Strategic Assessment for Shortleaf Pine

Rodney Will, John Stewart, Tom Lynch, Don Turton, Adam Maggard, Curtis Lilly, Kurt Atkinson

Key Points

Genetics

- Northern seed sources outperform southern seed sources when planted on northern sites, and southern seed sources outperform northern sources when planted on southern sites
- Western seed sources are more drought and fusiform rust resistant than eastern seed sources
- Rates of hybridization between shortleaf pine and loblolly pine have increased from 4% in shortleaf pine and 6% in loblolly pine in the 1950's in seed grown from mature trees to 47% in shortleaf pine and 25% in loblolly pine in current day seedling populations
- Shortleaf x loblolly pine hybrids resemble loblolly pine by exhibiting fast seedling/sapling growth rates and resemble shortleaf pine by exhibiting greater water use efficiency

Silviculture

- Emphasis on shortleaf pine silviculture has shifted from production forestry to objectives related to wildlife habitat and ecosystem restoration
- The ability of shortleaf pine to sprout after fire is a critical attribute that allows the use of fire to favor shortleaf pine over loblolly pine and over shortleaf x loblolly pine hybrids.
- To maximize survival of top-killed seedlings, seedlings should be smaller (0.6 to 1.6 cm GLD and 0.3 to 0.8 m tall) and sustain 50% or less crown scorch.

Climate and climate change

- Shortleaf pine is more drought tolerant than loblolly pine and exhibits greater water use efficiency
- The greater cold tolerance of shortleaf pine compared to loblolly pine could be due to the ability of shortleaf pine to better withstand ice/snow damage, extreme low temperatures, or winter soil moisture availability.
- High temperatures alone probably does not limit the southern range limit of shortleaf pine.
- The range of shortleaf pine will probably expand northward in response to climate change with little change in the southern portion of its current range
- More variable precipitation that is predicted under future climate scenarios will increase drought frequency and intensity and favor shortleaf pine relative to less drought tolerant species, but may increase susceptibility of shortleaf pine to drought along the western margin of its current range

Shortleaf Pine Management and Water Resources

- Managing shortleaf pine will likely produce the same effects on water quantity and quality as managing other pine species at a given location. The percentage of trees harvested, area disturbed, and the number of roads will far over-shadow any species effect on water.
- Restoration of more "open" ecosystems such as the shortleaf pine-bluestem ecosystem would likely increase streamflow, but as with harvesting it would have to be applied over large areas to increase water supply.
- Under a warmer and drier future climate gains in streamflow from harvesting and ecosystem restoration would be diminished because of a reduced input of water and higher evaporative losses.

Shortleaf Pine Growth and Yield

- Comprehensive growth and yield models for natural stands of even-aged and uneven-aged shortleaf pine have been developed.
- While mainly developed in the Interior Highlands, models for even and uneven aged forests are applicable throughout the Southeast.
- Biomass partitioning equations exist for mature shortleaf pine stands of different densities.

Key knowledge gaps/Uncertainties

1) What is causing the increase in shortleaf x loblolly pine hybrids and what is their effect on forest resiliency and productivity?
2) What is the best fire regime to manage population genetics of shortleaf pine?
3) How is management and wide scale planting of loblolly pine affecting the rate of hybridization between loblolly and shortleaf pine?
4) What is the rate of hybridization in seed orchard mother trees and half-sib seed produced that is grown in nurseries?
5) What is the effect of climate change on seed source selection?
6) How large is the variability in drought tolerance within shortleaf pine and can drought tolerance be used as a selection criterion for tree improvement programs?
7) What is the effect of seed source on the response to fire, drought, and other disturbances?
8) How can fire be used to bank advanced regeneration of shortleaf pine in natural regenerations systems?
9) How will climate change affect the range and productivity of shortleaf pine?
10) What is the effect of climate change on site suitability for shortleaf pine within the range?
11) Is the basal crook necessary as an adaptation to sprout following fire?
12) How does season of burn and fire intensity affect shortleaf pine resprouting?
13) What is the effect of different management strategies and silvicultural treatments on stream flow and soil water availability?

14) Will climate change affect the susceptibility or hazard area for shortleaf pine to littleleaf disease?

15) How will climate change affect susceptibility of shortleaf pine to pests and pathogens?

16) How will climate change affect wildfire frequency and intensity and how will that affect existing shortleaf pine stands and subsequent regeneration?

17) Is the preference of shortleaf pine for more xeric sites (compared to loblolly pine) due to superior drought tolerance or due to a history of more frequent fires on drier sites?

18) What are the proximate causes that limit the northern and southern range extremes for shortleaf pine?

19) How does the modeled growth and yield of shortleaf pine plantations compare to those of loblolly pine, especially for thinned plantations on cutover land based on modern plantation establishment technology and silviculture?

20) How is biomass partitioned among stand components for young stands and plantation grown shortleaf pine?

Introduction

Extensive summaries on shortleaf pine have already been compiled. Notable examples include a book chapter by Walker and Wiant (1966) which summarized silvicultural information and management recommendations for shortleaf pine. They included information related to growth, regeneration, intermediate treatments, and damaging agents. In 1986, the Symposium on the Shortleaf Pine Ecosystem was held in Little Rock, Arkansas. The proceedings from that meeting contain chapters on most topics related to shortleaf pine history, ecology, and forest management (Murphy 1986). In regards to management of shortleaf pine for restoration purposes, the conference “Shortleaf pine restoration and ecology in the Ozarks” was held in 2006 in Springfield, Missouri The proceedings from that meeting includes summaries related to history, ecology, genetics, regeneration, water quality, wildlife, growth and yield, and restoration efforts (Kabrick et al. 2007). In addition, summaries such as that contained in the Silvics of North America (Lawson 1990), silviculture guidelines (Baker et al. 1996), and other sources provide general and management information resulting from over 100 years of experience and research.

The goal of this work is not to repeat those previous summaries but rather to conduct a strategic assessment related to current and future issues and research needs for shortleaf pine management. Specifically, we compare shortleaf pine to loblolly pine, because the faster growing loblolly pine is the most common species alternative to the slower growing, hardier shortleaf pine. To that end, landowners must consider the tradeoff between fast growth and forest resiliency. We also focus on climate change and emerging conservation issues as these will frame future discussion and decisions related to shortleaf pine management. Throughout the assessment we identify topics of uncertainty that warrant additional consideration and research.

Life history and silvics

Shortleaf pine is one of the most important economic and ecological tree species in the southeastern United States. It tends to grow more slowly than other southern pine species during early years after establishment (Lawson 1990). Shortleaf pine occupies a variety of habitats from rocky uplands to saturated bottomland floodplains. Shortleaf pine is an important timber tree, providing a source of pulp, plywood, veneer, and lumber.

Shortleaf pine is monoecious (Krugman et al. 1974), carrying both male and female reproductive organs on the same tree. The strobili of both sexes emerge from late March in the southwestern areas of its range to late April in the northeastern sections. However, open-grown trees may produce strobili a few weeks earlier than those under forest conditions (Lawson 1990). Shortleaf pine usually does not produce a viable seed crop before the age of 20 (Lawson 1990). Seed fall occurs between late October and early November with some of the seeds remaining on the tree until the following spring (Lawson 1990, Yocom 1968). Good to excellent cone crops occur every three to ten years in the Northeast and every three to six years in the South (Lawson and Kitchens 1983). Seedling growth occurs early in the growing season, typically adding 0.3 to 1.0 m y^1 in height growth. Height growth typically finishes in early July, but seedlings can respond to late season precipitation with a new flush under moist soil conditions (Lawson 1990).

Shortleaf pine also has the ability to resprout following top damage when young. Usually shortleaf pine sprouts arise from dormant buds around the root collar, although sprouts may also arise out of needle fascicle buds, if the branches alone are minimally damaged (Little and Somes 1956). Within two to three months of establishment, shortleaf pine seedlings will typically develop a “J” shaped crook, or “double-crook”, at the soil surface. This crook harbors dormant buds in the primary leaf axils that are kept near the soil surface or buried under soil or duff. When a seedling or sapling is top-clipped by an animal or the crown is killed by fire, these dormant buds will produce multiple sprouts with and one or two eventually acting as a terminal leader (Mattoon 1915, Moore 1936).

Shortleaf pine seedlings grow a taproot at an early age. This consumes considerable resources in the early stages of seedling development and is a major reason why shortleaf pine can tolerate poor conditions (Lawson 1990). One condition shortleaf pine cannot tolerate is low light availability, and thus it is classified as an early seral species (Eyre 1980). Since shortleaf pine grows more slowly than many of its associated species, especially loblolly pine (Williston 1978a), its shade intolerance usually makes it unlikely to survive in areas of high competition without management intervention (Lawson and Kitchens 1986).

Shortleaf pine has the largest natural range of any pine species in the southeastern United States. Its natural range includes 22 states that span from New York south to northern Florida and west to eastern Oklahoma and covers more than 1,139,000 km^2 (Lawson 1990) (Fig.

1). The ability of shortleaf pine to tolerate a wide range of soil and site conditions is a major reason for its large distribution. Historically, the highest concentration of shortleaf pine was and is located in Arkansas (Smith 1986, Moser et al. 2007). Shortleaf pine on a good site attains heights of 25 to 30 m and diameters of 60 to 90 cm. Heights of nearly 40 m and diameters of 120 cm have been reported (Mattoon 1915). The maximum age for shortleaf pine is approximately 400 years, but it commonly lives 200-300 years (Mattoon 1915). The cylindrical taper, slow growth, and clear, straight bole make it an excellent tree for dimensional lumber, even moreso than its common pine associates (Virginia pine (*Pinus virginiana* Mill.), loblolly pine (*Pinus taeda* L.), and pitch pine (*Pinus rigida* Mill.)) (Mattoon 1915). The distinguishing characteristics of shortleaf pine are the needles and cones. Shortleaf pine tend to have closely knit crowns comprised of short needles (7.5 to 12.5 cm) in fascicles of two or three and have short (4.0 to 6.5 cm) egg-shaped cones.

Shortleaf pine grows in a wide range of climatic conditions. Annual precipitation averages between 100 cm in the northern and western sections of its range to 150 cm in the southern section (USDI Geological Survey 1970). Snowfall averages less than 40 cm annually over most of its range but may be twice that in higher elevations northward in the Appalachians into Pennsylvania. The region of best development for shortleaf pine is Arkansas, northern Louisiana, and the southern Piedmont (the Carolinas, Georgia, and eastern Alabama) where precipitation ranges from 115 to 140 cm (Lawson and Kitchens 1983, USDI Geological Survey 1970). Average annual temperatures across its range vary from 9 °C in New Jersey to 21 °C in southeast Texas. High variations between temperature and precipitation across its range may be responsible for the high adaptability and diversity within the species (Guldin 1986, Wahlenberg and Ostrom 1956). In the northeastern section of its range, seasons vary considerably in temperature, and rainfall is uniformly distributed throughout the year. The opposite is true in the southwestern section of its range; temperatures are warmer and less variable, whereas precipitation is more variable, i.e., rainfall events occur mainly during the winter and spring months, followed by sporadic precipitation in the summer. These highly variable conditions in shortleaf pine's physiological environment likely increase its ability to compete with other species that are adapted to less variable environments (Guldin 1986).

Due to the wide range and climatic variability across the range of shortleaf pine, it comes as no surprise that it grows on a wide variety of soils. Since most competitive trees prefer sandier soils, shortleaf pine is commonly found on soils with prominent clay textures in the surface and subsurface horizons (Guldin 1986). Shortleaf pine is usually found in soil order Ultisols, and in suborder Udults (Lawson and Kitchens 1983). On the Coastal Plain, Paleudults are the primary soil type. Paleudults have a thick horizon of clay accumulation lacking easily erodible materials. In the Piedmont, shortleaf pine is commonly found on Hapludults, which may have either relatively thin clay subsurface horizons or a subsurface horizon with easily erodible materials (Lawson 1999). In the Appalachian Highlands, soils are typically Dystrochrepts which are moist, are low in exchangeable bases, and have no free subsurface carbonates (Guldin 1986).

The optimal soils for shortleaf pine are deep, well-drained soils consisting of fine sandy loam or silty loam textures, which are primarily found on floodplains (Lawson and Kitchens 1983). Site indices for shortleaf pine on these sites may exceed 30 m at base age 50 (Williston and Dell 1974). These optimal locations occur in the Ozark Highlands of Arkansas and Missouri (Graney and Ferguson 1972). Soils with a high calcium content, high pH, or excessive internal drainage tend to cause poor growth in shortleaf pine (Lawson 1990). Even at optimal growing conditions, shortleaf pine typically won’t occupy the site indefinitely as other more competitive hardwoods and conifers prefer similar soils, especially in the southern section of its range (Baker and Balmer 1983). However, on drier, well drained and less fertile soils typical of the Piedmont, shortleaf pine is typically more abundant than loblolly pine in naturally occurring stands. The difference is partly attributable to shortleaf pine's larger root system, lower tolerance to poor soil aeration, and lower demand for nutrients (Lawson 1990).

Across its range, shortleaf pine is found at elevations ranging from 3 to 910 m, with optimal growth achieved at elevations between 150 and 460 m (Eyre 1980, Lawson 1990). Graney and Ferguson (1971, 1972) found that in the Ozark Highlands, site quality increased as slopes went from convex to concave and as latitude decreased.

Guldin (1986) hypothesized possible reasons for shortleaf pine being so prominent in western Arkansas and Oklahoma. To the south, competitive species such as loblolly pine dominate even though conditions are very favorable to shortleaf. To the north, ecologic, physiographic, and climatic factors favor oaks and interior pines. One of major factors influencing shortleaf pine distribution is fire. Due to its ability to resprout and thrive in locations that frequently burn, other species (such as loblolly pine) that do not resprout readily are selected against (Schultz 1997, Williams 1998). In short, shortleaf pine grows best where the majority of its faster growing co-occurring species struggle.

By far, the greatest problem facing eastern populations of shortleaf pine over 20 years old is the fungal pathogen known as littleleaf disease (Hepting 1971). This is most commonly a problem on heavy, poorly drained soils typical in the Piedmont (Hepting 1971). Littleleaf disease affects the roots of the trees and causes high susceptibility to a complex combination of factors, including poor aeration, damage to roots by nematodes, low fertility, and a toxic build-up of manganese. These all combine to cause a restriction of nutrient uptake, particularly nitrogen (Hepting 1971, Lawson 1990). Infected trees exhibit reduced growth rates and high mortality. Needles of infected trees will tend to be yellow with the end of branches retaining any lasting foliage (Williston and Balmer 1980). Infected trees also attract insects such as the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (Oak 1985). Fertilization with nitrogen may help to relieve some effects, but prevention via careful site selection is the best defense against littleleaf disease (Lawson 1990).

Campbell et al. (1953) and Campbell and Copeland (1954) provided maps and site hazard ratings for susceptibility to littleleaf disease. Susceptibility increases with soil erosion, firmness of subsoil consistency, shallowness of surface horizon, and subsoil mottling. The risk of littleleaf hazard on a site can be assessed several ways. If a stand is present, observing characteristics of the disease on individual trees throughout stand can be easily done (Mistretta 1984). Littleleaf sites can also be identified by a series of soil characteristics which include erosion, internal drainage, depth to reduced permeability, and subsoil mottling (grays and browns), all which can be observed through detailed sampling. Another method that can be used to identify littleleaf sites is the identification of internal drainage characteristics of the soil using soil maps (Mistretta 1984, Oak and Tainter 1988). Management options for infected shortleaf pine stands depend on the severity of the disease. If the proportion of trees infected is low (<10%), removing symptomatic trees and fertilizing the soil is likely the best option. If the percentage of trees infected is between 10-25%, removing symptomatic trees and replanting shortleaf at shorter rotations or converting to loblolly or other species is recommended. If the percentage of trees infected is greater than 25%, it is recommended to salvage the area and prepare the site before conversion to a different species (Anderson and Mistretta 1982, Mistretta 1984, Oak and Tainter 1988).

