RESTORATION OF LONGLEAF PINE— THE STATUS OF OUR KNOWLEDGE

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Abstract—By the fifth anniversary of the America's Longleaf Restoration Initiative in 2014, the decline in longleaf pine (*Pinus palustris* L.) appears to have been reversed. The area in longleaf pine-dominated stands currently exceeds 4 million acres, up from a low of about 3 million acres two decades ago. A major contribution to this reversal has been the recent establishment of more than 500,000 acres of longleaf pine plantations. However, the plantation approach has limitations in an environment where stand establishment costs exceed $300 per acre, when large-diameter sawlogs currently bring stumpage prices of $30 per ton or less, and when the most urgently-needed habitat is found in mature stands with well-developed understory flora. In addition, expanding the restoration of planted longleaf pine stands will require excluding hybrid Sonderegger pines (*P. ×sondereggeri* H.H. Chapm.) from longleaf pine seed orchards and nurseries, and developing silvicultural tactics for sustainable and lucrative pine straw harvests or other local niche markets. A broader and more inclusive approach to restoration might include identifying mixed-pine and pine-hardwood stands with a minor manageable longleaf pine component. Evidence from State surveys and FIA data suggests that such stands could add several million acres of restorable longleaf pine stands across the South. The silvicultural tactics in these stands are simple—harvest the non-longleaf pine component and restore prescribed burning. Not only would this bring an early economic return to the landowner, it would more quickly restore habitat conditions for the flora and fauna of interest in longleaf pine ecosystems. If the approach is feasible, expanding the use of prescribed fire on private lands will become more important, and perhaps more problematic, in restoration of longleaf pine ecosystems.

INTRODUCTION

In July 2014, a celebration was held in Washington DC to honor the fifth anniversary of America's Longleaf Restoration Initiative (ALRI), a program developed to bring Federal resources to bear to recover longleaf pine (*Pinus palustris* L.) across its former range. The ALRI began in 2009 with the publication of the Rangewide Conservation Plan for Longleaf Pine (ALRI, 2009) by an ad hoc Regional Working Group for America's Longleaf. This group is under the direction of three Cabinet-level Federal agencies—the Department of Defense, the Department of Agriculture (both the U.S. Forest Service and the Natural Resources Conservation Service), and the Department of the Interior (specifically, the U.S. Fish and Wildlife Service). The conservation plan laid out a 15-year mission to restore longleaf pine to at least 8 million acres on public and private lands across the South.

The driving force behind the restoration initiative was the catastrophic loss of area in longleaf pine forests over the past four centuries. The magnitude of the loss was calculated by Frost (1993) who concluded that before European settlement there were 74.0 million acres of forests where longleaf pine was dominant, plus another 17.0 million acres where longleaf pine was a component of mixed stands with hardwoods and/or other pine species.

A recent study based on FIA inventory data for the year 2010 puts the area of the longleaf pine-dominated stands at approximately 3.3 million acres. An additional 985,000 acres of the mixed longleaf pine-scrub oak type brings the Southwide estimate to 4.3 million acres (Oswalt and others 2012). This appears to show a reversal of the long-term decline in longleaf pine acreage (fig. 1), not only through better afforestation and reforestation, but also through more widespread use of prescribed burning and invasive species control (ALRI, 2014).

Of the 4.3 million acres in longleaf pine-dominated forest types, two common trends can be detected. First, a quarter of it is young; 758,000 acres is in the 0- to 10-year age class, and another 415,000 acres is in the 11- to 20-year age class (Oswalt and others 2012). Second, the large majority of young stands are planted

