

ARE LOCAL SEED SOURCES STILL RECOMMENDED FOR PLANTING SHORLEAF PINE IN SOUTHERN NEW JERSEY AND CENTRAL PENNSYLVANIA?

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ABSTRACT

Artificial regeneration could help offset the decline of shortleaf pine (*Pinus echinata*) populations, yet also address concerns related to climate change resilience. Provenance experiments are uniquely positioned to inform decisions regarding where to source seed for out-plantings designed to enhance regeneration success and climate resilience. Research from the late 1960s indicated that local seed sources should be used for shortleaf pine plantings in the Mid-Atlantic Region. The purpose of this research was to determine if recommendations for sourcing shortleaf pine seed in the Mid-Atlantic Region made over 50 years ago still apply. We revisited two shortleaf pine common garden trials in 2020, one in southern New Jersey (NJ) and the other in central Pennsylvania (PA), to evaluate performance of seed sources in their seventh decade after establishment. Our analysis indicated that local seed sources are still among the top-performers but that a few southern sources have closed the performance gap noted in the past at the NJ common garden. Therefore, some southern sources may be suitable for out-planting in southern NJ. The poor performance of all sources at the PA site, including the local source, support an earlier recommendation for more research on shortleaf seedling planting in central PA.

INTRODUCTION

Shortleaf pine (*Pinus echinata*) is a tree species found primarily in the Southeastern United States yet occurs as far inland as the lower Midwest (Oklahoma and Missouri) and as far north as the Mid-Atlantic (New Jersey and Pennsylvania) (Little 1971). Shortleaf pine grows on a wide range of sites and in association with a diversity of tree taxa, including oaks (*Quercus*), hickories (*Carya*), other southern pines (loblolly pine (*P. taeda*) and Virginia pine (*P. virginiana*), and more northern pines ([pitch pine, *P. rigida*] and eastern white pine [*P. strobus*]) (Lawson 1990). Although the species can occur on a range of landforms, shortleaf pine is most often associated with dry, well-drained to excessively well-drained soils or sites with a history of frequent burning (Lawson 1990). Because of shortleaf pine's tolerance of drought and frequent fire, the species is considered well adapted to projected future climate over the next century (Butler-Leopold and others 2018).

In recent decades, this species has undergone a population decline throughout its native range (Oswalt 2012). Research suggests that over much of shortleaf pine's range, regeneration and recruitment of new individuals is insufficient to replace senescent adult trees, contributing to the decline (Alberto and others 2013, Oswalt 2012). This shortleaf pine decline has been linked to several factors both historical and environmental, including exploitative timber harvesting,

wildfire suppression, insect pests (e.g., southern pine beetle [*Dendroctonus frontalis*]), and autogenic succession (Cunningham and Hauser 1989, Guyette and others 2007, Hanberry and others 2013). Currently, there is a concerted effort in conserving shortleaf pine to help counteract its range-wide decline (Anderson and others 2016).

Because of diminishing adult shortleaf pine abundance and seed sources, artificial regeneration, either direct seeding or seedling planting, may be the best option for reversing shortleaf pine population decline. Seedling planting can increase the probability of regeneration success as it bypasses uncertainties associated with earlier life stages. Planting nursery-grown shortleaf seedlings holds promise as a means to regenerate the species under a range of overstory structures (Kabrick and others 2015).

In the 1950s, the Southwide Pine Seed Source Study (SPSSS) was established to test the capacity to move seedlings across the distributions of southern pine species (Bragg and Hossain 2020). The SPSSS created a network of common garden experiments for the four major southern pine species, including shortleaf, installed across the Southeastern United States. As part of this larger effort, common garden trials for shortleaf pine were established on the Atlantic Coastal Plain near the northern edge of its native range at Green Bank, New Jersey (NJ) and outside of the species' range in the Central Appalachians at Blain, Pennsylvania (PA). Early results of the

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Citation for proceedings: Willis, John L.; Self, Andrew B.; Siegert, Courtney M., eds. 2022. Proceedings of the 21st Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SRS-268. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 262 p. <https://doi.org/10.2737/SRS-GTR-268>.

experiment at Green Bank indicated that local seed sources should be considered when planting shortleaf pine in NJ, but shortleaf pine may not be ideal for planting at sites north of its range in PA (Little 1969). At both sites, poor performance of southern provenances was linked to elevated winter injury, presumably due to lower winter hardiness (e.g., tolerance to low temperatures and heavier snow and ice loading).