Relative to other southern pines, shortleaf pine better withstands ice, wind, and sudden temperature changes and is unusually free of serious diseases (Hepting 1971). However, shortleaf pine may occasionally incur damage from the following agents: southern pine beetle (*Dendroctonus frontalis*), *Heterobasidion annosum*, *Phellinus pini*, Nantucket pine tip moth *(Rhyacionia* frustrana), redheaded pine sawfly *(Neodiprion lecontei*), loblolly pine sawfly *(N. taedae linearis),* Pales weevil *(Hylobius pales*), and pitcheating weevil *(Pachylobius picivorus),* as well as several other relatively unimportant diseases, root rots, damping off diseases, needle rusts, and insects (Baker 1972, Hepting 1971, Lawson and Kitchens 1983, Tainter 1986).

Loblolly pine

Loblolly pine is considered the most important pine species in terms of commercial value in the southeastern United States. Although loblolly pine is a medium lived tree compared to shortleaf pine, it responds well to silvicultural treatments and can be effectively managed in both even and uneven aged natural stands as well as in plantations. A major characteristic that differentiates shortleaf pine from loblolly pine is its juvenile growth pattern. Shortleaf pine grows relatively more slowly in its early years after establishment compared to loblolly pine (Lawson 1990).

Smaller than the range of shortleaf pine, loblolly pine's range is the second largest range of any pine species in the southeastern United States. It ranges across 14 states, from southern New Jersey south to central Florida and west to eastern Texas (Lawson 1990). It overlaps the natural range of shortleaf pine in many of its mid and southern localities. However, shortleaf pine is more drought tolerant and is able to extend its range further north (Guldin 1986) (Fig. 1). Annual precipitation for both species ranges from an average of 1,020 mm in the western parts of their range to 1,520 mm in the southern parts. Shortleaf pine's larger natural range is likely in part due its greater ability to thrive on lower quality sites compared to loblolly pine (Lawson 1990).

In contrast to shortleaf pine, which is very susceptible to littleleaf disease, only loblolly pine trees on high risk sites older than 50 years are susceptible to littleleaf disease (Oak 1985). Loblolly pine probably is not susceptible to littleleaf disease, because its roots are more evenly distributed through the soil profile and are better able to withstand waterlogged conditions. This allows for less root mortality and/or faster recovery from fungal infection, especially during or after waterlogged conditions (Walker and Oswald 2000).

Loblolly pine is susceptible to many of the same insects and diseases as shortleaf pine. Many of its new shoots are brittle and commonly break under snow and ice (Schultz 1997). The most important disease of loblolly pine is fusiform rust (*Cronartium fusiforme* Hedge. and Hunt ex Cumm.), a fungal pathogen that causes damaging cankers or galls on the stems and can appear at all growth stages of infected pines. Fusiform rust does not spread directly from pine to pine. Spores produced on the host oak are transported by wind and typically enter the pines through weak or tender stem tissue and form a spindle shape on the tree at the infected area caused by swelling (Anderson and Mistretta 1982). It is believed fusiform infection rates in loblolly pine are higher than they were previously, because fire suppression has allowed an increase in oak density (which act as an alternative host for fusiform rust). In addition, early selections for loblolly pine breeding programs appear to have included parent trees with a high susceptibility to rust (Burdsall and Snow 1977). Stands considered as “high hazard” sites for fusiform rust are ones that include 50% or more of the trees containing galls within 30 cm of the main stem. These sites can also be predicted using established distribution maps of infections zones (Anderson and Mistretta 1982). In comparison, shortleaf pine is fairly resistant to fusiform rust.

Competition

Since shortleaf pine grows more slowly than many of it associated species, especially loblolly pine (Williston 1978a), its shade intolerance usually makes it unlikely to survive in areas of high competition without management intervention (Lawson and Kitchens 1983). Hardwoods are the climax species on virtually all sites where shortleaf pine grows naturally (Lowery 1986). However, on sites where soil and moisture conditions favor shortleaf pine, or in situations where management intervention has occurred, shortleaf pine can dominate the site after overtopping its competition (McWilliams et al. 1986). Most hardwood species are impossible to completely eradicate from pine stands (Cain 1987, Cain and Yaussy 1984), and on productive sites, hardwoods such as sweetgum (*Liquidambar styraciflua* L.) and red maple (*Acer rubrum* L.) may eventually emerge through shortleaf pine's canopy and retake the site (Lawson 1990). This emphasizes the need for fire as a hardwood control agent in shortleaf pine ecosystems. Fire can also shift the understory component in mixed conifer stands to one dominated by shortleaf pine and understory grasses. Williams (1998) demonstrated how a single fire eradicated loblolly pine seedlings from a mixed pine site, while favoring shortleaf pine seedlings through their resprouting ability.

Diameter growth rates will decline after just a few years, if the pines are over stocked (Schultz 1997). McQuilken (1935) found that shortleaf pines become weak and spindly when crowded. As in most pines, this intolerance to shade usually suggests that even-aged methods of silviculture for shortleaf pine are easier and are more likely for successful regeneration (Guldin 1986, Lawson and Kitchens 1983). However, even under high densities, shortleaf pine will persist for a long time and will respond well to both overstory release (Lawson 1990, Yocom 1971) and understory release (Bower and Ferguson 1968). Uneven-aged management can be done successfully, but it is typically restricted to situations where large products and intensive intervention by foresters is possible (Williston 1978b).

Loblolly pine is considered shade intolerant and is an early successional species. It competes poorly with many deciduous trees, shrubs, and several pioneer grasses, herbs and forbs (Schultz 1997). Much like shortleaf pine, climax communities on loblolly pine sites will eventually convert to hardwood species (Schultz 1997), and control of hardwood vegetation is essential for successful regeneration of loblolly or shortleaf pine (Lawson and Kitchens 1983).

Basic Genetic Properties

Shortleaf pine belongs to the genus *Pinus* subsection *Australes*, a group of pines native to the southeastern United States, eastern Mexico, and islands the Caribbean Sea. Those found in the southeastern United States are known as southern yellow pines, and several of these species are related enough to hybridize with each other. During the Pleistocene glaciation, shortleaf pine lived along the coast of the Gulf of Mexico, but as the glaciers receded about 14,000 years ago, they migrated northward into their current range (Schmidtling 2007).

Like all pine species, shortleaf pine is diploid with 12 pairs of chromosomes (Mirov 1967) which correspond to 12 linkage groups—that is, sets of genes that tend to be inherited together—in molecular marker research (Echt et al 2011). Many molecular markers developed for use in loblolly pine function in shortleaf pine (Nelson et al 2007), as the two species are close relatives. The shortleaf pine genome is of similar size to other pine genomes. Shortleaf pine has a C-value (a measure of the DNA content of a chromosome) of 21.73 pg measured by laser flow cytometry and 22.77 pg measured by scanning Feulgen microspectrophotometry (Wakamiya et al 1993). These numbers translate to 21.4 gigabases and 22.5 gigabases for the haploid genome, respectively.

Provenance Testing and Geographic Diversity

Given its large geographic range, populations of shortleaf pine are expected to have local adaptations to climate. The Southwide Southern Pine Seed Source Study (SSPSSS) was established in 1951 to evaluate the range-wide variability and viability of shortleaf pine and loblolly pine seed sources (Schmidtling 2001). Posey and McCullough (1969) performed provenance tests on ten year old trees from the SSPSSS plantings in two common garden tests in Oklahoma. A planting in Pushmataha County, Oklahoma represented a north-south transect of the shortleaf pine range, and a planting in McCurtain County, Oklahoma represented an east-west transect of the shortleaf pine range. In these plantings, western shortleaf sources had significantly better survival and eastern gall rust (*Cronartium asclepiadeum f. sp. quercuum*) resistance than the eastern sources, and southern trees showed better growth in height and diameter than northern sources. While Posey & McCullough do not address it, the better survival of western sources may be associated with better drought adaptation, as well as better eastern gall rust resistance. Tauer (1980) revisited these trees ten years later and found the same trends and also determined that western source trees had significantly greater wood specific gravity than the trees of eastern origin.

Wells and Wakely (1970) examined more extensive ten year old plantings of shortleaf pine from the SSPSSS, employing 40 plantings of 23 seed sources across the shortleaf pine range. The plantings were divided into three study categories: the latitude series, the longitude series, and the intermediate series. The latitude series and the intermediate series were both designed to represent the latitudinal variation, though the latitude series encompassed a wider range than the intermediate series did. The longitude series represented an East-West transect across the shortleaf pine range. Since many of the plantings were originally established in the early 1950s, the drought from that era affected overall survival. The only provenance trend detected for survival was that trees from northern sources out-survived trees from southern sources in the northern plantings in New Jersey, Pennsylvania, and Missouri. Height (and by extension, volume) was the only other variable that significantly differed among provenances. The growth response was most significant in the latitude series. The results showed that southern sources outperformed northern sources in southern and central plantings, but the northern sources outperformed southern sources in northern plantings. While there was no longitudinal trend, trees from Ashley County, Arkansas consistently outgrew all other sources in the longitudinal series.

Gwaze et al. (2007b) measured a provenance test of shortleaf pine planted at two sites in Dent County, Missouri as part of the SSPSSS. At age 30, trees from northern sources outgrew trees from southern sources, and trees from New Jersey seed performed better than trees from the local Missouri seed. Additionally, trees from northern sources had better survival (62.2% for the New Jersey sources) than did the trees from southern sources (23.5%). These results agree with data from Wells and Wakely (1970) indicating that northern seed sources are generally better adapted to northern sites than are southern seed sources. Tauer & McNew (1985) used seed from 15 widely dispersed Oklahoma shortleaf pine stands in two plantings in eastern Oklahoma, one in the north and one in the south. After ten years, they reported that there was no statistical difference across seed sources for most traits (height, DBH, straightness, and crown rating) but that stand survival was lower at the northern planting, probably due to more xeric conditions there.

Most of these past surveys focused on optimal seed sources for achieving high survival and growth for various sites and assumed that climate would remain constant. As long-lived forest trees, shortleaf pines are well-adapted to climatic fluctuations, but those adaptations relate more for survival and not necessarily for optimal growth. Future provenance tests should be linked to the latest climate change models to predict the best sources of shortleaf pine for planting in various regions. Fortunately, much of the data produced by previous provenance test studies can be used in climate change predictions (Matyas 1994). In addition to the temperature and moisture effects of climate change, survival and recovery following disturbance such as drought, fire, ice storm may be more important than growth and volume production to maximize stand resiliency and to meet objectives related to ecosystem restoration. Provenance and seed source testing generally has not explored these traits. Given the strong selection pressures of disturbances such as fire, differing regional and local disturbance regimes may have caused population differentiation.

The genetic diversity of shortleaf pine has been studied using molecular markers. Population differentiation—the proportion of a species' diversity that can be accounted for by the differences among populations and not within populations—can be estimated with several statistics, including F_{ST}, G_{ST}, and $\Phi_{PT.}$. F_{ST} can be calculated from the results of codominant genetic markers, such as short sequence repeats, while G_{ST} can be calculated from the results of dominant genetic markers like amplified fragment length polymorphisms. The new Φ_{PT} metric (Excoffier et al. 1992) can be calculated for either kind of data. All involve complex statistical models. Population differentiation is a measurement of how isolated populations are to each other genetically. As a wind-pollinated, outcrossing forest tree with a largely contiguous range, it is expected that shortleaf pine will have a small amount of population differentiation for selectively neutral genetic markers.

Edwards and Hamrick (1995) estimated G_{ST} using 22 isoenzymes, which are polymorphic enzymes that can be differentiated and visualized on a starch gel. The researchers used up to 48 individuals from 18 sites that extended from the eastern to western portions of shortleaf pine's range. Generally, the sites represented the central and northern parts of the range, as the southernmost site was in southeastern Oklahoma. G_{ST} was ultimately estimated to be 0.026, indicating that most of shortleaf pine's diversity comes from within the populations and not among them.

Raja et al. (1997) used 23 isozyme systems covering 39 loci on 126 trees from 15 sites to estimate F_{ST}. The sites used in the study were evenly spread across shortleaf pine's geographic range. From this work, they estimated F_{ST} for shortleaf pine to be 0.089. The authors explain that their estimate for population differentiation is more than that of Edwards & Hamrick (1995) due to their study having more private alleles than the previous study. Private alleles are variants of markers that are not shared among populations, either because they originate in a population through mutation, or because they have been concentrated there through some evolutionary process. The site selection of Raja et al. (1997) also covers a greater north-south variation than did Edwards & Hamrick (1995), which may affect population differentiation, since provenance tests of shortleaf pine seed sources reveal that the trees are more variable according to north-south adaptation than to other factors (Wells & Wakely 1970).

Two studies of trees from the SSPSSS used molecular techniques to estimate population differentiation in shortleaf pine. Xu et al. (2008B) examined 93 shortleaf pines representing a rangewide sample of the species from that study using amplified fragment length polymorphism (AFLP). This technique generates dominant genetic marker data from pine DNA. A genetic marker technique is considered to produce dominant data when each locus can only be reported as having one allele (the dominant allele) present or absent. They estimated the population differentiation parameter G_{ST} to be 0.153, which is relatively high compared to other such estimates in this species but still represents a prolific outcrossing species. Stewart et al. (2010) reexamined the data from that study and estimated Φ_{PT} to be 0.057, which was in more agreement with previous studies. Stewart et al. (2010) also analyzed 90 trees from the SSPSSS representing a range-wide sample of the species with simple sequence repeats (SSR) also called microsatellites. These markers generate codominant genetic data. They estimated Φ_{PT} to be 0.080. Stewart et al. (2011) used 25 simplle sequence repeat markers to test 151 shortleaf pine seedlings from the same counties as those in the Southwide Southern Pine Seed Source Study and estimated Φ_{PT} at 0.146, though the rate may have increased due to the large number of shortleaf pine x loblolly pine hybrids identified in the study.

Improvement Programs and Nurseries

Shortleaf pine improvement has been a minor program compared to the improvement program for loblolly pine, the tree that dominates the southern timber industry. Due to loblolly pine’s faster growth rate and the strength of existing improvement programs, shortleaf pine tree improvement is largely restricted to areas outside of or on the periphery of the range of loblolly pine. In 2005-2006, approximately 2,300,000 shortleaf pine seedlings were produced compared to over 825,000,000 loblolly pine, 125,000,000 slash pine, and 33,000,000 longleaf pine seedlings (McNabb and Enebak 2008). Compared to the 2005-2006 season, loblolly pine and slash pine seedling production declined to 617,000,000 and 88,000,000 respectively for the 2010 – 2011 while longleaf and shortleaf pine production increased to 73,000,000 and 3,800,000. Of the shortleaf pine seedling production, 1,600,000 were bare-root were 2,100,000 are container-grown seedlings that were produced in Arkansas, Georgia, North Carolina, Oklahoma, South Carolina, Tennessee, and Virginia (Enebak 2011).