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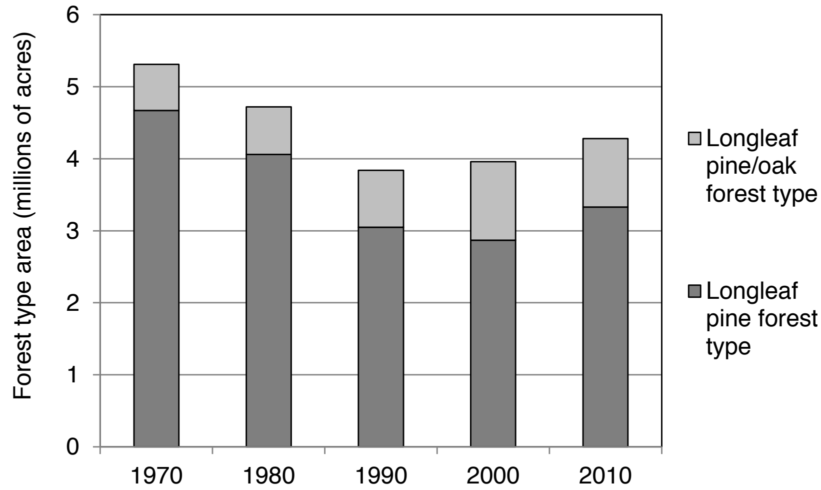

Figure 1—The trends in longleaf pine forest type and longleaf pine/oak forest type from 1970 to 2010. Adapted from USDA Forest Service, Forest Inventory and Analysis, Forest Inventory Online State Reports, August 2013.

relatively recently; of the 1.1 million acres of planted longleaf pine-dominated forests, 84 percent are ≤25 years old (Oswalt and others 2012). This suggests two conclusions—one, that new stand establishment is actively occurring, and two, that planting is generally the tool being used to do it. That has several implications for the short-term and long-term success of restoration.

THE PLANTATION APPROACH TO LONGLEAF PINE RESTORATION

Clearly, if a species is absent from a site, the first step in restoration is to reintroduce the species to the site, and planting is, by far, the most effective tool to meet that goal. However, there are some challenges to overcome with respect to establishment and management of planted longleaf pine stands in the context of restoration, especially on private lands.

Genetics— Seed Sources and Hybrids

Genetic improvement of longleaf pine has lagged behind that achieved for both loblolly pine (*P. taeda*) and slash pine (*P. elliottii* var. *elliottii*). Early genetic studies in longleaf pine showed significant heritable variation in growth and quality traits (Snyder and Namkoong 1978) and limited problems with diseases (Boyer 1990). Seed orchards and associated progeny tests were set-up by the USDA Forest Service's Southern Region and the Western Gulf Forest Tree Improvement Program[2] (Crane and Barbour 2009). The western gulf program subsequently rogued their orchards using progeny test data, however these orchards are owned by states without tree improvement programs. Only one advanced generation breeding program exists, consisting of an experimental population maintained at the Harrison Experimental Forest in south Mississippi (Nelson and others 2005). The established guidelines for seed source movement (Schmidtling 2001) still serve as the best information for seed source selection in consideration of planting programs. Utilizing proper seed sources consisting of multiple seed trees to ensure genetic diversity is a recommended practice (Echt and others 2011) and will need to suffice until more advanced tree improvement programs can deliver improved materials at appropriate scales. With the increased planting called for and being documented through the ALRI, care must be taken in evaluating early plantation success for disease incidence. In particular, brown spot needle blight (caused by Mycosphaerelia dearnessii) and fusiform rust (caused by Cronartium quercuum fsp. fusiforme) have the potential to cause significant losses in large-scale planting programs, and the potential for genetic selection for resistance exists and should be leveraged with ongoing programs. New genomic technologies also allow for reconstructing pedigree information in plantings of known seed sources, and these plantings could be used retrospectively to learn about the genetics of important traits such as disease resistance and emergence from the grass stage (El-Kassaby and Lstiburek 2009).

Beyond the limited availability of optimal seed sources for longleaf pine, there is the potential for increased hybridization with loblolly pine. Anecdotal and scientific evidence suggests that hybrids in pine planting stock may be more common than previously thought. Inter-species hybridization can erode the unique characteristics of the parental species and change their functional attributes in the ecosystem. If the goal is to restore the longleaf pine ecosystem, monitoring and maintenance of species integrity should be considered.

