

Updates on Longleaf Pine Ecology, Restoration, and Management

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Longleaf pine (*Pinus palustris* L.) forests and woodlands represent one of the world's most unique and biologically diverse ecosystems [1,2]. The longleaf pine ecosystem was historically one of the essential ecosystems in the southeastern United States due to its social, ecological, and economic value. Before European settlement, the longleaf pine ecosystem occupied 37 million hectares, ranging from eastern Texas to southeastern Virginia [3]. However, after European settlement, through extensive exploitation, fire suppression, and land use change during the 19th and 20th centuries, longleaf pines have become an endangered ecosystem in the United States [4]. After decades of restoration, the longleaf pine ecosystem currently reaches about 1.9 million ha [5].

The longleaf pine ecosystem provides high-quality timber and related forest products and an excellent wildlife habitat [6]. At present, some endangered species are dependent on this ecosystem, such as the red-cockaded woodpecker (*Picoides borealis*), gopher tortoise (*Gopherus polyphemus*), and black pine snake (*Pituophis melanoleucus*) [7]. In addition, longleaf pine forests have significant potential for carbon storage [8], as trees can reach a lifespan of up to 450 years [9]. Conserving and restoring longleaf pine forests has become the priority of natural resource management in the southeastern United States. Thus, it is necessary to study the longleaf pine ecology. This Special Issue selected nine papers that aim to discuss new knowledge of longleaf pine forests from different perspectives to achieve the sustainability of this species and its ecosystem.

The existence of longleaf pine relies on its sporadic seed production. Based on the observations of cone production and tree diameters from individual trees at multiple sites across the historical range in the previous years, Chen and Willis [10] found that three-year cycles dominate cone production dynamics; however, other cycles also exist. Taylor's law, the correlation between average and variance, is applicable in cone production for most trees. No significant correlation was found between tree diameter (or basal area) growth and cone production among trees across sites. These results provide new information on cone production at the individual tree level and narrow down the possible biological mechanisms. The results may be used in developing strategies for managing and modeling longleaf pine cone production.

The longleaf pine ecosystem needs periodic prescribed burning to suppress competition from broadleaf trees. Without prescribed burning, longleaf pine forests gradually degrade into broadleaf forests. Here, Gilliam [11] examined the effects of fire exclusion on longleaf pine in a unique urban interface of a university campus with remnant longleaf pine stands (University of West Florida Campus). Due to chronic fire exclusion, the open-canopy longleaf pine forests were transitioned into closed-canopy forests with the increased prevalence of broadleaf trees, such as *Quercus virginiana* and *Magnolia* spp., resulting in the complete absence of longleaf pine regeneration. The exclusion of prescribed burning also appeared to decrease soil fertility (e.g., increases in acidity). It is a fact that the longleaf pine is a fire-dependent ecosystem. However, frequent prescribed burning (e.g., 3–5 years)



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needs more trained burners, and the burnings affect the local environment (e.g., air and water pollution).

Historically, longleaf pine forests and woodlands dominated the Coastal Plain of the southeastern region of the USA. However, there were spatial and temporal changes in the distribution of the longleaf pine ecosystem due to over-harvesting, fire exclusion, and land use change (for agricultural development). Hanberry et al. [12] analyzed the combined data of 255,000 trees from land surveys between 1810 and 1860 with other historical descriptions in the past two centuries to quantify longleaf pine's distribution and change. They found that longleaf pine predominantly constituted 77% of historical Coastal Plain trees, and upland oaks (*Quercus*) contributed another 8%. While pine trees still dominate these forests today (58% of all trees), most are planted loblolly (*Pinus taeda* L.) and slash pines (*Pinus elliottii* Engelm.). Broadleaf trees, such as water oak (*Quercus nigra* L.), live oak (*Quercus virginiana* Mill.), sweetgum (*Liquidambar styraciflua* L.), and red maple (*Acer rubrum* L.), have increased their proportions in comparison to historical surveys. This study confirms that longleaf pine initially dominated over 25–30 million ha of Coastal Plain forests. However, it declined to 7.1 million ha by 1935, dropped to 4.9 million ha by 1955, and reached a low point of about 1.3 million ha in the mid-1990s; after that, restoration efforts contributed to a recovery to 2.3 million ha in the past two decades. The federal agencies (e.g., the USDA Forest Service) continuously restore longleaf pine through different approaches. With climate and land use change, new areas outside the historical range may be possible for the longleaf pine ecosystem. Tatina et al. [13] detected the boundary change between historical pine and oak–pine open forests after comparing the tree composition and densities from historical and contemporary forest inventory data in Mississippi's Coastal Plain ecological province. Their results indicated that the historical open forests dominated by fire-tolerant longleaf pine with a pine density of 88% in all trees were converted to loblolly and slash pines in monocultures with a density of 45%. Contemporary forests are closed forests with a higher tree density (336 trees ha^{−1}) than the historical open woodlands (168–268 tree ha^{−1}). The ecotonal boundary of the northern Coastal Plain between historical pine and pine–oak woodlands has shifted, and the spatial area of the pine component has decreased from 88% to 34% due to the encroachment of the oak component. The unique historical forest landscape in the region became homogenized through forestation. These results may have implications for developing regional forestry strategies and management practices to restore longleaf pine forests (or woodlands) across its historical range.