In Oklahoma, shortleaf pine tree improvement began with the Oklahoma State University Department of Forestry in 1965 when the Kiamichi Research Station was transferred from the Horticulture Department. Professor Clayton Posey led the early tree improvement projects, which included shortleaf pine, as well as loblolly pine and eastern cottonwood. In 1980, the Kiamichi Research Station under the supervision of Superintendent Ben Smith became a member of the Western Gulf Forest Tree Improvement Program (Lantz and McKinley 2003). Beginning in 1968, Forestry Services of the Oklahoma Department of Agriculture, Food, and Forestry partnered in these tree improvement efforts. In 1985, Forestry Services took sole control of this work and continues to provide the staff and operational expenses to manage the orchard, collect seed, and conduct the breeding work.

Missouri and Arkansas have been collaborating on shortleaf pine improvement since the early 1960s in a breeding project in the Mark Twain National Forest in Missouri, the Ozark National Forest in Arkansas, and the Ouachita National Forest in Arkansas. The first seeds of this project were collected in the early 1980s, and a second generation was collected in 2003. This program focuses on generating seed for shortleaf pine restoration of endangered ecosystems, especially for habitat related to the red cockaded woodpecker (Studyvin and

Gwaze 2007). This program is also part of a program that provides shortleaf pine seed for sale in Missouri (Gwaze et al. 2007A).

The Western Gulf Forest Tree Improvement Cooperative also maintains a shortleaf pine breeding program (Lowe and van Buijtenen 1990). Cooperating members of the program produce first and second generation improved shortleaf pine seedlings for purchase. Bulk orders can be made from the International Forest Company (Moultrie, GA), and smaller orders can be purchased from the Arkansas Forestry Commission. Oklahoma Forestry Services, which has recently been increasing production, offers genetically improved shortleaf pine seedlings through the Albert Engstrom Forest Regeneration Center in Goldsby, OK. In general, however, the efforts to improve shortleaf pine for planting are small compared to the improvement programs for loblolly pine. In the future, some areas, especially more xeric and northern places, could benefit from expanded shortleaf pine breeding.

The breeding programs focused on shortleaf pine growth and productivity may have inadvertently included some shortleaf x loblolly pine hybrids. The lack of a basal crook and fast growth are desirable traits for tree breeders and seedling producers, but they are also traits that are typical for hybrid trees (Lilly et al. 2012a). During selection, orchard managers may be inadvertently selecting for these traits in order to produce superior lines. Additionally, shortleaf pine tree improvement orchards are generally located near loblolly pine orchards. Since artificial regeneration of this species is important to its future, it is critical that the genetic integrity of planting be maintained. As yet, it is unknown whether hybrids maintain shortleaf pine's resiliency to disturbance, cold, and drought, so managers should be aware of this potential problem. However, more research is required to determine whether improved shortleaf pines have hybrid character or not.

The United States Forest Service maintains seed orchards for shortleaf pine in North Carolina, Mississippi, Louisana, and Arkansas (Barbara Crane, USFS, personal correspondence). In Oklahoma, Forestry Services operates a shortleaf pine seed orchard that produces seedlings well adapted to the westernmost portion of the range. State-run seed orchards are maintained in Tennessee, Georgia, Arkansas, and Texas (Diane Warwick, TN Department of Forestry, personal correspondence; Russ Pohl, Georgia Forestry Commission, personal correspondence; David Bowling, Arkansas Forestry Commission, personal correspondence; and Fred Raley, Western Gulf Forest Tree Improvement Program, personal correspondence). A state-run seed orchard in Kentucky also exists, but seed has not been collected from it in some time (Timothy Sheehan, Kentucky Division of Forestry, personal correspondence).

Hybridization and Introgression

Shortleaf pine is known to hybridize with several species. Hybrids of shortleaf pine and slash pine (*P. elliotii*) may outperform either species on dry sites (Schmitt 1968). Hybrids of shortleaf pine and loblolly pine (*P. taeda*), as well as backcrosses, have been relatively easy to reproduce (Schmitt 1968). Shortleaf pine also has been crossed with longleaf pine (*P. palustris*) and even a hybrid of two other trees called Sonderegger pine (*P. taeda x elliotti*) (Snyder and Squillance, 1966). Of these hybrids, two have received attention for their possible commercial value: shortleaf pine x slash pine hybrids and shortleaf pine x loblolly pine hybrids.

Shortleaf pine x slash pine hybrids appear to have hybrid vigor—that is, they outperform their parent species—in their growth performance (Schmitt 1968). Also their resistance to fusiform rust (*Cronartium fusiforme*) is similar to the rust-resistant of the shortleaf pine parent and not the susceptible slash pine parent. Past work also emphasized seed production of what was believed to be a possibly “promising” improved tree (Wakeley et al. 1966). However, little work with this hybrid has continued today, and no natural shortleaf pine x slash pine hybrids have been reported.

Shortleaf pine x loblolly pine hybrids are considerably more important for breeding and ecology reasons than shortleaf x slash pine hybrids. The earliest report of artificial hybrids was made by Schreiner (1937), who made successful crosses at the Institute of Forest Genetics in Placerville, California. First generation shortleaf pine x loblolly pine crosses have many traits that are intermediate of the two parent species, including the sizes of needles and cones and the number of needles per fascicle. Loblolly pine generally has three needles per fascicle—and sometimes two, four, or five—and shortleaf pine has two or three needles per fascicle. The hybrids have two or three needles per fascicle but have more three needle fascicles than shortleaf pine (Little and Righter 1965; Snyder and Hamaker 1978).

Hybrid performance varies by study. Benson et al. (1982), as well as Schultz (1997), reported that the hybrids were intermediate to their parent species in growth and survival. Schoenike et al. (1977) indicated that hybrids (which were identified by morphology) have intermediate growth to loblolly pine and shortleaf pine. Other studies have reported more dominance of loblolly pine traits. Mergen et al. (1965) observed the hybrids as being more like loblolly pine (that is, having faster growth). Sluder (1970) reported that hybrids grew about as quickly as loblolly pines. Lilly et al. (2012a) also found that the hybrid saplings grew as quickly as loblolly pine saplings but maintained the superior leaf-level water-use efficiency of shortleaf pines. The hybrids in their study also lacked the strong basal stem crook found in shortleaf pine saplings, a trait with is thought to imbue fire resistance.

One major advantage of loblolly pine x shortleaf pine hybrids is their disease resistance. Shortleaf pine is susceptible to littleleaf disease, and loblolly pine is susceptible fusiform leaf rust. Interestingly, western trees of both species are more resistant to their respective pathogens (Bryan 1973; Squillace 1976), a trend that may be related to natural introgression (Hare & Switzer 1969). Schoenike et al. (1977) found that hybrids grown in the Piedmont of South Carolina were resistant to both littleleaf disease and fusiform rust, and Benson et al. (1982) reinforced these results. Other studies also showed that hybrids are resistant to fusiform rust (La Farge and Kraus 1980; Florence and Hicks 1980; Kraus et al 1982; Kraus 1986).

Zobel (1953) was the first to propose that loblolly pine x shortleaf pine natural hybrids occur. He observed numerous trees in Texas that appeared to have traits intermediate to shortleaf pine and loblolly pine. At the time, natural hybrids of loblolly pine and slash pine (called Sonderegger pine) were well-known and relatively common, and there was interest in hybrid pines for tree improvement. At first, identifying natural hybrids could only be accomplished through morphological measurements. While morphological data is easy to acquire, traits are subject to complex genetic and environmental effects. Nonetheless, researchers generated several studies of loblolly pine x shortleaf pine hybrids using morphological measurements. Mergen et al. (1965) found 10 out of 40 trees sampled from Harrison County, Mississippi and 4 out of 22 trees sampled from Greene County, Mississippi were likely hybrids according to analysis with a suite of morphological characters. They did note that there was a great deal of variation of characters within species as well. Hicks (1973) proposed that research using morphology proceed with the use of six traits: needle length, fascicle sheath length, number of needles per fascicle, terminal bud width, cone length, and seed weight, but he did not identify any hybrids in his study. Abbott (1974) conducted a morphological hybrid study after he found an "atypical" tree in an Oklahoma State University seed orchard. In his thesis, 19 loblolly pine and 12 shortleaf pine selections were studied using a hybrid index that incorporated needle length, number of needles per fascicle, cone length, seed weight, and fascicle sheath length. One loblolly selection and three shortleaf pine selections were hybrid, according to his index. Cotton et al. (1975) and Schoenike et al. (1977) both used morphological measures to search for natural hybrids in Texas and North Carolina, respectively, but neither found obvious hybrids.

Advancements in biochemistry gave geneticists more tools for the identification of hybrids. Hare and Switzer (1969) found protein banding evidence that some loblolly pine trees from Texas may have some shortleaf pine genetics. They concluded that this hybrid character may explain why loblolly pines from the region exhibit greater fusiform rust resistance than pines in the east. Florence and Hicks (1980) examined 29 loblolly pines, shortleaf pines, and suspected hybrids (identified by morphology) using protein banding patterns on acrylamide gels. Their protein banding patterns generally confirmed the morphological classifications.

Later, even more advanced isoenzyme (also called isozymes or alloenzymes) techniques were employed to identify hybrids. Edwards and Hamrick (1995) and Raja et al. (1997) both identified hybrids using isoenzyme techniques in shortleaf pine populations. Both studies found that hybrids between shortleaf pines and loblolly pines were more prevalent in the west than in the east. Edwards and Hamrick (1995) reported 4.6% of shortleaf pines west of the Mississippi River were hybrids and 1.1% of the shortleaf pines east of the Mississippi River were hybrids. They relied on one isoenzyme marker (the isocitrate dehydrogenase, or IDH, maker) to identify their hybrids. Note that by using only this marker, they could only identify F1 hybrids and half of all backcrosses by the rules of Mendelian genetics. Raja et al. (1997) indicated that the hybridization rate was higher than that, classifying 16% of the shortleaf pines west of the Mississippi River as being hybrids and 4% of shortleaf pines east of the Mississippi River as hybrids. Their study employed 39 loci, and the range of sampled trees extended further south than did the range used by Edwards and Hamrick (1995). Chen et al. (2004) used isoenzymes and a chloroplast DNA marker (which identifies the paternal parent species) to identify hybrids in Montgomery County, Arkansas, where the sympatric range of loblolly pine and shortleaf pine transitions into the allopatric range of shortleaf pine. The sympatric range of loblolly pine and shortleaf pine is the range in which the two species can naturally co-occur. The allopatric ranges of the species are the ranges in which they do not co-occur. They found 12.5% hybrid pines in the shortleaf pine population, some of which were in the shortleaf pine allopatric range and some of which were not heterozygous for the IDH marker, indicating that genes were being transferred over generations or over distances via loblolly pine pollen.

DNA-based genetic markers have displaced isoenzymes as the leading method for genotyping pine trees because they are less expensive, technically simpler, and more abundant. Xu et al. (2008a) used amplified fragment length polymorphisms (AFLP) and the isocitrate dehydrogenase isoenzyme marker to determine the hybridization rates in 93 shortleaf pine and

102 loblolly pine trees from the SSPSSS, trees representative of geographically diverse populations from the 1950s. They found that the hybridization rate between these two species was 16.3% and 2.4% in shortleaf pine populations west of and east of the Mississippi River, respectively. In the loblolly pine trees of the study, the rate was 4.5% and 3.3% west and east of the Mississippi River, respectively. These results support the theory that hybridization is more common in the west than in the east. Stewart et al. (2010) followed up on Xu et al. (2008a) to test the same trees (though 3 shortleaf pine trees were omitted from the dataset due to degraded DNA) with the simple sequence repeat method, employing 42 markers, plus the isocitrate dehydrogenase isoenzyme marker. They found that the hybridization rates were 7.5% in shortleaf pine west of the Mississippi River and 0% in shortleaf pine east of the Mississippi River. In loblolly pines, 9.1% of the trees west of the Mississippi River were hybrids and 3.3% of the trees east of the Mississippi River were hybrids. Interestingly, while the estimates for the rates were similar, there was disagreement between the two studies as to which of the trees were actually hybrids.

To test for changes in the hybridization rate between the SSPSSS population collected in the 1950s and young, naturally regenerated loblolly and shortleaf pine from modern stands, Stewart et al. (2011) used 25 simple sequence repeat markers to test 165 loblolly pine saplings and 151 shortleaf pine saplings sampled from the same counties that the trees from the SSPSSS originated. They found that the hybridization rate in shortleaf pine stands had increased to 54% in the west and 40% in the east. The rates in loblolly pine stands had increased to 20% in the west and 29% in the east. These increases are alarming, because introgression—the process of genes moving from one species to another through hybridization and backcrossing—

is a known cause of extinction (Allendorf et al. 2001). Given the previously reported hybrid vigor, it is likely that fire suppression over the last 60 or more years may be allowing hybrids to encroach into shortleaf pine habitat because the hybrids lack the strong basal stem crook that is thought to give shortleaf pine seedlings increased fire tolerance (Lilly et al. 2012a). More research is necessary to confirm the role of fire as a selection pressure to eliminate loblolly pine x shortleaf pine hybrid seedlings. However, managers who wish to prevent hybrid encroachment into shortleaf pine habitat should consider employing a prescribed fire when saplings can still be top-killed by fire.

In addition to fire suppression, allowing the survival and proliferation of loblolly pine x shortleaf pine seedlings, widespread establishment of loblolly pine plantations may be increasing the incidence of cross-pollination. Stewart et al. (in press B) did a case study of hybrids using 25 short sequence repeat markers on nearly 400 shortleaf pine saplings and nearly 100 adult shortleaf pine trees spread across 4 sites in the Caney Creek Wilderness in the Ouachita National Forest in Arkansas, which is located just within the allopatric range of shortleaf pine. The stands were different distances downwind of extensive loblolly pine plantations, ranging from a hundred meters to 10 km away from the nearest plantation. They found that hybridization was higher in the stand nearest to the plantation than in the stand furthest away. They also found that there were more hybrids in the parent trees than in the progeny, indicating that hybridization had been going on for some time at the site and that the hybrids may be selected for in the long run.

Given that introgression with loblolly pine may be a threat to shortleaf pine, further study on the phenomenon should be encouraged. The development of a fast DNA-based hybrid identification system could help foresters find where hybridization is occurring in their forests. Better understanding what factors lead to natural hybridization could help managers better administer their lands for maintaining shortleaf pine’s genetic integrity. Additional information about where in the shortleaf pine range hybrids are the most serious problem will also help strategic planning in the forests of the South.

Past human activity probably has increased the level of hybridization between loblolly pine and shortleaf pine, and managers should be aware of these effects in weighing their options for managing shortleaf pine in an ecologically sustainable way. Forest managers should consider terrain, climate, fire regime, and other local conditions which may affect the process of hybridization. Guldin (2007) states that fire is needed to restore shortleaf pine, and fire may also serve to remove most hybrids and help retain the genetic integrity of shortleaf pine. To that end, reintroduction of fire as a management tool is a potentially critical part of the future of successful shortleaf pine management.

The rapid increase in loblolly pine x shortleaf pine hybrids since the 1950’s implies perturbations to the ecological interactions that previously maintained the genetic integrity of both species. Shortleaf pine is particularly at risk, because it originates almost entirely from natural regeneration, unlike loblolly pine with over 12 million ha of plantation in the Southeast (Fox et al. 2007). While loblolly pine x shortleaf pine hybrid seedlings are readily establishing, they may have trouble persisting and regenerating in a future climate with longer and more frequent droughts as well as increased risk of wildfire. Replacement of pure shortleaf pine with hybrids may reduce the resiliency of southern pines to future disturbances and climate regimes and may eventually result in extirpation of the pine component from areas of the Southeast.

The next needed step is to confirm that fire will eliminate hybrids in natural stands and determine the type and intensity of fire necessary to do so.