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In studies with shortleaf pine (*P. echinata* Mill.) in the Ouachita Mountains, the prevalence of hybrids between loblolly pine and shortleaf pine especially in native stands appears to be increasingly common. This may be due to increasing overlap between the species in pollen flight and conelet receptivity resulting from changing climatic conditions, coupled with increasing proximity to loblolly pine plantations (Stewart and others 2012, Tauer and others 2012). Shortleaf pine is unique among southern pines in that it sprouts prominently if top-killed (as by fire) when young, an attribute correlated to the unique presence of a basal crook on shortleaf seedlings and saplings (Lilly and others 2012). Among the traits of the hybrids between loblolly pine and shortleaf pine is a much less well developed basal crook, which results in less effective sprouting, implicating fire as a tool to maintain the genetic integrity of shortleaf pine by eliminating the hybrids (Lilly and others 2012, Stewart and others 2014). As a result, The Forest Service's Southern Region (Region 8) is undertaking a major effort to genetically test second-generation shortleaf pines in their seed orchards (fig. 2), and removing those trees that are hybrids between loblolly and shortleaf pine.

Figure 2—Pure shortleaf seedlings (with crook) and putative hybrids (without crook) naturally regenerated from beneath a second-generation shortleaf pine seed orchard on the Kisatchie National Forest. (photo by James M. Guldin)

Anecdotal observations suggest that similar considerations might apply with respect to Sonderegger pine, the hybrid between loblolly and longleaf pines. First described by Chapman (1922), Sonderegger pines emerge from the grass stage sooner and grow more rapidly than longleaf pine (Wells and Wakeley 1970), and they tend to have heavier branches and forks with multiple stems in the upper canopy. Several longleaf pines in the first-generation seed orchard managed by the USDA Forest Service at the Stuart Nursery in Louisiana show what appears to be this attribute typical of Sonderegger pine (fig. 3). As a result, Region 8 and the Southern Research Station are expanding their genetic testing into longleaf pine seed orchards, again with the goal of removing the influence of Sonderegger hybrids on seedlings provided for outplanting in longleaf pine restoration efforts.

Economics and Markets

Longleaf pine plantations are costly to establish. Assuming one is reforesting a cutover site, recommendations to establish a planted stand of longleaf pine might include chemical site preparation and possibly mechanical site preparation. Planting 500-600 trees per acre incurs costs for buying containerized longleaf pine seedlings, and contracting with a planting crew to plant them. All of these costs together can easily exceed $300 per acre for stand establishment (Dooley and Barlow 2013). At a $300 investment per acre and assuming a 6 percent compound interest rate, the compounded costs of stand establishment will grow to more than $1700 per acre after 30 years. The standing volume of an average longleaf pine plantation after 30 years can be expected to be in the ballpark of 60 green tons per acre (Gonzalez-Benecke and others 2012). Current stumpage prices for pine pulpwood are roughly $10 per green ton (Timber-Mart South 2015). This suggests if a landowner was growing longleaf pine for commercial fiber production on a 30-year rotation (itself an unlikely supposition), stumpage prices for pine pulpwood would have to rise considerably to break even on an investment with a 6 percent internal rate of return.

Longer rotations bring additional financial concerns for owners of planted longleaf pine stands. Through the latter part of the 20th century, experts repeatedly advised landowners that the real value for longleaf pine timber products is in large-diameter longleaf pine sawlogs, which commanded premium stumpage prices because of the high quality of lumber they produce. Unfortunately, the start of the 21st century has not been kind to landowners who have pursued this strategy. As an example, pine sawtimber stumpage prices in south Alabama and elsewhere in the South have fallen from nearly $60 per ton in the late 1990s to below $30 per ton in 2012-2015 (Timber-Mart South 2015).

Figure 3—Possible presence of Sonderegger pine (hybrid between loblolly and longleaf pine) in a first-generation seed orchard on the Kisatchie National Forest. (photo by James M. Guldin)

In addition, logging technology is changing, with cutting machines and forwarders replacing loggers with chain saws and skidders for felling and bucking pine sawlogs. Changes in mill technology are also leading to the processing of smaller sawlogs. As a result, it is increasingly difficult to sell sawlogs larger than 24 inches in diameter at the large end to timber buyers.

Finally, long rotations are very difficult to justify economically when stand establishment costs are high and early returns from thinning are limited. Yields that might be expected in a typical 80-year even-aged rotation in a typical planted longleaf pine stand could include thinning at age 30 (12 tons per acre), age 45 (19 tons per acre), and age 60 (24 tons per acre), and a final standing volume of 90 tons per acre (two-thirds of which is sawtimber) at age 80 (Gonzalez-Benecke and others 2012). Carrying a high stand establishment cost over an 80-year rotation is not an economically robust investment.

