Hybridization Leads to Loss of Genetic Integrity in Shortleaf Pine: Unexpected Consequences of Pine Management and Fire Suppression

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ABSTRACT

Hybridization between shortleaf pine and loblolly pine is causing loss of genetic integrity (the tendency of a population to maintain its genotypes over generations) in shortleaf pine, a species already exhibiting dramatic declines due to land-use changes. Recent findings indicate hybridization has increased in shortleaf pine stands from 3% during the 1950s to 45% for present-day natural regeneration. This drastic increase in hybridization is likely because of increased and wide-spread planting of loblolly pine and reduced selection pressure against loblolly pine and hybrids caused by fire suppression. Because shortleaf pine is more fire and drought tolerant than loblolly pine, loss of genetic integrity of shortleaf pine may reduce the resiliency and adaptability of southeastern conifer forests in the face of climate change and other stressors. Loblolly pine may also be at risk, with hybrids increasing in natural stands of loblolly pine from 4% in the 1950s to 27% at present.

Keywords: shortleaf pine, loblolly pine, hybrids, introgression

Shortleaf pine (*Pinus echinata* Mill.) and loblolly pine (*Pinus taeda* L.) are both important hard pine species (subgenus *Pinus* [diploxylon]) with extensive ranges across the southeastern United States. Shortleaf pine has the largest natural range of any of the southern pines (Little 1971) and the range of loblolly pine is smaller and more southern, but still quite extensive. Historically, the two species natu-

rally shared an extensive geographic area (i.e., were sympatric), with loblolly pine generally found on more mesic sites and shortleaf pine generally found on more xeric sites. According to Mohr (1897), shortleaf pine was more abundant in much of its range than was loblolly pine before European settlement. Schultz (1997) reported that in the original southern forests, loblolly pine was a minor species on both the up-

lands and the lowlands, but that it was more common on moist sites not subject to frequent fires.

The historical fire regime and the two pine species' response to fire is believed to have played a role in their natural distribution. Shortleaf pine was common on sites frequented by fire. Guyette et al. (2006, 2007) report a mixed intensity burn occurred on average every 8.5 years before 1810 in the Ozarks. Such fires were critical to shortleaf pine abundance, in part because of the ability of seedlings and saplings to sprout (Figure 1) when top-killed by fire (Mattoon 1915, Wright and Bailey 1982, Lawson 1990). In contrast, loblolly pine was not common on fire-prone sites (Schultz 1997), being less fire resistant, especially at the seedling and sapling stages of development (Williams 1998).

As mentioned, a large portion of loblolly pine and shortleaf pine ranges are sympatric, allowing for possible hybridization between the two species. It is thought that

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Figure 1. Shortleaf pine sprouts 60 days after top-kill by a fire that occurred on April 14, 2010 on the Big Piney Ranger District of the Ozark–St. Francis National Forest, Arkansas.

hybridization is normally prevented by different flowering times in the two species, but under certain climatic/weather conditions hybridization may occur (Dorman and Barber 1956), and natural hybrids of shortleaf pine and loblolly pine have been reported (Zobel 1953, Hare and Switzer 1969, Edwards-Burke et al. 1997 and Stewart et al. 2010). The questions are where, when, and why do they hybridize, and what are the consequences?

A Brief History of Shortleaf Pine and Loblolly Pine Management

Since the inception of pine management in the southeastern United States during the 1930s and 1940s, loblolly pine has been the favored species. Schultz (1997, p. 1–3) clearly states why: "loblolly pine is the ideal tree for site restoration and forest management" and, that loblolly pine is "the most hardy and versatile of all of the southern pines, in terms of its ability to reproduce and grow rapidly on diverse sites." In contrast, shortleaf pine has not been favored because of slow early growth, and in some places its susceptibility to littleleaf disease, caused by a complex of factors including low soil nitrogen, poor soil drainage, and the funguslike *Phytophthora cinnamomi* Rands (Dorman 1976, Mistretta 1984).