Management efforts should be undertaken to conserve the genetic integrity of shortleaf pine and preserve important traits not found in the more productive hybrid and loblolly pine genotypes. Assuming that larger hybrid pines (> 10 to 15 cm ground line diameter) are resistant to top-kill from fire in a manner similar to loblolly pine, the window of opportunity to kill hybrids is the seedling or sapling stage. Waiting too long may produce an irrevocable change, resulting in permanent loss of shortleaf pine from large areas and a less resilient forest.

Silviculture

The methods of managing shortleaf pine based on its underlying natural history have been well documented. Important resources are listed directly below. While the biology and management concepts may not change, the technology and objectives do change. The biggest technological advance has been the advent of effective herbicides that selectively kill hardwoods and herbaceous plants. This provides the ability to more easily manage both natural and artificial regeneration of the relatively slow growing, shade intolerant shortleaf pine. What the herbicides don’t do is selectively control loblolly pine or shortleaf x loblolly pine hybrids. For that reason, fire is necessary to reduce loblolly pine genotypes and needs to be employed in areas where both species occur and shortleaf pine is desired instead of loblolly pine. Fire must be used to target loblolly pine or hybrid seedlings/saplings before they become large enough to survive top-kill through thick bark and other adaptations.

With the exception of the frequency and timing of prescribed fire, natural regeneration systems for shortleaf pine are similar to those for loblolly pine. In fact, prescriptions for uneven-aged silviculture lump loblolly pine and shortleaf pine (Baker et al. 1996). Likewise, even-aged silviculture for shortleaf pine using artificial regeneration is similar to that for loblolly pine. Given the greater emphasis on loblolly pine plantation culture, more advanced genotypes (to include clonal varieties) exist for loblolly pine. While treatments such as site preparation and competition control might be necessary for establishment of shortleaf pine artificial regeneration, the positive growth response to these and other silvicultural inputs is less compared to the response of loblolly pine, especially while young (Schultz 1997)

Even though the life history and traditional silviculture related to shortleaf pine are well documented, objectives change over time that may require development or modification of silvicultural systems. One objective that recently has become more important is restoration of shortleaf pine-grass woodlands for wildlife and biodiversity. Often times, overriding management objectives or agency mandates preclude the use of herbicides on these areas, making the use of fire essential. For that reason and others related to encouraging shortleaf pine over loblolly pine in naturally regenerated stands, the use of fire as a management tool is discussed below.

Resources related to silviculture

1) Detailed discussion of shortleaf pine life history and growth potential (Mattoon 1915).
2) Synopsis of most aspects of shortleaf pine silviculture including growth, site index, regeneration (natural and artificial), intermediate treatments (thinning, release,

nutrition), damaging agents, wildlife, range, and watershed management (Walker and Wiant 1966).

3) Bulletin from State and Private Forestry discussing most aspects of shortleaf pine silviculture and management (Williston and Balmer 1980).
4) Symposium proceedings that includes most aspects of shortleaf pine silviculture and management (Murphy 1986). Specific topics include ecology (Guldin), site quality (Graney), natural regeneration (Lawson), artificial regeneration (Barnett et al.), tree improvement (Kitchens), stocking (Sander), stand dynamics (Smalley), herbaceous competition (Dougherty and Lowery), woody competition (Lowery), growth and yield (Murphy), water (Miller), wildlife (Wigley), and damaging agents (Tainter).
5) Chapter in Silvics of North America on shortleaf pine which summarizes life history (Lawson 1990).
6) Forest Service technical report detailing uneven-aged silviculture (Baker et al. 1996).
7) Proceedings from a symposium on shortleaf pine restoration (Kabrick et al. 2007). Topics include wildlife (Masters), restoration management (Guldin), direct seeding (Mann and Gwaze), fire (Stambagh et al.), site preparation (Gwaze et al.), and several woodland restoration case studies (Tuttle and Houf; Hasenbeck; Ladd et al.; Hedrick et al.; Nigh).

Shortleaf pine and fire

Shortleaf pine is fire-adapted, as it possesses traits that allow it to withstand or recover from fire. However, fire is not necessary for regeneration, growth, or reproduction. As a species, on the other hand, shortleaf pine may be fire *dependent*, because fire suppression appears to facilitate introgression with loblolly pine (Stewart et al. 2011). In this sense, fire serves as a selective pressure against hybrid survival and contributes to continued species integrity of shortleaf pine.

Shortleaf pine has long been recognized as a fire resistant species (Garren 1943) and is favored by frequent, low intensity surface fire (Schwilk and Ackerly 2001). While it does not have serotinous cones or a grass stage, shortleaf pine does have attributes such as thick, platy bark (Lawson 1990) that develops at an early age (Guldin 1986) and resistance to fire scar rot (Guyette et al. 2007). It has low amounts of flammable resin and has the ability to resprout after top-kill (Mattoon 1915).

Of these adaptations, the most important, and what sets shortleaf pine apart from the other southern pines, is the ability of seedlings and saplings to prolifically sprout from the basal crook following top-kill. This ability provides shortleaf pine with a competitive advantage when intermixed with species that do not normally sprout, such as loblolly pine (Williams 1998). Sprouting in shortleaf pine occurs from dormant buds that developed in the axils of primary needles (Stone and Stone 1954). These buds are harbored in a unique basal double-crook just above the root collar. The crook's development usually occurs during the first few months of seedling establishment with May being identified as typical (Wakeley 1954). However, crooking may not occur until ages 3 to 9 for slower growing, shaded seedlings (Little and Somes 1956). Formation of compression and tension wood just above the cotyledon causes the seedling to tilt so that it is horizontal; shortly after, it resumes upward growth through a similar process, leaving a horizontal section 2.5 to7.5 cm long (Mattoon 1915; Stone and Stone 1954). Almost all naturally regenerated shortleaf pines have a basal crook (Lilly et al. 2012b; Mattoon 1915; Stone and Stone 1954). In contrast, very crowded nursery growing conditions can reduce the frequency of shortleaf pine crooking (Stone and Stone 1954; Lilly et al. 2012a; Wakeley 1954).

The lethal temperature range of dormant plant tissues generally is between 93 and 108 ^{o}C (Kayll 1968) and decreases to approximately 60 ^{o}C for metabolically active tissue (Hare 1961). The basal crook has been widely speculated to increase the odds of sprouting by keeping the bud cluster closer to soil surface where the heat from a fire is lower. In addition the crook facilitates the accumulation of soil and duff above the dormant buds cluster which further insulates them from the heat of a fire. Temperature reached at the basal crook during fire correlated to shortleaf pine sprouting, and sprouting did not occur on charred stem segments (Lilly et al. 2012b) substantiating the importance of the crook in protecting buds from fire damage. Therefore, while the crook is not necessary for sprouting, it probably does increase the likelihood of sprouting following surface fire. The importance of the basal crook decreases as individuals grow, and the thickening bark insulates the cambium.

Fire as a management tool

Fire appears necessary to perpetuate shortleaf pine ecosystems. Fire scar studies show that low frequency burns every two or three years were common in historical shortleaf pine ecosystems in the Missouri Ozarks and that large scale (stand replacing) fires occurred during times of extreme drought approximately every 20 years (Guyette et al. 2006; Guyette et al. 2007). This fire regime resulted in even-aged and uneven-aged patches of shortleaf pine across the landscape (Guyette et al. 2007). In the absence of fire, climax communities in these ecosystems trend towards hardwood species (Guyette et al. 2007). Due to competition from hardwoods and the lack of pine sapling and seedling recruits in mature, undisturbed shortleaf pine forests, it is estimated shortleaf pine may be reduced to 10% of its historical levels in a few centuries without fire (Batek et al. 1999). The practice of controlled or prescribed fire is recommended to promote pure stands of shortleaf pine (Guyette et al. 2007). While low intensity surface fires typical of prescribed fires help maintain shortleaf pine stands, wildfires can damage existing shortleaf pine forests (Guyette et al. 2007). The frequency and intensity of wildfires might increase as a result of increased temperatures and drier conditions from climate change.

Fire is the most widely used silvicultural tool in the southeastern United States with almost 3.2 million ha annually treated with prescribed fire (Wade et al. 2000). There are many benefits to prescribed fires: they can increase yield due to thinning dense young stands, control disease, control unwanted vegetation, create habitat, improve visual aesthetics, reduce fuels, provide cheap site preparation, and make recreational activities and working easier and safer in the woods (Crow and Shilling 1980). Disadvantages and difficulties related to prescribed fire include air pollution and related public safety issues due to smoke, unpredictable and destructive behavior (especially on steep slopes), need for trained personnel, liability to neighbors, and a limited number of days suitable for burning (Lawson 1986).

In shortleaf pine silviculture, prescribed fire can be used for site preparation in both natural and artificial regeneration systems. Slash reduction and competition control can be accomplished using fire as site preparation before plantation establishment. For natural regeneration, fire can eliminate litter and duff to expose mineral soil for seed germination (Barnett et al. 1986, Crow and Shilling 1980).   After regeneration, fire can safely be employed to reduce competition and open up the midstory once the shortleaf pine trees reach greater than 10 to 15 cm in ground line diameter, 2.5 to 5.0 m in height, and 8 to 15 years of age (Cain and Shelton 2002; Dey and Hartman 2005; Lawson 1990; Mattoon 1915).

Another possible use of fire in shortleaf pine silviculture is to accumulate advanced regeneration. Repeated dormant season fires prevent transition of shortleaf pine from seedling to sapling size categories (Cain and Shelton 2002). However, repeated burns can increase shortleaf pine seedling frequency compared to competing species (Dey and Hartman 2005) and can shift understory dominance to shortleaf pine (Williams 1998). Natural regeneration of shortleaf pine is often successful by relying on seed fall following a hot summer burn that kills hardwood competition and exposes mineral soil (Cain 1987). However, seed fall is often unpredictable (Shelton and Wittwer 1996). In these cases, banking advanced regeneration may be an important opportunity to increase regeneration success. For instance, Dey and Hartman (2005) and Williams (1998) recommend burning on 1 to 3 year intervals to reduce competing species until advanced shortleaf pine regeneration can be augmented by new seed fall.

Seedling size and fire intensity strongly affect shortleaf pine resprouting. Lilly et al. (2012b) found that sprouting is sensitive to fire damage and intensity and that sprout survival decreases with seedling size. To maximize survival of top-killed seedlings, seedlings should be smaller (0.6 to 1.6 cm GLD and 0.3 to 0.8 m tall), sustain 50% or less crown scorch, and have crook temperatures below 83°C. In addition, it is important to wait at least one a year after fire to assess seedling sprout success, as significant mortality can occur during the growing season that appears to be proportionately greater for larger seedlings (Lilly et al. 2012b).

Season of burn is important for shortleaf pine survival, having better sprout survival associated with dormant season burns (Cain and Shelton 2000; Grossman and Kuser 1988; Guyette et al. 2007). While survival rates from dormant season prescribed burns typically are close to 90%, results are variable, and some dormant season burns can kill a majority of seedlings (Elliot and Vose 2005; Ferguson 1957). Using fire scar analysis, Guyette et al. (2007) noticed that most shortleaf pines exhibiting fire scars had survived dormant season fires (October to March), suggesting that growing season burns were either uncommon or caused tree mortality. Cain and Shelton (2000) conducted a study in the upper coastal plain of southeastern Arkansas. They found that no sprouting occurred from a summer (August) burn, but a dormant season burn (January) resulted in 95% survival from sprouting when measured two growing seasons later. Grossman and Kuser (1988) burned seedlings as late as April, and reported that all sprouted. Survival of these sprouts were 100% in stumps less than 10 cm GLD but declined greatly with GLD from 10 to 20 cm (Grossman and Kuser 1988).

Reasons for greater survival following dormant season fires may relate to carbohydrate reserves and temperature. Stored root reserves which could be used for sprouting are consumed in spring growth. A spring burn might destroy the photosynthesizing portion of the plant before it can replenish its reserves (Hare 1961). However, Chapin et al. (1990) discusses that studies emphasizing the magnitude of stored carbohydrate depletion following clippings fail to point out that substantial carbohydrates still remain. A more intuitive reason to attribute higher sprouting survival after dormant season burns is related to higher ambient temperatures in the summer. Dormant season fires occur when ambient temperatures are cooler and when soil moisture is typically greatest. Both these factors will reduce the temperature that plant tissues reach. As shortleaf pine sprouting is negatively correlated to basal crook temperature (Lilly et al. 2012b), it is reasonable to assume that lower temperatures prevalent in dormant season fires are related to decreased mortality.

Loblolly pine and fire

With the exception of formation of the basal crook and prolific sprouting following top-kill, loblolly pine exhibits similar resistance to fire as shortleaf pine does. Thick bark insulates the cambium, and survival is likely once the trees are large enough so that their foliage escapes the direct effects of the fire (beginning when approximately 3-5 m tall and 7 cm dbh) (Schultz 1997). As such, fire can be used to manage loblolly pine stands for midstory hardwood release. Loblolly pine seedlings will sprout when top-clipped above the location of the cotyledons. However, loblolly pine is less able to survive top-clipping than shortleaf pine, because it has fewer sprouting buds (Campbell 1985; Little and Somes 1956). Loblolly pine loses its ability to resprout much sooner than shortleaf pine does, typically around 3 years old (Campbell 1985; Mattoon 1915; Schultz 1997). Most importantly in regards to topkill from fire, the dormant buds for loblolly pine are held higher and are more susceptible to fire. Because of the lack of crooking and lower sprouting capacity, the critical time to influence the stand composition using fire is the seedling stage. Williams (1998) determined that one prescribed fire can shift the understory species composition from a mix of loblolly and shortleaf pine to one dominated by shortleaf pine.

Elimination of pine seedlings that are not shortleaf pine is particularly important for reducing survival of shortleaf x loblolly pine seedlings. Lilly et al. (2012a) found that hybrid seedlings often had an ‘s’ shaped bend in the lower stem, but lacked a functional crook that would lower the height of the dormant buds. They presumed that fire offers the opportunity to discriminate against these hybrid seedlings (as well as pure loblolly pine seedlings) and regenerate pure shortleaf pine and maintain long-term species integrity of shortleaf pine.

Fire has been and will be an essential tool for managing shortleaf pine. Given the increasing incidence of hybridization between shortleaf and loblolly pine, reintroducing fire to areas where it was common in the past is more important than ever. Replacement of pure shortleaf pine with loblolly pine or loblolly pine x shortleaf pine hybrids will reduce the resiliency of southern pines to respond to future disturbance and climate regimes and may eventually result in extirpation of the pine component from areas of the Southeast. The next needed step is to confirm that fire will eliminate hybrids in natural stands and the type and intensity of fire necessary to do so. Given the important role of fire and the advantages shortleaf pine seedlings possess, it is essential that breeding programs include the basal crook trait as a selection criteron. Even if the trait is not expressed in all nursery seedlings grown at high density, it is important to ensure the trait is passed to future generations. High planting density in the nursery leading to failure of crook expression can be overcome in the field by planting seedlings several cm below root collar to protect the dormant buds from fire, much the way the crook does in naturally grown seedlings.

Shortleaf pine and drought

Even though the precipitation range along the edge of the western ranges for both loblolly and shortleaf pine (1020 mm) are similar (Lawson 1990; Baker and Langdon 1990), it is generally accepted that shortleaf pine is more drought tolerant than loblolly pine, because it more frequently occurs and exhibits greater competitiveness on drier sites (e.g., Lawson 1990). Shortleaf pine seedlings have greater root:shoot ratios than loblolly pine seedlings (Zak 1961) which may increase shortleaf pine seedlings/saplings resistance to severe drought. However, growth rates of the two species are similar on more xeric sites (Schultz 1997), and we are not aware of direct comparisons of survival in response to drought on sites where both species co-occur. Loblolly pine has the capability to grow and reproduce on locations that were thought to be too harsh as they are outside its natural range. For instance, loblolly pine has been planted and outperforms shortleaf pine in the Ouachita Mountains of Oklahoma (Lambeth et al. 2005) and can naturalize as far west as Stillwater, Oklahoma. Recent problems with 'volunteer' loblolly pine associated with plantations establishment in the Ouachita Mountains of Oklahoma have necessitated pre-commercial thinning and indicates that the ability to reproduce does not limit the westward expansion of loblolly pine.