A key alternative for landowners managing longleaf pine stands over longer rotations is to take advantage of unique markets. One example is to sell high-quality sawlogs in the specialized market for utility poles, which brings a premium stumpage price; another is to consider harvest of pine straw, which can be quite profitable (Roise and others, 1991). Local market development for high-quality dimension lumber is urgently needed. However, without access to niche markets, the only way to generate a positive return over a sawtimber rotation is for a landowner to be comfortable with a low internal rate of return of about 4 percent or less.

Habitat in Planted Stands

The main reason for concern about the loss of longleaf pine ecosystems across the South is the loss of habitat for fauna and flora associated with mature open forests and woodlands. Species such as gopher tortoise (*Gopherus polyphemus*), red-cockaded woodpecker (*Picoides borealis*), Bachman's sparrow (*Peucaea aestivalis*), northern bobwhite (*Colinus virginianus*), bluestem grasses (*Andropogon* spp.) and wiregrass (*Aristida stricta* Michx.) thrive in open woodlands maintained by frequent fire.

This is not the kind of habitat that is associated with young pine plantations, including longleaf pine plantations. Planted stands quickly develop into an early stem exclusion stage (cf. Oliver and Larsen 1996), when crown closure in plantations reduces understory development to the point where native forbs and grasses are suppressed. In addition to the constraint on development of legumes and grasses for which longleaf pine ecosystems are known, the lack of ground-layer biomass reduces foraging habitat for gopher tortoise as well as nesting and foraging habitat for northern bobwhites. Depending on subsequent silvicultural activities, the period during which understory vegetation is suppressed may last for two to three decades.

There is also a considerable difference in the ease with which new understory plant communities can become established in planted stands of longleaf pine, depending on whether the site has a history of agricultural use. Converting land from forest to agricultural use not only removes the woody vegetation, but plowing and planting crops also degrades the understory woodland flora that had existed prior to conversion (Walker and Silletti 2006). Restoration of forest land that has never been in agricultural production is relatively easy; in addition to replanting trees, reintroduction of prescribed burning associated with some precommercial or commercial thinning promotes natural development of the existing seed bank and rootstocks of understory forbs, legumes, and grasses, even in poletimber stands. However, restoration of longleaf pine ecosystems planted on abandoned agricultural land requires not only planting longleaf pine, but also direct seeding or planting of the complex of native warm season grasses and legumes (Kaeser and Kirkman 2014, Norden and Kirkman 2014). The cost of restoration of understory plants adds to the financial commitment a landowner may make.

In summary, the approach to restoration of longleaf pine through establishment of new plantations will continue to be important, but remains challenging both economically and ecologically. There are issues to ponder genetically as well, though those seem manageable. This begs the question about whether a second approach, in addition to the plantation model might be considered.

MANAGEMENT OF EXISTING MIXED PINE STANDS

Several of the issues with the plantation approach to restoring longleaf pine stands might be addressed by a different approach—actively managing the composition of immature and mature mixed-species pine and pine-hardwood stands that are not dominated by longleaf pine, but that contain a minor and manageable component of longleaf pine. This approach involves first identifying these stands, and then using commercial thinning to remove most, if not all, of the trees other than longleaf pine, to convert the stand to a longleaf pine-dominated stand. That would be followed by initiation of cyclic prescribed burning as the subsequent step to restore the understory plant community.

Quantifying a Minor Manageable Component of Longleaf Pine

Managing stands that are essentially understocked with longleaf pine has some support in silviculture research in southern pines from the latter part of the

20th century. The classic work of Croker and Boyer (1975) on the Escambia Experimental Forest in south Alabama clearly established the feasibility of using the shelterwood method to obtain natural regeneration of longleaf pine. The recommendation of leaving 30 square feet per acre after the seed cut was based on work by Boyer (1979) who noted that stand-level seed production declined at residual basal areas greater than 40 square feet per acre and less than 30 square feet per acre. Based on this, one suggestion for a lower limit of longleaf pine basal area in a mixed stand would be 30 square feet per acre. The prescription would retain all the longleaf pines, harvest most or all of the other trees, conduct any supplemental midstory removal that might be necessary through harvest or as a mechanical or chemical intermediate treatment, and initiate cyclic prescribed burning. The goal would be to either maintain an understocked pine woodland condition dominated by longleaf pine, or develop a second age cohort of naturally-regenerated longleaf pine seedlings beneath the residual longleaf pine overstory in a manner approximating the shelterwood-with-reserves method.

