Shortleaf Hybridization: Should We Be Concerned?

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Hybridization and Introgression Defined

Occasionally, closely related species can hybridize, that is fertilize each other and produce offspring that have a mixture of genes from both parent species. Some hybrids are themselves infertile or poorly adapted, such as the mule (a hybrid of a male donkey and a female horse that cannot sire nor bear offspring). Many hybrids, however, can reproduce. Shortleaf pine x loblolly pine hybrids are fertile with both parent species and other hybrids.

A backcross occurs when a hybrid sexually crosses with a parent species. The resulting offspring will have ¾ of their genes from that parent species, because half of their genes come from the non-hybrid parent and the other half come from the parent that has 50% of both species' genes (Fig. 1). Repeated hybridization and backcrosses result in a process known as introgression. Introgression can result in the movement of genes from one species to another or the blurring of the distinctions of species.

Many plant and animal species are threatened or have gone extinct from hybridization and introgression.[4]

Shortleaf Pine Hybridization

Hybridization naturally occurs between shortleaf pine and loblolly pine.[3] About 4% of shortleaf pine trees grown from seed collected in the 1950s had significant hybrid character.[11,5] Generally, more hybrids are observed west of the Mississippi River than east of it, presumably because weather is more variable in the west, and that may cause shortleaf pine to flower later or loblolly pine to flower earlier, allowing an overlap in fertility periods.[1] However, by the turn of the twenty-first century, the frequency of hybrids increased to 47% among seedlings identified as shortleaf pine (Fig. 2).[6]

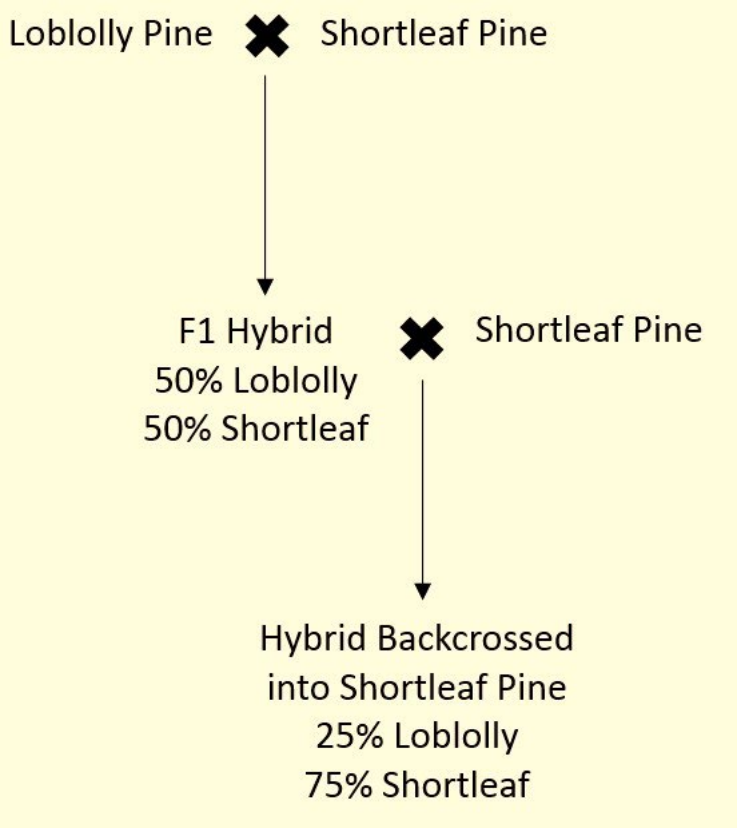

Figure 1: An F1 hybrid occurs when a shortleaf pine and loblolly pine cross. When an F1 hybrid crosses with a parent species, the resulting offspring are considered to be backcrossed.

Shortleaf-loblolly hybrids are described as having "…a definite trend toward intermediacy2..." In general, hybrids have needles that are of intermediate length relative to the parent species and have two or three needles per fascicle (as opposed to 3 needles per fascicle for loblolly pine and 2 and occasionally 3 needles per fascicle for shortleaf pine). Hybrids demonstrated grow rate similar to loblolly pine and had water use efficiency and an ability to resprout after topkill that was similar to that of shortleaf pine.[2,7]

