine nurseries (Marx et al. 1984). In some cases, a blend of micronutrients was applied to pine seedlings during the summer (Hopmans and Flinn 1983, Landis 1979, Maxwell 1988, Munson 1982). In general, however, Mn fertilizers were not applied before 1980 because most routine soil tests at that time did not include Mn, and most nursery soils were acid and not deficient in Mn. Since then, opinions vary as to when seedbeds need to be fertilized with Mn (figure 8).

Since $MnSO_4$ forms a variety of hydrates (monohydrate, tetrahydrate, pentahydrate, and heptahydrate), the amount of Mn applied in experiments is not always certain. In theory, anhydrous $MnSO_4$ contains 36 percent Mn, the monohydrate contains 32 percent Mn, and the tetrahydrate contains 24 percent Mn (van den Driessche 1984). Therefore, the exact amount of Mn applied during previous research (table 3) is unknown since the hydrate tested was not specified.

Currently, less than 5 percent of pine seedbeds in the United States are fertilized with Mn before sowing. Managers who do apply $MnSO_4$ before sowing do so at a rate of 2 to 11 kg/ha of Mn based on soil tests (Aldhous and Mason 1994, Davey 2002, Maxwell 1988). Due to economics, $MnSO_4$ is the preferred source and can be applied before and after sowing. Applying 35 kg/ha of $MnSO_4$ (table 4) might cost $100/ha (2022 USD). If a foliar test indicates less than 20 ppm Mn, then a liquid product, containing either $MnSO_4$ or $MnCl_2$, might be applied over the top of pine seedlings. Application of more expensive chelated products to pine seedlings appears to have no added benefit. Deficient pines respond well after a foliar application of $MnSO_4$ (Lange 1969), but pines have not responded well to fritted Mn sources (Jokela et al. 1991).

Phosphorus Fertilization

At some nurseries, high rates of P + Ca fertilization resulted in chlorosis and stunting of pine seedlings (Shoulders and Czabator 1965, Steinbeck et al. 1966). At that time, some believed increasing P levels in plants would reduce uptake of Mn and Fe (Neilsen et al. 1992, Shoulders and Czabator 1965). Although a high rate of TSP (1,152 kg/ha of P) induced Cu and Zn deficiencies and caused chlorosis on young *Populus* cuttings (Teng and Timmer 1990), the treatment did not result in a Mn deficiency. In fact, the treatment slightly increased soil solution Mn. Likewise, when greenhouse-grown loblolly pine seedlings were fertilized with Na_2HPO_4, foliar P concentration increased but foliar Mn was not affected (Rowan and Steinbeck 1977). Evidence is lacking to support the assumption that a high rate of TSP will produce a Mn deficiency in bareroot conifer seedlings.

Calcium Fertilization

Foliar Mn reached deficient levels (1 to 19 ppm) when soils contained more than 10,000 ppm Ca (Landis 1988, Nakos 1979). Likewise, applying 10,000 ppm Ca to container-grown media reduced foliar Mn to an undetectable level and resulted in chlorosis of Douglas-fir needles (van den Driessche 1984). In some soils, applying lime to increase soil

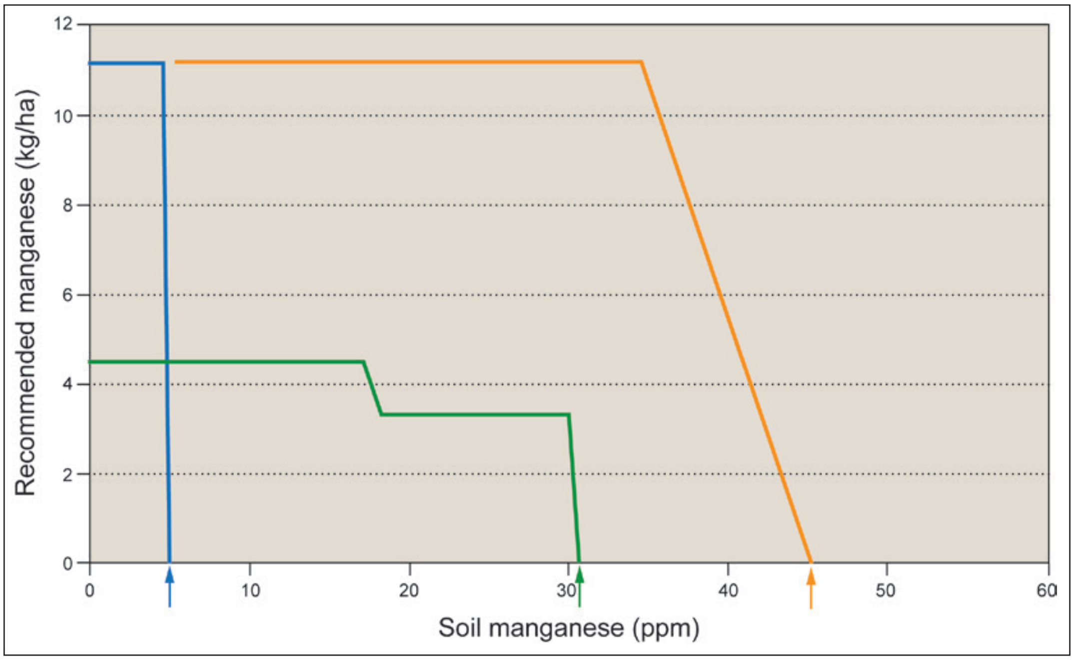

Figure 8. This graph demonstrates three opinions regarding the trigger value for fertilizing pine seedbeds with Mn. Some agronomists set 45 ppm soil Mn (Mehlich 3) as a satisfactory level (orange arrow – line) while others use a 30-ppm (green arrow – line) or 5-ppm trigger value (blue arrow – line).

Table 4. A partial list of Mn fertilizers sold as liquids (L), granules (G), wettable powders (WP), or water-soluble powders (WS). Manganese oxide is not water soluble.

Trade name	Common Name	Type	%	% N	% S	Formula
Wolf Trax™	Mn oxide + Mn sulfate	WP	33			$MnSO_4 \bullet 1H_2O + MnO$
Brant®	Manganese sulfate	WP	31		18	$MnSO_4 \bullet 1H_2O$
Southern Ag	Manganese sulfate	WP	29		17	$MnSO_4 \bullet 1H_2O$
Frit™ 287 G	Mn oxide + Mn sulfate	G	28		6	Mn in crushed glass
Lebosol® Mangan	Manganese carbonate	L	28			$MnCO_3$
Ele-Max®	Manganese carbonate	L	27	3		$MnCO_3$
Nutriseed™ ZnMn	Manganese carbonate	L	16			$MnCO_3$
NitraMar™	Manganese nitrate	L	15	7		$Mn(NO_3)_2$
Tiger-sul	Manganese oxide	G	15		65	MnO
Brant® EDTA	EDTA	L	13			$Mn(C_{10}H_{16}N_2O_8Na_2)$
Mineral Research	Manganese chloride	L	7			$MnCl_2 \bullet 4H_2O$
Britz	Manganese sulfate	L	7		4	$MnSO_4$ in kraft lignin
Ultra-Che®	EDTA	L	6	3		$Mn(C_{10}H_{16}N2O_8Na_2)$
Biomin®	Manganese sulfate	L	5	1	3	$MnSO_4$ in glycine and citric acid
13-13-13	Manganese oxide	G	0.4	13	9	MnO
20-20-20	EDTA	WS	0.025	20		$Mn(C_{10}H_{16}N2O_8Na_2)$

pH to near neutrality will produce a Mn deficiency in some row crops (Foy 1992, Siebielec and Chaney 2006). In a bareroot nursery, applying 2,240 kg/ha of dolomite will increase soil Ca and might lower extractable Mn slightly (figure 4). At one loblolly pine nursery, applying a total of 2,984 kg/ha of Ca (lime plus gypsum) caused summer chlorosis (pH 6.7) without producing a Mn deficiency (South 2021). Although applying Ca before sowing pine (pH < 7.0) may cause Mg and Fe deficiencies, it is unlikely to induce a Mn deficiency. Mn and Ca in pine foliage are closely correlated (Hill and Lambert 1981).

Nitrogen Fertilization

Since several N fertilizers can lower soil pH, it has been suggested that N fertilization might induce in Mn toxicity (Bengtson 1970, Foy 1984, Lingle and Wight

1961). Although improper use of N can certainly injure pine seedlings, billions of bareroot pine seedlings have been fertilized with N without symptoms of Mn toxicity. For example, 450 kg/ha of N produced more growth on loblolly pine (at pH 4.8 soil) than 150 kg/ha (Marx 1990). Although foliar Mn concentration increased to 1,400 ppm, there was no sign of stunting. Other conifer trials have also shown that extra N fertilization did not induce Mn toxicity (Birchler et al. 2001, Rowan and Steinbeck 1977, Woods 1983, Yongliang et al. 2002). At some nurseries, soil Mn is actually lower after seedbeds are fertilized with N and then irrigated (Radwan et al. 1979) (figure 9).

Iron Fertilization

When chlorotic seedlings are related to high pH soil, a foliar application of Fe can reduce chlorosis (Korstian et al. 1921, South 2021). In contrast, if chlorosis appears after acid soil (< pH 5.0) becomes saturated, then the problem is most likely Mn toxicity. Too much Mn in the soil or water can induce an Fe deficiency (Lafond and Laflamme 1970, Morrison and Armson 1968, Olson and Carlson 1950). One way to reduce an Fe deficiency induced by Mn toxicity, is to apply Fe (Bryson and Mills 2014, Lafond and Laflamme 1970). For example, one nursery (pH 4.1 to 4.5) applied three applications of Fe (1.0 kg/ha/application) and successfully reduced chlorosis and restored growth of pines (Shoulders and Czabator 1965).

Manganese after Outplanting Pine Seedlings

Sometimes bareroot pine seedlings are lifted and shipped with less than 100 ppm foliar Mn (table 1). Does the foliar Mn affect plantation growth? Only a few studies have examined the effect of foliar Mn on seedling performance. On a site in Alabama, there was no relationship between foliar Mn in the nursery (118 to 861 ppm Mn) and height growth of loblolly pine after 3 years (Larsen et al. 1988). Likewise, on five sites in Texas, there was no relationship (P =0.65) between foliar Mn and height of shortleaf pine 8 months after planting. Shortleaf pine height averaged 169 and 186 mm (LSD_{05} = 30 mm) for two treatments that averaged 234 and 502 ppm Mn at planting, respectively (Bryson 1980). When needles contain more than 100 ppm Mn, then outplanted pines might not benefit from fertilization with Mn (Jokela et al. 1991, Larsen et al. 1988, Sypert 2006, Vogel and Jokela 2011).

On Mn-deficient sites, nutrient loading with Mn and S in the nursery might increase height growth of pines after planting. At a nursery in South Africa, container seedlings were fertilized five times with $MnSO_4$, and growth after outplanting in the field increased significantly (P = 0.0001) (de Ronde et al. 1988). Assuming 40 mm of irrigation with 3,100 ppm Mn, the total rate applied in the nursery would equal 1,240 kg/ha of Mn.

Conclusion

Additional nursery research using the scientific method is needed to investigate several questions: (1) What is the adequate Mn range for pine needles? (2) Will an ineffective foliar application (280 g/ha of Mn) of a row-crop chelate (Last and Bean 1991) also be ineffective when applied to pine seedlings? (3) In a high pH soil, will pine seedlings develop a Zn deficiency before a Mn deficiency? (4) Will an application of MnO persist longer in a nursery soil than an application of $MnSO_4$? (5) At what rate does weathering convert unavailable Mn to available Mn? (6) Will foliar Fe applications to ponderosa pine seedlings reduce Fe chlorosis caused by low soil pH and high soil Mn? Exploration of these and other nutrient questions will benefit the science of growing quality seedlings.

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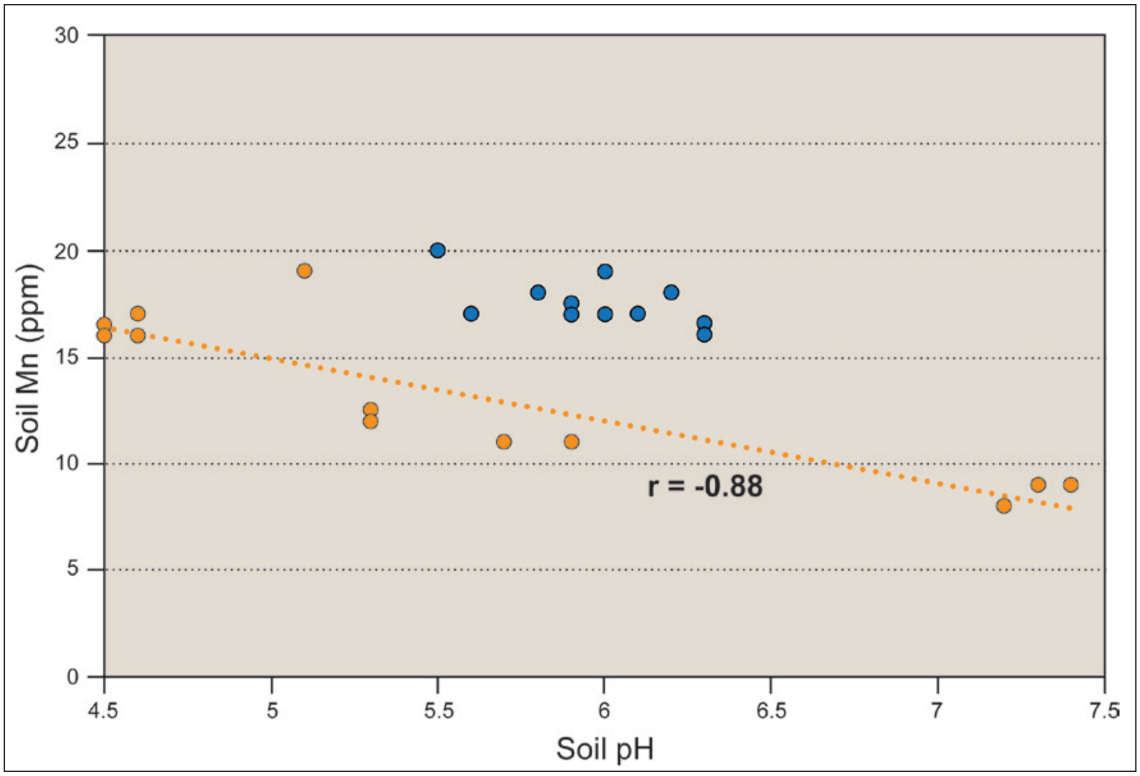
Acknowledgments

I thank the nursery managers who shared their experiences with Mn fertilization. I thank J.B. Jett, Eric Jokela, John Mexal, Barbara Hawkins, Tom Starkey, Nelson Thiffault, and Diane Haase for reviews of earlier drafts of this manuscript.