A second approach to quantifying the lower threshold for a minor manageable longleaf pine component might be through research on rehabilitation of understocked pine stands. Resource analysts with the Forest Inventory and Analysis Program of the U.S. Forest Service consider a stand with 60 percent stocking as the lower limit of full stocking (USDA Forest Service 1972). However, stand development in the Farm Forestry Forty demonstrations at the Crossett Experimental Forest in south Arkansas (in mixed loblolly-shortleaf pine stands) showed a relatively rapid recovery from cutover understocked conditions in the first two decades of management (Reynolds 1969, Reynolds and others 1984). Baker and Shelton (1998) expanded upon those early observations with a study of stand growth and yield in response to five levels of understocking. They concluded that loblolly-shortleaf pine stands on medium sites that were cut back to as little as 30 percent stocking were able to recover to fully stocked conditions within 15 years. The fact that stands could recover from slightly understocked conditions was not surprising, but stands with 30 percent stocking do not give a visual impression that they would be able to recover that rapidly. In the absence of better data specifically for longleaf pine stands, the 30-percent stocking figure might be a second point of departure to quantify the lower limit of a minor but manageable longleaf pine component in mixed stands.

Estimates of Area in Mixed Longleaf Pine Stands

Among the reasons this approach to restoration of manageable mixed pine stands might be fruitful is the potential increase in area of longleaf pine that could be in restorable condition. The report on longleaf pine area published by Oswalt and others (2012) is based on an analysis of FIA data where longleaf pine accounts for a plurality of stocking on the plot. This resulted in two predominant FIA forest types: longleaf pine (where longleaf pine clearly made up a plurality of stand stocking), and longleaf pine-oak (where scrub oaks made up a plurality of stocking and longleaf pine accounted for 25- to 50 percent of stand stocking.) This is the area where longleaf pine was never lost, or where it is being recovered using planted stands.

A case study within the natural range of longleaf pine might illustrate the potential gains in recovery of longleaf pine using this approach. As previously stated, the area of longleaf pine-dominated forests, according to FIA data, is roughly 4.3 million acres (Oswalt and others 2012). But FIA data can also provide a rough estimate of the area that might be available for restoration in stands with a minor component of longleaf pine that could possibly attain a plurality of longleaf pine stocking with the removal of more prominent species in the stand.

One analytical approach includes all FIA plots with at least one longleaf pine ≥5.0 inches diameter at breast height (d.b.h.) and in which longleaf pine may or may not be the dominant species. This results in an estimate of 7.9 million acres of stands within the natural range of longleaf pine in which some portion of stand basal area includes longleaf pine (fig. 4). This analysis probably excludes most of the 758,000 acres of planted longleaf pine stands ≤ 10 years old, because they would not contain trees ≥ 5.0 inches d.b.h. Assuming that stands with longleaf pine basal area from 20- to 50 percent of stand basal area might qualify as having a minor manageable longleaf pine component (fig. 4), the South may have 1.825 million acres of stands where longleaf pine is a minor manageable component, and in which restoration might be used to create longleaf pine-dominated stands.

A second analysis includes all FIA plots that have two or more species that are ≥5.0 inches d.b.h. and where longleaf is not the dominant species (fig. 5). Stands in this analysis total 4.11 million acres across the natural range of longleaf pine. Again, assuming that stands with longleaf pine basal area from 20- to 50 percent of stand basal area might qualify as having a minor manageable longleaf pine component (fig. 5), the South may have an additional 1.24 million acres of stands in which longleaf pine is not the dominant species but where restoration to create longleaf pine-dominated stands might be considered.

