BIOMASS ACCUMULATION PATTERNS OF NUTTALL OAK SEEDLINGS ESTABLISHED UNDER THREE STAND CONDITIONS

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Abstract—To gain a better understanding of bottomland oak seedling development under various stand conditions, we studied biomass accumulation on 1-0 bareroot Nuttall oak (*Quercus nuttallii* Palm.) seedlings planted in a mature bottomland hardwood stand after harvesting. Harvest operations in fall 1998 created three residual stand conditions which applied treatment conditions that left overstory residual stocking levels of 0, 25, and 50 percent. During the third growing season, we randomly selected eight plants from each stand condition, excavating and separating them into leaf, stem and root tissues. We used oven-dried mass to calculate leaf weight ratio, stem weight ratio and root weight ratio for each sample plant. Our findings indicate that, regardless of stand condition, artificially established Nuttall oak seedlings differed little in biomass accumulation and distribution of accumulated biomass among tissues. While trends in the data indicate that seedlings established under zero percent stocking tended to increase biomass accumulation, high error terms associated with treatment means precluded definitive delineation of differences in seedling biomass accumulation among tissue types under the various stand conditions. However, root weight ratios and stem weight ratios suggest that seedlings established beneath partial canopies may have experienced more moisture stress than seedlings established under zero percent stocking.

INTRODUCTION

Silviculturists have yet to develop reliable practices for regenerating bottomland hardwood stands that produce an adequate component of the highly desired bottomland oaks (*Quercus* spp.). Several factors may contribute to the difficulty of developing sufficient advance oak reproduction in bottomland stands, one of which may be related to the structure of mature stands (Oliver and others 2005). Mature bottomland hardwood stands often have an intact overstory and a dense midstory layer that together can reduce light availability in the understory to less than 10 percent of full sunlight (Gardiner and Yeiser 2006, Lockhart and others 2000). While acorns are able to germinate, evidence suggests that seedling growth and survival may be limited by the understory light regime (Gardiner and Hodges 1998, Hodges and Gardiner 1993). Accordingly, workers often identify insufficient light as a primary factor limiting growth of advance oak reproduction in mature bottomland hardwood stands.

Evidence of the potential for light to limit bottomland oak seedling growth has been demonstrated by Gardiner and Hodges (1998), and Guo and others (2001). Gardiner and Hodges (1998), who studied cherrybark oak (*Quercus pagoda* Raf.) seedling biomass accumulation under controlled levels of light, reported that cherrybark oak seedlings exhibited a quadratic response to light availability. Greatest biomass accumulation occurred under moderate light levels (27-53 percent of full sunlight), and relatively low and high light availabilities resulted in diminished biomass accumulation (Gardiner and Hodges 1998). The decreased biomass accumulation under low light availability was attributed to insufficient photosynthetically active radiation, whereas decreased biomass accumulation under full sunlight was attributed to moisture stress.

Silvicultural practices to reduce canopy cover and increase understory light availability have been successfully applied in bottomland hardwood stands. Such practices have spanned a range of intensities—from midstory removals, gap formation, and partial stand harvests. Midstory removals generally target stems subordinate to the overstory leaving the canopy intact; gaps typically are formed by removing canopy vegetation in small (≤ 0.5 ha) areas of the stand; and partial harvesting may remove a range of basal area from the stand, often leaving relatively few residual stems to form a sparse canopy. Although practitioners have an array of options for influencing the light environment in the understory of mature bottomland hardwood stands, we lack an understanding of how bottomland oak seedlings develop under differing stand conditions that result in various understory light regimes.

Our purpose was to quantify biomass accumulation and distribution among tissue types for Nuttall oak (*Quercus nuttallii* Palm.) seedlings, which were artificially established under three stand-stocking levels. We hypothesized that seedlings established under the various stocking levels would show differing responses to light availability, e.g., those established under partial canopies would exhibit increased biomass accumulation and a more balanced distribution of biomass among root and stem tissues than seedlings established in the open.