Figure 9. A nitrogen (N) fertilization trial installed at the Union Camp Nursery (Capron, VA) included four sources of N applied at 224, 336, and 448 kg/ha during the growing season (Villarrubia 1980). On June 30, 1978, untreated plots (blue dots) ranged from pH 5.5 to 6.3 and averaged 17 ppm Mn (Mehlich 1). On September 12, 1978, soil treated with N (orange dots) averaged 13 ppm Mn. Irrigation and rainfall leached some Mn and some Mn was taken up by seedlings. Fertilization with sodium nitrate reduced soil acidity to pH >7.1, while ammonium sulfate increased acidity to pH <4.7. Urea and ammonium nitrate treatments averaged pH 5.4 and pH 5.2, respectively.



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Forest Nursery Seedling Production in the United States—Fiscal Year 2021

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Abstract

Forest nursery production for the 2021 planting season was more than 1.37 billion tree seedlings (including about 22.8 million container seedlings imported from Canada). Approximately 71 percent of seedlings were produced as bareroot stock. Only a small portion (3 percent) of seedlings were hardwood species. Based on this total number of seedlings and estimated planting densities in each State, more than 2.6 million ac (1,716,192 ha) were planted. Approximately 82 percent of production and planting occurred in the southern States, while 13 and 5 percent were planted in the western and eastern States, respectively.

Background

This annual report summarizes forest nursery seedling production in the United States. The number of seedlings reported is used to estimate the number of acres of forest planting per year. Prepared by the U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis (FIA) and State and Private Forestry, this report includes State-by-State breakdowns, regional totals, and an analysis of data trends. Universities in the Southern, Northeastern, and Western Regions of the United States made an effort to collect data from all the major producers of forest and conservation seedlings in the 50 States. Forest and conservation nursery managers provided the information presented in this report. Because all data are provided voluntarily by outside sources and some data are estimated, caution must be used in drawing inferences.

Methodology

State and Private Forestry, in collaboration with Auburn University, the University of Idaho, and Purdue University, produced the data for this report. These universities collected forest tree seedling production data directly from the forest and conservation nurseries that grow forest tree seedlings in their region of the United States (Auburn University collected from 12 States in the Southeast, the University of Idaho collected from 17 States in the West, and Purdue University collected from 21 States in the Northeast and Midwest). The estimate of planted acres for each State was calculated using FIA estimates of planting densities. In addition, FIA average annual estimates of tree planting area based on ground-plot data that States collected during 5-, 7-, or 10-year periods is included. FIA estimates of acres of trees planted by State may not correlate with nursery production surveys because nurseries do not report shipments across State lines. Total acres by region, however, provide a reasonable estimate of planted acreage. Data collected are reported for both hardwood and conifer species by bareroot and container seedlings produced (table 1) and by estimated acreage planted of each (table 2).

Table 1. Hardwood and conifer tree seedling production for each State and each region during the 2021 planting year.

State	Hardwood bareroot seedlings produced	Hardwood container seedlings produced	Total hardwood seedlings produced	Conifer bareroot seedlings produced	Conifer container seedlings produced	Conifer container seedlings imported	Total conifer seedlings produced	Total seedlings produced
Southeast								
Florida	2,161,613	60,066	2,221,679	52,304,000	5,118,500	—	57,422,500	59,644,179
Georgia	4,616,621	500	4,617,121	203,854,180	148,341,600	—	352,195,780	356,812,901
North Carolina	440,000	—	440,000	60,700,000	13,925,193	—	74,625,193	75,065,193
South Carolina	647,000	—	647,000	159,299,000	—	—	159,299,000	159,946,000
Virginia	877,750	—	877,750	31,202,121	442,686	—	31,644,807	32,522,557
Regional Totals	**8,742,984**	**60,566**	**8,803,550**	**507,359,301**	**167,827,979**	**0**	**675,187,280**	**683,990,830**
South Central								
Alabama	3,719,200	—	3,719,200	100,785,667	36,683,624	—	137,469,291	141,188,491
Arkansas	9,573,490	—	9,573,490	85,009,925	166,875	—	85,176,800	94,750,290
Kentucky	530,400	—	530,400	56,760	—	—	56,760	587,160
Louisiana	—	—	—	—	53,677,288	—	53,677,288	53,677,288
Mississippi	—	177,000	177,000	74,184,000	11,003,000	—	85,187,000	85,364,000
Oklahoma	511,746	4,100	515,846	3,457,948	21,500	—	3,479,448	3,995,294
Tennessee	1,405,000	—	1,405,000	2,315,000	—	—	2,315,000	3,720,000
Texas	—	—	—	81,014,000	—	—	81,014,000	81,014,000
Regional Totals	**15,739,836**	**181,100**	**15,920,936**	**346,823,300**	**101,552,287**	**0**	**448,375,587**	**464,296,523**
Northeast								
Connecticut	—	—	—	—	—	—	—	—
Delaware	—	—	—	—	—	—	—	—
Maine[1]	—	3,500	3,500	—	—	3,984,760	3,984,760	3,988,260
Maryland	912,788	480,200	1,392,988	684,525	7,620	—	692,145	2,085,133
Massachusetts	500	20,000	20,500	—	200	—	200	20,700
New Hampshire	13,542	—	13,542	158,677	—	—	158,677	172,219
New Jersey	50,936	—	50,936	70,562	—	—	70,562	121,498
New York	134,500	—	134,500	492,600	—	—	492,600	627,100
Pennsylvania	531,665	40	531,705	3,155,945	200	—	3,156,145	3,687,850
Rhode Island	—	—	—	—	—	—	—	—
Vermont	37,100	925	38,025	1,300	—	—	1,300	39,325
West Virginia	—	—	—	—	—	—	—	—
Regional Totals	**1,681,031**	**504,665**	**2,185,696**	**4,563,609**	**8,020**	**3,984,760**	**8,556,389**	**10,742,085**
North Central								
Illinois	744,550	4,503	749,053	56,600	1,884	—	58,484	807,537
Indiana	1,684,879	500	1,685,379	468,600	—	—	468,600	2,153,979
Iowa	690,975	—	690,975	138,250	—	—	138,250	829,225
Michigan[1]	1,480,500	101,666	1,582,166	16,040,090	11,243,025	—	27,247,415	28,829,581

State	Hardwood bareroot seedlings produced	Hardwood container seedlings produced	Total hardwood seedlings produced	Conifer bareroot seedlings produced	Conifer container seedlings produced	Conifer container seedlings imported	Total conifer seedlings produced	Total seedlings produced
Minnesota[1]	470,856	—	470,856	2,040,090	—	485,970	2,526,060	2,996,916
Missouri	892,985	—	892,985	465,695	—	—	465,695	1,358,680
Ohio	500	—	500	—	—	—	—	500
Wisconsin[1]	1,335,786	—	1,335,786	3,262,331	1,342,040	392,040	4,996,411	6,332,197
Regional Totals	**7,301,786**	**106,669**	**7,407,700**	**22,435,956**	**12,586,949**	**878,010**	**35,900,915**	**43,308,615**
Great Plains								
Kansas	—	12,200	12,200	—	47,925	—	47,925	60,125
Nebraska	279,370	5,000	284,370	468,700	680,665	—	1,149,465	1,433,735
North Dakota	13,150	19,930	33,080	684,390	72,450	—	756,840	789,920
South Dakota	729,625	1,700	731,325	290,550	2,425	—	292,975	1,024,300
Regional Totals	**1,022,145**	**38,830**	**1,060,975**	**1,443,640**	**803,465**	**0**	**2,247,105**	**3,308,080**
Intermountain								
Arizona	—	400	400	—	650	—	650	1,050
Colorado	63,700	32,516	96,216	12,025	137,445	—	149,470	245,686
Idaho[1]	12,250	45,885	58,135	1,390,180	4,539,872	880,820	6,810,872	6,869,007
Montana[1]	92,300	35,163	127,463	—	486,179	86,356	572,535	699,998
Nevada	—	1,446	1,446	—	177	—	177	1,623
New Mexico	—	7,000	7,000	—	112,000	—	112,000	119,000
Utah	—	—	—	—	—	—	—	—
Wyoming	—	—	—	—	—	—	—	—
Regional Totals	**168,250**	**122,410**	**290,660**	**1,402,205**	**5,276,323**	**967,176**	**7,645,704**	**7,936,496**
Alaska								
Alaska	—	—	—	—	—	—	—	—
Pacific Northwest								
Oregon[1]	700,00	1,269,500	1,969,500	37,227,000	31,270,774	15,582,044	84,079,818	86,049,318
Washington[1]	546,709	59,483	606,192	25,792,130	25,499,190	1,414,360	52,705,680	53,311,872
Regional Totals	**1,246,709**	**1,328,983**	**2,575,692**	**63,019,130**	**56,769,964**	**16,996,404**	**136,785,498**	**139,361,190**
Pacific Southwest								
California	1,517,800	30,000	1,547,800	3,348,447	20,745,987	—	24,094,434	25,642,234
Hawaii	—	158,226	158,226	—	2,497	—	2,497	160,723
Regional Totals	**1,517,800**	**188,226**	**1,706,026**	**3,348,447**	**20,748,484**	**0**	**24,096,931**	**25,802,957**
Totals	**37,419,786**	**2,531,449**	**39,951,235**	**950,395,588**	**365,573,471**	**22,826,350**	**1,338,795,409**	**1,378,746,644**

[1] Totals include an estimate of container conifers produced in Canada; bareroot imports for Maine and containers for other States.

Table 2. Estimated hardwood and conifer tree seedling acres planted for each State and each region during the 2021 planting year.

State	Hardwood acres planted	Conifer acres planted	Total acres planted	FIA estimated acres planted[9]
Southeast				
Florida[2]	4,039	104,405	108,444	150,006
Georgia[2]	8,395	640,356	648,751	212,353
North Carolina[2]	800	135,682	136,482	108,401
South Carolina[2]	1,176	289,635	290,811	88,362
Virginia[2]	1,596	57,536	59,132	57,031
Regional Totals	**16,006**	**1,227,613**	**1,243,620**	**616,153**
South Central				
Alabama[2]	6,762	249,944	256,706	218,748
Arkansas[2]	17,406	154,867	172,273	89,136
Kentucky[3]	1,219	130	1,350	1,142
Louisiana[2]	—	97,595	97,595	160,561
Mississippi[2]	322	154,885	155,207	140,495
Oklahoma[2]	938	6,326	7,264	31,659
Tennessee[2]	2,555	4,209	6,764	24,386
Texas[2]	—	147,298	147,298	126,044
Regional Totals	**29,202**	**815,256**	**844,458**	**792,171**
Northeast				
Connecticut[3]	—	—	—	—
Delaware[2]	—	—	—	515
Maine[5]	6	6,641	6,647	4,069
Maryland[2]	2,533	1,258	3,791	—
Massachusetts[3]	47	—	48	—
New Hampshire[3]	31	365	396	402
New Jersey[3]	117	162	279	—
New York[5]	224	821	1,045	2,077
Pennsylvania[3]	1,222	7,256	8,478	1,847
Rhode Island	—	—	—	—
Vermont[3]	87	3	90	—
West Virginia[3]	—	—	—	—
Regional Totals	**4,268**	**16,507**	**20,774**	**8,910**
North Central				
Illinois[3]	1,722	134	1,856	1,667
Indiana[4]	2,593	721	3,314	2,413
Iowa[5]	1,152	230	1,382	—
Michigan[2]	2,877	49,541	52,417	6,330
Minnesota[2]	856	4,593	5,449	8,403
Missouri[3]	2,053	1,071	3,123	223
Ohio[3]	1	—	1	2,173
Wisconsin[6]	1,670	6,246	7,915	8,256
Regional Totals	**11,201**	**62,401**	**73,602**	**29,465**

State	Hardwood acres planted	Conifer acres planted	Total acres planted	FIA estimated acres planted[9]
Great Plains				
Kansas[2]	22	87	109	1,012
Nebraska[2]	517	2,090	2,607	—
North Dakota[2]	60	1,376	1,436	—
South Dakota[2]	1,330	533	1,862	164
Regional Totals	**1,929**	**4,086**	**6,015**	**1,176**
Intermountain				
Arizona[2]	1	1	2	-
Colorado[2]	175	272	447	669
Idaho[2]	106	12,383	12,489	10,016
Montana[2]	232	1,041	1,273	4,506
Nevada[2]	3	—	3	—
New Mexico[2]	13	204	216	—
Utah[2]	—	—	—	—
Wyoming	—	—	—	846
Regional Totals	**528**	**13,901**	**14,430**	**16,037**
Alaska				
Alaska[2]	—	—	—	—
Pacific Northwest				
Oregon[7]	5,627	240,228	245,855	118,350
Washington[7]	1,732	150,588	152,320	96,376
Regional Totals	**7,359**	**390,816**	**398,175**	**214,726**
Pacific Southwest				
California[8]	3,440	53,543	56,983	36,986
Hawaii[8]	352	6	357	568
Regional Totals	**3,791**	**53,549**	**57,340**	**37,554**
TOTALS	**74,285**	**2,584,128**	**2,6582,413**	**1,716,192**

[1] Acres planted were estimated assuming:
[2] 550 stems/acre.
[3] 435 stems/acre.
[4] 650 stems/acre.
[5] 600 stems/acre.
[6] 800 stems/acre.
[7] 350 stems/acre.
[8] 450 stems/acre.

[9] FIA = Forest Inventory and Analysis; average annual acreage planted estimated for all States on 5-year cycles, except for Alabama, Louisiana, Mississippi, and North Carolina, which are on 7-year cycles, and for Alaska, Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, and Washington, which are on 10-year cycles. Data generated by Andy Hartsell, USDA Forest Service.

Assumptions

The following assumptions were used in compiling this report.

1. *The number of seedlings reported by the participating forest and conservation nurseries was the number of shippable seedlings produced for distribution in the 2021 planting season (i.e., seedlings that were planted from fall of 2020 through spring of 2021).*

Some species of forest seedlings require two or more growing seasons to reach accepted forest and conservation seedling size standards, so not all seedlings in production at a nursery at any given time are considered shippable (i.e., available for distribution). Therefore, only shippable seedlings were counted.

2. *All seedling production reported in this survey met the grading standards for the respective nurseries (i.e., cull seedlings were not included in the estimates).*

Production estimates are often based on seedbed inventories of seedlings meeting grading standards. For cases in which nurseries ship seedlings by weight, as opposed to examining and counting each seedling, landowners and tree planters often plant every seedling that is shipped to them.

3. *Seedling production data were collected from all the major nurseries that produced forest and conservation tree seedlings for the planting season.*

Considerable effort was made to contact all major producers of forest and conservation seedlings. The universities collecting the survey data reported, with few exceptions, that the major producers were included in the results.