However, the primary reason for dominance of loblolly pine in southern forests today is that the species has been the backbone of southern pine tree improvement programs (for the reasons given by Shultz (1997) mentioned previously) for 50 years and has been extensively planted by forest industry. Intensive silvicultural inputs and the success of the tree improvement programs have increased yield of loblolly pine plantations from approximately 90 ft^3 ac^{-1} per year (6.3 m^3 ha^{-1} per year) in natural stands to currently over 350 ft^3 ac^{-1} per year (24.5 m^3 ha^{-1} per year) in plantations (Fox et al. 2007). These dramatic increases in growth have led to establishment of over 30 million ac of pine plantations in the southeastern United States, composed primarily of loblolly pine and to a lesser extent slash pine (*Pinus elliottii* Engelm.; Fox et al. 2006). Consequently, loblolly pine plantations have replaced natural stands of shortleaf pine, mixed shortleaf pine–upland hardwood stands, and, in particular, mixed loblolly–shortleaf pine stands in the upper Gulf Coastal Plain. In addition, loblolly pine plantations of both North Carolina and Arkansas–Oklahoma origin have been established, primarily by forest industry, outside its native range into the Interior Highlands of Oklahoma, Arkansas, and Missouri. These areas were traditionally dominated by pure shortleaf pine stands and mixed shortleaf pine–oak and oak–pine stands. As a consequence of the focus on loblolly pine through the last half of the 20th century, shortleaf pine has been largely ignored and unmanaged across much of its range, and it is diminishing in numbers of trees and stands.

The exclusion of fire has contributed to the decline of shortleaf pine in natural stands. Young shortleaf pines generally sprout after fire, whereas loblolly pine does not. Without fire on naturally fire-prone sites, loblolly pine survives and will outgrow shortleaf pine, whereas fire selectively eliminates loblolly pine regeneration (Williams 1998). In other areas, fire suppression gives later successional hardwoods an advantage. Accumulation of duff and litter as well as greater understory shading prevents shortleaf pine regeneration. In the Ozark Mountains, with fire excluded, Guyette et al. (2007) predict shortleaf pine numbers will be reduced by 80% and then stabilize within 200 years; Moser et al. (2007) reached a similar conclusion for shortleaf pine across the South. Several recent estimates are that shortleaf pine ecosystems have already been reduced by more than 40% in the last half

a century (Guldin et al. 1999, South and Buckner 2003).

One outcome of these management strategies is the juxtaposition of many loblolly pine plantations of various sources (diversified flowering times) with naturally occurring shortleaf pine stands and an increase in abundance of naturally regenerated loblolly pine in fire-prone areas previously dominated by shortleaf pine. This increased interspersion may enhance the opportunity for these two species to hybridize. If shortleaf pine is a more prolific sprouter after fire than shortleaf pine × loblolly pine hybrids, as our data suggest (Lilly et al. 2012, in press), fire suppression could also increase the chance of hybrid establishment and survival.

The probable existence of natural hybrids between loblolly pine and shortleaf pine has been a topic of discussion since at least the early 1950s (Zobel 1953), but of limited concern. Schreiner (1937) reported that viable artificial hybrids of shortleaf pine × loblolly pine had been produced at the Institute of Forest Genetics in Placerville, California, indicating that natural hybrids could occur, and, as noted earlier, because of occasional environmentally induced overlapping flowering times, some natural hybridization does occur. Extensive hybridization may lead to hybrid zones, and as hybrids are established, they can further invade shortleaf pine habitat (Buggs 2007). The questions then are how common is hybridization across the ranges of loblolly pine and shortleaf pine? Has the amount of hybridization changed over time and with forest management practices? Will hybridization have an effect on the long-term integrity of each species, and, finally, are there management opportunities to counter the impact of hybridization?

Early Notes on Hybrids

Artificial Hybrids

Early descriptions of shortleaf pine × loblolly pine hybrids relied on morphological traits. Characterization of artificial hybrids showed that the first generation (F$_1$) trees were generally intermediate compared with their parents for many of the traits examined. Little and Righter (1965) described the F$_1$ hybrids as looking something like a loblolly pine but with small cones with stout, sharp prickles, intermediate needle anatomy, and two or three needles per fascicle. Snyder and Hamaker (1978) reported shortleaf pine × loblolly pine hybrids to be

distinct and intermediate; useful identifying traits included needle length, fascicle sheath length, number of rows of stomata, needle diameter, and number of stomata per centimeter of needle length. Schultz (1997) reported that the F_1 hybrids tend to be intermediate to their parents for growth and survival. Mergen et al. (1965) noted large environmental effects, such that mean values for traits in one environment for either parent or F_1 could overlap values for the other groups in other environments. However, they noted a general tendency for intermediate values for hybrids for most traits, but that vegetative traits of hybrids tended to more closely resemble loblolly pine (the faster-growing species) than shortleaf pine. There was little indication of hybrid vigor for the cross, and all these studies were from crosses using shortleaf pine as the female parent. The reciprocal cross is considered by most to be more difficult to produce and was not studied.