Climate change has raised concerns about where to source seedlings. Local seed sources have been recommended for parts of shortleaf's range (Little 1969); however, this suggestion was made over 50 years ago and under a different climate. Updated recommendations are needed to support shortleaf pine conservation efforts where seedling planting is being considered. The Green Bank, NJ and Blain, PA common garden studies are uniquely positioned to help inform shortleaf pine conservation efforts involving artificial regeneration on contrasting sites in the Mid-Atlantic Region (i.e., Coastal Plain vs. Appalachians).

The purpose of this research was to evaluate the performance of shortleaf pine provenances planted at the Green Bank and Blain sites in year 62 and 66, respectively, of these experiments. Based on an early report linking performance to latitude of seed origin (Little 1969), we hypothesized that the southern seed sources originating farther from the planting sites will have lower survival and growth rate than seed sources closer to the planting or those better adapted to climate at the study sites. By revisiting these long-term studies, we hope our results will aid future managers and researchers to make informed decisions on where to source shortleaf pine seedlings for enhanced regeneration success in southern New Jersey and central Pennsylvania.

METHODS

Study Site Description and Design

The study site at Green Bank, NJ (Burlington County) is located in the Outer Coastal Plain (OCP) Physiographic Province. The OCP has flat to slightly undulating topography and is underlain by unconsolidated marine deposits dominated by sand. Climate at Green Bank is predominantly humid continental with mean January low temperature, mean July high temperature, and mean annual precipitation of -3.9 °C, 29.4 °C, and 119.4 cm, respectively (Arguez and others 2010). The Green Bank common garden was planted in a former seedling nursery in the Wharton State Forest. The study site is underlain by two soil types (USDA Soil Survey Staff 2021). The dominant (75 percent of the area) is mapped as Galloway sand with 0 to 5-percent slope. The second is mapped as Downer loamy sand with 0 to 5-percent slopes.

The study site at Blain, PA (Perry County) is in the Ridge and Valley Physiographic Province of the Central Appalachians.

Climate at the Blain site is humid continental with mean annual precipitation as rain, mean July high temperature, and mean January low temperature of 109.6 cm, 28.9 °C, and -6.1 °C, respectively (Arguez and other 2010). The planting location is flat to gently sloping and somewhat poorly drained. The dominant soil series is Blairton silt loam formed within silty colluvium derived from shale and siltstone over acid, silty residuum weathered from shale and siltstone (USDA NRCS Soil Survey Staff 2021).

At both sites, multiple seed sources were planted in a randomized block design. Seed sources from seven States were planted in 1958 at Green Bank, NJ: New Jersey (NJ), Virginia (VA), South Carolina (SC), Tennessee (TN), Georgia (GA), Missouri (MO), and Louisiana (LA). At Blain, six seed sources were planted in 1954: PA, TN, Arkansas-Stone County (AR-S), Arkansas-Ashley County (AR-A), Oklahoma (OK), and Texas (TX). Seed was collected from at least 20 trees at each geographic source (Wells and Wakeley 1970). All seed sources were replicated four times (i.e., four blocks). The seed sources were randomly assigned to planting units within each block. Every planting unit representing a seed source had 121 trees planted as 11 rows with 11 trees within each row. Trees were planted on a 1.8 m x 1.8 m spacing. In order to minimize edge effects with adjacent plantings, the interior 49 trees (seven rows with seven trees per row) were tagged for long-term monitoring.