DISCUSSION

Reliance on restoration of longleaf pine ecosystems using planted stands on abandoned agricultural lands or in reforestation of cutover stands that did not support longleaf pine will continue to be a fundamental objective under the Rangewide Conservation Plan for Longleaf

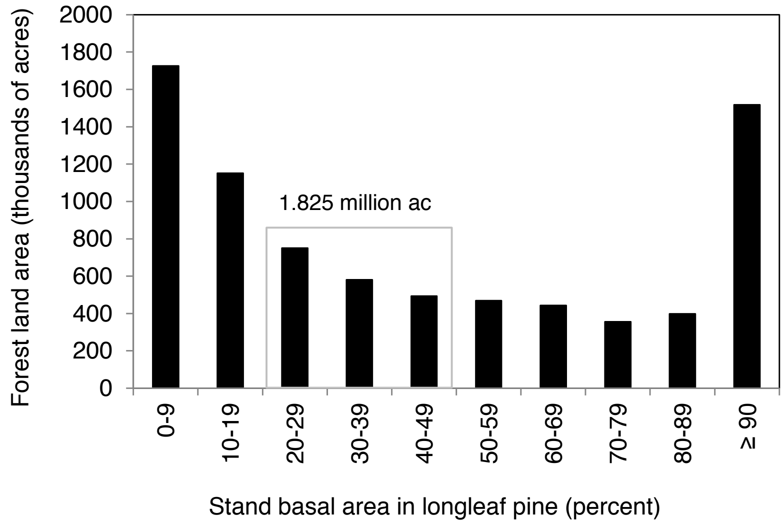

Figure 4—Forest land area by stand basal area classes where longleaf pine may or may not be the dominant species. Data include all FIA plots that have at least one longleaf pine ≥ 5.0 inches in diameter at breast height.

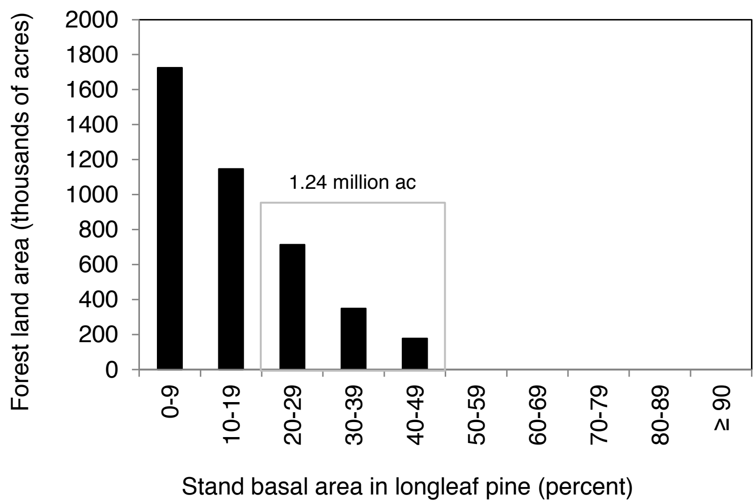

Figure 5—Forest land area by stand basal area classes where longleaf pine is not the dominant species. Data include all FIA plots that have at least one longleaf pine ≥5.0 inches in diameter at breast height.

Pine. The best way to re-establish longleaf pine on sites adapted to longleaf pine without a seed source is to use planting. The nursery practices to raise containerized longleaf pine seedlings and the details of the silviculture required to establish new planted stands are well documented. However, the practice is expensive, and development of appropriate habitat for species at risk from loss of native pine ecosystems may take two decades to establish, if not longer.

Silvicultural practices developed in southern pines in the latter part of the 20th century offer an alternative approach to augment existing plantation restoration efforts. Looking at those studies from a 21st-century perspective suggests that understocked pine stands can often be effectively managed and used to recover full stocking over time, not just for a timber resource but also for habitat associated with mature pine forest ecosystems. We suspect that if these stands have a manageable longleaf pine component in them and have never been in agricultural use, restoration of functional habitat appropriate for the species of conservation concern in longleaf pine stands can occur more quickly, and potentially at a much lower cost to the landowner, than it can through the creation of new plantations.