Natural Hybrids

When naturally occurring trees thought to be hybrids (putative hybrids) of shortleaf pine × loblolly pine were found, the morphological traits shown as useful to identify artificial hybrids were not as helpful. For example, when Mergen et al. (1965) applied their set of traits to putative hybrids they were able to clearly separate the parents, but only 14 of the 62 individuals identified as putative hybrids fell in their hybrid category. They noted that the putative hybrids, although generally intermediate, tended to be similar to shortleaf pine in reproductive morphology but resembled loblolly pine in vegetative traits. They suggested some of the putative hybrids were backcrosses (an F_1 × to either parental species), as had Zobel (1953). Hicks (1973) took a statistical approach to the question of the most appropriate traits to use and concluded that needle length, fascicle sheath length, number of needles per fascicle, terminal bud width, cone length, and seed weight were the most useful in distinguishing shortleaf pine, loblolly pine, and their hybrids.

One reason the existence of hybrids is of interest was illustrated by the work of Abbott (1974). Because of an "atypical" loblolly pine tree in an Oklahoma State University seed orchard, he examined 19 loblolly pine and 12 shortleaf pine first-generation orchard selections. The trees were from southeast Oklahoma or adjacent areas in Texas or Arkansas, the far northwestern edge

of the natural range of loblolly pine. Abbott (1974) constructed a hybrid index using needle length, number of needles per fascicle, cone length, number of seeds per gram, and fascicle sheath length. He found that the atypical loblolly pine was intermediate for all traits, i.e., a hybrid (1 of 19 = 5%), as were three of the shortleaf pine orchard selections (3 of 12 = 25%). He concluded that hybridization must occur relatively frequently in the sampled areas. Cotton et al. (1975), looking for natural hybrids in 16 stands within a 60-mi radius of Nacogdoches, Texas, concluded that hybrids may exist but at a low frequency. Schoenike et al. (1977) reported that in the Clemson Experimental Forest, South Carolina, putative hybrids occurred at a frequency of about 1 in 10,000 trees (0.01%). Why hybrids were selected into seed orchards, in particular if they are so uncommon, is of interest. Do they have some advantage?

Early Studies of Hybrids— Hybridization Greater in Western Populations

Natural hybridization between shortleaf pine and loblolly pine has been difficult to study using morphological characters because morphology varies by individual tree and environment. Also, introgression (backcrossing and intercrossing of F_1's with other F_1's and with either parent species) occurs, which renders morphology even less reliable. Researchers thus turned to biochemical methods to resolve identification questions. Hare and Switzer (1969) analyzed seed proteins to compare eastern and western sources of loblolly pine to shortleaf pine and found that eastern loblolly pine showed 34% seed protein similarity to shortleaf pine, while western sources of loblolly pine showed 88% similarity. They concluded that the frequency of hybridization was variable across the sympatric portion of these species' ranges, but higher in the West. Florence and Hicks (1980) used seed megagametophyte protein banding patterns to examine putative hybrids and concluded that introgression did occur, probably with most gene flow from loblolly pine into shortleaf pine.

Using isoenzymes, Edwards and Hamrick (1995) and Raja et al. (1997) also noted that western populations exceeded eastern populations in the level of hybridization between shortleaf pine and loblolly pine. Raja et al. (1997) reported 16% of the trees from

western populations were hybrids as were 4% in eastern populations.

When Raja et al. (1998) sampled stands of shortleaf pine in the Mount Ida, Arkansas, area in the early 1990s they found 15% of trees to be hybrids. The samples were seed from trees in what were thought to be pure natural shortleaf pine stands, several miles north of any native loblolly pine. To confirm or discount these results, Chen et al. (2004) sampled native pine stands across a southeast to northwest transect of Montgomery County, Arkansas, which included Mount Ida. These stands were mixed loblolly pine/shortleaf pine in the southeast part of the county and pure shortleaf pine, up to 20 mi north of the closest known loblolly pine stands, in the northwest corner of the county. Chen et al. (2004) concluded that the percentage of hybrid trees was relatively high (12.5%) but showed no apparent pattern across the sample transect. Chen et al. (2004) found apparent hybrids in shortleaf pine stands beyond the natural range of loblolly pine, as had Edwards and Hamrick (1995) and Raja et al. (1997).