2020 Remeasurement

We revisited Green Bank and Blain test sites in the summer of 2020 to obtain updated data on the monitored trees. Our measurements at Green Bank focused primarily on the stem diameter, total height, and survival assessment of the trees. We measured the diameter at breast height (DBH; 1.4 m above the ground) with diameter tapes and recorded to the nearest tenth of a centimeter. Tree top height (height) was measured to the nearest tenth of a meter from at least two angles approximately one tree height from the subject tree using the ultrasound function of a Haglof Vertex Laser Geo unit. Only the number of live trees was recorded at the Blain study site.

Statistical Analysis

Our analysis evaluated shortleaf pine responses at stand and tree levels. The experimental unit (ExU) is the 49 tagged trees planted for each replicate of the seed source experiment (n=28 and n=24 at Green Bank and Blain study sites, respectively). Two response variables were used for testing stand-level patterns: survival and basal area. Survival (SURV) was estimated as the percent of original 49 tracked trees tallied as live in 1962, 1967, 1972, and 2020. Basal area (BA) was calculated by summing the basal area of live trees in each ExU based on the 2020 measurement, which was then expanded to the area per hectare. Tree-level responses

were tested using top height and DBH of live trees from the 2020 inventory summarized by ExU. Tree-level means for height and DBH were calculated based on all trees (mHT and mDBH, respectively). The maximum DBH (xDBH) and height (xHT) in each ExU were also included as tree-level responses. Analysis of the Blain study site was based on descriptive summaries of 2020 survival only.

Statistical tests were performed on the Green Bank data using RStudio version 1.1.456. We tested our hypothesis using analysis of variance (ANOVA) and correlation analysis. We used one-way ANOVA for a randomized block design to evaluate the effect of seed source on several response variables. The LA seed source was excluded from ANOVA models testing for seed source effects on tree-level attributes since only two of the four blocks had surviving trees in 2020. When significant seed source effects were detected by ANOVA, all pairwise comparisons of seed source means were performed using Tukey's Honest Significant Difference method. We used correlation analysis (Pearson's product-moment correlation) to test for associations between the response variables and geographic and climatic variables related to seed source origin (table 1). Statistical significance was assessed when $p \leq 0.05$.

Table 1—Descriptions of geographic and climatic variables used in Pearson product moment correlation tests based on year 62 data from Green Bank

Distance from seed source to planting site (DIST): Euclidean distance from center of origin county to the Green Bank site; kilometers
Latitude (LAT): Universal Transverse Mercator latitude for center of origin county; meters
Longitude (LON): Universal Transverse Mercator longitude for center of origin county; meters
Altitude (ALT): Elevation in meters above sea level for center of origin county
Annual precipitation (PREC): Mean annual precipitation for origin county; centimeters
Annual temperature (TEMP): Mean annual temperature for origin county; Celsius
Mean January low temperature (JALO): Mean of the low temperatures in January for origin county; Celsius

Note: Climatic variables are 30-year averages for 1981–2010.
Source: Arguez and others 2010.

RESULTS

Seed Source Effects

Survival variation among seed sources was evident early in the experiment at Green Bank (fig. 1). Mean survival at year 5 (1962) ranged from a high of 94 percent for the NJ source to a low of 22 percent in the LA source. By year 15 (1972), all out-of-State seed sources averaged <67 percent survival, while mean survival of the local NJ source remained above 90