If removing all other pine species in mixture with longleaf pine creates stand conditions that a landowner thinks are too understocked, it is probably feasible to retain a mixed stand as long as the percentage of longleaf is increased to some degree. This could be important if a broader suite of habitat values can be maintained through retention of a mixed-dominance pine component (Lavoie and others 2011) and again, if the stands do not have an agricultural history and the native understory flora can be brought back through prescribed burning.

The surprising element of this approach is the area that could potentially be restored. If converting stands with a minor manageable longleaf pine component into longleaf pine-dominated stands proves fruitful, the area that could potentially be restored in a relatively simple manner would increase by a range of from 1.24 million to more than 3 million acres. That would make dramatic progress toward achieving the 8 million acres targeted for achievement by 2025 in the Rangewide Longleaf Conservation Plan.

It would be relatively easy to make a start at this on Federal and State lands simply by adopting some modifications in existing silvicultural prescriptions for stands with a minor manageable longleaf pine component to increase the percentage of longleaf pine through thinning and re-establishment of cyclic prescribed burning. The challenge on public and private lands would be to expand the use of prescribed burning, which is increasingly constrained by air quality regulations especially in heavily populated areas. A doubling of area in longleaf pine stands being restored would double the need for annual prescribed burning to create and maintain open forest and woodland habitat. This may be difficult to accomplish in the current social and political climate.

LITERATURE CITED

America's Longleaf Restoration Initiative (ALRI). 2009. Rangewide conservation plan for longleaf pine. Atlanta, GA: America's Longleaf Restoration Initiative. 42 p. http://www.americaslongleaf.org/media/86/conservation_plan.pdf. [Date accessed: January 29, 2015]

America's Longleaf Restoration Initiative (ALRI). 2014. 2013 Range-wide accomplishment report. Atlanta, GA: America's Longleaf Restoration Initiative, Longleaf Partnership Council. 19 p. [Date accessed: January 29, 2015]

Baker, J.B.; Shelton, M.G. 1998. Rehabilitation of understocked loblolly-shortleaf pine stands—I. recently cutover natural stands. Southern Journal of Applied Forestry. 22(1): 35-40.

Boyer, W.D. 1979. Natural regeneration of longleaf pine. Journal of Forestry. 77(9): 572-575.

Boyer, W.D. 1990. Pinus palustris Mill., Longleaf pine. In: Burns, R.M., Honkala, B.H., tech. cords. 1990. Silvics of North America. Vol. 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture: 405-412.

Chapman, H.H. 1922. A new hybrid pine (*Pinus palustris* x *Pinus taeda*). Journal of Forestry. 20: 729-735.

Crane, B. and Barbour, J. 2009. Status of longleaf pine seed orchard resources in support of restoration. In: Proceedings of the 30th southern forest tree improvement conference. Blacksburg, VA: 74-76. http://www.rngr.net/publications/tree-improvement-proceedings/sftic/2009/status-of-longleaf-pine-seed-orchard-resources-to-support-restoration.pdf [Date accessed: July 7, 2015]

Croker, T.C., Jr.; Boyer, W.D. 1975. Regenerating longleaf pine naturally. Res. Pap. SO-105. New Orleans, LA: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 21 p.

Dooley, E.; Barlow, R. 2013. Special report: 2012 costs and cost trends for forestry practices in the South. Forest Landowner. July/August, 22-28. http://digital.graphcompubs.com/publication/?i=171803&p=24. [Date accessed: February 3, 2015].

El-Kassaby, Y.A.; Lstiburek, M. 2009. Breeding without breeding. Genetics Research. 91(2): 111-120.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In: Hermann, S.M., ed. The longleaf pine ecosystem: ecology, restoration and management. In: Proceedings of the Tall Timber fire ecology conference No. 18. Tallahassee, FL: Tall Timbers Research Station: 17-43.

Gonzalez-Benecke, C.A.; Gezan, S.A.; Leduc, D.J. [and others]. 2012. Modeling survival, yield, volume partitioning and their response to thinning for longleaf pine (*Pinus palustris* Mill.) plantations. Forests. 3: 1104-1132.

Kaeser, M.J.; Kirkman, L.K. 2014. Field and restoration guide to common native warm-season grasses of the longleaf pine ecosystem. Unnumbered publication. Newton, GA: Joseph W. Jones Ecological Research Center at Ichauway, in partnership with the Georgia Native Plant Society. 71 p.