Xu et al. (2008a) and Stewart et al. (2010) reported that the Isocitrate Dehydrogenase (*IDH*) isoenzyme locus alone was not entirely reliable in identifying hybrids, which some of the earlier studies had relied on, at least in part. Still, almost all studies on hybridization between loblolly pine and shortleaf pine have observed more hybridization west of the Mississippi River than east of it (Hare and Switzer 1969, Edwards and Hamrick 1995, Raja et al. 1997, Xu et al. 2008a). Stewart et al. (2010), used 42 microsatellite markers and the *IDH* locus and reported similar results, that 4.5% of loblolly pine grown from seed collected in the 1950s Southwide Southern Pine Seed Source Study (SSPSSS) were hybrids with shortleaf pine, 3.3% east of the Mississippi River and 9.1% west of the river. Similarly, 3.3% of the shortleaf pine, also of SSPSSS origin, was hybrids, 0 and 7.5% east and west of the Mississippi River, respectively. Most likely, more hybridization in the west is caused by a more variable climate, as weather affects the timing of pollen shed and strobili receptivity (Dorman and Barber 1956).

Stewart et al. (2010) also found apparent hybrids in shortleaf pine stands beyond the natural range of loblolly pine. Why are these hybrids occurring?

Recent Studies of Hybrids

Important questions remain: Is the level of hybridization changing and if so, is it anthropogenically induced. What effect will increased levels of hybridization have on the long-term integrity of these species? If intensive management of loblolly pine throughout the sympatric range of these two species is in part responsible for the high level of hybridization found, are there serious implications regarding shortleaf pine management? Will the potentially overwhelming loblolly pine background pollen cloud put the future of the shortleaf species at risk?

Recent studies by Xu et al. (2008b) and Stewart et al. (2010, 2011, 2012) were designed to estimate and compare levels of hybridization present in the 1950s rangewide samples of loblolly pine and shortleaf pine (the SSPSSS plantings) with levels found in present-day natural regeneration of loblolly pine and shortleaf pine sampled from the same counties. Stewart et al. (2011) also compared the level of hybridization in native pure shortleaf pine stands of varying distance from an area of intensive loblolly pine management.

Results and Implications—Population Genetics, Large Changes

Genetic measures of intraspecies population differentiation are important and of interest because they reflect the genetic health and integrity of the populations. Population differentiation is a measure of how much of the species' diversity originates among populations versus how much is found within populations. Species with low population differentiation, such as outcrossing wind-pollinated forest trees such as shortleaf pine, can be expected to have low population differentiation (0–10%), because genes can move relatively freely through the range. Species with more isolated populations can be expected to have high population differentiation (80–100%), indicating that the populations are more distinct from each other. Population differentiation is measured using genetic data (microsatellites, amplified fragment length polymorphism, morphological characters, and more) and a mathematical model. Analysis of the SSPSSS data showed that intraspecies population differentiation nearly doubled in both shortleaf pine and loblolly pine from the 1950s (Stewart et al. 2010, Xu et al. 2008a) to present day (Stewart et al. 2012). These genetic changes suggest that most populations of both species are becoming more distinct, i.e., populations are increasing in genetic differentiation from other populations of the same species, relative to what is considered "normal" for pine species. Increased population differentiation can lead to a loss in genetic diversity in a species and may be caused by an increase in hybridization levels, habitat fragmentation, management practices, and/or changes in selective pressures due to the suppression of fire (Stewart et al. 2012).

The southeastern United States is an intensively managed landscape, including many disturbances that interrupt what was once a more contiguous forest. Knapp et al. (2001) and Sork et al. (2002) have shown that wind-dispersed pollen typically contributes little or nothing to distant trees, making habitat fragmentation a potential cause of population differentiation. Jump and Peñuelas (2006) reported population differentiation was higher in fragmented forests than in continuous ones. Measures of population differentiation are approximately inversely related to gene flow, so as habitat fragmentation reduces gene flow, population differentiation will increase. Forest managers should be aware of the effects of forest fragmentation on naturally regenerated pines.

The present-day extensive plantations of loblolly pines throughout the southeastern United States produce very large pollen clouds that will move into nearby remnant stands of native shortleaf pine and loblolly pine. Raja et al. (1998) observed that artificial regeneration (seed from a seed orchard) decreased population diversity while natural regeneration enriched diversity in shortleaf pine. Because these pollen clouds from pine plantations will be genetically less heterogeneous than those in naturally regenerating pine stands, the result will be a general stand level reduction in pollen diversity. The effect could increase population differentiation of remaining loblolly pine and shortleaf pine natural stands.