Shortleaf pines probably are more drought tolerant than loblolly pine. However, the perception of differences in drought tolerance might be overstated and may be confounded with previous fire history as drier, more xeric sites are more likely to burn. With the basal crook adaptation of shortleaf pine that protects dormant buds from fire and higher sprouting capacity, frequent fire discriminates against loblolly pine. Frequent, widespread fire on a regional basis may have extirpated loblolly pine from areas that are pure shortleaf pine, i.e., Ozark and Ouachita Mountains of Arkansas and Oklahoma. Likewise, more frequent fires on xeric sites may have facilitated shortleaf pine dominance on drier sites where the species co-occur. For instance, historical fire return frequencies as short as 1.9 years have been measured in the Ozark Mountains of Arkansas on dry ridge tops (Engbring et al. 2008). This return interval would be frequent enough to prevent establishment of loblolly pine.

Shortleaf pine seedlings have leaf-level traits that are consistent with greater drought resistance. Compared to loblolly pine, shortleaf pine has smaller needles, smaller stomatal diameter, and lower stomatal density, traits that are related to reduced water consumption (Knauf and Bilan 1977; Mitton et al. 1998; Tyree and Sperry 1988). At the stand level, shortleaf pine was recorded to use less water than an adjacent stand of similar sized loblolly pine (Ting and Chang 1985). Water use efficiency (WUE) is the measure of a plant's ability to acquire carbon per unit of water loss and is usually an indicator of drought tolerance (Larcher 1995). Lilly et al. (2012a) found both instantaneous and long-term estimates of WUE agree that shortleaf pine seedlings have higher WUE than loblolly pine seedlings. Water use efficiency increases with drought and is confounded, if individuals are experiencing different levels of water stress. However, Lilly et al. (2012a) measured WUE under well-watered conditions in a nursery. While greater WUE is good for an individual, it may not be helpful in the presence of competitors which would consume the unused water, nor is WUE under well watered conditions indicative of survival during drought. To truly ascertain the full ecological implications related to WUE, a comparison of long-term WUE is needed that accounts for tree size and directly relates WUE to survival, competition, stress, and growth.

Loblolly pine x shortleaf pine hybrid seedlings exhibited WUE intermediate to shortleaf and loblolly pine. Additionally, Florence and Hicks (1980) noted that shortleaf pine and loblolly pine x shortleaf pine hybrids in east Texas were located together on more xeric sites than loblolly pine. The similar drought tolerance of hybrids to shortleaf pine combined with the growth rates of hybrid saplings that are similar to loblolly pine may be facilitating the recent increase of hybrids and indicate their potential for continued expansion in the future.

While planting shortleaf pine rather than loblolly pine on more xeric sites is a safe course or action, uncertainties exist related to drought tolerance. For instance, separating the effects of drought and fire regime on species distributions could better delineate sites where planting shortleaf pine is necessary and provide the information needed to make predictions about shortleaf and loblolly pine distributions in a changing climate. Additional research on mechanisms of drought resistance combined with genetic screening may lead to drought resistant lines of shortleaf pine. This effort is likely to be successful, as shortleaf pine family differences in adjustment of water potential components in response to drought have been identified (Choi 1992). Lastly, the role of fire and drought have on hybrid survival and expansion need to be determined to better manage the shortleaf pine genetic resource.

Temperature

The northern range of shortleaf pine extends through northern Arkansas, southern Missouri, eastern Kentucky, West Virginia, and southern New Jersey and includes isolated pockets in central Pennsylvania. This limit roughly follows the 10^{o}C average temperature isotherm (Lawson 1990). In contrast, the northern range of loblolly pine extends from southern Arkansas to southern Tennessee, South Carolina, eastern North Carolina, eastern Virginia, and Delaware stopping where annual temperature reach 13^{o}C (Baker and Langdon 1990). The northern limit of loblolly pine is speculated to be related to low winter temperature and snow and ice damage (Baker and Langdon 1990). In addition, cold temperature might have an indirect effect on reproduction. For instance, cold damage to newly emerged female strobili of loblolly pine (which emerge earlier than those of shortleaf pine) may limit reproduction (Gulden 1986). Hocker (1956) statistically compared climate within the loblolly pine natural range and areas adjacent to it and found that winter precipitation and average temperature were best correlated to loblolly pine distribution. He further speculated that winter temperature may have an indirect effect through its influence on soil water uptake and availability. If low winter moisture availability due to cold temperature is a limitation for northward expansion of loblolly pine, then this may partly explain the more northern range of the more drought tolerant shortleaf pine. Likewise, Fletcher and McDermott (1957) found that the northern range of shortleaf pine in Missouri was best related to winter precipitation (17” between Nov-April) as well as the presence of loess derived soils blocking its expansion. One of the difficulties in determining the proximate reason for northern range limits is that mortality related to cold can be a lengthy process whereby temperature stress may predispose trees to other disturbance agents (Wells and Rink 1984).

Variability in the response to ice and snow may also relate to the different northern range limits of shortleaf and loblolly pine. In particular, loblolly pine is susceptible to damage from ice and snow which can break the terminal leader, branches, or even snap the main stem (Schultz 1997). In comparison, shortleaf pine most often suffers bending, but not breaking (Boggess and McMillan 1954). In the northern part of loblolly pine's range, damaging storms occur every three years (Schultz 1997) which no doubt affects tree vigor, competitiveness and ability to reproduce.

Both species have been planted well beyond the northern limits of their range with successful establishment as far north as central Illinois. These plantings have variable success and often suffer from periodic cold or ice/snow damage (Wells and Rink 1984). Several of these plantings allowed direct comparison of cold tolerance between loblolly pine and shortleaf pine. Damage to loblolly pine and shortleaf pine plantations were observed following severe cold temperatures of the winter of 1950-1951 in southern Illinois (Boggess and McMillan 1954). Events of that winter included a temperature swing from 11 to -20^{o}C between one afternoon and the next morning as well as minimum low temperatures of approximately -28^{o}C. Of more than 20 plantations examined, damage to shortleaf pine was minimal with all trees recovering. In contrast, 3 of 8 loblolly pine plantations exhibited severe damage (> 50% of trees exhibiting complete or partial mortality). Similarly, damage from ice storms in 1950 and 1952 were recorded in central Illinois (Boggess and McMillan 1954). Overall, loblolly pine suffered much more damage than did shortleaf pine. One area that had loblolly pine and shortleaf pine plantations of the same age had 60% damage to the loblolly pines with the majority of the damage consisting of stem breakage. In contrast, only 30% of shortleaf pines were damaged, and the majority of the damage was bending from which many trees recovered. In comparison, the more northerly species, red pine (*P. resinosa*) and white pine (*P. strobus*), planted in the same area did not suffer any damage.

The southern range of loblolly pine extends to the Gulf Coast and to the central part of the Florida peninsula (max mean annual temperature 24°C). Shortleaf pine extends to within 10-50 km of the Gulf Coast, the northern panhandle of Florida, and southeast Georgia (max mean annual temperature 21°C). There has been little attention paid to the proximate causes related to the southern range limit of shortleaf pine, perhaps because there is no reason to consider moving shortleaf pine southward, as related southern pines that are faster growing naturally occur beyond the range of shortleaf pine. The southern limit of shortleaf pine may be related to edaphic properties as it appears to abruptly stop at the transition to the sandier, wetter lower Coastal Plain and Coastal Prairie. However, shortleaf pine does grow on lower Coastal Plain sites in North Carolina and further north. Therefore, ascribing the southern limit to soils alone is not possible. More intense competition from southern species in combination with edaphic features may limit its distribution. It is unlikely that temperature alone limits the southern range of shortleaf pine. Shortleaf pine is able to withstand higher maximum temperatures and evaporative demand as well as lower precipitation in the Interior Highlands than those experienced in northern Florida.

Climate change

Furniss et al. (2010) summarized many of the effects of climate change projected by the Intergovernmental Panel on Climate Change (IPCC) 2001 report (IPCC 2001. http://www.ipcc.ch/index.htm#.TydfeZi4JAw Accessed January 30, 2012) on water and forests. As mentioned previously, the climate across the range of shortleaf pine varies considerably. Within its current range, temperatures are expected to rise 2.5° (east) to 5° (south central) C for all seasons by the end of the 21st Century. Annual precipitation is expected to decrease approximately 5% in western parts of the shortleaf pine range but increase 5% in the east and increase up to 10% in the north. Annual distribution of precipitation is expected to change (longer dry periods) and precipitation extremes are expected to intensify. Temperature change predictions are considered to be more reliable than precipitation projections (Furniss et al., 2010).

An example of possible recent changes in climate comes from the updating of the USDA plant hardiness zone map in January 2012 (http://planthardiness.ars.usda.gov/PHZMWeb/). This new map pushes plant hardiness zones northward by approximately one 2.4° C zone. The reason for the shift is the incorporation of more recent temperature data (1976-2005) compared to an older, shorter time interval for the 1990 version (1974-1986) (http://www.ars.usda.gov/is/pr/2012/120125.htm). While USDA does not endorse climate warming as the reason for redrawing the map, the maps certainly imply warmer temperatures during the period between 1986 to 2005. Plant hardiness zones were developed based on extreme low temperatures. The historical range of shortleaf pine roughly corresponded to zone 6a which has a minimum extreme low temperature of -23.3° C. If controlled by extremely low temperatures, the range of shortleaf pine might be expected to shift northward close to 150 km in some places and potentially include areas such as central Missouri and most of Ohio.

The most common way to predict future species ranges is through the climate envelope approach whereby species distributions are expected to move such that the future climate of a species range is similar to that of the current range. In other words, if the 10° C average temperature isotherm pushes 100 km north, and all else remains the same, then the range of shortleaf pine also will shift 100 km northward. This approach has been criticized, because it fails to account for edaphic requirements, competitive interactions among species, disturbance, and dispersal rates (e.g., Lo et al. 2010). These non-climate factors have a large influence on species range. For instance, shortleaf pine does not penetrate central Missouri, largely due to loess soils (Fletcher and McDermott 1957), nor does shortleaf pine occur in the Mississippi River Valley due to edaphic, hydrologic, and land use factors.

The USDA Forest Service conducted a detailed prediction of climate change effects on distributions of eastern tree species (Iverson et al. 2008) using the climate envelope approach that also included elevation, soils information, and current land use to determine potential suitable habitat 100 years into the future. The model did not account for changes in land use, land cover, disturbance, or human activities. Six climate scenarios were considered based on three global circulation models (ranging in mean temperature increase from 2.1° to 7° C and precipitation increases of between 39 and 99 mm y^{-1}). Species-specific maps for range distributions are available at http://www.nrs.fs.fed.us/atlas/tree/tree_atlas.html. Loblolly pine is predicted to have net gain of suitable habitat between 33% and 61% (Fig. 2). For shortleaf, a net increase in suitable habitat is predicted between 43% and 77%, resulting in a shift in the northern range limit (Fig. 3). For both species, there is very little predicted loss of suitable habitat, and both species are predicted to generally increase in importance value (based equally on trees per acre and basal area). While the approach of Iverson et al. (2008) is useful, it is limited in that it pertains to maximum potential habitat. Current agents such as land use, competition, fire, pest and pathogens, etc. constrain current species ranges and will do so in the future. The limitation of their analysis is apparent in that the current predicted suitable range differs substantially from the actual current range.

In addition to climate change effects on species distributions, climate change will affect species occurrences and dominance within their current ranges. Near the northern portion of the range, increasing temperature might increase the competitiveness of loblolly pine or other tree species relative to shortleaf pine. On the other hand, increased variability in precipitation will increase the frequency and intensity of droughts and may increase the competiveness and dominance of shortleaf pine. Higher temperature and more frequent drought may have an indirect positive effect on shortleaf pine by increasing frequency or intensity of fire. The potential effects of climate change are difficult to predict, especially since human activities that modify disturbance regimes control regeneration may overwhelm any possible effects due to climate.

Deciding whether to plant loblolly or shortleaf pine based on potential climate change is difficult. On sites with better soil moisture holding capacity, loblolly pine will probably exhibit excellent survival and superior growth, especially if employing site preparation and competition control which may increase availability of soil moisture. On drier sites, however, planting shortleaf pine might be considered as a potential strategy for increased drought in the future. In addition, effects of lower or more variable precipitation, higher temperatures increase evaporative demand and can exacerbate the effects of drought. With higher temperature and more frequent drought, the risk of wildfires may increase. If so, this is another reason to consider managing for shortleaf pine (both natural and artificial regeneration systems) on drier, more fire-prone sites. A greater understanding of key factors influencing shortleaf pine range, site suitability, and productivity are needed as it relates to changing climate.

Water Resources and Shortleaf Pine

Streamflow for water supply and the support of aquatic life may be the most important ecosystem services supplied by forested watersheds (NRC, 2008). Forests in the United States provide drinking water to more than 180 million people. Throughout the native range of shortleaf pine, about 80% of municipal water supply comes from forest watersheds (USFS 2012, http://www.fs.fed.us/water/ accessed January 27, 2012).

The shortleaf pine region (SPR) covers a wide range of climates, geology, and other properties important to the generation of streamflow. Average annual precipitation and streamflow can be as high as 2000 mm and 1000 mm in the southern Appalachian Mountains to slightly below 1000 mm and 250 mm, respectively, along the western edge of the region in Oklahoma (Satterlund, 1972 and Pettyjohn et al.,1983).

Shortleaf Management Effects on Water Quantity:

Numerous watershed studies have been conducted across the shortleaf pine region (SPR), covering a variety of climatic, soils, topographic and geologic conditions and silvicultural treatments and have been summarized in the citations that follow. The results of these studies are too numerous to repeat here, so the reader should consult the references for more site-specific and detailed information. Almost all of these studies evaluated the effects of timber harvest on streamflow from forests of hardwoods, mixed pine-hardwood, or other pines (such as eastern white pine and loblolly pine) or conversions of some forest type to loblolly pine (Jackson et al., 2004 and Beasley et al., 2004). However, the results of these studies can be extrapolated to shortleaf pine, because it would be unlikely that the changes in streamflow observed would be different, if shortleaf pine was used instead of loblolly pine or another coniferous species. Other factors such as regional physiography and the silvicultural practices in use would likely have a greater influence on the water balance and water quantity than the species of pine (Miller, 1989).

Bosch and Hewlett (1982) summarized streamflow data from 94 forest and shrub watersheds around the world. They developed separate linear regressions for different cover types for the relationships between the percent reduction in cover and increased annual streamflow. For a given percent removal of trees (or percent afforestation), streamflow increased (or decreased) linearly. Conifers exhibited the greatest increase (decrease) in streamflow for a given removal (re-growth) of trees. Variability in response was high, because data was collected from different regions around the world. The magnitude of the streamflow increase following a certain amount of harvest was found to be greater in areas with greater mean annual precipitation.