4. *All seedlings reported in this survey were produced for reforestation and conservation projects.*

Some of the nurseries that participated in this survey also produce seedlings for ornamental use, Christmas tree production, or other horticultural purposes. Private nurseries were asked to report only seedling production destined for conservation and reforestation planting.

5. *Forest tree seedlings remain in the general area where they are produced.*

Forest and conservation seedlings are routinely shipped across State borders and at times across international borders. It is assumed that, on average, the number of seedlings imported into a State is equal to the number of seedlings exported from that State. In some States, a significant number of seedlings are produced in Canada and imported for planting in those States. Estimates of the number of seedlings shipped from Canada were obtained from Canadian nurseries that routinely export seedlings to the United States.

6. *Dividing the number of seedlings shipped from forest and conservation nurseries by the average number of stems planted per acre in a specific State is an appropriate proxy of the number of acres of trees planted during the planting season.*

These estimations do not include direct seeding or natural forest regeneration activities. Average tree planting densities for each State were provided by FIA.

7. *Respondents to the production survey reported only hardwood and conifer trees produced.*

Nurseries were asked not to include shrubs in their production estimates. Many conservation and restoration plantings include shrubs and herbaceous plants to address wildlife, biodiversity, or other management objectives. Using only tree production to estimate acres planted results in an underestimate of planted acreage where a mixed planting of shrubs and trees occurred.

Data Trends

More than 1.37 billion forest tree seedlings were planted in the United States in fiscal year (FY) 2021. This production level is an approximately 9-percent increase from FY 2020 (figure 1). The increase is attributable, in part, to a return of operations following the coronavirus pandemic. Seedling production in the Southern United States has increased annually from 2012 through 2021 (figure 2). In the Eastern United States, seedling production generally declined from 2012 to 2020, but nearly doubled from 2020 to 2021 because many nurseries had ceased lifting operations during the pandemic (figure 2). In the Western United States, production has fluctuated over time (figure 2). Some of the year-to-year variation is attributed to inconsistent participation from nurseries during data collection and shifting planting needs following wildfires,

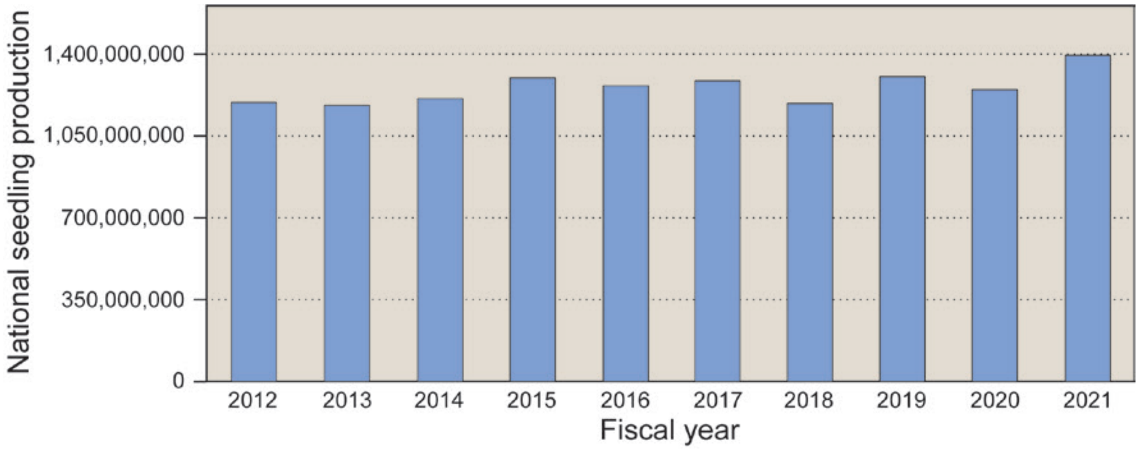

Figure 1. Total annual forest nursery seedling production in the United States for fiscal years 2012 through 2021. Sources: this report, Haase et al. (2019, 2020, 2021), Harper et al. (2013, 2014), Hernández et al. (2015, 2016, 2017, 2018)

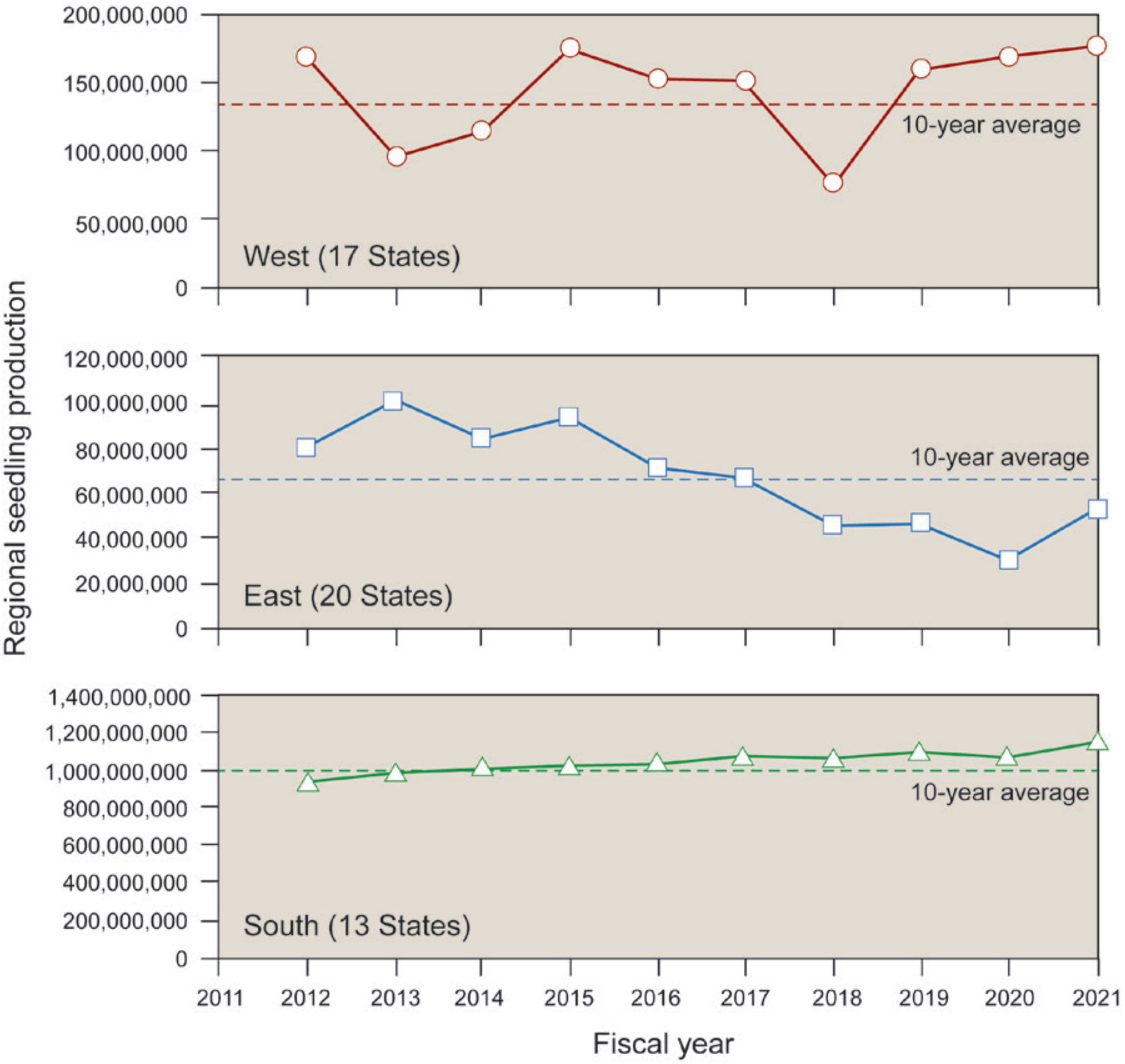

Figure 2. Annual forest nursery seedling production by region for fiscal years 2012 through 2021. Ten-year production averages are: 142,277,318 (west), 69,851,412 (east), and 1,044,440,614 (south). Sources: this report, Haase et al. (2019, 2020, 2021), Harper et al. (2013, 2014), Hernández et al. (2015, 2016, 2017, 2018)

pests, and harvests. Based on the total number of seedlings shipped and the average number of seedlings planted per acre in each State, more than 2.6 million ac (1,072,310 ha) of tree seedlings were planted during the fall 2020 through spring 2021 planting season.

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Acknowledgments

The authors thank the U.S. Department of Agriculture, Forest Service, Washington Offices of the Forest Inventory and Analysis program, and the State and Private Forestry Deputy Area for their support.

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Survival and Growth of Four Floodplain Forest Species in an Upper Mississippi River Underplanting

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Abstract

Forest restoration efforts commonly occur in degraded ecosystems. For the floodplain forests of the Upper Mississippi River, the combination of aging canopy trees and expansion of invasive species such as reed canary grass (*Phalaris arundinacea* L.) can shift forested ecosystems to open meadows. Before this shift occurs, there may be opportunities to proactively underplant. Our study reports 2-year survival and growth of four tree species (swamp white oak (*Quercus bicolor* Wild.), silver maple (*Acer saccharinum* L.), hackberry (*Celtis occidentalis* L.), and sycamore (*Platanus occidentalis* L.) planted under a moderate canopy of silver maple (approximately 60 percent overstory cover) across three elevational gradients. Swamp white oak had high survival across all three of the elevational zones and showed limited effects by herbivory or insects. Growth and survival of sycamore and hackberry depended on the elevational zone; sycamore performed better on lower elevational sites and hackberry did better on higher elevational sites. Our results highlight the potential for underplanting in floodplain forests as a proactive restoration strategy, with consideration given to local site conditions.

Introduction

Anthropogenic expansion, utilization, and manipulation of the natural environment, which includes the intentional and unintentional introduction of nonnative species, have resulted in the development of a relatively new field of ecology and natural resource management—restoration (Galatowitsch 2012). While restoration has multiple subdisciplines (e.g., restoration ecology, restorative silviculture, and others), an overarching theme is management action focused on reestablishing composition, structure, and/or function of an ecosystem (Nunez-Mir et al. 2015). While some restoration efforts focus on restoring to some prior time period, often pre-European colonization, other restoration efforts also are couched under the broad theme of restoration that focuses on restoring ecosystem structure and/or function (but not necessarily individual species) in such a way that the restored ecosystem may be better adapted to future conditions (Stanturf et al. 2014).

Restoration efforts often focus on highly degraded ecosystems or ecosystems that have moved to a novel state (Hobbs et al. 2006). Numerous studies across multiple ecosystems note that restoration practices for ecosystems in these conditions often result in significant inputs of time and money, and these inputs may not guarantee immediate or long-term (> 5 years) success (Diagne et al. 2021, Fantle-Lepczyk et al. 2022, Hoffmann and Broadhurst 2016). To use resources more efficiently, basic knowledge of ecosystem function and response is important to avoid overinvestment in techniques that have little effect, or underinvestment in techniques beneficial to restoration success.

As opposed to the systems described above, some ecosystems may be considered degraded, but have not yet shifted to a novel state. These ecosystems may be affected by disturbances, but still maintain enough resistance or resilience to maintain ecosystem function (Millar et al. 2007). Such ecosystems are often not considered priorities for restoration, but may represent opportunities where restoration interventions could be applied in a more efficient way to increase resilience and maintain ecosystem function before a shift to a novel state (Dudney et al 2018).

Novel environmental conditions in the 19th through 21st centuries in the Upper Mississippi River (UMR) resulted from extensive land clearing; artificial river modifications culminating in the impoundment of the system via a series of locks and dams; expansion of native and nonnative invasive species; and increased hydrologic variability due to changes in regional weather patterns and land uses that have altered floodplain forest successional processes (Guyon et al. 2012, Cosgriff and Vandermyde 2019). Invasive species also may contribute to future shifts of these forests to alternate ecosystem states (Miller-Adamany et al. 2019). Forests that are highly resistant and resilient to current and future potential ecosystem shifts include healthy, mature overstory trees and newly regenerating individuals. When a disturbance does occur, mortality of overstory trees can be compensated through regeneration of individuals which will grow into the overstory. Forests with less resilience have potential to shift to a novel state. These forests may have an intact overstory or may have some mortality with invasive understory species establishing. Regeneration is limited under those conditions. Finally, forests that have shifted to a novel state have almost no overstory, no regeneration, and are dominated by a range of native and nonnative invasive herbaceous species. Often, the most visible examples of this shift from forest to an alternative state in the UMR are wet meadow habitats dominated by invasive reed canary grass (*Phalaris arundinacea* L.) occurring within historically forested areas (Bouska et al. 2020)

Researchers and managers have been exploring and testing multiple means for controlling the exclusionary, nonnative reed canary grass in the UMR to allow for the regeneration of native tree species (Adams et al. 2011, Thomsen et al. 2012, Clark and Thomsen 2020). Although short-term and highly intensive management options are available for controlling reed canary grass, seedlings face additional challenges due to the dynamic nature of the floodplain and increased pressure from herbivory. These factors can result in limited survival of the planted trees, and thereby limited success in restoring floodplain forest function (De Jager et al. 2013a). In addition, focusing restoration efforts on these invasive wet meadow sites may come at the expense of potentially lower cost interventions in forests that retain some components of a forested habitat but are on a potentially reversible trajectory towards a future ecosystem shift.

Challenges to regeneration in floodplains are well-documented from other systems, including invasive plants and browse pressure from small rodents, beavers (*Castor canadensis* Kuhl), and white-tailed deer (*Odocoileus virginianus* [Zimmerman]) (Guyon et al. 2012). Two historically important floodplain forest species in the UMR, American elm (*Ulmus americana* L.), and green ash (*Fraxinus pennsylvanica* Marsh.), face serious threats from pathogens and nonnative pests such as Dutch elm disease (caused by the fungus *Ophiostoma ulmi*) and emerald ash borer (*Agrilus planipennis* Fairmaire) (Nisbet et al. 2015, Ramano 2010). Even with control of competing vegetation and herbivory, regeneration treatments often fail in the UMR, indicating that other complicating factors, such as hydrologic variability, inadequate understanding of floodplain species silvics, and inappropriate stock types for artificial regeneration may also affect regeneration success (De Jager et al. 2019, Hammes et al. 2020).

Our overarching goal was to conduct an applied, *in situ* experiment to quantify how elevation (as a surrogate for hydrology) and herbivory influence the survival and growth of four different tree species established through artificial regeneration in a mature silver maple (*Acer saccharinum* L.) floodplain forest ecosystem with no well-established natural regeneration. Questions of interest were: (1) how does planted seedling survival and growth vary across gradients of hydrology in the UMR floodplain? and (2) how do survival and growth patterns vary across species and stock conditions? Data collected to address these questions can increase our basic understanding of the early growth dynamics of four understudied floodplain species, help match seedling species to environmental conditions to improve survival outcomes in restoration work, and aid in applied decision making related to floodplain forest restoration and management.