For decades forest management practices have emphasized fire suppression. Removing fire from an ecosystem adapted to its presence upsets the balance of that ecosystem. Shortleaf pine and loblolly pine are both considered fire resistant, but shortleaf pine is considerably more so at a young age because shortleaf pine seedlings more readily sprout after top-kill (Mattoon 1915, Wright and Bailey 1982, Lawson 1990). Changes in the role of fire in the ecosystem may change the rate at which each species expands or fails to do so, because both species are early successional and require bare mineral soil for germination and full sun for maximum growth (Waggoner 1975, Baker and Langdon 1990, Lawson 1990). For shortleaf pine, lack of fire could isolate stands, reduce regeneration success, increase the hardwood component, favor loblolly pine as the pine component, and perhaps increase the success of shortleaf pine loblolly pine hybrids, thus increasing population differentiation.

Stewart et al. (2010) reported that the correlation of genetic distance and geographic distance (i.e., a measure of the relationship between the degree of genetic differences from population to population and their physical separation) from the 1950s to present-day samples increased in shortleaf pine but decreased in loblolly pine. For shortleaf pine, the increase in correlation makes sense in light of the increase in population differentiation. The shortleaf pine populations are losing diversity.

A decrease in the correlation of genetic distance with geographic distance in loblolly pine is possibly caused by the increasing use of genetically improved loblolly pine in plantations. Because a limited number of genetic sources are planted across extensive areas, the geographic diversity of loblolly pine could decrease, as shown for shortleaf pine artificial regeneration (Raja et al. 1998). There are two primary tree improvement cooperatives for loblolly pine that produce genetically improved loblolly pine seed to produce seedlings for planting across much of the South. Even though the cooperatives maintain diverse breeding populations, extensive plantings of genetically improved material (generally about 20 open-pollinated families per orchard) will reduce the diversity of the pollen clouds and the subsequent genetic diversity of naturally regenerated stands.

Results and Implications— Hybridization, a Dramatic Increase

Stewart et al. (2012) found that hybridization and introgression in present-day natural regeneration of both shortleaf pine and loblolly pine was very high: 114 hybrids of 316 sample trees, 36.1% compared with 4.0% in the 1950s (Figure 2). Loblolly pine showed an increase from 4.5% hybrids in the 1950s to 27.3% in present day, and shortleaf pine increased from 3.3 to 45.7%. The dramatic increase in hybrids was observed across the range of both species (it is important to note that the re-collections
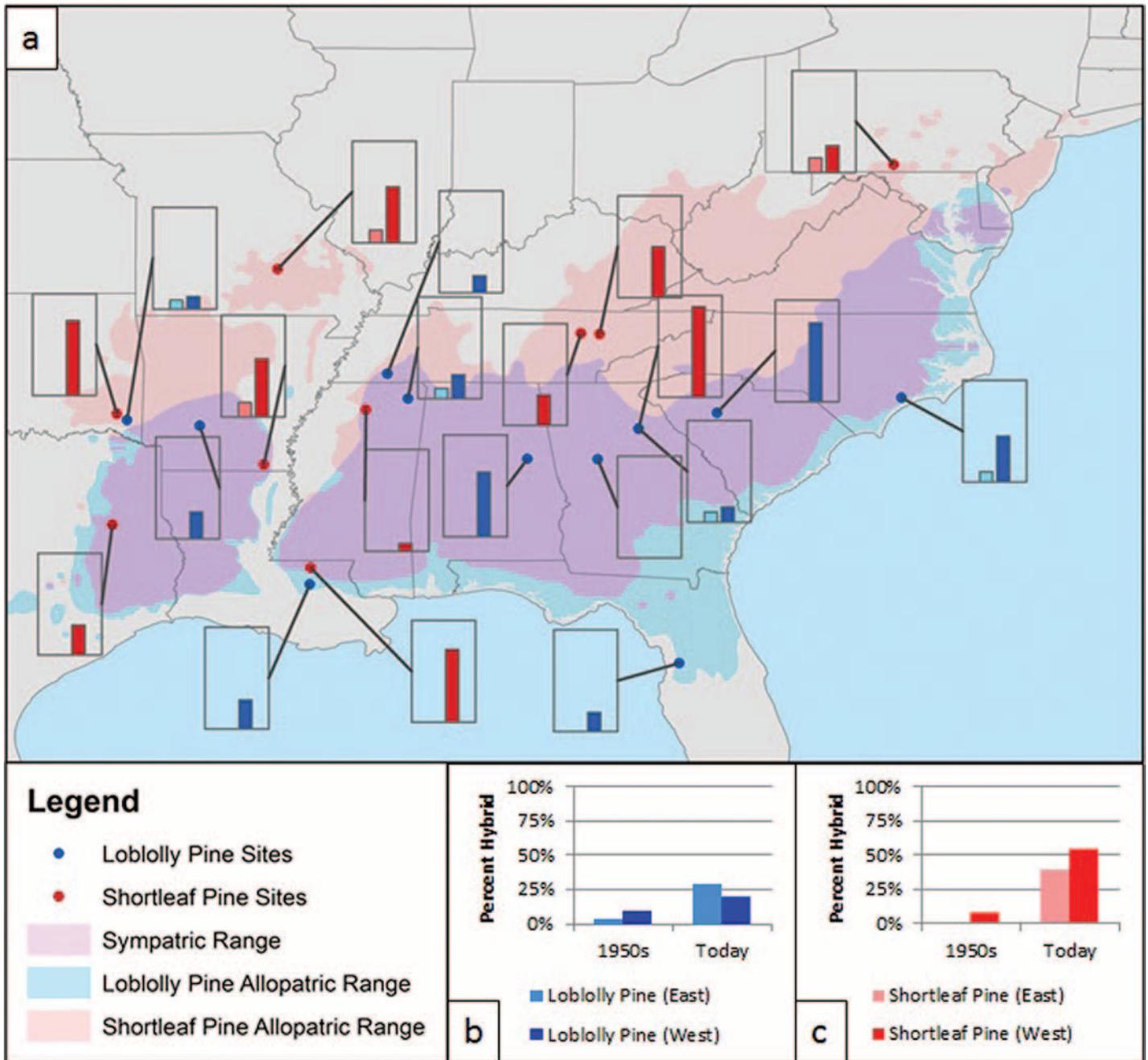
Figure 2. Hybrid proportion of shortleaf pine and loblolly pine over time and range. The rate of hybridization of loblolly pine and shortleaf pine has increased since the 1950s. (a) Map of the ranges of loblolly pine and shortleaf pine, including their sympatric (or shared) range, along with sample sites. The graphs indicate premanagement hybrid percentages on the left and present-day hybrid percentages on the right. The height of each graph is 100% hybrid. (b and c) The percentage of individuals with hybrid character from premanagement trees and modern trees for (b) loblolly pine and (c) shortleaf pine.