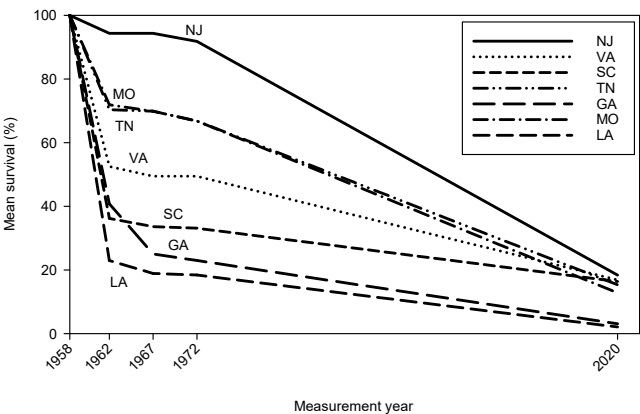


Figure 1—Mean survival of seven shortleaf pine provenances over a 62-year period of the common garden experiment in Green Bank, NJ. Survival in 1958 represents seedlings at the time of planting (late winter), while others are estimates from either during or the end of that year's growing season.

percent. In 2020, mean survival of all seed sources fell below 20 percent and the LA seed source survived in just two of the four original blocks. Seed sources formed two groupings based on 2020 mean survival. The low survival grouping at year 62 consisted of LA and GA sources, both with mean survival below 5 percent. Mean survival of sources falling in the higher survival grouping ranged from 13 percent for the MO source to 18 percent for the NJ source. Based on survival rankings, the SC source went from the third lowest at age 15 (33 percent) to the third highest at age 62 (16 percent).

Compared to the Green Bank study, 2020 survival was substantially lower in the 66-year-old common garden planting near Blain, PA (table 2). No provenance exceeded 10 percent survival. Although not tested statistically, the PA seed source had the highest survival, followed by TN. Both the PA and TN planting were the only ones with survivors in all four of the original blocks.

Table 2—Mean percent survival and number of experimental units (ExU) with at least one survivor for six seed sources in year 66 of the common garden planting at Blain, PA

Seed source	Mean survival	Surviving ExUs
	percent	number
PA	9.3	4
TN	7.2	4
AR-S	3.1	3
OK	1.5	2
AR-A	0.5	1
TX	0.5	1

Note: Seed sources are listed in ascending order of proximity to the Blain site (i.e., closest to farthest).

Seed source was a significant source of variation in the ANOVA model for 2020 survival ($p < 0.001$). Tukey's HSD test detected significantly greater survival in NJ, VA, and SC sources than in GA and LA sources (fig. 2A). No differences in survival were detected between GA and LA sources or MO with any of the seed sources. Seed source was a significant factor in the ANOVA model for 2020 BA ($p < 0.001$). Tukey's HSD detected significantly lower BA in the GA plantings compared to both SC and VA (fig. 2B). The BA of the LA plantings were significantly lower than NJ, SC, TN, and VA according to Tukey's HSD. According to ANOVA, seed

source was a significant factor in the model for 2020 mDBH ($p = 0.002$), but not in the model for xDBH. Tukey's HSD test determined that the mDBH of the GA trees was significantly greater than trees sourced from NJ, MO, and TN (fig. 2C). An effect of seed source was detected in ANOVA models for 2020 mHT ($p = 0.010$) and xHT ($p = 0.004$). Tukey's HSD tests for mHT determined that trees sourced from GA were on average taller than trees sourced from NJ and MO (fig. 2E). Tukey's HSD test revealed the mean xHT of MO trees was significantly less than trees from several sources, including NJ, VA, SC, and GA (fig. 2F).