Methods

Regional Description and History

The UMR basin encompasses multiple forest ecosystems and ecotones from the headwaters of the Mississippi River beginning at Lake Itasca, MN, to its confluence with the Ohio River in Cairo, IL. Multiple indigenous tribes note locations of spirituality (e.g., Bdote at the confluence of the Minnesota River and Mississippi River in Minnesota and Trempealeau Mountain near modern-day Trempealeau, WI) (Anfinson 2003). These Tribes are the stewards of these ecosystems. Current ownership of these lands, especially in the Minnesota and Wisconsin portions of the navigable portion of the UMR, is primarily Federal, with small areas of State, municipal, Tribal, and privately owned land.

The U.S. Army Corps of Engineers (USACE) is the primary Federal agency responsible for management of UMR navigation and was the agency given authorization by the U.S. Congress to develop the lock and dam system in the 1930s (Nanda and Ports 2004). The USACE-St. Paul District manages the portion of the UMR that flows from the headwaters in northern Minnesota to Lock and Dam 10 at Guttenberg, IA. Most USACE lands in the St. Paul District, acquired to support development of the 1930s navigation project, along with substantial U.S. Fish and Wildlife Service (USFWS) ownership, are incorporated into the Upper Mississippi River National Wildlife and Fish Refuge. Land management is broadly defined in the context of a series of navigation pools and associated floodplains, with the area of impounded water upstream from the lock and dam being referred to as a navigation pool and numbered according to the number of the lock that impounds it.

Site Description

The study site is within the Kains Switch South (KSS) forest management site, a USACE site located on the western edge of the Mississippi River floodplain between river mi 668.2 and 670.3 within navigation Pool 9 (figure 1). The site is approximately 5 miles (8 km) south of New Albin, IA, and the Minnesota/Iowa border in Allamakee County, IA. The KSS encompasses 660.5 ac (267.3 ha) of USACE-owned lands and is within one of the largest contiguous tracts of floodplain forest of the USACE-St. Paul District.

The floodplain forest at KSS is representative of the broader UMR floodplain forest. Silver maple makes up almost 60 percent of the tree species' importance value on the site, with remaining species being primarily green ash, American elm, eastern cottonwood (*Populus deltoides* Bartr.), and black willow (*Salix nigra* Marshall) (figure 2). Average basal area in this forest is 148 ft^2/ac (34 m^2/km^2), with a quadratic mean diameter of 14.7 in (37.3 cm). Average annual inundation duration during the growing season for the site ranges from 0 to 101 days with a mean of 35 days (Van Appledorn et al. 2018). Areas higher in elevation (and with typically shorter inundation durations) generally have lower overstory density (approximately 50 to 100 ft^2/ac [approximately 11 to 23 m^2/km^2]). Boxelder (*Acer negundo* L.) and black walnut (*Juglans nigra* L.) are present in these areas. Green ash is a common component of the midstory and understory. Given the presence of the invasive emerald ash borer in the region, young ash will most likely be killed before reaching the forest canopy (Herms and McCullough 2014). Regeneration of other tree species is virtually nonexistent.

USACE forest management guidelines and priorities focus on maintaining important ecosystem functions, such as providing habitat for the numerous wildlife species of concern that are inhabitants or seasonal migrants of the floodplain forest or seasonal migrants (Guyon et al. 2012). Because many wildlife species of concern within these management areas are dependent on large forest tracts with relatively closed canopies and some large-diameter trees, maintenance of forest cover with large trees present is a management priority for the agency. Consideration of how these forests will regenerate and replace the current cohort of overstory trees present on the landscape, which are expected to reach natural senescence within the next 50 to 75 years, is important for long-term management at the landscape level. Canopy green ash mortality has accelerated forest canopy loss in discrete locations within the management area as well, necessitating an active management approach.

Experimental Design

We used elevation gradients as a surrogate for a suite of environmental conditions believed to influence forest composition and structure (e.g., soil moisture, nutrient availability, texture, and inundation regime). We divided the distribution of elevations at KSS into three quantiles and mapped these quantiles to identify high (highest elevation quantile: 626.5 to 628.5 ft [190.9 to 191.6 m]), intermediate (moderate elevation quantile: 624.5 to 626.5 ft [190.3 to 190.9 m]), and low (lowest elevation quantile: 622.5 to 624.5 ft [189.7 to 190.3 m]) elevational zones (figure 1). Within each of the three zones, locations with intermediate canopy coverage (approximately 60 percent closed) were identified using first-return light detection and ranging (lidar) data (Sattler and Hoy 2020), followed

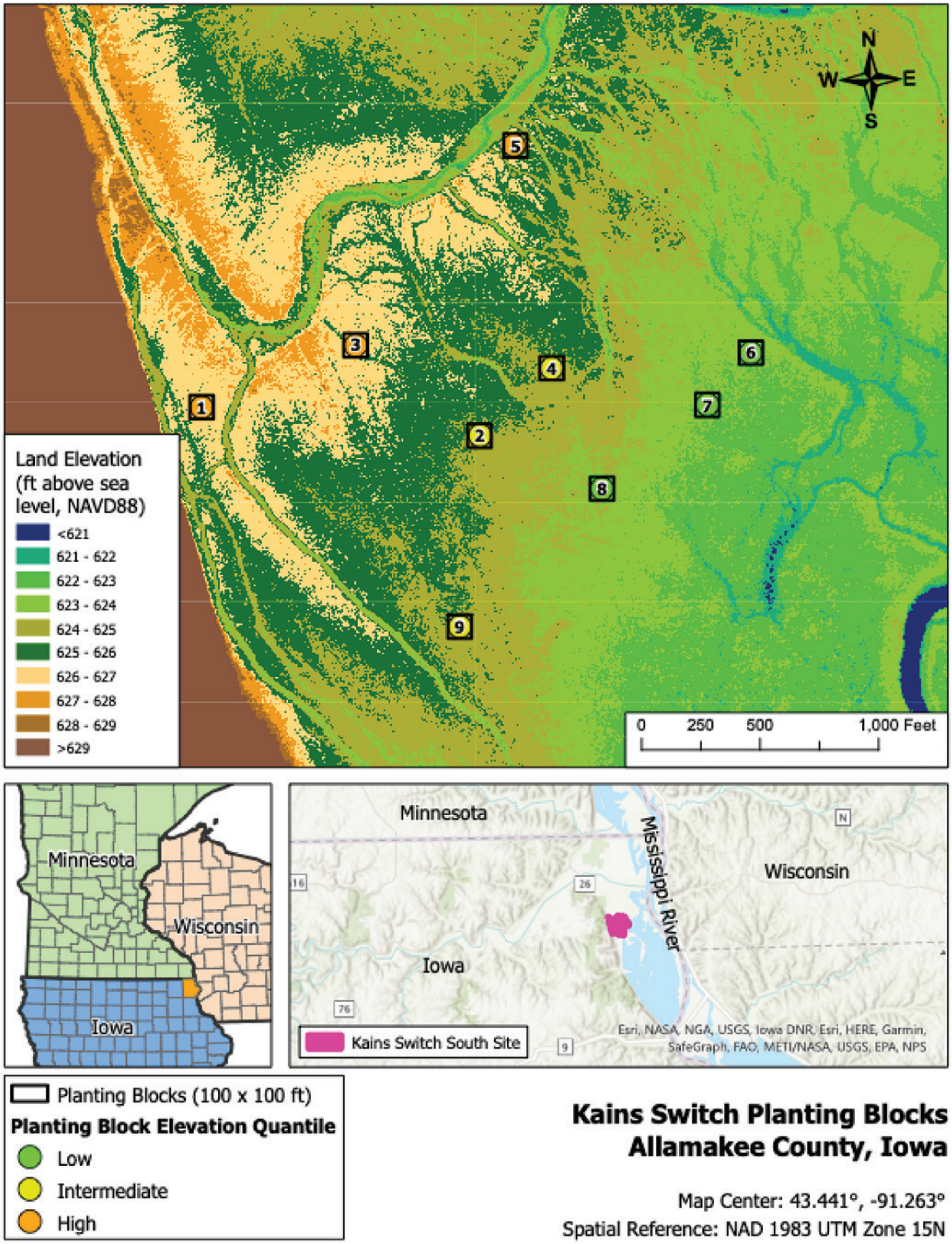

Figure 1. These maps show the Kains Switch South (KSS) planting study at various spatial scales. KSS is located along the Mississippi River near the borders of Iowa, Minnesota, and Wisconsin. Planting locations were located based on NAVD88 images and grouped into three elevational categories: low, intermediate, and high.

Figure 2. The floodplain forest ecosystem within Kains Switch South forest management area in northern Iowa consists of a mix of hardwood species. (Photo by Laura Reuling, 2021)

by on-site assessments to confirm canopy densities. The final plots were randomly selected from the set of viable locations identified during the on-site assessments. Plot size was 0.143 ac (578 m^2). Three plots that had similar overstory canopy coverage (approximately 60 percent overstory canopy) were selected within each zone, resulting in a total of nine plots (figure 3). Competing vegetation was present on most plots but was variable in composition and density; one of the highest elevation sites had high densities of reed canary grass, but wood nettle (*Laportea canadensis* L.), giant ragweed (*Ambrosia trifida* L.), and rice cutgrass (*Leersia oryzoides* L.) were more prevalent competitors across most sites.

Figure 3. Crews gridded out study plot locations early in the 2020 growing season before seedlings were planted. (Photo by Andrew Meier, 2020)

Figure 4. Each seedling was measured for height, as shown on this hackberry, shortly after planting in June 2020. (Photo by Andrew Meier, 2020)

Within each of the 9 plots, a total of 64 seedlings were planted in an 8 by 8 grid with 10- by 10-ft (3- by 3-m) cell sizes. containing 16 individuals representing each of the following species: swamp white oak (*Quercus bicolor* Willd.), silver maple, sycamore (*Platanus occidentalis* L.), and hackberry (*Celtis occidentalis* L.). Orientation of the grid was north/south. Species' cell assignments were randomly assigned, and placement within each cell was also random. Specific information on each species is listed in table 1.

Seedlings were planted May 21 and 22, 2020, by staff from the USACE and USFWS; staff received training on tree planting. Initial seedling measurements were collected 1 week later by staff at the University of Minnesota. Measurements included species, basal diameter, height, and notes regarding initial seedling vigor, health, and evidence of herbivory (figure 4). Each individual seedling (figure 5) was mapped within the plot to provide a detailed record for future measurements. During the 2020 and 2021 field seasons, field crews applied herbivory protection (PlantSkydd®) once annually in June. Later in the growing season (late June or early July), competing vegetation was controlled manually with a brush saw to maintain a free-to-grow condition. End-of-growing-season measurements (same as initial variables) occurred in September 2020 and October 2021. An additional survival assessment occurred in June 2021.

Data Summary

Percent survival, average height, and basal diameter growth were summarized by species, time period, and elevational zone. Linear regression was used to explore relationships between individual species diameter and height growth. A linear trend line was added to plotted data to visually determine positive, negative, or neutral trends. Data are publicly available (Windmuller-Campione et al. 2022b).

Table 1. Seedling stock size, nursery information, and average initial measurements with associated standard errors in parentheses for the four species planted at Kains Switch South. Size descriptions are nursery classifications and not field measured.

Species	Nursery size specifications	Nursery	Average basal diameter in (SE)	Average height in (SE)
Silver maple	21 to 30 in tall	Iowa Department of Natural Resources	0.37 (0.01)	29.3 (0.37)
Sycamore[1]	11 to 20 in tall	Iowa Department of Natural Resources	0.29 (0.01)	21.3 (0.29)
Hackberry	2 to 3 ft tall	Schumacher's Nursery (MN)	0.29 (0.01)	30.9 (0.35)
Swamp white oak	2-0 stock	Wisconsin Department of Natural Resources	0.50 (0.01)	39.6 (0.71)

[1] Sycamore stock were visually noted to be in poorer condition than other species.
1 in = 2.54 cm

Figure 5. This photo shows a sycamore seedling and surrounding understory vegetation on the study site after planting. (Photo by Andrew Meier, 2020)

Results

Survival

Survival varied across species, elevational zones, and measurement periods (figure 6). Swamp white oak seedlings had high survival across all three elevational zones with limited effects from browse and other disturbances. By October 2021, the high elevational zones had the highest percentage of healthy swamp white oak seedlings (61 percent). Although some mortality of sycamore occurred during the 2020 growing season, the high elevational zone had 70 percent, or 33 individual seedlings, still noted as healthy in October 2021. In the intermediate and low elevational zones, however, sycamore mortality increased during the 2021 growing season and a higher percentage of trees were dead by October 2021. Silver maple mortality was low in 2020 across all zones, but, similar to sycamore, silver maple mortality was substantially higher in the intermediate and high elevational zones in 2021. Hackberry had very low mortality in any measurement period in the intermediate and high elevational zones, but had substantial mortality in 2021 in the low elevational zone.

In general, the number of seedlings noted as healthy declined over the 2-year period, a pattern that was relatively consistent across species and elevational zones (figure 6). Swamp white oak and sycamore still had a high percentage of healthy individuals in October 2021. Silver maple had large decreases in the percentage of healthy seedlings across all three elevational zones starting in June 2021. A large proportion of silver maple seedlings were affected by browse. The browsing vector was not identified, but many silver maple seedlings showed substantial levels of insect defoliation earlier in the growing season, so ungulate browsing may not be the primary driver of defoliation on the site.

Growth

Seedling diameter and height growth varied across species, elevational zones, and time (figure 7). Over the two growing seasons, sycamore showed positive linear growth across the three elevational zones with some trees growing as much as 3.5 ft (1.1 m) in height and 0.3 in (0.76 cm) in diameter between June 2020 and October 2021 (figure 7). There were no obvious relationships between height and diameter growth across the three elevational zones for hackberry. Swamp white oak showed variable relationships between height and diameter growth across the three elevational zones with slight positives in the low and intermediate elevational zones and a slight negative relation in the high elevational zones. Although silver maple had positive linear relationships between diameter and height for both the high and the intermediate elevational zones, many of the height changes were negative due to browse (figure 7).

Discussion

Floodplain forests are a dynamic ecosystem (De Jager et al. 2019). Conditions across a management unit are not uniform (Windmuller-Campione et al. 2022a), and slight changes in elevation, which have nonlinear relationships with hydrology (Van Appledorn et al. 2021), can influence the short-term survival of planted seedlings. Among the four species and three elevational zones in this study, the number of healthy seedlings varied, highlighting the importance of quantifying microsite characteristics.