were done by species and were to be representative of that species, as were the 1950s SSPSSS collections; so if there was a bias, it would have been against hybrids). Except for a single loblolly pine population sample from Georgia, all populations of present-day samples of natural regeneration contained hybrid trees. The percentage of hybrids ranged from a low of 7.7% hybrids in a Mississippi shortleaf pine stand to 88.9% in a Georgia shortleaf pine stand. Hybrids among loblolly pine east of the Mississippi River increased from 2.3 to 29.2%, and west of the river from 9.1 to 20%. Hybrids among shortleaf pine east of the Mississippi increased from 0 to 39.8% and west of the river from 7.5 to 54%. Of these hybrids in the present-day samples, 4.4% were first-generation (F_1) trees, 2.4% in loblolly pine populations and 6.6% in shortleaf pine populations. No first-generation hybrids were found in the 1950s samples.

Hybridization can threaten a taxon in a variety of ways, through the generation of poorly adapted hybrids, the generation of hybrids with greater vigor than one or both of the contributing species, or the introgressive extinction of one or both species (Simberloff 1996, Allendorf et al. 2001). Discovering whether introgression is a natural

process or anthropogenic is crucial to understanding how or whether to manage the issue (Allendorf 2001). Given the timescale (about 55 years) for the large increase in introgression Stewart et al. (2012) reported it is almost certainly in large part human caused.

Human causes for introgression include introduction of other species, habitat fragmentation, and habitat modification (Allendorf and Luikart 2007). All these may have had an impact on loblolly pine and shortleaf pine. Loblolly pine is being planted outside of its range and as a replacement for shortleaf pine harvested or lost through natural succession. Stewart et al. (2010, 2012) have reported high levels of introgression of loblolly pine genes into shortleaf pine in the Pennsylvania and Missouri allopatric populations, as well as across its sympatric range. This is indirect evidence that human plantings of loblolly pine (e.g., Maple 1966 reports on 15-year-old loblolly pine planted in northern Arkansas) have affected the genetic makeup of naturally regenerating shortleaf pine, because the closest naturally occurring loblolly pine pollen sources are approximately 75+ mi distant in Pennsylvania and 100+ mi in Missouri. Long-distance wind transport of pollen can not be dismissed as a possibility, but it is highly unlikely to have had a significant effect on the occurrence of hybrids (Dyer and Sork 2001, Bohrerova et al. 2009). Hybrids in loblolly pine populations were also found across its range.