Stednick (1996) updated the analysis performed by Bosch and Hewlett (1982) as additional watershed study data became available. Stednick also divided the data by hydrologic region (Table 1). The greatest increases in streamflow occur when a watershed is clear-cut. Increases resulting from thinning are a function of the percent of cover removed. Based on the regressions, clear cutting a pine-forested watershed in the SPR could increase first-year annual streamflows from 184 to 615 mm. Actual results for specific locations and watershed conditions vary considerably from the predicted means.

Table 1. Regression model statistics and coefficients for streamflow increase versus percent harvested area for watersheds in the shortleaf pine region (SPR) and by hydrologic region (from: Stednick, 1996). Data includes all forest types except for the central plains data that was collected from watersheds initially covered mostly by shortleaf pine.

Hydrologic Region	**#**	**n**	**Slope**	**r^2**	**SE**	**P value**	**Threshold for response**
Appalachian Mountains and Highlands	2	29	2.78	0.65	74	0.0001	20

Eastern Coastal Plain and Piedmont	3	7	1.84	0.02	97	0.0051	45
Central Plains (includes Ouachita and Ozark Mountains)	8	7	6.15	0.31	197	0.0009	50

Two studies on shortleaf pine-forested watersheds were conducted in the Ouachita Mountains of Arkansas and Oklahoma. Following clear cut harvesting and site preparation (broadcast burning), first year average (across 3 replicate watersheds) streamflow increased 100 mm in the Arkansas study, but average (across 3 replicate watersheds) streamflows decreased 100 mm in the Oklahoma study. The decrease in streamflow in the Oklahoma study was attributed to an increase in infiltration and deep soil percolation resulting from sub-soiling along the contour that was part of the site preparation. Streamflow increased an average of 50 mm during the second year after harvest (Miller, 1984). In three of the watersheds in the Arkansas study, 50% of the basal area was removed, and they were broadcast burned and allowed to regenerate naturally as part of an uneven-aged management system. Average steamflow increased 100, 74 and 65 mm, the first, second and third years following harvesting. (Miller et al. 1988). Through time, as vegetation recovers following harvest in the SPR, streamflow may return to pre-harvest quantities in 3 to 7 years (Jackson et al., 2004 and Beasley et al., 2004).

Both Bosch and Hewlett (1982) and Stednick (1996) determined a threshold response (Table 1), defined as the smallest change in cover that can results in a detectable change in streamflow in watershed studies. Theoretically, removing no trees would produce no change in streamflow, but removing a small number of trees would produce a change too small to detect. Increases in streamflow resulting from managing pines are also a function of spatial distribution of tree removal over a watershed. Trees removed in blocks have been found to produce a greater increase in streamflow than when the same number of trees is removed evenly throughout a watershed (Jackson et al., 2004).

Prescribed fire is often used in site preparation and restoration of shortleaf pine-bluestem ecosystems. Low intensity prescribed fires have only minor and very temporary effects on streamflow (Jackson et al., 2004 and Van Lear and Waldrop, 1989). Streamflow increases from pine-bluestem restoration would likely occur as a result of the reduction in tree cover rather than fire effects on soils.

Shortleaf Management Effects on Water Quality:

As with water quantity, most of the water quality studies done in the SPR have been performed on sites occupied by different forest types. However, water quality effects are more a function of the amount of soil disturbance created by the harvesting and silvicultural methods applied, site characteristics (climate, soils, slope, etc.), and the density of roads than forest type (Miller 1989).

Sediment is the non-point pollutant of greatest concern resulting from forest management operations. Sediment yields ranging from 110 to 3000 kg/ha in the first year following harvesting and site preparation have been reported in watershed studies in the SPR. The low value was from a site in West Virginia that was harvested "carefully" using BMPs (low soil disturbance) (Jackson et al., 2004 and Beasley et al., 2004). The high value was from a site in East Texas where the site preparation consisted of shearing, windrowing, and burning (high soil disturbance) (Beasley et al., 2004). The differences in magnitude were also likely a function of differences in climatic factors (rainfall amounts and intensities) that occur throughout the shortleaf pine region. Harvested sites in the SPR usually return to pre-harvest sediment yields in 2 to 7 years after harvest as vegetation quickly regenerates (Jackson et al., 2004 and Beasley et al., 2004)

Results from watershed studies in the SPR have shown that disturbances, harvesting, site preparation, and fire slightly increase nutrient concentrations and loads in streams. These increases have been found to be short-lived (1 year or less) and not a threat to site productivity and water quality when normal modern forest practices are employed. Changes in biogeochemical cycles may occur if forests are converted from one type to another (e.g., hardwood to pine). In most cases inputs of nutrients from atmospheric deposition are greater than nutrient losses. (Jackson et al., 2004).

Forest roads have often been described as the greatest long-term source of sediment from forestry operations. There is nothing unique about roads in shortleaf pine forests compared to other forest types. Road erosion is mostly a function of slope, age, traffic, frequency of maintenance activities (grading), soil erodibility, and rainfall amounts and intensities. Total road erosion in a watershed is related to road density, which depends on harvesting and silvicultural methods. Rates of road erosion from road segments measured in the SPR range from 4.5 Mg/ha/yr on a well-constructed and established road in West Virginia (Jackson et al., 2004), 80 Mg/ha/yr on a newly constructed road in Oklahoma (Turton and Vowell, 2000), to 258 Mg/ha/yr on the Coweeta Experimental Forest in North Carolina (Jackson et al., 2004). Road erosion rates from individual road segments are high but only create a water quality problem if the sediment is delivered to a stream. Sediment delivery from a road system in a watershed is a function of road density, topography, and travel distances to stream channels. Miller et al. (1985) determined that about 7% of the road segment erosion measured in a study in the Ouachita Mountains in central Arkansas actually entered steams. Busteed et al. (2005) used GIS inventories of road systems in two watersheds in the Ouachita Mountains in Oklahoma and determined that about 5-7% of the roads drained directly into streams.

Shortleaf Pine, Climate Change and Water Resources

Based on simple water balance, a decrease in annual precipitation and an increase in temperature (like that projected for the western part of the SPR) would likely produce a decrease in streamflow. Likewise, an increase in annual precipitation and a slight increase in temperature (like that projected for the eastern part of the SPR) would likely increase streamflow. Based on Global Circulation Model predictions, median changes in streamflow are expected to be -2 to -5% and +2 to +5% from west to east across the SPR, respectively. Flood severity, stream temperatures, and sedimentation (from more extreme events) are also expected to increase (Furniss, et al., 2010).

As stated previously, changes in streamflow from forest management are likely the same for all pines in the SPR. The same is likely true for climate change effects on streamflow; climate change will overshadow vegetation type. Shortleaf pine is thought to be more drought resistant than other pines found in the SPR such as loblolly pine. However, better survival won't mitigate the effects of reduced precipitation and increased temperatures on streamflow. It's also possible that the SPR will recede eastward if precipitation decreases below 1000 mm along the western edge of the SPR.

When water resources become scarce, we may look for ways to mitigate the effects of climate change such as managing forests to improve water yields. As previously stated, small watershed studies have shown that streamflow increases after a certain percentage of forest cover is removed. Therefore, it seems logical that if we reduce forest cover in a basin, we can increase streamflow. Putting this concept into practice over a large land area is, however, problematic and likely ineffective (NRC, 2008) for a number of reasons:

1. Streamflow increases from forest harvest are short-lived, especially in the SPR, as vegetation recovers quickly (Stednick, 1996). Land would have to be kept in a perpetual harvest state, which may be incompatible with other uses.
2. The magnitude of streamflow increases from forest harvest are lower in regions with lower precipitation (Stednick, 1996). If climate change reduces precipitation, gains in

streamflow from forest harvest will be smaller, and more land would have to be harvested to produce useful streamflow increases.

3. Large areas within a drainage basin would have to be managed to produce a measureable effect on streamflow. A minimum of between 50% to 20% (moving west to east) of the land in a watershed in the SPR would have to be harvested to generate a statistically significant increase on streamflow (Stednick, 1996). This may be incompatible with other management goals (such as wildlife) and not possible given the mix of private and public land that exists in the SPR.
4. Increased streamflow could come at the cost of decreased water quality from more frequent disturbance needed to keep large portions of a watershed in a “harvested” state.

On the other hand, gains in streamflow may be produced as a side-effect of managing forests differently to mitigate the effects of climate change. It’s possible that forests may have to be managed to ensure forest survival under a drier and warmer climate. Thinning may be one approach used to reduce competition for soil water. Climate change may justify converting more hectares of highly stocked pine and pine-hardwood forests to pine-grassland cover types. Such changes could increase streamflow if the conversion is “permanent” but would have to be carried out over large areas of a drainage basin. Long-term measurements of streamflow under such conversions are currently not available.

The growth and yield of shortleaf pine

Information concerning the growth and yield of shortleaf pine is not nearly as comprehensive as that available for the other three major southern pines despite the fact that shortleaf has the most extensive range and is second in volume only to loblolly pine. This was noted by Paul Murphy (1986) in his classic review of the growth and yield of shortleaf pine. It is still the case today, although a number of significant works relating to shortleaf pine have become available since that time. In particular, comprehensive growth and yield models for natural stands of even-aged and uneven-aged shortleaf pine have been developed (Lynch et al. 1999; Huebschmann et al. 2000). However, no comprehensive growth and yield model for shortleaf pine plantations has been developed since that of Smalley and Bailey (1974) which was developed for unthinned old-field plantations. This is a notable deficiency, since in recent years there has been renewed interest in the establishment of shortleaf pine plantations. Although some of the major works cited by Murphy (1986) will be noted here, readers are referred to Murphy (1986) for a comprehensive list and discussion of shortleaf pine growth and yield research prior to 1986.

Murphy (1986) discussed classification of growth and yield information in a way that is still useful today. Growth and yield studies may be classified as descriptive, predictive or inferential according to their purpose. Descriptive studies focus on observations that describe a notable phenomenon such as a stand with unusually high stocking. Inferential studies use statistically designed experiments. For example, an inferential study may be designed to find the residual basal area stocking that results in the largest cubic foot volume growth. Inferential studies are usually limited in size and scope, as well as the number of variables measured.

Predictive studies are designed to develop equations that can predict growth and yield at future times. Well-designed predictive studies include a range of variables important for prediction of growth and yield, which typically include stand density, site index, and age or time in stand development. Ideally, the full ranges of variables that may be of interest for prediction should be included, as well as each combination of such variables that may occur. Preferably, predictive studies are based on re-measured plots for accurate determination of growth, although historically some have been based on temporary plots. Thus, well-designed predictive studies can consist of 200 plots or more and may last a number of years depending on the number of plot measurements obtained.

Because of the time and expense required for inferential and predictive studies, Murphy (1986) noted that inventory data are sometimes used to develop growth and yield models. Continuous Forest Inventory (CFI) plots maintained by private landowners or forest industry or FIA plots established and maintained by the USDA Forest Service are usually the source of these data. Murphy (1986) noted the following six potential drawbacks of the use of inventory data to develop growth and yield models: (1) plot isolations are lacking; (2) often, there are important variables which may not have been measured; (3) plots must usually be screened to remove unwanted plots, requiring many plots to be initially available; (4) plots representing uncommon or rare combinations of stand variables may be lacking; (5) plot history is generally not available; and (6) predictive models based on inventory data may not well represent growth and yield for managed forests. Nevertheless, Murphy (1986) felt that models based on inventory data could be useful for interim results. Data used for the development of growth and yield models may be temporary plots or permanent (remeasured) plots. Where temporary plots are used, no actual growth measurements are made; thus as Murphy (1986) points out, assumptions must be made to make growth predictions based on temporary plots.

As Murphy (1986) indicates, there are three types of growth and yield models: stand-level, size-class distribution, and individual tree. Stand-level models generally provide predictions at the stand level in terms of yields per acre – there is no breakdown of yield into size classes, such as dbh classes. However stand-level models usually require a minimum of independent variables for their use – generally age, site index, and density. Size class distribution models provide more detailed predictions, usually stand and stock tables. Individual tree models are capable of providing the most detailed predictions but also require more detailed input for their use. Individual tree models usually require inputs of individual tree diameter and height or a stand table from which these can be derived.

Information for natural even-aged forests

USDA Forest Service Miscellaneous Publication 50 (USDA Forest Service 1929) is one of the earliest comprehensive publications for southern pine yield. It provides site index curves and yield tables for all four southern pines, including shortleaf pine. The shortleaf pine yield tables are based on 188 temporary plots located throughout the southern U.S. Yields are given in cubic feet per acre and board-feet per acre for normally stocked stands of various ages and site indices. The fact that yields are given only for normally-stocked stands represents a drawback for modern use of these yield tables. Fully-stocked stands having normal density were once considered ideals for management. However, this is no longer the case. Use of these yield tables for non-normal stands involved application of ratios of actual-to-normal basal area per acre, but it was difficult to project these ratios to future times. The fact that these tables are based on temporary plots also makes them problematic for use for growth projections. The tables presented in Miscellaneous Publication 50 are based on graphical analyses, and therefore, there are no underlying equations for yields. Murphy (1986) notes that the site index curves were sometimes still used and the information contained in Miscellaneous Publication 50 are still valuable as a reference for research.

Schumacher and Coile (1960) is another early source of growth and yield information for shortleaf pine. This work provides yield equations which are an advantage over Misc. 50 which provides results in tabular form only. It is based on 74 temporary plots from a somewhat restricted geographical range. It is a stand-level model which provides per-acre predictions of forest yields. The model is based on a "well-stocked" concept, somewhat similar to normal stocking. Therefore, to use the Schumacher and Coile (1960) model for predictions one must make assumptions concerning the development of stocking percentages through time.

Variable-density stand level growth and yield equations were first provided by Murphy and Beltz (1981) and Murphy (1982) for natural, even-aged shortleaf pine. The equations were based on permanent inventory plots established and maintained by USDA Forest Service Forest Inventory and Analysis (FIA) for the Southern Research Station. Data were from Arkansas, Louisiana, east Texas, and eastern Oklahoma. The equations can be used to project stand basal area and volumes to future times. As indicated above, these equations may not well-represent the yields that can be obtained in managed forest stands.

The Shortleaf Pine Stand Simulator (SLPSS) (Lynch et al. 1999; Huebschmann et al. 1998) is an individual tree forest growth and yield simulator for managed stands of natural even-aged shortleaf pine. The simulator is based on over 200 permanently established plots located in western Arkansas and southeastern Oklahoma on the Ozark and Ouachita National Forests. Plots were established in combinations of age, basal area per acre, and site index categories that attempted to cover most combinations of these variables that would be encountered in management. Twenty-five plots from an earlier thinning experiment established by Frank Freese near Hot Springs, Arkansas, were incorporated in the study. At establishment, plots were thinned to a residual basal area level according to the study design and hardwood control was accomplished using chemical herbicide. On all residual shortleaf pine trees, individual tree dbh was measured and the distance and azimuth to the plot center was recorded. Total height and height to crown base was recorded on a subset of trees on the plot. Each 1/5th acre measurement plot was surrounded by an isolation strip 33 feet wide which received the same thinning and herbicide treatment as the measurement plot. Thus, the competitive atmosphere at the edge of the measurement plot should be similar to that in the interior of the plot. Plots were established during the period from 1985-1987 and remeasured 4-5 years later.