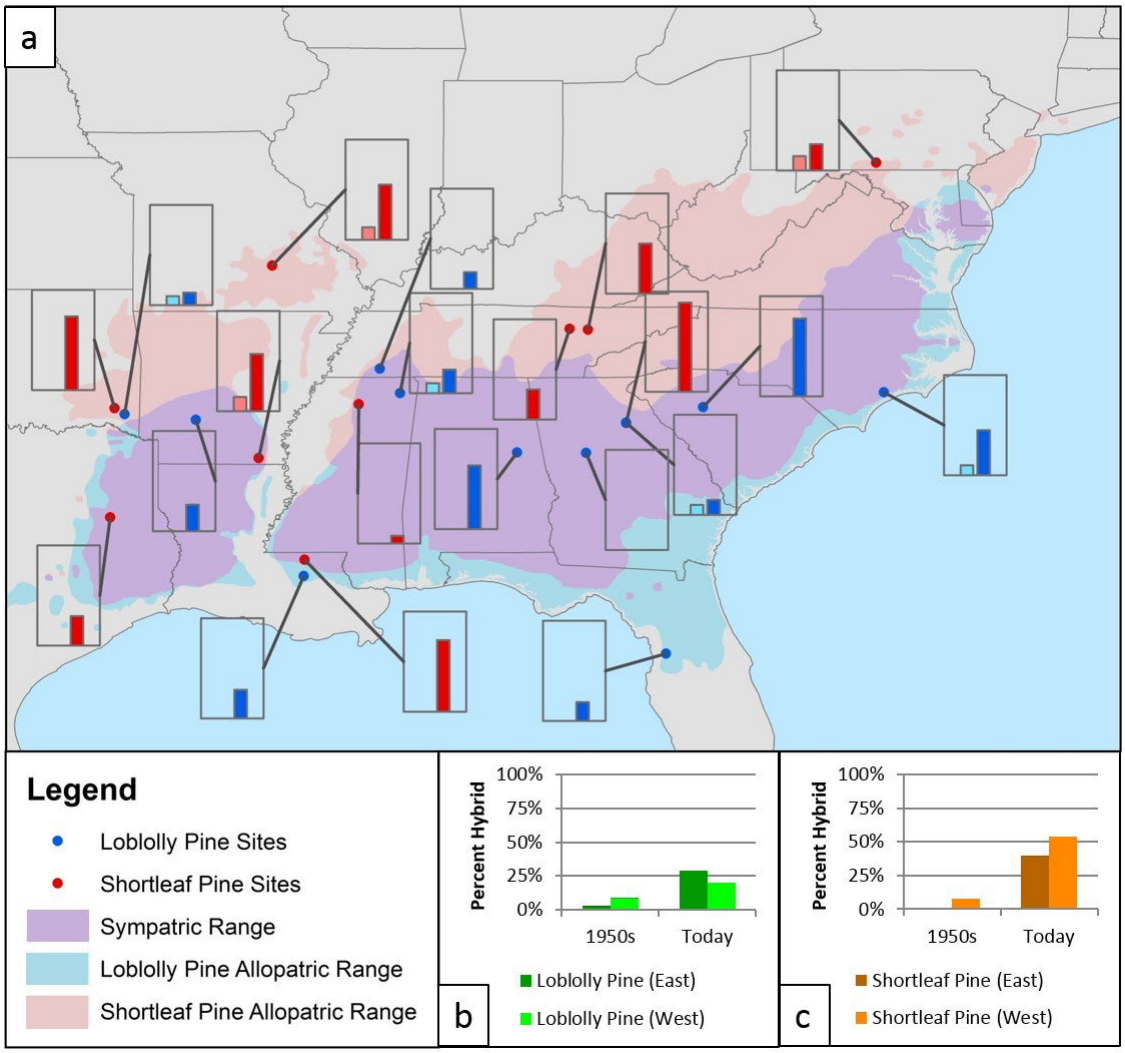

Figure 2: The rate of hybridization between shortleaf pine and loblolly pine increased dramatically in sites across the ranges of both species. The map (a) indicates the allopatric and sympatric ranges of shortleaf pine and loblolly pine. The sites indicated on the map correspond to locations sampled in the 1950s and in the 2000s. The bar graphs indicate the frequency of hybrids at each site, with the 1950s samples on the left and the 2000s samples on the right and the top of each box representing 100%. Hybridization occurred both east and west of the Mississippi River in (b) loblolly pine sites and in (c) shortleaf pine sites. Source: Tauer et al., 20129

Some hybrids exhibited an intermediate basal crook.[2] The basal crook is a bend in the stem of shortleaf pine saplings and seedlings that lowers a segment that contains dormant buds to the surface of the soil where it is covered by soil and duff. The location of the buds below or near the soil surface helps protect them from damage due to fire and presumably facilitates resprouting. The intermediate crook, however, does not lower the tissue very much at all, so it does not appear to be effective in allowing the hybrids to recover from fire (Fig. 3). One study showed that continued biennial prescribed fire eliminates loblolly pine and hybrids from open canopy woodlands.[7]