Habitat fragmentation may lead to the isolation of populations, but it can also result in the mixing of previously distinct gene pools (Rhymer and Simberloff 1996). For loblolly pine and shortleaf pine, habitat fragmentation could cause an increased level of cross-pollination. The time periods for pollen flight and female strobili receptivity of both species generally do not overlap but may occasionally because of unusual seasonal weather conditions. However, if habitat fragmentation isolates local populations, female strobili may show extended receptivity (Schultz 1997) and might even be pollinated by another species. The extensive planting of nonlocal loblolly pine may also increase the overlap of pollination and receptivity times. The timing of pollen shed and strobili receptivity of these nonlocal sources on nonnative sites is not known; however, the Woodbridge et al. (1995) heat sum model suggests local conditions might strongly influence nonlocal source flowering timing to be close to local. Schmidtling's

Figure 3. Sample differences in the degree of basal crook expression as exhibited in loblolly pine (left), hybrid (center), and shortleaf pine (right).

(1971) common garden observations on shortleaf pine showed all sources, from New Jersey to Louisiana, with overlapping flowering in a Mississippi planting, which also suggests that the nonlocal sources should be very close to the local in flowering time. Nevertheless, just a few days difference could result in overlap and hybrids.

Habitat modification can create corridors for the two species to more often enter each other's habitat (Rhymer and Simberloff 1996). For loblolly pine and shortleaf pine, a large sympatric range already existed, but the two species maintained somewhat different niches, with loblolly pine on mesic sites where fire was uncommon and shortleaf pine commonly on xeric and fire-prone upland sites. Habitat modification, in particular extensive planting of loblolly pine in shortleaf pine habitats, could create corridors between loblolly pine and shortleaf pine habitats that in the past did not exist and were maintained by fire.

Climate change has the potential to affect the ranges of loblolly pine and shortleaf pine, and perhaps increase the co-occurrence of the species. Climate change has already been implicated in the creation and movement of hybrid zones and introgression (Buggs 2007). Potential warmer springtime temperatures could accelerate shortleaf pine pollen shed and increase the overlap of the two species' flowering times, with a subsequent increase in hybridization. In addition, climate change could result in hybrid zones, where the hybrids actually have an advantage over one or both parents.

The removal of fire as a selection pressure to eliminate nonfit phenotypes is another possible reason for an increased number of hybrid individuals. Fire kills loblolly pine regeneration, but has little effect on shortleaf pine regeneration due to its ability to sprout (Williams 1998). Hybrids do not sprout as vigorously as shortleaf pine and do not have the fire survival adaptation of a basal crook (Figure 3; Lilly et al. in press, Liu et al. 2011); consequently, regular fires should reduce the frequency of hybrids. Lilly et al. (2012, in press) also noted that shortleaf pine × loblolly pine hybrids appear to combine the faster growth rate of loblolly pine and some of the drought tolerance of shortleaf pine. These results suggest fire suppression would favor survival of hybrids and their growth rate would make them competitive; consequently, the proportion of hybrids in regenerating populations would increase over time, and as we have seen, could result in more hybrids than in the past.

In a study of the effects of proximity of loblolly pine plantations on introgression in

naturally regenerating shortleaf pine, Stewart et al. (2011) estimated the level of hybridization in native shortleaf pine mature and sapling populations of varying distances from an area of intensive loblolly pine management. The sample area, the Caney Creek Wilderness Area near Mena, Arkansas, is a relatively undisturbed, naturally regenerated shortleaf pine–dominated wilderness area. Stewart et al. (2011) reported that the percent of hybrids for both mature and sapling populations showed significant positive correlations with proximity to the loblolly pine plantations. They also reported a significant positive correlation between geographic distances and genetic distances (a measure of differences) among the populations. For stands that were only 0.2–6.2 mi from the nearest loblolly pine plantations, such correlations with distance are of note. These data show that the level of hybridization among the populations decreased with distance from the loblolly pine plantations.