The measurements described above provided data for the development of individual tree growth equations in SLPSS. Equations were developed for individual tree basal area growth (Lynch et al. 1999). Individual tree height prediction was accomplished using a height-diameter equation (Lynch et al. 1999, Lynch and Murphy 1995). Individual tree survival was assessed using an equation which predicted probability of shortleaf pine survival based on individual tree and stand level variables (Lynch et al. 1999). Parameters were fitted to a crown ratio equation (Lynch et al. 1999) that was used to predict the crown ratios of individual shortleaf pine trees in even-aged natural stands. SLPSS uses a polymorphic site index equation which was previously developed by Graney and Burkhart (1973). This equation can be used to predict the average total heights of dominant and codominant shortleaf pine trees at various ages growing in even-aged natural stands given user-supplied site index. The equation can also be used to obtain site index given user-supplied age and dominant height. Individual tree cubic-foot and board-foot volumes were obtained in the simulator by using the shortleaf pine taper equation developed by Farrar and Murphy (1987). Equations from Saucier et al. (1981) were used to calculate weight per cubic foot for shortleaf pine trees of given dbh and total height. This information was applied to cubic foot volumes obtained from the taper equations discussed above to obtain weight information for SLPSS.

In order to predict future forest conditions, SLPSS needs an input of initial (current) values. Input required as initial values includes site index, current age, merchantability specifications, and current stand table. One may also input plot data from an inventory. SLPSS will project the stand to a specified future value, and predict future stand and stock tables, where stock tables are presented for cubic feet, board-feet, and green weight pounds per acre. Thinning can be conducted in SLPSS as well, where thinning may be to a specified residual basal area per acre or to a specified residual stand table. After thinning the residual stand may be grown a specified number of years to another thinning or to harvest.

Lynch et al. (1999) presented results from trials of SLPSS with site index 60 ft (base age 50 years) indicating maximum Mean Annual Increment (MAI) in basal area ranging from about 2.5 to 6 ft^2/acre/year and in cubic volume ranging from 65 to 100 ft^3/acre/year, for stands with initial basal areas ranging from 30 to 120 ft^2/acre at age 20. MAI curves converged by age 100 years. Trials with initial stocking of 71 ft^2/acre of basal area at age 20 and site indices ranging from 50 to 80 feet at index age 50 years showed maximum MAI for cubic foot volume ranging from 80 to 115 ft^3/acre/year and occurring around age 42.

Lynch et al. (1991) provide an interim growth and yield projection system which uses the initial measurements of same study used to parameterize SLPSS to develop stand volume per acre- and basal area per acre relationships. Basal area projection equations described by Murphy (1982), and Murphy and Beltz (1981) are used to project to future forest conditions. This interim model was used prior to the completion of SLPSS but SLPSS would now be preferred for applications.

Rose and Lynch (2001) used the data described for SLPSS above to test a new method of estimating parameters in the basal area growth equation. They used a system of equations to predict basal area growth in four ranked dbh classes on each plot. The parameters in the system were estimated using seemingly unrelated least squares. They compared the results to an equation estimated using ordinary least squares regression (OLS) in the traditional way on an independent data set obtained by random selection. The new method showed improved Mean Square Error (MSE) and Fit Index (FI) but the OLS equation had a lower mean absolute error.

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Budhathoki et al. (2008a; also see Budhathoki et al. 2006) fit a new individual tree basal area increment equation for natural, even-aged shortleaf pine individual trees using data from additional measurements of the plots upon which SLPSS is based (described above). Data from the first three measurements were used. Budhathoki et al. (2008a) used mixed-effects estimation to account for the grouping of individual trees on plots. The equations of Lynch et al. (1999) were all fit using OLS which assumes that all individual trees in the dataset are mutually independent. However, basal area increments for individual trees located on the same plot are correlated. When mixed-effects analysis is used, a plot-level random effect can be specified to account for this correlation. Also, equations fit using mixed-effects methods have the potential to be calibrated for local use. According to the Akaike Information Criterion (AIC) the fit of the mixed-effects model was superior to a similar basal area growth model fitted by OLS.

Mixed-effects modeling methods were also used by Budhathoki et al. (2008b) to develop a diameter-height equation for shortleaf pine growing in even-aged natural stands. Additional measurements were incorporated into the dataset used to develop SLPSS (described above). A plot-level random effect was incorporated into the diameter-height model to account for the grouping of trees on plots in the dataset. This grouping may violate the assumption of independent errors when OLS techniques are used to fit diameter-height equations to individual trees located on plots. Budhathoki et al. (2008b) determined that the fit of the mixed-effects equation was superior to an equation fitted by OLS according to the AIC. Shrestha et al (in press, also see Shrestha 2010) developed a revised probability of survival equation for individual shortleaf pines. Mixed-effects models were tested in this study but it was concluded that OLS estimates were better for prediction in this case.

A system of equations for the annual growth of the loblolly-shortleaf pine type in Louisiana was developed by Cao and McDill (2002) using FIA data. They tested methods of interpolation used when periodic growth measurements are used to fit annual growth equations. The Forest Vegetation Simulator (FVS) (http://www.fs.fed.us/fmsc/fvs/) has the capacity to predict shortleaf pine growth and yield.

Schulte and Buongiorno (2004; also see Schulte et al. 2000) developed a matrix model for naturally-occurring shortleaf and mixed hardwood forests. The growth matrix they developed is density and site dependent. The data are from over 1,000 FIA (Forest Inventory and Analysis) plots maintained by the USDA Forest Service. Since these are inventory plots, they may not reflect the yield that could be obtained in managed shortleaf pine stands. When the model was used to simulate some long-term scenarios, it predicted that shortleaf pine would be eventually replaced by hardwoods if no major disturbance occurred (and presumably in the absence of hardwood control).

As Murphy (1986) notes, a study installed in natural even-aged forests on the Sinkin Experimental Forest in Missouri by the North Central Experiment Station (now the Northern Research Station) has provided much useful information (Brinkman et al. 1965, Sander and Rogers 1979, Rogers and Sander 1985). In this inferential study, there were four residual basal area treatments plus a control which were replicated in a 30 year old shortleaf pine stand three times.

Murphy et al. (1992) describe the volume and basal area development on a thinning experiment installed by Frank Freese in the 1960's. The final measurements on the study were made in 1987 when 25 remaining study plots were incorporated into the data base that was used to develop SLPSS as described above. This smaller scale inferential study provides interesting information regarding the development of shortleaf pine forests after thinning treatments.

Wittwer et al. (1996) describe a thinning experiment located in naturally-occurring even-aged shortleaf pine in southeastern Oklahoma near the western edge of the shortleaf pine natural range in an inferential study in which plots were located in a small geographic area. They found that thinning significantly improved the growth of crop trees, since diameter growth of residual crop trees in thinned stands was significantly greater than was the case in unthinned stands. Previously unthinned shortleaf pine was thinned to 30, 50 and 70% full stocking, and an unthinned control was also included. Five years after thinning, net periodic annual basal area growth was 6.7, 7.9, and 8.6 ft^2/acre/year in the 30, 50 and 70% full stocking treatments but only 4.5 ft^2/acre/year in the unthinned control, largely due to mortality. For a comparable component of crop trees, periodic annual diameter increment was 0.42, 0.35, and 0.29 on the 30, 50, and 70% full stocking respectively but only 0.24 in/yr on controls. Periodic annual volume increments were not significantly different among treatments and ranged from 183 to 213 ft^3/acre/year.

A shortleaf pine thinning experiment similar to that described by Wittwer et al. (1996) was established on land owned by an industrial forestry concern some miles to the east and on a better site (site index about 70 feet at 50 years). Sabatia et al. (2006, 2007, 2009) used destructive sampling to establish individual tree biomass equations for shortleaf pine on this site. A system of equations was developed for the components of individual shortleaf pine tree above ground biomass including bolewood, treebole, branches, foliage, and whole tree. Bark biomass can be obtained by subtracting bolewood biomass from tree bole biomass. Thinning had a significant influence on the equations. Trees ranged from 7- 40 cm in dbh and were 46-53 years old. The plots in the thinning experiment had treatments of 50, 70% full stocking or unthinned control. Sabatia et al. (2008) indicate that the equations might be used for naturally-occurring shortleaf pine in southeastern Oklahoma having dbhs in the range from 7-40cm and the equations have potential to be applied in other areas. A similar study was conducted by Gwali et al. (in press; also Gwali 2008) on a relatively poorer site than the one used by Sabatia et al. (2009). Trends were similar to those reported by Sabatia et al. (2009)

Sabatia et al. (2009, 2010) used the equations described above to estimate plot biomasses on the thinning experiment so that the effects of thinning on shortleaf pine biomass components could be determined. The unthinned control plots had significantly more total biomass, bole biomass, bark biomass and foliage biomass but less branch biomass 16 years after the thinning to 50 or 70% full stocking. As a proportion of total biomass, foliage biomass was similar among thinning treatments. In the 50% full stocking treatment bark biomass proportion was significantly smaller than in the other treatments. Bolewood biomass proportion was significantly smaller in the 50% treatment than in the control. Branch biomass proportion was significantly greater in the thinned treatments than in the control. The results seem to support the assertion that thinning increases branch biomass relative to bole biomass 16 years after thinning.

A model of shortleaf pine needle litterfall was developed by Huebschmann et al. (1999) using data collected over seven growing seasons in the shortleaf pine thinning study sites described above by Wittwer et al. (1996) and Sabatia et al. (2008, 2009). The model related stand-level and weather variables to litterfall quantities. It could be used to help forecast fuel loads or production amounts of needle litterfall as a forest product. Variables significantly related to needle litterfall quantities included spring temperatures when the needles were produced, needlefall during the two previous seasons, and site index.

Stand density and stocking

Lynch et al. (2007) used unthinned control plots on the natural shortleaf pine thinning experiments described by Wittwer et al. (1996) and Sabatia et al. (2009) above to develop maximum size-density relationships for shortleaf pine. These unthinned control plots already had density sufficient to exhibit competition-induced mortality at the beginning of the thinning studies. They had never been previously thinned and contained virtually no hardwood competition due to early herbicide treatments. Three maximum size-density relationships were developed. The first was a maximum size-density relationship between the logarithm of number of trees per acre and the logarithm of quadratic mean diameter. This was the classic maximum size-density relationship described by Reineke (1933) who also developed a maximum size density equation for shortleaf pine. Reineke (1933) used this type of relationship as the basis for his Stand Density Index (SDI). The second relationship was the 3/2 power law relationship between the logarithm of mean tree volume and the logarithm of number of trees per acre. The third relationship was an equation relating the logarithm of Lorey's mean height (a basal area weighted mean) and number of trees per acre. Lynch et al. (2007) showed that the third relationship could be derived from the other two. In fact, any two of the three relationships can be used to derive the third. Because of their interrelationships, the three equations were fitted together in a system using three-stage least squares. Analysis of the data confirmed that 3/2 was appropriate for the slope of the line between the logarithm of mean tree volume and the logarithm of number of trees per acre. The slope of the line between the logarithm of number of trees per acre and the logarithm of quadratic mean diameter was -1.7762. Measurements of the graph given by Reineke (1933) for the relationship between the maximum number of trees per acre and quadratic mean diameter indicate a slope of -1.8. The estimated line indicates a maximum stand density index of 473.5 trees per acre. This represents the maximum number of shortleaf pine trees per acre associated with a stand having a quadratic mean diameter of 10 inches. Both slopes are steeper than the value of -1.6 postulated by Reineke (1933) for a variety of species. The slope of the line between the logarithm of Lorey's mean height and the logarithm of number of trees per acre was = -0.3740. Rogers (1983) developed a thinning guide for shortleaf pine. The stocking chart of Rogers (1983) is also reproduced in the article by Wittwer et al. (1996). Stand basal area, number of trees and quadratic mean diameter can be used to locate a point on the stocking chart. Stocking percent for the stand can then be read from the chart. Two lines, the "A" line (100% stocking) and the "B" line (60% stocking) contain the area on the chart that represents stands that fully utilize growing space. Use of the chart with these lines may serve to guide thinning decisions.

Regeneration for Natural Even-aged Stands

Lynch et al (2002, 2003) developed a model to predict the probability of obtaining specified levels of shortleaf pine reproduction (stems per acre) 9-10 years after thinning and comprehensive hardwood control. The model is based on counts of reproduction made 9-10 years following thinning and hardwood control on 182 plots. These plots were part of the database described for SLPSS above. The model was based on the logistic equation. The model related regeneration to residual overstory basal area, site index, and stand age. Probability of regeneration success was negatively related to overstory basal area and site index. The negative relation to site index may be due to the more vigorous hardwood competition (even following hardwood control) on better sites.

An analysis of long-term data for shortleaf pine seed production was presented by Shelton and Wittwer (1996). The data were obtained during a 9-year period from 1965 to 1974 in the Ozark and Ouachita Mountains of southern Missouri, mid-to-western Arkansas, and southeastern Oklahoma. During this time there were two good seed crops and one “bumper” seed crop. Seed production ranged from an annual mean of 84,000/acre in the western portion of the Ouachita mountains to 167,000/acre in the southern Ozark mountains and was positively correlated to stand age but negatively correlated to hardwood and pine basal areas. The authors concluded that for the majority of the study area shortleaf pine seed production would be sufficient to obtain natural regeneration.

The effect of shortleaf pine reproduction cutting method and hardwood retention on shortleaf pine regeneration was analyzed by Wittwer et al. (2003). They provide a review of some of the work relating to shortleaf pine regeneration prior to 2003. They found that seed production in the first year after harvest correlated with shortleaf pine residual density, with higher residual densities producing more seed. However, 4 years after harvest there was no significant difference in seed production among cutting methods, which they thought was due to response of residual seed trees in seed tree and shelterwood stands. They also found that seed crops were lower in the western part of the Ouachita Mountains.

Information for Natural Uneven-aged Stands

Murphy (1986) remarked that there was relatively little information available for natural uneven-aged stands, which is still the case, although some important works have become available since that time. Murphy and Farrar (1985) developed a stand-level model for uneven-aged shortleaf pine based on inventory data. Initial values of merchantable basal area, sawtimber basal area, and site index can be used to predict future merchantable and sawtimber basal area as well as cubic foot and board-foot volumes. Although the model is based on inventory data, the plots were located in forests which were managed according to an uneven-aged regime by an industrial forestry concern.

Huebschmann et al. (2000) describe an individual tree model for the description of growth and yield of uneven-aged shortleaf pine forests. The data were obtained from permanently established inventory plots maintained by an industrial forestry concern and located in naturally-occurring shortleaf pine forests under uneven-aged management. There is overlap in the data bases for Huebschmann et al. (2000) and Murphy and Farrar (1985). The data were obtained from 152 plots distributed over six counties in the mid-western portion of Arkansas. The model of Huebschmann et al. (2000) consists of an individual tree basal area increment model, a probability of individual tree survival model, an ingrowth model which predicts the annual number of shortleaf growing past the 5.1 inch limit of merchantability, diameter-height models and hardwood basal area growth models. The hardwood basal area growth model was used to describe the growth in basal area of a small component of hardwood contained in these forests. There is also a hardwood basal area ingrowth model. The procedure for estimating shortleaf pine volume and weight is the same as indicated for the even-aged version of SLPSS above. The taper equations of Farrar and Murphy (1987) are used to obtain cubic foot and board-foot volumes. Weights are obtained using the equations from Saucier et al. (1981) together with the taper equations as described above.

The growth and yield system of Huebschmann et al. (2000) was incorporated into SLPSS software, so the input requirements are very similar to the requirements for the even-aged version described above. Upon entering SLPSS, the user is asked whether it is desired to project an even-aged stand or an uneven-aged stand. If one indicates the desire to project an uneven-aged stand, the equations of Huebschmann et al. (2000) are used. Initial inputs required are a stand table or inventory plots, site index, merchantability specifications and initial hardwood basal area. Since uneven-aged forests do not have an age, initial age is not required. Site index is problematic in uneven-aged stands, but it is recommended that the cores used to determine site index be free from evidence of suppression. The uneven-aged version of SLPSS will then project stand conditions according to the specified elapsed time. Future stand and stock tables will be predicted with cubic feet, board-feet, and weights per acre for the merchantable and sawtimber portions of the projected stand. One may simulate partial cuts as are often performed according to cutting cycles for an even-aged stand. The simulation will indicate stand and stock tables for removals as well as for the residual stand.