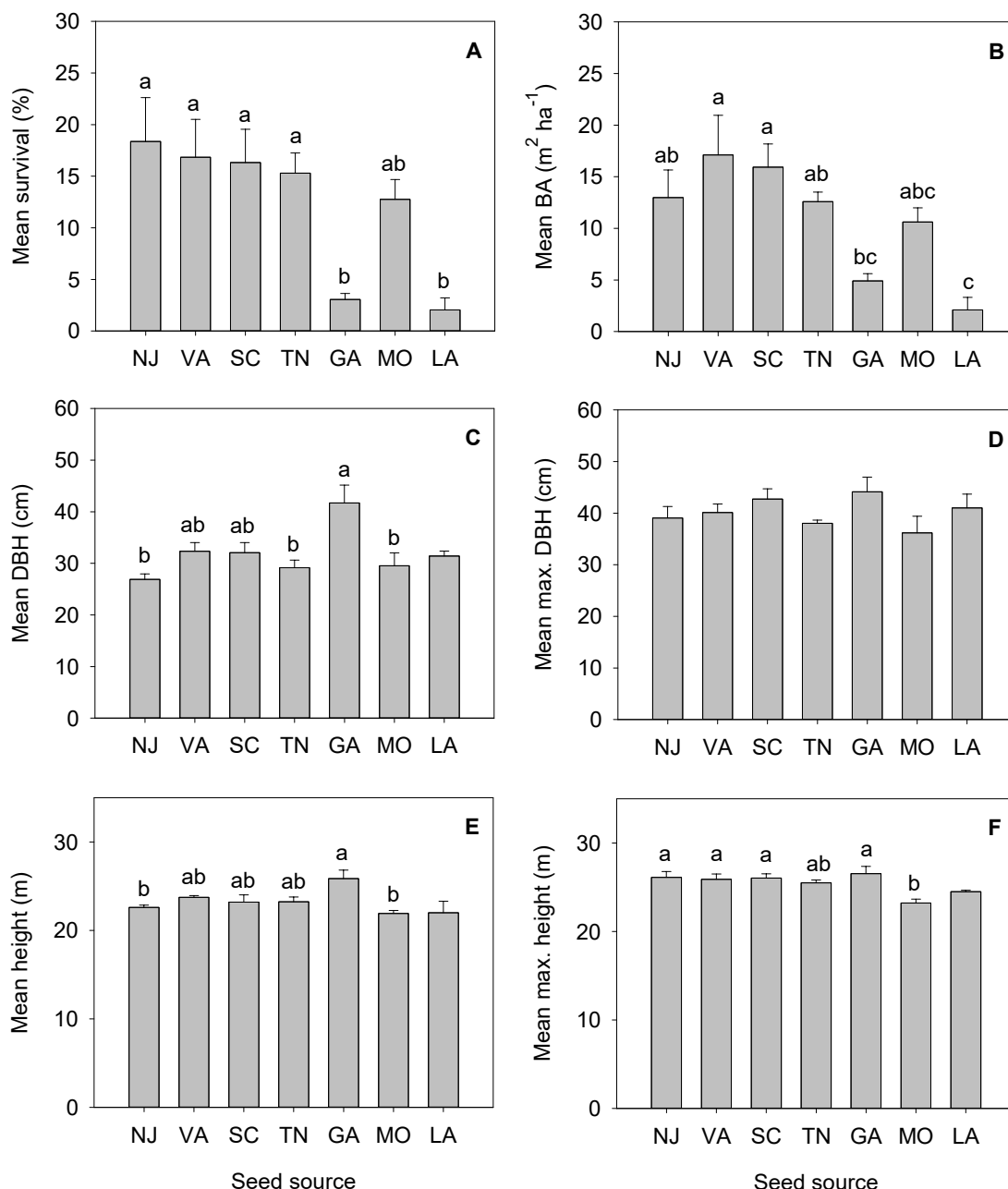


Figure 2—Mean survival (A), BA (B), DBH (C), maximum DBH (D), height (E), and maximum height (F) of shortleaf pine in year 62 (2020) of the common garden experiment in Green Bank, NJ. Seed sources are ranked from left to right based on increasing distance from county of origin to Green Bank. Seed source was a significant factor in ANOVA models for variables where lowercase letters are present (except D). State means with the same letter are not statistically different according to Tukey's HSD. Louisiana not included in ANOVA models for variables shown in figures C-F. Error bars equal one standard error.