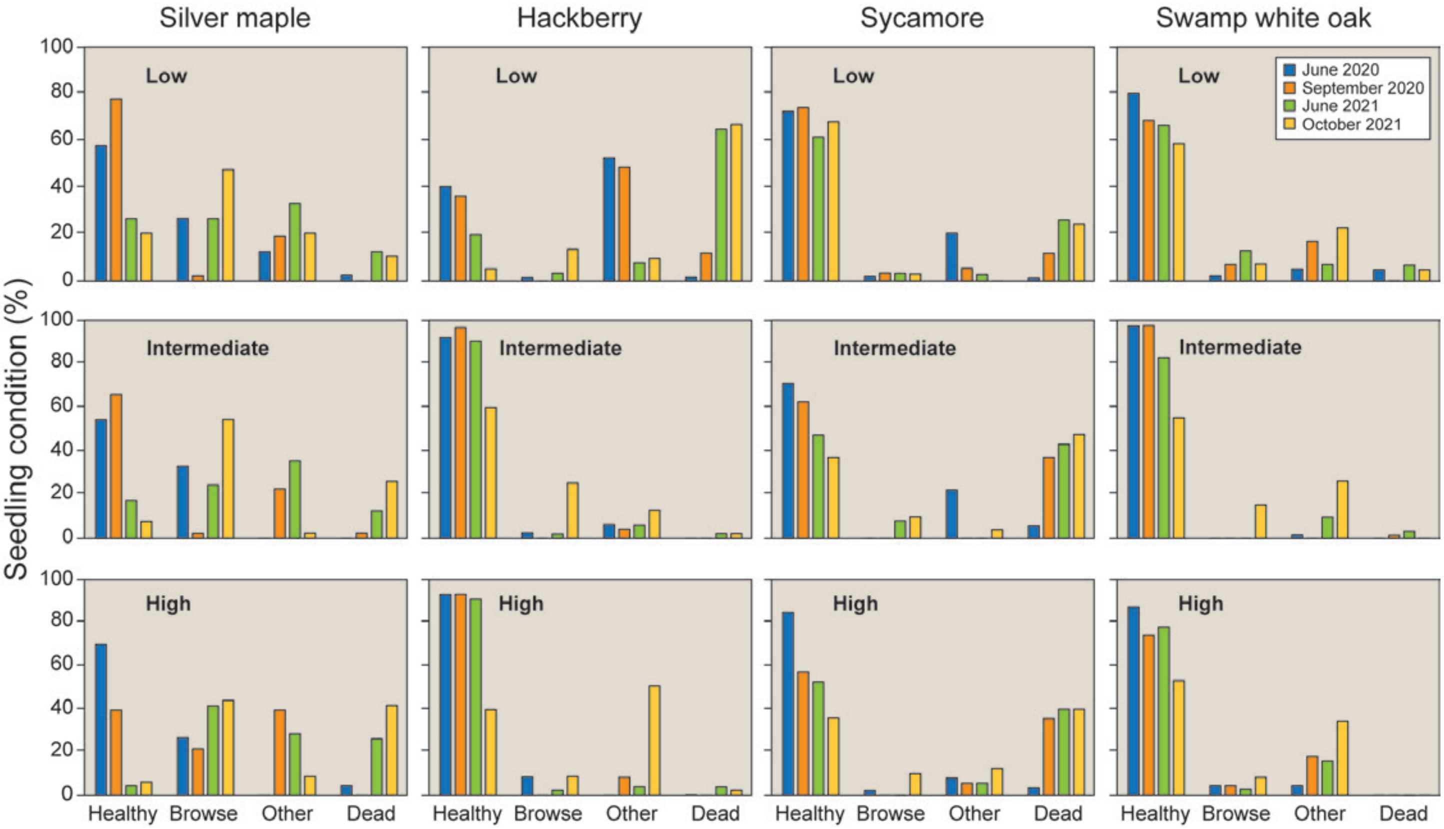

Figure 6. Seedling condition changed over time by elevational zone (low, intermediate, or high) and by species. The "Other" category included dieback, insects, wilt, or leaf drop.

Out of the four species planted, swamp white oak maintained the greatest healthy status and had the least impact from browse over the 2-year period (figure 6). PlantSkydd® was likely an adequate form of browse protection for this species, although we did not have an untreated control. Swamp white oak has emerged as a preferred choice for regeneration and restoration work within wet forested systems, both in floodplains and within wet black ash (*Fraxinus nigra* Marsh.) forests in the northern Lake States region (D'Amato et al. 2018, Hammes et al. 2020, Iverson et al. 2016). Early results from our study support the evidence that swamp white oak can survive under variable hydrological conditions including within low elevational zones (which had 60 percent of swamp white oak seedlings noted as healthy after 2 growing seasons). Height and diameter growth for this species, however, were limited during the 2 years (figure 7). Additional seasons of monitoring would be beneficial to fully understand the height and diameter growth potential of these seedlings because many oak species focus resources on root development during the first few years (Rogers 1990). This shift in resource allocation to a well-established root system could provide opportunities for underplanting, especially as overstory canopies of silver maple and cottonwood begin to reach maturity. Finally, given the already observed changes in the hydrologic regimes of the UMR (Guyon et al. 2012), the silvics of swamp white oak may allow this species to be more resilient to fluctuating water levels within and between growing seasons due to climate change (De Jager et al. 2013b).

The percentage of healthy silver maple seedlings was relatively low within all elevational zones (figure 6). Silver maple also suffered a high amount of insect damage which negatively affected height. Large cohorts of first-year silver maple natural regeneration can occur along the UMR, but additional research on silvics of silver maple as a seedling and sapling would be beneficial (Gabriel et al. 1990).

Hackberry and sycamore seedling survival and growth varied across elevational zones (figures 6 and 7). Sycamore is a common species occurring under varying conditions in floodplain forested systems (Bragg and Tatschl 1977). Hackberry performed best in the intermediate elevational zones, but had a large decrease in the number of healthy seedlings in the high elevational zone during the 2021 growing season. In other floodplain ecosystems, hackberry is considered a species common in higher elevations (Hale et al. 2008).

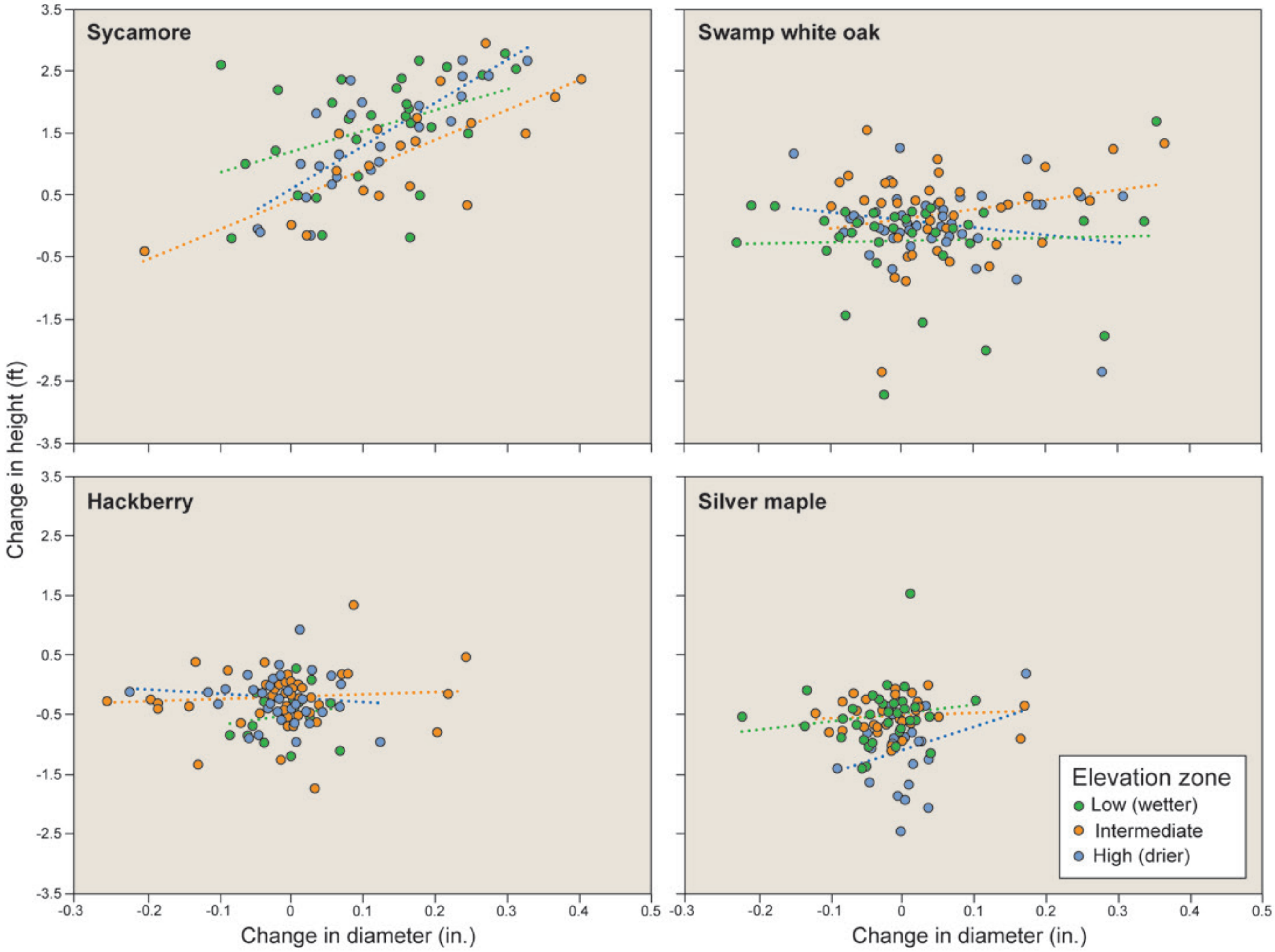

Figure 7. The relationship between changes in diameter and height between June 2020 and October 2021 varied by species and elevational zones.

An important caveat of our study is that these results represent just 2 years of data. During the establishment phase, planted or naturally regenerated seedlings are susceptible to impacts from the local environment and broader regional weather patterns (e.g., drought in 2021) (Oliver and Larson 1996). Additional years of monitoring and measuring would be useful to quantify seedling survival, growth, and development. Management actions that include artificial tree regeneration in floodplain forests cannot rely solely on early results to determine success or failure. In fact, assessments of planting success or failure would likely be more appropriate 3 to 5 years postplanting.

Regeneration is a key process within sustainable forest ecosystem management (Nyland 2016). Our short-term results highlight the importance of understanding the site when developing regeneration planting strategies. This study demonstrates that seedlings can be established under moderate light environments (60 percent overstory canopy) and across different elevational zones, providing opportunities for proactive restoration or underplanting to occur prior to canopy decline and the subsequent establishment of invasive species. In this study, understory vegetation was manually controlled with brush saws for 2 years. Accounting for the time and resources required for vegetation control could be important when considering the scale of planting. Even with this limitation, proactive underplanting may provide an opportunity for increased efficiency in resource utilization and the ability to treat greater areas. With underplanting, natural resource managers may consider multiple planting periods (e.g., planting at year 1, 3, and 5) compared with planting all at once to increase the potential of hitting recruitment windows with flooding. Longer term assessments of species' survival and growth would be beneficial especially given the multiple stressors that could affect seedling survival and growth in a floodplain forest environment.

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Acknowledgments

The authors express a sincere thank you to the project partners that have made this work possible including the U.S. Army Corps of Engineers, the U.S. Geological Survey, and individuals within the University of Minnesota. We appreciate all individuals who assisted with the planting, weeding, and data collection including Mike Tuma, Alan Toczydlowski, R. Lane Moser, Ella Gray, Marshall Johnson, Mackinzie Schaffer-Smiley, Sara Rother, Sierra Williams, and many others. Funding for this project was provided by Northern Forest CESU agreement between the U.S. Army Corps of Engineers and University of Minnesota (W912HZ-18-2-0004), Minnesota Agriculture Experiment Station (MIN-42-108), and the U.S. Army Corps of Engineers Upper Mississippi River Restoration Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Afforestation of the Gobi Desert: A Nursery Protocol for Producing High-Quality *Haloxylon ammodendron* Seedlings

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Abstract

Conservation and restoration of degraded arid lands in Mongolia depend upon protecting the remnant forests from further degradation and restoring denuded sites. Worsening environmental conditions, driven by climate change, intensify the need for active restoration. *Haloxylon ammodendron* (C.A. Mey.) Bunge. is a candidate plant species for restoration, but low water availability constrains its germination and establishment. Thus, active restoration requires massive production of high-quality seedlings. Here we present a nursery protocol for producing high-quality container seedlings with high percentages of germination and seedling establishment. We tested three representative field soils as growing media with three watering regimes. All treatment combinations produced high-quality seedlings, though there were differences in shoot height, root collar diameter, shoot and root biomass, and root length. We conclude that field soils reflective of outplanting conditions can be used for seedling production, and the nursery watering regime can be adapted to local conditions if a minimum moisture level can be maintained.

Introduction

Arid lands characterize more than 40 percent of the Earth's land surface, contribute 40 percent to global net primary productivity, and support more than 38 percent of humanity (Wu et al. 2019). Climate change threatens these sensitive ecosystems (Li et al. 2019, Huang et al. 2016) by causing severe and widespread droughts (Dai 2013) that often lead to desertification (D'Odorico et al. 2013). It is not surprising, therefore, that desertification affects drylands of central Asia (Byambadorj et al. 2020, Mandakh and Dash 2013, Nyam-Osor et al. 2021). These biodiversity hotspots (Leadley et al. 2010) are highly sensitive to climate change (Seddon et al. 2016).

In the absence of reduced greenhouse gas emissions (Lioubimtseva and Henebry 2009), sustainability of central Asian ecosystems is at risk. Revegetation efforts (Wu et al. 2019) could halt (or reverse) desertification (Zhang et al. 2016) and mitigate climate change by sequestering carbon in plant biomass (Schulze et al. 2000). Restoration initiatives in central Asia use the genus *Haloxylon*, known as the "forest of the desert" (Jia et al. 2008, Li et al. 2019, Zhu and Jia 2012), given its broad distribution in middle and central Asia, from northwest China to Afghanistan and Iran (Buras et al. 2012, Guo et al. 2005, Thevs et al. 2013). Species of *Haloxylon* occur as tall shrubs or small trees (figure 1). These plants prefer sandy soils (Khassanov et al. 1994); growth and survival decrease with increasing presence of silt and clay in the soil (Kayo 2019). *Haloxy-*

Figure 1. *Haloxylon ammodendron* occurs as tall shrubs or small trees in the Gobi Desert region of Mongolia. (Photos by Ser-Oddamba Byambadorj)

lon trees present xeromorphic and halophytic adaptations (Chang et al. 2019) by regulating water uptake and transpiration (Gong et al. 2006, 2015; Höhl et al. 2020; Ma et al. 2007; Xu et al. 2007). *Haloxylon* trees have deep roots (Wei et al. 2007) and branches with high water-use efficiency that limit photorespiration and transpiration (Ashraf and Harris 2013). These characteristics lead to increased photosynthetic yield (Doubnerová and Ryšlavá 2011, Sage 2004, Sage et al. 2012).