Lavoie, M.; Kobziar, L.; Long, A.; Hainds, M. 2011. Problems and needs for restorationists of longleaf pine ecosystems: a survey. Natural Areas Journal. 31(3): 294-299.

Lilly, C.J.; Will, R.E.; Tauer, C.G. [and others]. 2012. Factors affecting the sprouting of shortleaf pine rootstock following prescribed fire. Forest Ecology and Management. 265: 13-19.

Nelson, C.D.; Lott, L.H.; Gwaze, D.P. 2005. Expected genetic gains and development plans for two longleaf pine third-generation seedling seed orchards. In: Proceedings of the 28th southern forest tree improvement conference, June 20-23, 2005, Raleigh, NC: North Carolina State University, Department of Forestry and Environmental Resources: 108-114.

Norden, H.; Kirkman, K. 2014. Field guide to common legume species of the longleaf pine ecosystem. Unnumbered publication. Newton, GA: Joseph W. Jones Ecological Research Center at Ichauway, in partnership with the Georgia Native Plant Society. 72 p.

Oliver, C.D.; Larsen, B.C. 1996. Forest stand dynamics. New York: John Wiley and Sons. 544 p.

Oswalt, C.M.; Cooper, J.A.; Brockway, D.G. [and others]. 2012. History and current condition of longleaf pine in the Southern United States. Gen. Tech. Rep. SRS-166. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 51 p.

Reynolds, R.R.; Baker, J.B.; Ku, T.T. 1984. Four decades of selection management on the Crossett Farm Forestry Forties. Bulletin 872. Fayetteville, AR: University of Arkansas, Arkansas Agricultural Experiment Station. 43 p.

Reynolds, R.R. 1969. Twenty-nine years of selection timber management on the Crossett Experimental Forest. Res. Pap. SO-40. New Orleans, LA: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 19 p.

Roise, J.P.; Chung, J.; Lancia, R. 1991. Red-cockaded woodpecker habitat management and longleaf pine straw production: an economic analysis. Southern Journal of Applied Forestry. 15(2): 88-92.

Schmidtling, R.C. 2001. Southern pine seed sources. Gen. Tech. Rep. SRS-44. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 25 p.

Snyder, E. B.; Namkoong, G. 1978. Inheritance in a diallel crossing experiment with longleaf pine. Res. Pap. SO-140. New Orleans, LA: U.S. Department of Agriculture Forest Service Southern Forest Experiment Station. 40 p.

Stewart, J.F.; Will, R.E.; Robertson, K.M.; Nelson, C.D. 2014. Frequent fire protects shortleaf pine (*Pinus echinata*) from introgression by loblolly pine (*P. taeda*). Conservation Genetics. DOI 10.1007/s10592-014-0669-x. [Date accessed: February 3, 2015].

Stewart, J.F.; Tauer, C.G.; Nelson, C. D. 2012. Bidirectional introgression between loblolly pine (*Pinus taeda* L.) and shortleaf pine (*P. echinata* Mill.) has increased since the 1950s. Tree Genetics and Genomics. 8: 725-735.

Tauer, C.G.; Stewart, J.F.; Will, R.E. [and others]. 2012. Hybridization leads to loss of genetic integrity in shortleaf pine: unexpected consequences of pine management and fire suppression. Journal of Forestry. 110(4): 216-224.

Timber-Mart South, 2015. Southwide average prices. http://www.timbermart-south.com/prices.html. [Date accessed: May 6, 2015].

USDA Forest Service. 1972. Forest survey handbook, FSH 4813.1. Washington, DC: U.S. Department of Agriculture. 254 p.

Walker, J.L.; Silletti, A.M. 2006. Restoring the ground layer of longleaf pine ecosystems. In: Jose, S.; Jokela, E.J.; Miller, D.L., eds. 2006. Ch. 10. The longleaf pine ecosystem--ecology, silviculture, and restoration. New York: Springer Science+Business Media, LLC: 297-325.

Wells, O.O.; Wakeley, P.C. 1970. Variation in longleaf pine from several geographic sources. Forest Science. 16(1): 28-42.