Table 3—Pearson product-moment correlations and test results for associations between the six response variables and seven geographic and climatic variables based on year 62 data collected at Green Bank

Response variables	Geographic and climatic variables						
	DIST	LAT	LON	ALT	PREC	TEMP	JALO
SURV	-0.631 ^b	0.696 ^b	0.524 ^b	-0.003	-0.529 ^b	-0.606 ^b	-0.580 ^b
BA	-0.604 ^b	0.577 ^b	0.533 ^b	-0.030	-0.574 ^b	-0.474 ^a	-0.437 ^a
mDBH	0.283	-0.590 ^b	-0.134	-0.042	0.031	0.571 ^b	0.584 ^b
xDBH	0.005	-0.392 ^a	0.123	-0.264	0.079	0.477 ^a	0.494 ^a
mHT	-0.023	-0.389 ^a	0.157	-0.164	-0.073	0.435 ^a	0.465 ^a
xHT	-0.438 ^a	-0.128	0.555 ^b	-0.501 ^b	-0.040	0.319	0.363

^aStatistically significant at $p \leq 0.05$.

^bStatistically significant at $p \leq 0.01$.

Influence of Geography and Climate

According to Pearson correlation tests (table 3), all but one significant correlation was moderate in strength (i.e., $|r|=0.334$ - 0.667). Survival and BA were significantly correlated with nearly all geographic and climatic variables, except altitude of the county of seed origin. Correlations between distance from source county to the planting site with both survival and BA were negative. The only strong correlation ($|r|>0.667$) detected was between survival and latitude, a positive correlation. Survival and BA were negatively correlated with all climatic variables. Of the climatic variables, survival was most strongly associated with mean annual temperature of the county of origin, while BA was most strongly associated with mean annual precipitation of the county of origin. Correlations with mean January low temperature were stronger for survival than BA. Latitude of origin was the only geographic variable significantly correlated with mDBH, xDBH, and mHT, which were negative. The tree-level variable xHT was negatively correlated with both distance from origin and altitude of origin and positively correlated with longitude of origin. The variables mDBH, xDBH, and mHT were positively correlated with both mean annual and January low temperatures.

DISCUSSION

A geographic pattern in survival and growth of shortleaf pine seed sources was evident at years 10 and 14 of the Green Bank (NJ) and Blain (PA) common garden trials, respectively, which was linked to variation in winter injury among the seed sources (Little 1969). Partly because of these early results, we hypothesized that seed sources originating farther from the study sites, especially those from southern-most sources, would have lower survival and growth than local seed sources or ones better adapted to the climate of the planting site. The results presented for stand-level attributes (i.e., survival and basal area) at both common gardens

supported this hypothesis. Our analysis showed that the southern-most sources (LA and GA) had substantially lower survival and basal area than central and northern sources over the 62-year study at Green Bank. Interestingly, LA and GA sources had the poorest survival out to stand age 15 in a Missouri common garden comparing the same seed sources as the Green Bank study (Gwaze and others 2007). Our hypothesis was also supported by correlation tests revealing associations between geographic variables and the stand-level attributes of the NJ common garden in year 62. Positive correlations with latitude of origin and stand-level attributes are likely more indicative of adaptation to climate, while negative correlations with distance from origin county to Green Bank may reflect local adaptation in the shortleaf pine seed sources more generally. Gwaze and others (2007) also detected a north-to-south trend to shortleaf pine seed source performance in two common garden trials in Missouri with more northern sources out-performing the local MO source.

Most of the results for tree-level attributes (i.e., top height and stem diameter) did not support our hypothesis. For example, the GA seed source out-performed several others based on average diameter and height in 2020, including the local NJ source. However, the GA source also had one of the lowest survival rates during the 62-year study. By stand age 15, the mean survival rate for GA-sourced trees was just 22 percent. Therefore, the GA specimens surviving to 2020 have grown in low-density stand conditions for nearly a half century. We surmise that the larger size of surviving GA-sourced trees is more of a reflection of density-dependent growth than inherent growth superiority over the local seed source. Furthermore, the higher survival of the NJ source (>90 percent out to age 15) maintained stands with high tree density, intense competition, and less growing space per capita, which, in turn, yielded smaller trees on average after 62 years.