Despite adaptations to dry climates, *Haloxylon* species are at risk (Enkhchimeg et al. 2020, Lioubimtseva and Henebry 2009) due to extensive harvesting for pharmaceuticals and firewood (Jiang and Tu 2009) and to the use of succulent stems as fodder for livestock (Akhani et al. 1997, Song et al. 2006). Since 1980, *Haloxylon* species abundance has decreased by 70 to 80 percent in Turkmenistan, Kazakhstan, and Uzbekistan (Rachkovskaya 2003, Rachkovskaya et al. 2003, Rathore et al. 2012, Thevs et al. 2013).

Mongolia supports 2 million ha of *Haloxylon* forest in the arid southern region (Dorjsuren 2009), representing 13 percent of the total national forest inventory. Even though half of this forest is protected, significant degradation has occurred (Khaulenbek et al. 2018). Thus, the Government of Mongolia supports several forest restoration initiatives, including the Mongolia-Korea Joint Green Belt Plantation Project (Stanturf et al. 2020) that has already restored 1,490 ha of desert land during the last decade (Khaider et al. 2019).

Physiological and morphological studies show that *Haloxylon* trees absorb groundwater at great depth (Yang et al. 2007) when they have reached maturity (Sheng et al. 2004). During the initial phase of seedling growth, surficial water from rainfall evaporates rapidly, contributing to poor seed germination and poor survival of *Haloxylon* (Meshkov et al. 2009). Therefore, successful restoration in these habitats may be improved through use of nursery-grown seedlings, which tend to have higher establishment rates compared with seed (Middleton 1998, Nosrati et al. 2013). Although production of high-quality seedlings requires more resources initially, improved field performance can offset these costs (Haase et al. 2021).

Several field studies have investigated germination, emergence, and establishment of *Haloxylon* seedlings (Li et al. 2017; Song et al. 2005, 2006; Tobe et al. 2004, 2005), but few (Wang et al. 2019) have focused on nursery practices to produce high-quality *Haloxylon* seedlings. The objective of this study was to evaluate germination and development of nursery-grown *Haloxylon* seedlings grown in three field soils collected from different desert sites using three watering regimes.

Materials and Methods

Experimental Site

We conducted this study at the forest nursery of the Korea-Mongolia Joint Green Belt Plantation Project located at Bayanzag (44°5'25.73"N, 103°42'38.47"E) at an altitude of 1100 m in Bulgan soum (Dal bag), Umnugobi province, 675 km south of the capital Ulaanbaatar. Bayanzag belongs to the East Gobi semi-desert steppe region (Grubov 1982). Mean annual precipitation in the area is 137 mm (measured at Saikhan station in Bulgan soum), with 80 to 90 percent occurring in the summer and autumn months. Mean annual air temperature is 6.2 ± 1.1 °C, and summer average temperature is 19.8 ± 0.45 °C. The mean air temperature of the warmest month (July) is 24.2 °C, while that of the coldest month (January) is -13.8 °C (NAMEM 2019). The growing season starts in May and ceases at the end of September with the first autumnal frosts. Annual temperature and precipitation were measured during the 3-year study using a HOBO H21-USB Micro Station (Onset Computer Corp, USA) (figure 2).

Seed Collection and Germination Assessment

Bulk seed samples were collected in December 2013 from natural *Haloxylon ammodendron* (C.A.Mey.) Bunge. stands in the Gurvantes region of the Umnugobi province (43°27'55"N, 101°16'35.77"E). Seeds were stored in airtight containers and refrigerated at 5 °C for 5 months until the experiment began in spring 2014. Seed-quality traits were determined according to the Mongolian National Standard (MNS 2887: 2009) and included germination capacity, germination energy, and 1,000-seed weight (g). Germination capacity and energy were determined on 4 replicates of 50 seeds, each sown on filter paper in 9-mm plastic petri dishes. Deionized water was added to each dish until half the volume of each seed was immersed (about 5 ml). The Petri dishes were covered with lids and held for 8 to 16

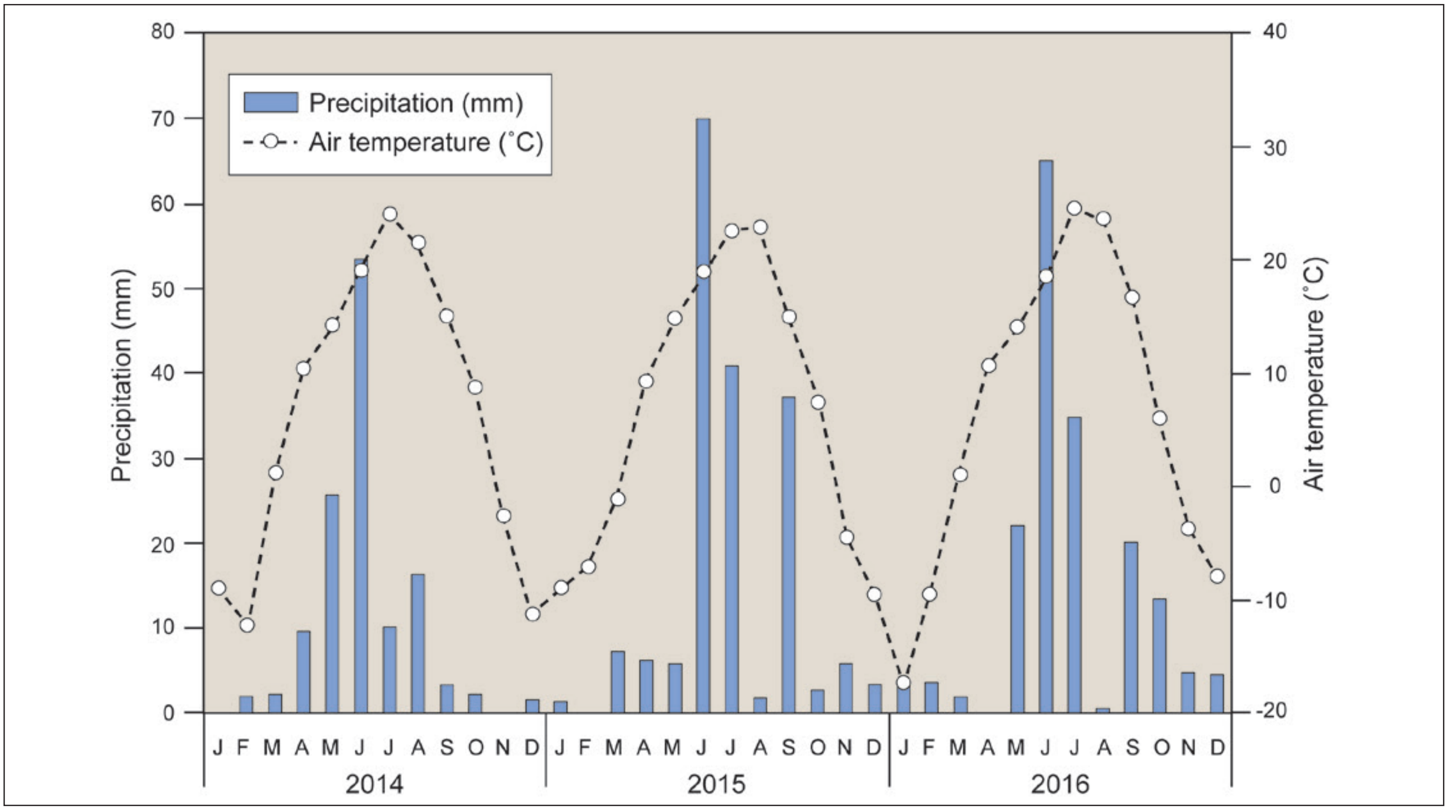

Figure 2. Average monthly temperature and precipitation during the experiment were measured on site.

h at 25 °C under continuous illumination (3000 lux) in a plant growth chamber (GC-300TL, Lab Companion, JEIO TECH Co. Ltd.). Seeds were considered germinated when the radicles emerged. Germinated seeds were counted and removed daily. Germination capacity is the proportion of total germinated seeds to total sown seeds and is expressed as a percentage. Germination energy (also expressed as a percentage) is one of the commonly employed indices of germination speed (ISTA 1999) and was computed as the proportion of total germinated seeds after 3 days to that of total germinated seeds after 5 days.

Soil Type and Analysis

Three soil types were used to evaluate emergence and seedling development. The soil types used are commonly distributed in the study region (table 1). The most dominant soil types are Arenic Yermic Calcisols (in desert areas) and Arenic Calcisols (in saxaul forested areas) (Batkhishig 2016, FAO 2015). Soils were collected from their respective regions to a depth of 20 cm and used without any further processing. Each soil type was used to fill 300 polybag containers (10 by 20 cm; 37.7 cm^3 volume) for a total of 900 containers in the study.

Each of the three soil types were sampled, air dried, sieved to 2 mm, and analyzed for physical and chemical properties (ISO 2006). Particle size composition was determined by the pipette method (Burt 2004), soil organic matter (SOM) by the oxidation method of Walkley and Black (Nelson and Sommers 1996), calcium carbonate content by the volumetric method (ASTM 1996), pH by using a glass electrode pH meter on a 1:2.5 air-dried soil/distilled water mixture (MNS ISO 10390: 2001), and electrical conductivity (EC) by using a platinum electrode on a 1:5 air-dried soil/distilled water mixture. Available phosphorus (P_2O_5) was measured by molybdenum blue colorimetry after ammonium carbonate digestion (MNS 3310: 1991). Nitrate-nitrogen (NO_2-N) was determined by sodium acetate digestion and spectrocolorimetry. Potassium (K_2O) was analyzed by flame spectrometry (Burt 2004).

Emergence Assessment

In April 2014, 6 seeds were sown in each of 900 polybag containers at a depth of 0.5 cm. The total percentage of seedlings emerged 4 weeks after sowing was recorded. Emergence rate was estimated by a

Table 1. Physical and chemical analysis of three local soil types used as growing media for *Haloxylon ammodendron* seedlings.

		Soil type		
Characteristic	**Units**	**Gobi red soil-Ferric Calcisols (Soil 1)**	**Gobi sandy loamy light-brown soil-Arenic Yermic Calcisols (Soil 2)**	**Sandy Gobi brown soil-Arenic Calcisols (Soil 3)**
		Parameters		
pH	water	8.643	8.133	8.597
$EC_{2.5}$	dS/m^{-1}	1.385	0.139	0.250
$CaCO_3$	%	0.270	8.117	0.420
Organic matter	%	0.113	1.555	0.261
$N\text{-}NO_3$	mg//kg	0.707	0.467	1.740
		Soil texture		
Sand	%	74.73	60.83	82.97
Silt	%	17.56	24.73	9.61
Clay	%	7.72	14.45	7.42
		Soluble anions		
CO_3^{2-}	mg/100gr	0.000	0.000	0.000
HCO_3^-	mg/100gr	1.930	1.223	1.173
Cl^-	mg/100gr	1.650	0.247	0.467
SO_4^{2-}	mg/100gr	8.693	0.160	0.517
		Soluble cations		
Ca^{++}	mg/100gr	2.073	1.168	1.173
Mg^{++}	mg/100gr	0.537	0.287	0.173
Na^+	mg/100gr	9.607	0.148	0.777
K^+	mg/100gr	0.055	0.028	0.035
		Mobile		
P_2O_5	mg/100g	3.020	2.057	4.663
K_2O	mg/100g	4.873	6.960	8.363

modified index of germination rate (Rozema 1975) as follows:

$$\text{Emergence rate} = \sum \frac{100Gi}{nti}$$

where n is the total number of seeds and Gi is the number of seedlings emerged on day ti (ti=0, 1, 2, 3 ....).

During emergence assessment, containers were irrigated every 3 days for 25 min with a soaker hose (Smile Spray Hose, SML 6-6 Namkyung Company Ltd) capable of delivering 18 L min^{-1}. At the end of the 4-week emergence assessment, a single seedling (healthy and undamaged) was left in each container to be used for evaluation of seedling growth in response to soil and watering treatments.

Watering Regimes

After seedling emergence (May 2014), containers were watered to field capacity every 3 days for 1 month to assure seedling establishment. After establishment, three watering regimes (low, medium, and high) were applied to each of the three soil types by irrigating for 25 min at intervals of 3, 7, or 14 days (Nyam-Osor et al. 2014; 2018). Irrigation was applied during the growing season (May to September) for 3 years (2014 through 2016) (figure 3). For logistical reasons related to the automatic watering system, seedlings assigned to each treatment combination were kept together in a group, though environmental conditions throughout the study area were otherwise fairly uniform.

Seedling Measurements

At 10-day intervals throughout the 3 growing seasons, 50 seedlings were randomly selected from each treatment group and measured for height and root collar diameter (RCD). At the end of the experiment (September 2016), 15 randomly selected, healthy seedlings per treatment were harvested and measured for shoot height, RCD, root length, fresh weight, and dry biomass. Shoot height was measured from the root collar to the tip of the young shoot. Root length was measured from the root collar to the tip of the tap root. RCD was measured with a digital Vernier caliper at the base of the stem (Thompson and Schultz 1995). All harvested seedlings were separated into shoots and roots. Soil particles were rinsed from the roots. After fresh weight was measured, root and shoot samples were oven dried at 80 °C for 48 h and weighed for dry biomass (Cregg and Zhang 2001).