Studies suggest that since dramatic change in hybridization has occurred over the last 50 years, it likely originates from human activity.[6] Factors such as habitat fragmentation (the interruption of once continuous forests with fields, towns, and other land uses), habitat modification (altering terrain features for roads, reservoirs, and so on), planting of loblolly pine on shortleaf pine sites, and hybridization in seed orchard genetic sources may be contributing to increased incidence of cross fertilization. Fire exclusion from the southeastern United States, which historically had a frequent fire return interval, allows hybrids to persist on shortleaf pine sites once the hybrids become established.[10]

Management Options for Reducing Hybridization and Introgression

Shortleaf pine was once the dominant pine species across much of the southeastern United States. Nonindustrial private landowners should be encouraged

Figure 3: The basal crook is an important adaptation to fire in shortleaf pine (right). Loblolly pine (left) lacks a basal crook, and hybrids have an intermediate crook (middle) that does not lower the buds beneath the surface to protect them from fire. Credit: Curtis Lily

to plant and maintain shortleaf pine when objectives related to productivity are not the primary concern. Shortleaf pine seedlings currently available from commercial sources are largely free of hybrids.[7]

While slower growing than loblolly pine, shortleaf pine is more resilient to disturbance and potential climate change.

Prescribed fire can be used to eliminate hybrid and loblolly pine seedlings and saplings from shortleaf pine dominated sites.[8] It should be noted that the window of opportunity to kill hybrids and unwanted loblolly pines using prescribed fire is only during the seedling and sapling stages. Once larger, loblolly and hybrid pines are less susceptible to fire, because their thick bark protects them from fire.

Prescribed fire must be incorporated into efforts to conserve or restore shortleaf pine. Governmental and nongovernmental agencies such as the US Forest Service, state forestry, and The Nature Conservancy will play a crucial role as they have the ability to manage landscapes with prescribed fire. Using fire is problematic across landscapes with fragmented ownership or near cities and towns where large-scale and frequent burning is difficult to accomplish. Shortleaf pine is more drought, fire, cold, and ice tolerant than loblolly pine. These attributes of shortleaf pine increase resilience of southeastern forests, and diluting these shortleaf pine traits through hybridization and introgression may increase the threat posed by disturbances such as wildfire, drought, and climate change.

References

[1]Dorman K.W., Barber J.C. 1956. Time of flowering and seed ripening in southern pines. Paper 72, U.S. Forest Service Southern Experimental Station. 17pp.

[2]Lilly, C.G., Will, R.E., and Tauer, C.G. 2012. Physiological and morphological attributes of shortleaf x loblolly pine F1 hybrid seedlings: is there an advantage to being a hybrid? Canadian Journal of Forest Research. 42:238-246.

[3]Mergen F., Stairs G.R., Snyder E.B. 1965. Natural and controlled loblolly x shortleaf pine hybrids in Mississippi. Forest Science. 11: 306-314.

[4]Rhymer J.M., Simberloff D. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics. 27: 83-109.

[5]Stewart J.F., Liu Y., Tauer C.G., Nelson C.D. 2010. Microsatellite versus AFLP analysis of pre-management introgression levels in loblolly pine (Pinus taeda L.) and shortleaf pine (Pinus echinata Mill.) Tree Genetics and Genomes. 6:853-862.

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

[7]Stewart J.F., Will R.E., Robinson K.M., Nelson C.D. Work under way.

[8]Stewart J.F., Will R.E., Robinson K.M., Nelson C.D. 2014. Frequent fire protects shortleaf pine (Pinus echinata) from introgression by loblolly pine (P. taeda). Conservation Genetics. DOI 10.1007/s10592-014-0669-x.

[9]Tauer C.G., Stewart J.F., Will R.E., Lilly C.J., Guldin J.M., Nelson C.D. 2012. Hybridization leads to loss of genetic integrity in shortleaf pine: unexpected consequences of pine management and fire suppression. Journal of Forestry. 110: 216-224.

[10]Will R.E., C.J. Lilly, J. Stewart, S. Huff and C.G. Tauer. 2013 Recovery from topkill of shortleaf pine X loblolly pine hybrids compared to their parent populations. Trees: Structure and Function. 27:1167–1174.

[11]Xu S., Tauer C.G., Nelson C.D. 2008. Natural hybridization within seed sources of shortleaf pine (Pinus echinata Mill.) and loblolly pine (Pinus taeda L.) Tree Genetics and Genomics. 4: 849-858.