Lhotka and Loewenstein (2011) developed an individual-tree diameter growth model of uneven-aged managed oak-shortleaf pine in the Missouri Ozarks. The data were obtained from permanent inventory plots located in the Pioneer Forest, which has been managed by single tree selection since the 1950's. Diameter growth models were developed for each species based on 290 permanent plots. Parameters were fit using mixed-effects estimation procedures. The authors tested calibration of the models by using additional data to estimate random effects. The best results were obtained when using 1 and 3 trees for calibration.

Economic information for natural uneven-aged stands and comparison with even-aged stands

The economic and ecological benefits and trade-offs from using uneven-aged silviculture with naturally-occurring loblolly-shortleaf forests were investigated by Shulte and Buongiorno (1998). Their simulations showed good economic returns with uneven-aged silviculture and hardwood control. Retaining a modest hardwood component reduced income but increased diversity. Maximizing diversity led to significant income reductions.

Schulte and Buongiorno (2002) used nonlinear programming to identify optimal uneven-aged management regimes for naturally-occurring shortleaf pine forests. They found the best regimes in terms of guiding maximum diameter and hardwood control. Site productivity determined the optimal maximum diameter.

An economic comparison of even-aged (naturally-regenerated) versus uneven-aged silviculture for pine stands in southern Arkansas was conducted by Redmond and Greenhalgh (1990). These stands often contain a shortleaf pine component. They found that the uneven-aged system could be better, if the owner has a 7% alternative rate of return and the initial stand is moderately understocked. However if the stand is severely understocked or well-stocked so that a liquidating harvest can be conducted, then even-aged management is financially superior.

SLPSS (Lynch et al. 1999) was used to perform an economic evaluation of the shortleaf pine – bluestem grass ecosystem on the Ouachita National Forest. As part of the evaluation, the value of a breeding pair of red-cockaded woodpeckers was estimated in terms of timber revenues forgone by conversion to the lower densities and longer rotation ages entailed by conversion to the shortleaf pine-bluestem grass ecosystem (Zhang et al. 2010, Huebschmann 2000). The study determined that while economic impacts of conversion to shortleaf pine-bluestem could be significant on a stand level, the regional economic impact was minimal (Huebschmann et al. 2002, 2000; Hueubschmann 2000). As part of the study, Huebschmann et al. (2004) developed a bid price equation for National Forest timber sales in western Arkansas and eastern Oklahoma.

Information for Plantations

As Murphy (1986) indicates, plantations may be categorized as old-field or non-old-field (forest or cutover). Plantation growth and yield information is often also categorized as being for thinned or unthinned stands. Many of the early southern pine plantations were established on old field sites and often were not thinned. Murphy (1986) cites a number of plantation studies published prior to 1986 for shortleaf pine. Most were inferential studies, which were not really designed to provide predictive equations for shortleaf pine growth and yield.

The size-class distribution model of Bailey and Dell (1974) is a shortleaf pine growth and yield model that provides predictive equations. This model is based on data from unthinned shortleaf pine plantations located on old field sites. The model provides stand and stock tables for various sites, age from seed, and planting density. Diameter distribution information is based on the Weibull function. The model includes equations that predict values of the Weibull diameter distribution parameters based on dominant height and surviving number of trees. It includes a survival equation that can be used to estimate surviving number of trees based on the number of trees planted from seed and dominant height. Dominant height can be estimated from site index curves for shortleaf pine plantations. The surviving number of trees per acre at a given age can be used with the Weibull distribution to predict the stand table at that age. A height-diameter equation can be used to estimate heights for each dbh class, so that cubic volumes within classes can be computed to provide predicted stock tables for given ages. The volume equation of Smalley and Bower (1968) for shortleaf plantation in the Tennessee, Georgia and Alabama highlands were used to obtain predicted stock tables based on the predicted stand tables and predicted average heights in each diameter class. Site index equations used in this yield prediction system were those of Smalley and Bower (1971) for shortleaf plantations in the highlands of Tennessee, Georgia and Alabama.

Apparently, the model of Smalley and Bailey (1974) is still the most comprehensive growth and yield model available for shortleaf pine plantations. Future research needs include up-to-date plantation models for thinned plantations on cutover land based on modern plantation establishment technology and silviculture.

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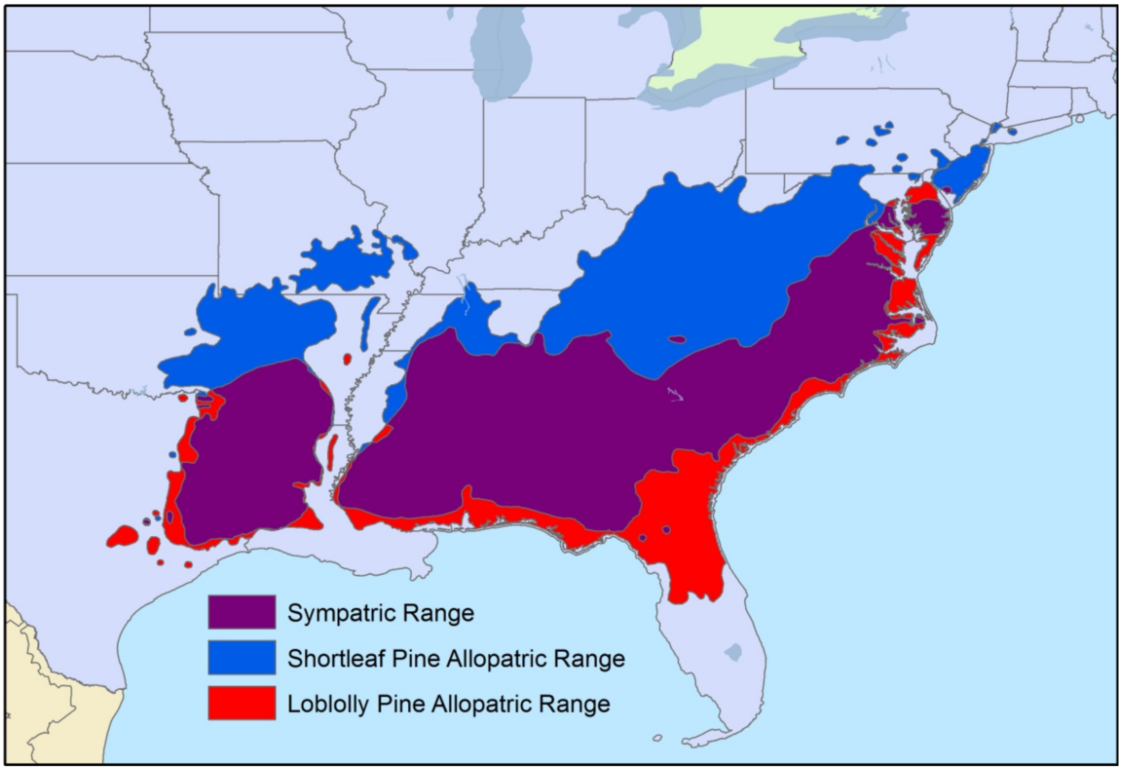

Figure 1. Range map of shortleaf and loblolly pine

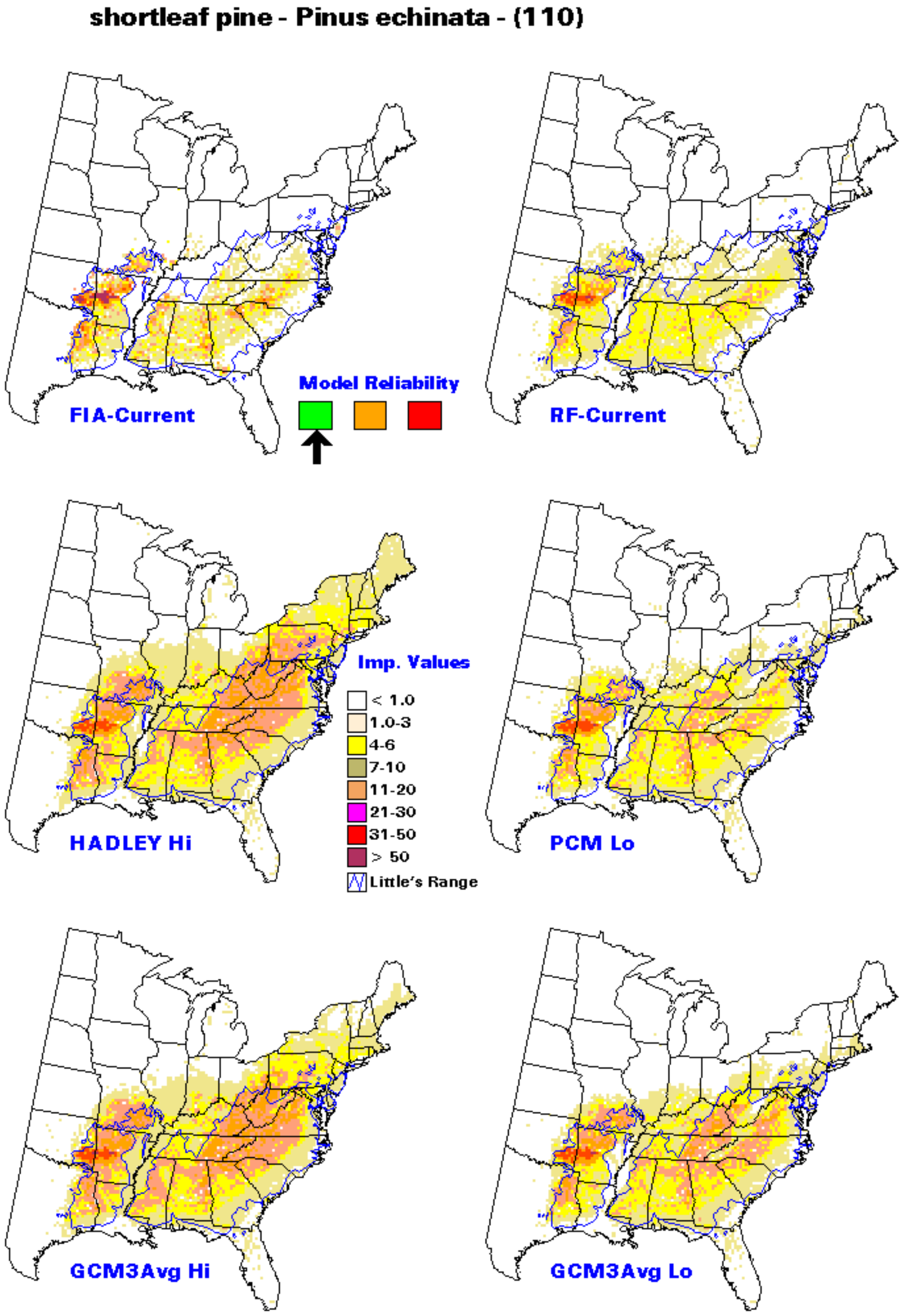

Figure 2. Summary of potential changes and differences in importance values for shortleaf pine based on the harshest scenario (Hadley Hi) & the mildest scenario (PCM Lo) ; as well as the average of all the three GCM models (Hadley, PCM & GFDL) for the high carbon and low carbon scenarios. http://www.nrs.fs.fed.us/atlas/tree/summ6pp_110.html

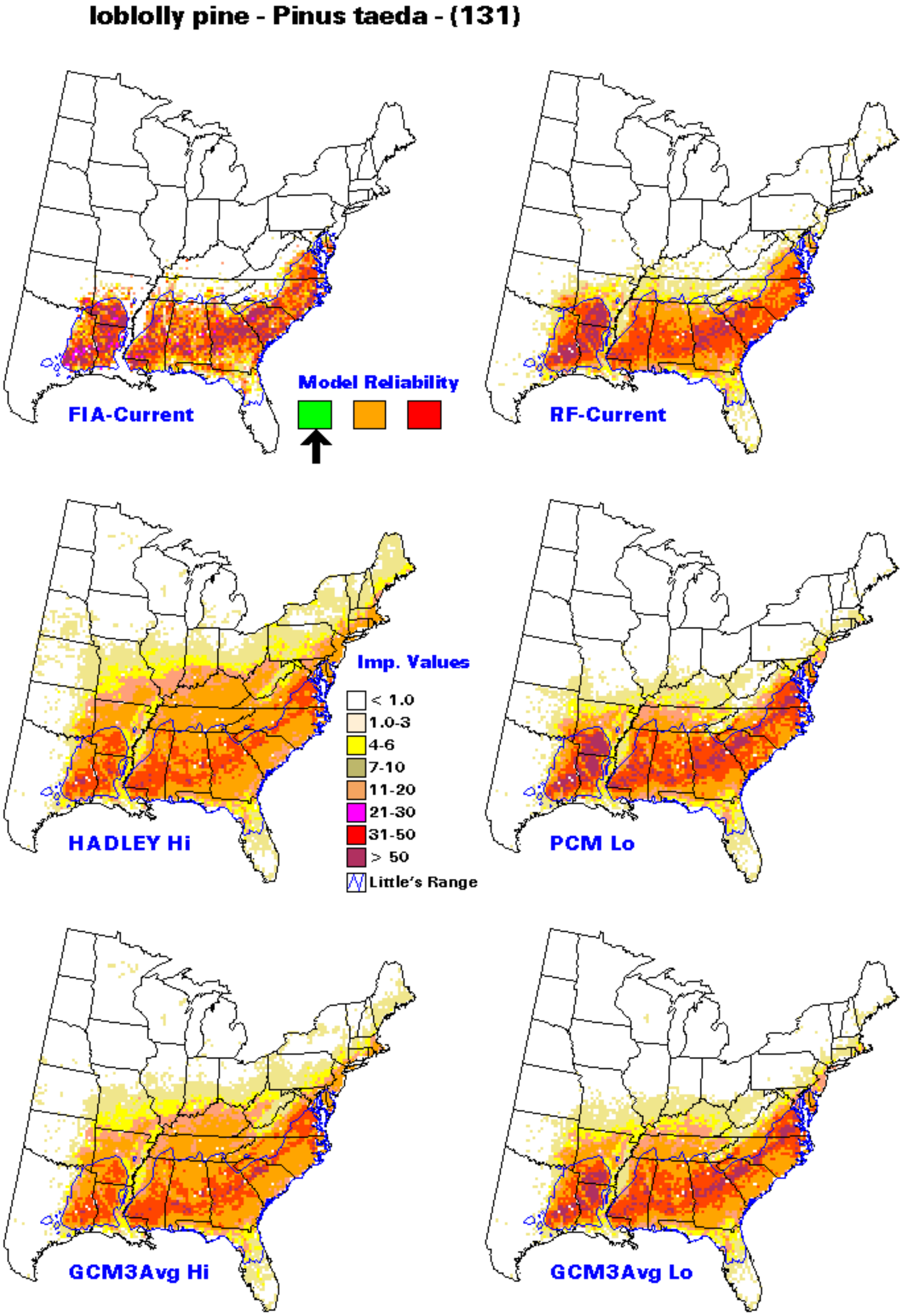

Figure 3. Summary of potential changes and differences in importance values for loblolly pine pine based on the harshest scenario (Hadley Hi) & the mildest scenario (PCM Lo) ; as well as the average of all the three GCM models (Hadley, PCM & GFDL) for the high carbon and low carbon scenarios. http://www.nrs.fs.fed.us/atlas/tree/summ6pp_131.html