Statistical Analysis

The experimental design for this project was a completely randomized design with 100 replications (polybag containers) of 9 treatments consisting of a 3 by 3 factorial (soil type by watering regime) (figure 4). Irrigation logistics constrained arrangement of the containers, but we are confident that environmental gradients did not have an influence in the relatively uniform study area. The SAS version 9.4 software package (SAS Institute Inc. 2014) was used to analyze the data with two-way analysis of variance

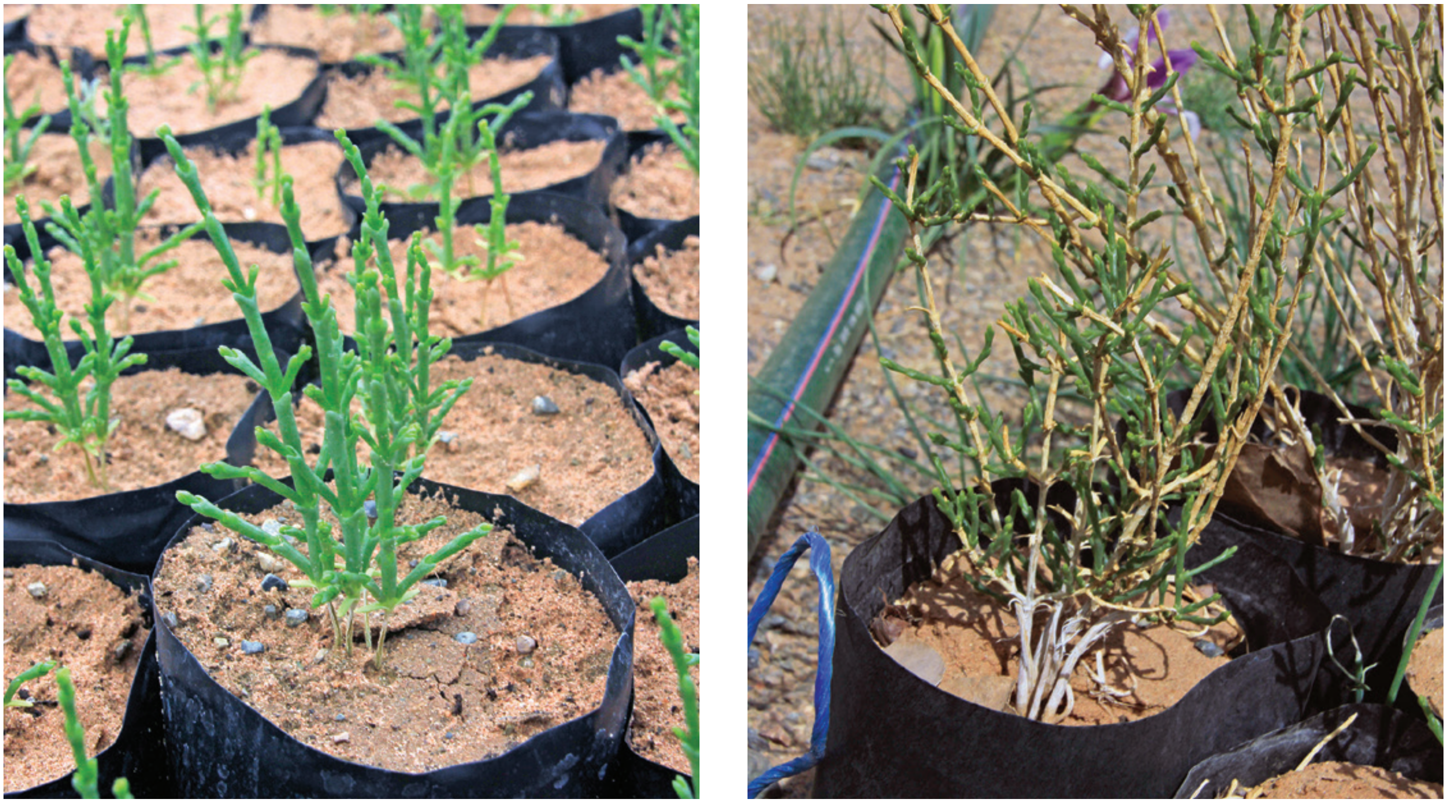

Figure 3. *Haloxylon ammodendron* seedlings were assessed for 3 years to evaluate development in response to soil type and watering regime. (Photos by Ser-Oddamba Byambadorj)

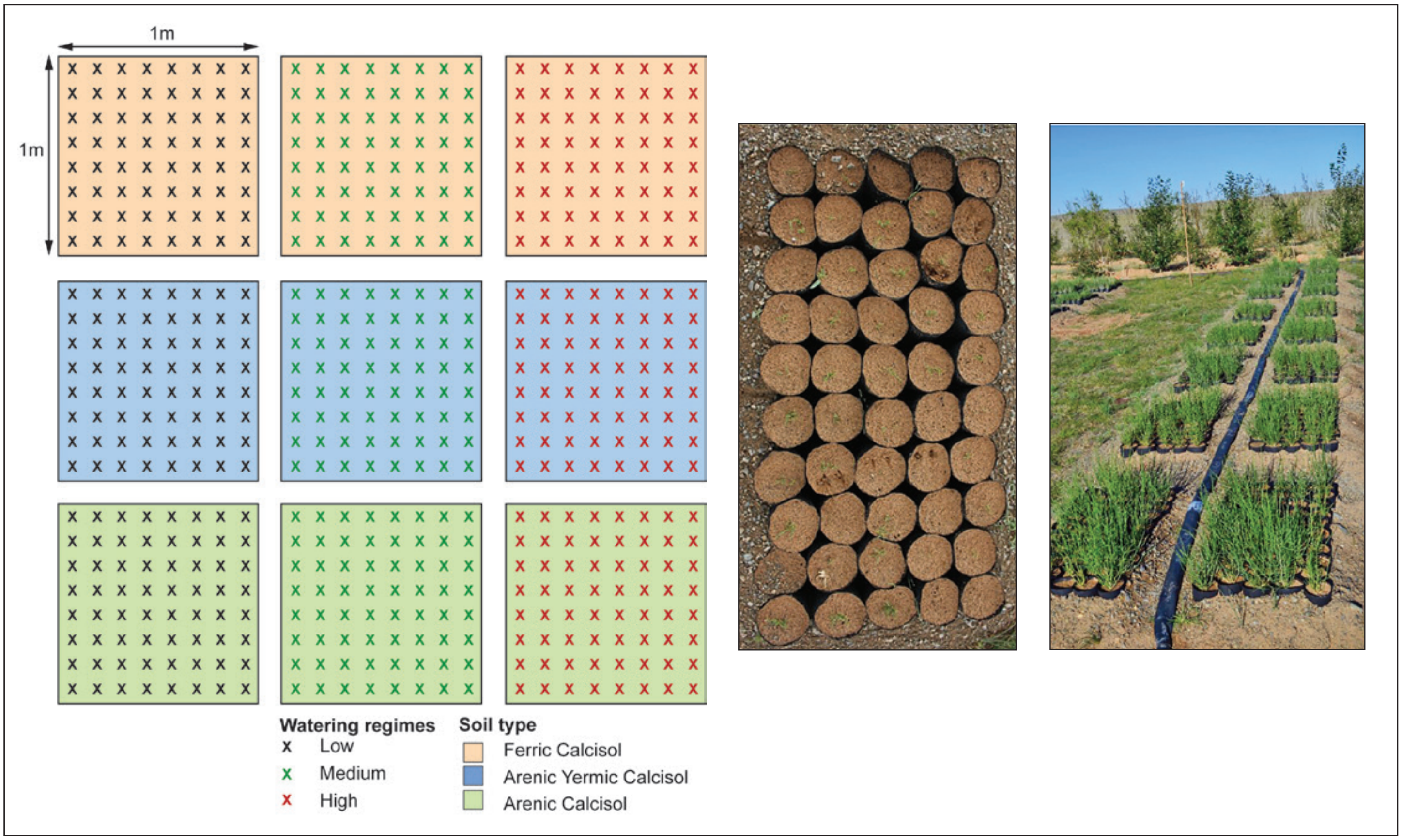

Figure 4. The experimental design for the 3-year study to assess *Haloxylon ammodendron* seedling development included replications of each soil type and watering regime. (Photos by Ser-Oddamba Byambadorj)

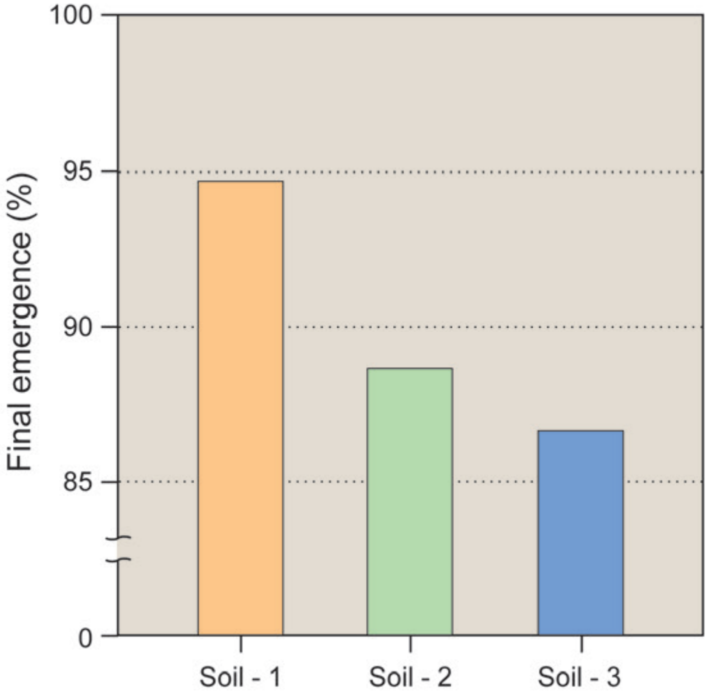

Figure 5. Average total emergence (n=100 containers) of *Haloxylon ammodendron* seeds varied by soil type.

(ANOVA) and Duncan's multiple range test was used for multiple comparisons. Seedling growth and biomass data were normally distributed. ANOVA for the effects of time and treatment on morphological traits was conducted with time and treatment as a fixed effect and plot as a random effect.

Results

Soil Characteristics

Soil physical and chemical characteristics differed among the three soil types (table 1). Soil 1 was the most alkaline with the highest amounts of HCO_3, Cl^-, SO_4^{2-}, Mg^{++}, and Na^+ and, consequently, high EC. Soil 2 had much higher calcium carbonate and organic matter compared with the other two soils. Soil 3 had the highest nitrogen (N), phosphorus (P), and potassium (K) concentrations.

Seed Germination and Emergence

Weight of 1,000 seeds averaged 3.24 ± 0.09 g. The germination capacity and germination energy were 92 and 74 percent, respectively. Seeds sown directly in containers had a lower emergence rate than seeds tested in the laboratory. Nevertheless, after 10 days, emergence was greater than 60 percent regardless of soil type. Final emergence 4 weeks after sowing was more than 85 percent, with Soil 1 having the highest value (figure 5).

Seedling Morphology

In the first growing season, all seedlings initially grew slowly, had accelerated growth in the middle of the season, and grew slowly again toward the end of the season (figure 6). At the low and high watering regimes, seedlings grown in Soil 3 were taller than those grown in the other two soils at the end of the season. In the medium watering regime, seedlings in Soil 1 were tallest. Diameter growth (RCD) followed a similar pattern as height growth. Seedlings growing in Soil 2 had the smallest RCD values regardless of watering regime (figure 6). Height and diameter growth patterns during the second and third growing seasons were similar to the first growing season (figure 7).

At the end of the study (three growing seasons), seedling morphology differed significantly by soil type and watering regime (figure 7 and table 2). Root systems were well developed regardless of treatment (figure 8). Biomass values differed significantly by soil type but not by watering regime (figure 9, table 3). Both root and shoot biomass were largest in seedlings grown in Soil 3 and smallest in seedlings grown in Soil 2.

Table 2. Statistical analysis of height and root collar diameter (RCD) as a function of different treatments at the end of three growing seasons.

	Height			RCD		
Source of variation	DF	F value	Pr > F	DF	F value	Pr > F
Soil type	2	3.18	0.0436	2	7.38	0.0008
Watering regime	2	23.12	<.0001	2	3.98	0.0203
Soil type * watering regime	4	3.70	0.0063	4	0.63	0.6396

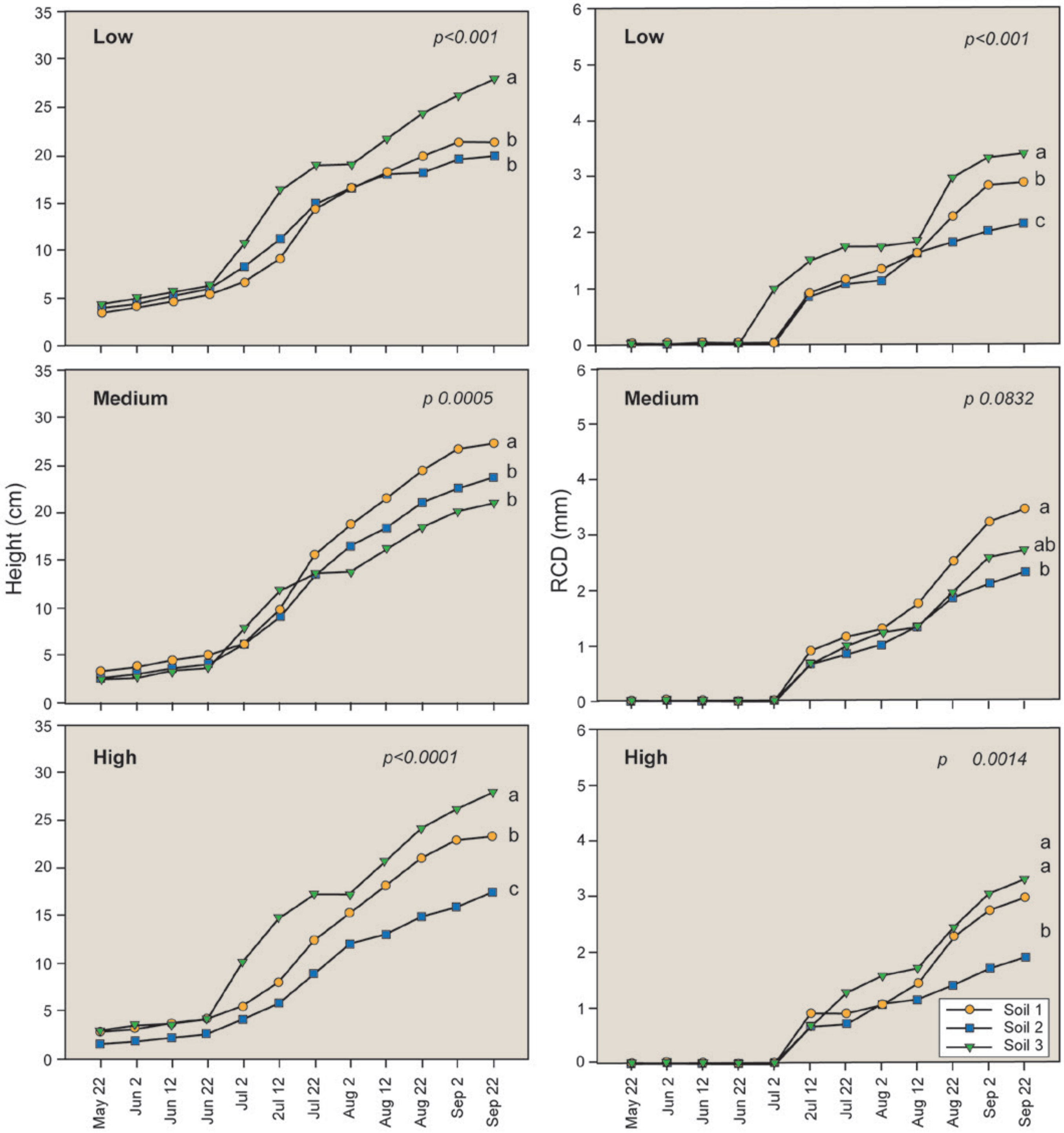

Figure 6. Shoot height and root collar diameter at the end of the first growing season varied (2014) by watering regime (low, medium, and high) and soil type (n = 50).