A tree-level result that did support our hypothesis was the negative correlation between distance from source county and maximum top height, suggesting a decrease in tree performance with increasing distance the seed was moved. Since the height of free-to-grow trees is more responsive to physical site conditions (e.g., site quality) than stand density (Avery and Burkhart 2002), this negative association could be linked to an increased mismatch between shortleaf genotypes and the planting site with increasing seed transportation distance. Winter injury (e.g., snow and ice loading) was cited as a factor to help explain poor performance of southern genotypes out to year 10 at Green Bank (Little 1969). Shoot injury caused by late frosts could have also disproportionately affected development of southern genotypes growing in Green Bank, a site near the northern limit of shortleaf's natural range.

The NJ source was the undisputed top-performer out to year 10 of the Green Bank study. Based on the 10-year results, Little (1969) recommended local seed sources for planting in southern NJ. Our results suggest that the local NJ source is no longer the top-performer after 62 years. By 2020, the VA, SC, and TN sources closed the performance gap with the local source. Although statistical differences were not detected among these 4 sources at age 62, the nominally greater basal area and tree size for VA and SC sources implies that Coastal Plain sources south of NJ may be suitable for planting in southern NJ. Several other common garden studies have also suggested that moving seeds a modest distance northward may be preferable to deploying local sources for southern pine artificial regeneration (Schmidtling 1995, Tauer 1980, Wells and Wakeley 1970).

The 64-year results of the common garden study near Blain, PA, albeit limited to just survival, indicate that local sources will likely yield best results for shortleaf pine plantings in central PA. However, the poor performance of all sources at the Blain test site also suggest that shortleaf pine may not be suitable for planting at similar sites (i.e., sites with similar soil, topography, and climate) north of the species' current range. Early results clearly show how poorly shortleaf pine performed out to year 14. For example, survival ranged from 1 percent in the southern-most source (TX) to 35 percent in the local PA source. Winter injury was likely the main culprit explaining poor performance at Blain, but deer browse may have also contributed (Little 1969). Some have posited that planting shortleaf pine in the PA Ridge and Valley should prioritize south-facing sites underlain by sandstone at elevations less than 305 m above sea level, especially where frost pockets are unlikely to form (Little 1969). We concur with the early recommendation that shortleaf pine planting should be experimental in central PA until results indicate otherwise.

CONCLUSIONS

Results of the Green Bank and Blain common gardens out to the seventh decade continue to support the early recommendation to source shortleaf pine seedlings from populations best adapted to planting sites in southern NJ and central PA. However, the poor performance of all sources at Blain, PA indicates that additional experimental research is likely needed to determine appropriate genetics to deploy and site types to select when planting shortleaf pine north of its natural range in central PA. Although local sources are still viable options for shortleaf artificial regeneration in southern NJ, our study suggests that some southern sources are also suitable for out-planting on NJ Coastal Plain sites. This finding has implications not only for shortleaf pine artificial regeneration in NJ, but for climate change adaptation strategies at the northern edge of shortleaf pine's natural range. Since a warming climate is expected to favor genotypes adapted to warmer conditions, the deliberate northward movement of southern shortleaf pine seed may help enhance resilience of NJ Coastal Plain forests to future climate. Artificial regeneration would also create an opportunity for deployment of genetically improved shortleaf pine planting stock. However, one must also anticipate winter injury and associated performance setbacks in more southern sources, especially in the first few decades before climate has ameliorated for a given seed source. For example, the SC source went from one of the poorest performers to one of the top-performing sources in year 62. This suggests the performance of the SC source may have improved as climate warming ameliorated growing conditions at Green Bank. Future research at these common garden trials could investigate seed source variation in climate sensitivity based on the radial growth of individual trees over the last seven decades.

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