The Stewart et al. (2011) Caney Creek Wilderness data suggest that even a short distance of a few miles or less is important to limiting interspecific hybridization between loblolly pine and shortleaf pine. It is worth note that over the last 80 or more years the level of hybridization has apparently not changed significantly in these populations, except perhaps for a small increase in the number of hybrids at the southern edge of this area where loblolly pine plantations are only 0.2 mi away. The authors suggest that a mile or so distance between shortleaf pine and loblolly pine may be sufficient to minimize hybridization. Stewart et al. (2011) suggest the Caney Creek Wilderness example illustrates how local conditions and distance can affect local hybridization levels.

Conclusions

Although increased hybridization will have little effect on plantation management that uses artificial regeneration using improved genetic stock, hybridization may have negative effects on our natural forest ecosystems. Loblolly pine, shortleaf pine, and their hybrids likely provide many of the same structural and functional roles within forests. However, introgression, particularly into shortleaf pine, may reduce the resilience of our southeastern forests if the hybrids are intermediate in physiological and morphological traits. Shortleaf pine is more drought tolerant, more tolerant of fire, and potentially more tolerant to temperature extremes, thus better able to survive and grow

under possibly harsher climatic conditions in the future. The uncertainty of future climate conditions and future management actions make it particularly important to maintain the full range of genetic potential within our natural populations.

Management and other human activities may be stressing the genetic integrity and reducing the genetic diversity of our southern pines, shortleaf pine in particular. South and Buckner (2003) reported that in the 1990s, over 21 million ac of loblolly pine was planted or direct seeded, often with nonlocal material, while during that same time period less than 500,000 ac of shortleaf pine were established. Since 1990 the total pine plantation acreage has increased to over 30 million ac, mostly because of additional establishment of loblolly pine plantations (Fox et al. 2006). Clearly, loblolly pine plantations are displacing natural pine forests, including forests that had varying components of shortleaf pine. At the same time, Smith et al. (2001) report that more than 70% of the roughly 21 million ac of forestland lost in the South in the 20th century was formerly southern yellow pine. No doubt much of this land was previously forest containing some shortleaf pine as well. The net result is an estimated 40% decline in shortleaf pine acreage in the 20th century (South and Bucker 2003). Increased landscape fragmentation through increased population density and exurban development may further stress the genetic integrity and diversity of native pine species (Wear 2002).

The consequences of human development and management activities in the forests of the southeastern United States are many, including

1. Many stands of native shortleaf pine have been harvested and replaced with loblolly pine plantations, or in the absence of fire and management, replaced by hardwoods.
2. There is less natural regeneration of loblolly pine, and what does occur is reduced in diversity by pollen from extensive plantations of improved loblolly pine of lowered diversity.
3. There is little natural regeneration of shortleaf pine across much of its range because of land-use change and fire suppression, and what does occur is reduced in diversity.
4. This loss in abundance of natural stands of shortleaf pine and loblolly pine has nearly doubled intraspecific population

differentiation in both species, confirming that genetic integrity, i.e., the tendency of a population to maintain its genotypes over generations, in remaining natural stands of both species is being lost.

5. Hybridization and introgression in samples of present-day natural regeneration of both species is very high. In loblolly pine an increase from 4.5% hybrids in the 1950s to 27.3% in present-day samples, a 600% increase. In shortleaf pine, hybrids increased from 3.4 to 45.7%, a 1,300% increase.
6. The abundance of loblolly pine plantings around remnant shortleaf pine leads to increased hybridization. However, even a limited separation of just a few miles or less may significantly reduce hybridization levels.
7. Lack of fire appears to favor encroachment of loblolly pine on natural shortleaf pine sites, reducing shortleaf pine numbers and thus diversity.
8. Lack of fire may convey a hybrid advantage in that hybrids tend to grow fast like loblolly pine, retaining some of the drought hardiness of shortleaf pine. However, hybrids have a poorly developed crook and are less well adapted to fire than pure shortleaf pine.

Through habitat modification, climate change, fire suppression, and seed/seedling movement via artificial regeneration, human activity is altering the genetic makeup of native stands of loblolly pine and shortleaf pine. Management practices regarding these two species need to be reexamined to determine their ecological efficacy. Loblolly pine and shortleaf pine managers should consider factors such as terrain, climate, fire regime, and other local conditions that may affect hybridization levels. Guldin (2007) states that fire is needed to restore shortleaf pine, and we think fire may also serve to remove most hybrids and help retain the genetic integrity of shortleaf pine. To that end, reintroduction of fire or maintaining active prescribed burning programs, especially at a large scale in contiguous unfragmented forest conditions, is probably the best chance to maintain a resilient native forest and retain shortleaf pine as a significant structural and functional component of southern pine forests into the future.

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