Discussion

All treatment combinations resulted in good seedling establishment. At the end of the establishment phase, roots were at least 20 to 25 cm long, sufficient for them to find an environment containing more moisture and less salinity than in superficial soil horizons (Matsui et al. 2018, Tobe et al. 2005, Wang et al. 2019). Height and RCD differed among some treatments, but all treatments resulted in a good balance between aboveground and belowground biomass allocation. The mean root-to-shoot ratio after 3 years was approximately 0.8 (data not shown) independent of treatments, considered a well-balanced ratio (Evert 2006).

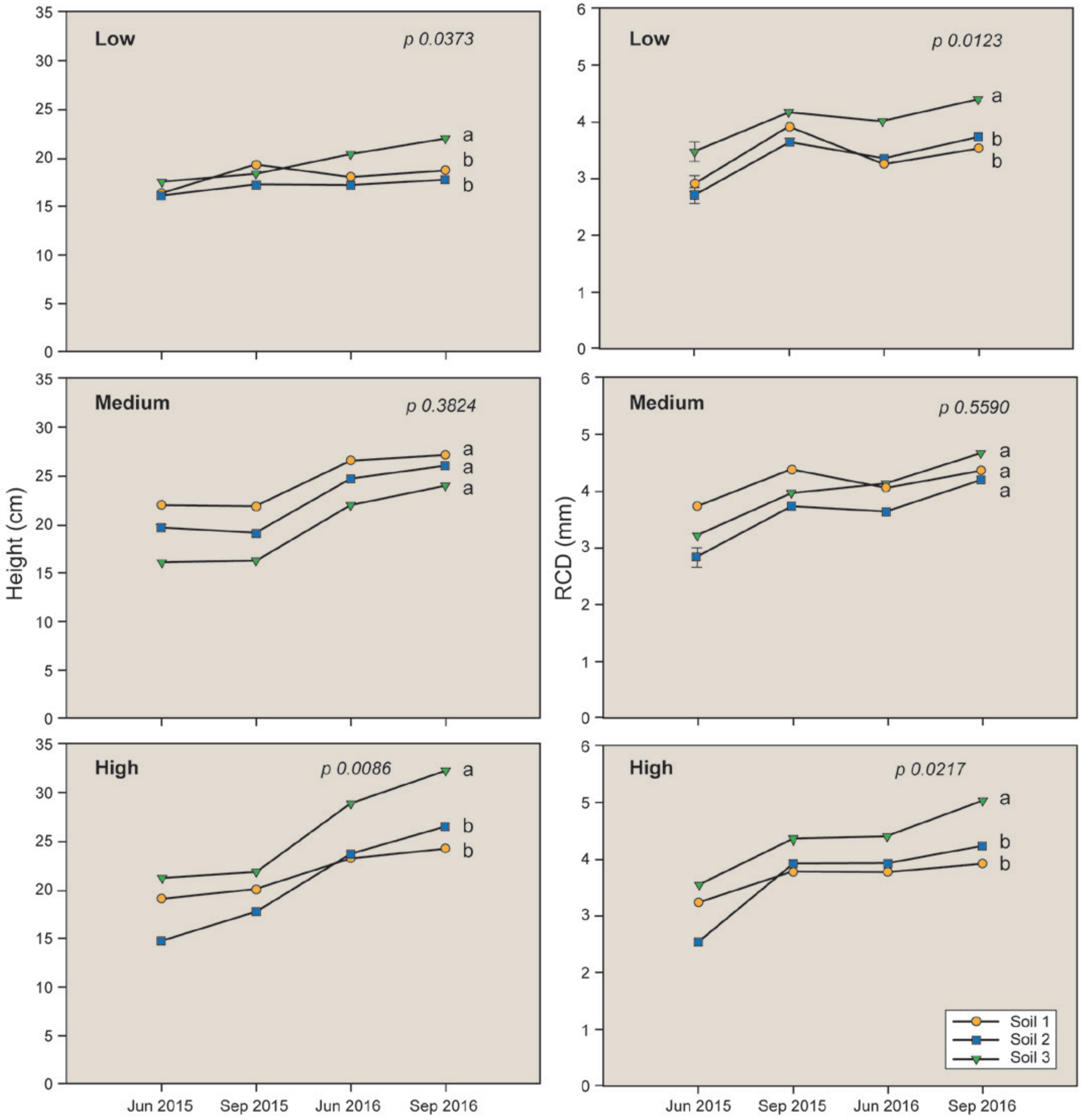

Figure 7. Shoot height and root collar diameter during the second and third growing seasons tended to be highest for Soil 3 (n = 50).

Table 3. Statistical analysis of biomass partitioning as a function of different treatments at the end of three growing seasons.

		Root biomass		Shoot biomass	
Source of variation	**DF**	**F value**	**Pr > F**	**F value**	**Pr > F**
Soil type	2	10.24	<.0001	7.75	0.0007
Watering regime	2	0.63	0.5358	0.90	0.4078
Soil type * watering regime	4	1.78	0.1369	1.44	0.2239

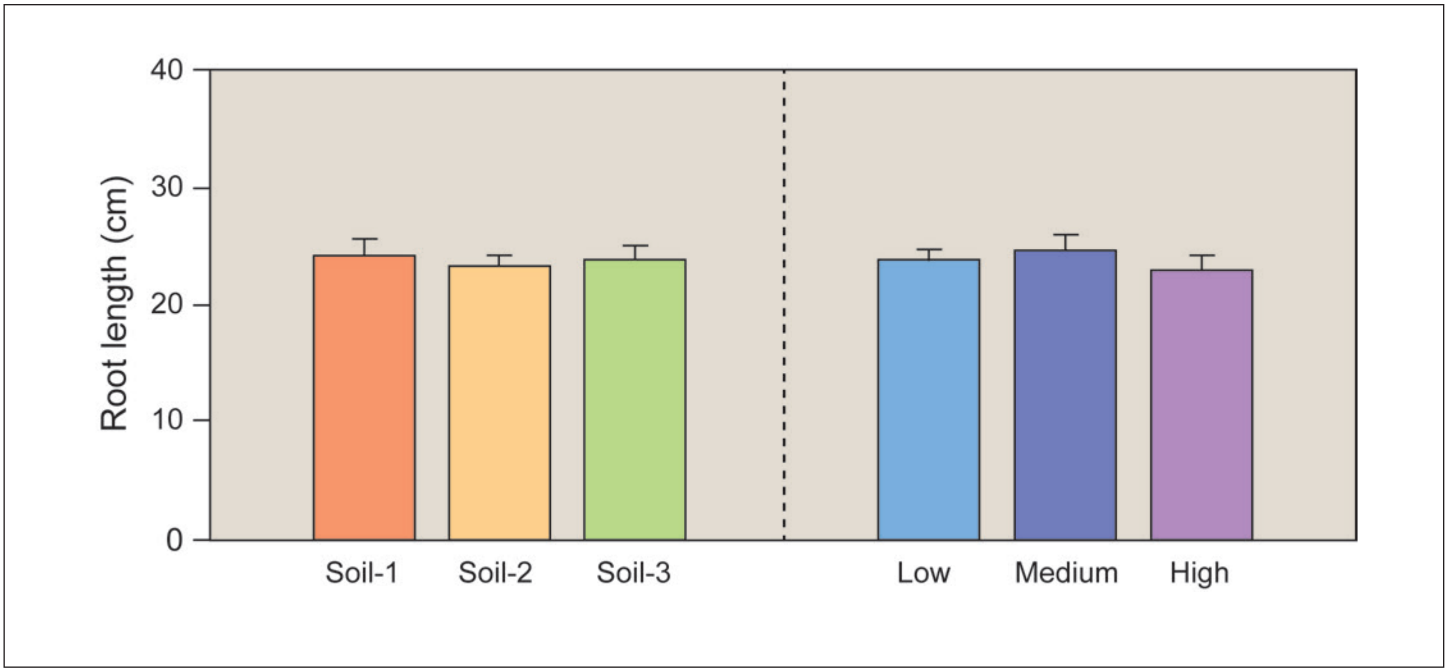

Figure 8. Root length at the end of the third growing season varied little among soil types or watering regime (n = 15).

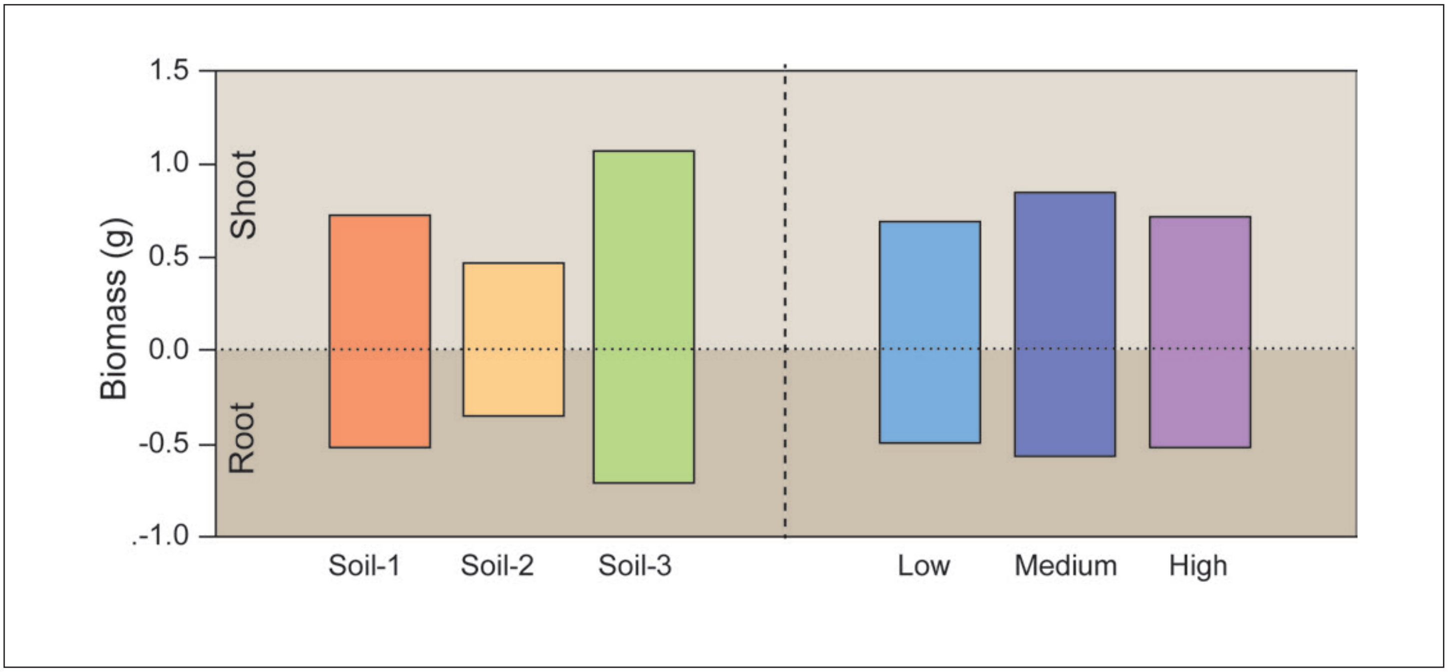

Figure 9. Aboveground and belowground biomass partitioning at the end of the third growing season varied among soil types and watering regime (n = 15).

Height growth slowed during the second season. This growth pattern is similar to results from a previous study with *Haloxylon ammodendron* (Zhang et al. 2016). The authors suggested that a change in biomass partitioning slowed shoot growth and increased root biomass to increase water uptake (Wei et al. 2007). We did not harvest seedlings at the end of the first and second growing seasons to examine biomass partitioning, thus we cannot be certain if this explains the growth patterns in this study. Future investigations could examine the annual pattern of biomass partitioning to better understand how this might represent an adaptation to the arid environment (Wei et al. 2007, Zhu and Jia 2012). Future research could also examine if the use of soil from the designated outplanting site will result in seedlings being preconditioned to their future field environment.

Figure 10. Propagation of *Haloxylon* can be done successfully in a nursery, and could be a significant contributor to restoring this species to the landscape. (Photo by Ser-Oddamba Byambadorj)

Our results highlight the possibility of using soil from the designated outplanting site instead of traditional growing media to produce high-quality *Haloxylon* seedlings in forest nurseries. The most important factor is that the growing medium functions well under the nursery growing conditions (Altmann 2021). Even though the soil used in our study was not sterilized and not modified physically (by sifting) or chemically (by adding compost or other amendments) before using, seedling growth was acceptable, and no disease occurred. Being able to replace traditional growing media may be an economically favorable approach for forest nursery production (though it must be done in an environmentally sustainable manner), particularly when large-scale restoration activities are underway for these arid lands.

Conclusions

Given the likelihood that future climate conditions in central Asia will be hotter and drier, we believe that the focus during the next few decades should center on protecting and arresting further degradation of arid ecosystems. In Mongolia, reforestation and afforestation of arid lands depend upon *Haloxylon* species due to their tolerance of arid conditions. Because natural regeneration of this species is poor, however, propagation protocols in local nurseries are necessary (Khaulenbek et al. 2018). The protocol suggested here demonstrates that high-quality container seedlings can be grown with field soils from the designated outplanting sites using adequate watering regimes (figure 10). Preliminary results for outplanting these seedlings in desert sites near the nursery indicate that 96 to 100 percent survived with slight differences by year-of-planting (Khaider et al. 2019). We will continue long-term evaluation of these afforestation efforts.

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Acknowledgments

Korea-Mongolia Joint Green Belt Plantation Project supported this work. The authors thank the staffs of the Korea-Mongolia Joint Green Belt Plantation Project and the members of the Laboratory of Forest Genetics and Ecophysiology, the National University of Mongolia for their assistance in laboratory and field work. The article is an activity within the work of IUFRO Task Force Transforming Forest Landscapes for Future Climates and Human Well-being. We acknowledge the useful discussions and shared ideas of the Task Force members, and the support of Michael Kleine, IUFRO Deputy Director.

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