In recent decades, the government and private landowners have made efforts to restore longleaf pine forests. After analyzing the national forest inventory data during two time periods (2009–2015 and 2016–2021), Potters et al. [14] indicated increases in the estimated number of longleaf pine trees and the area of the longleaf pine forest type, as well as a growth in mean plot-level longleaf pine carbon and importance value. However, they also found a decrease in the overall forest area containing longleaf pine in other forest types. Their results indicate a pattern in which longleaf pine-dominated forests are becoming more widespread through restoration efforts. In contrast, forests where the longleaf pine was less critical (e.g., mixed broadleaved forests) have shifted to other forest types. Additionally, the number of longleaf seedlings and small trees has decreased across most states and forest types. Based on this trend, it is suggested that the opportunity window to expand the longleaf forest-type footprint through the restoration of forests with a minor longleaf overstory component may be closing on a large scale.

Restoring and managing longleaf pine forests requires an estimate of tree growth rate and yield for landowners with varied objectives. Site index is usually used in growth and yield prediction. Here, VanderSchaaf [15] reviewed and examined sixteen existing equations to estimate the site index in naturally regenerated longleaf pine forests for their behavior across site quality and age conditions. Nine of these sixteen equations were polymorphic, but all were base-age invariant. No equation is superior to the others. This study can serve as a reference to determine which equation is most appropriate for a particular situation.

Prescribed burning could not only kill unwanted plant species but could also have adverse effects on soil carbon, nutrients, and water. These adverse effects were usually ignored. Dunson et al. [16] examined the effects of prescribed burning on soil chemical properties. Sampling and measuring were conducted in 36 plots at three sites with two different burn intervals (2–3 years and biannually) in eastern Texas. These sites varied by overstory species, such as with longleaf pine and shortleaf pine (*Pinus echinata* Mill.) in the overstory at one site, a mix of loblolly pine and shortleaf pine at another, and longleaf and loblolly pines at the third. They found short-term responses in soil chemical properties after repeated burning, including nitrogen in the forms of ammonium and nitrate, the carbon-to-nitrogen ratio, and electrical conductivity; these indices decreased following prescribed burning regardless of the overstory species. Oswald et al. [17] used the same sites and studied the effects of prescribed burning on soil water infiltration and physical properties. They found a significant increase in soil water infiltration rates between pre-burn and post-burn, pre-burn and green-up, and between the two different burn intervals. Soil strength initially decreased slightly but then increased over time. Soil-stable aggregates increased significantly over time, and soil physical properties changed significantly, including soil bulk density, pore space, water-stable soil aggregates, and soil strength. Repeated burning treatments could have short-term (2–3 years) effects on soil physical properties and soil water infiltration rates, regardless of overstory species.

Interactions exist between the longleaf pine ecosystem and the atmosphere, which is the source of ecological services. Monitoring water consumption dynamics across the geographic range of the longleaf pine restoration areas could indicate their possible hydrological variations. Chen et al. [18] used the derived data from remote sensing (1979–2022) to characterize the water consumption dynamics and effects on cone production at three geographic margins in the longleaf pine's range (i.e., Bladen Lake State Forest, Escambia Experimental Forest, and Kisatchie National Forest) under varying climatic conditions. They found that the mean annual transpiration at Escambia was approximately 431 mm, but it was 500 mm at Bladen and Kisatchie. Mean monthly transpiration had two peaks (June and October) at Escambia but only one (August) at Bladen and Kisatchie. The mean annual evapotranspiration reached approximately 900 mm at Kisatchie and about 791 mm at Escambia and Bladen. The mean annual transpiration/evapotranspiration ratio was about 0.65 at Bladen and 0.55 at Escambia and Kisatchie. Hydrological regimes existed in these areas, such as evapotranspiration correlated with specific humidity across the sites on a monthly scale but not on a yearly scale; negative relationships existed between precipitation and the ratios of transpiration/precipitation and evapotranspiration/precipitation on a yearly scale across the sites; the same is true for the relationships between precipitation and the specific humidity/precipitation ratio on monthly and yearly scales. Cone production was usually highest in years with moderate water consumption. The results provide a baseline for longleaf pine forests' hydrological requirements and their interactions with the atmosphere across broad spatial and temporal scales.

In short, it is critical to continue to improve our understanding of the spatial and temporal dynamics in the longleaf pine ecosystem to achieve its sustainability in the changing environment. The nine publications in this Special Issue, representing a small sample of the current scientific research, provide new information about ecological processes related to the longleaf pine ecosystem from different perspectives. These results may have implications for longleaf pine management, conservation, and restoration. Further research is expected to monitor and better manage the longleaf pine ecosystems, especially under projected climate and land use changes.

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