METHODS

The study was conducted in a mixed-species bottomland hardwood stand located about 10 km east of Anguilla in Sharkey County, MS (32° 58' N, 90° 43' W). In fall 1998, we sectioned the stand into two blocks, each having three, 1.7-ha experimental plots that were assigned one of three residual stocking levels. Using tables published by Goelz (1995), we then harvested trees on the plots to their assigned treatment level, which included 0 percent residual stocking, 25 percent residual stocking or 50 percent residual stocking. Harvesting

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operations were conducted using conventional chainsaw felling, and merchantable logs were removed from the site with a grapple skidder. After harvesting, the site was prepared for planting by severing at groundline with a chainsaw all stems greater than 2.5 cm diameter at breast height (d.b.h.) that were not marked as leave trees. Site preparation also included reducing slash piles to the ground by cutting upright branches from felled crowns. The stand was planted by hand in March 1999 with 1-0 bareroot Nuttall oak seedlings obtained from the Mississippi Forestry Commission Nursery in Winona, MS. Residual stand conditions following the harvest are listed in table 1, and a more detailed description of the site, stand, harvest levels, and planting methods can be found in Ware and Gardiner (2004).

We sampled Nuttall oak seedling biomass in the summer of 2002 by randomly selecting eight seedlings from each treatment plot in a randomly chosen block. Each sample seedling (24 total) was excavated by hand and dissected into root, stem and leaf tissues. Though we would have preferred to sample more seedlings in each treatment plot, we were limited by the time required to properly excavate sample seedlings. In the course of this study, two technicians worked three months to excavate the 24 sample seedlings. Soil was washed away from excavated root tissues and all tissue types were oven-dried at 70 °C before dry mass was measured on a balance. The relative distribution of mass among each tissue type was calculated with the following equations. Leaf weight ratio (LWR) = leaf mass ÷ total seedling mass; stem weight ratio (SWR) = stem mass ÷ total seedling mass; root weight ratio (RWR) = root mass ÷ total seedling mass.

Response variables, including leaf mass, stem mass, root mass, total seedling mass, LWR, SWR and RWR, were analyzed according to a completely random design. Analysis of variance was performed and Duncan's Multiple Range Test was used to separate treatment means. All tests were conducted at an alpha of 0.05.

RESULTS AND DISCUSSION

Seedling Establishment

Third-year findings on survival, height and diameter growth of Nuttall oak seedlings planted under the three residual stand stocking levels are reported in Ware and Gardiner (2004). In brief, third-year survival averaged 77 percent for all treatments, and this survival resulted in more than 570 established seedlings per hectare across the study site (Ware and Gardiner 2004). Height growth was greatest on seedlings established under 0 percent residual canopy where they were 59 percent taller (mean height = 152 cm) than seedlings established under the 25 and 50 percent residual stocking treatments (Ware and Gardiner 2004). Root-collar diameter growth tracked height growth as Nuttall oak seedlings established under zero percent stocking showed diameters 45 percent greater (mean diameter = 17.8 mm) than seedlings established under 25 and 50 percent residual stocking (Ware and Gardiner 2004).

Seedling Biomass Accumulation

Though Ware and Gardiner (2004) observed differences in height and root-collar diameter growth, dry mass within tissue types did not vary for Nuttall oak seedlings established under three stand stocking levels (fig. 1). Three years after outplanting, average seedling mass was 138.2 ± 36.9 g; root tissue comprised 38 percent, stem tissue comprised 50 percent and leaf tissue comprised 12 percent of total seedling mass (fig. 2). Mean seedling and tissue weights appeared to increase with decreasing stand stocking (figs. 1, 2). However, these trends were not significant, and treatment differences may have been obscured by high error terms associated with treatment means. Regardless of statistical significance, the response observed in our data for Nuttall oak did not follow the pattern observed for cherrybark oak raised under neutral density shade cloth (Gardiner and Hodges 1998).

Seedling Biomass Distribution

Nuttall oak seedlings established under the various stand stocking levels did show differing proportions of biomass distributed among root and stem tissues (fig. 3). Seedlings established under zero percent stocking showed a 36 percent higher SWR than seedlings established under the 25 and 50 percent stocking levels (fig. 3). The RWR for seedlings established under zero percent stocking was 25 percent less than RWRs of seedlings raised under 25 percent stocking (fig. 3). Three years after establishment, Nuttall oak seedlings raised under the various stand stocking levels accumulated similar proportions of biomass in leaf tissue (fig. 3).

Our findings appear contrary to reported biomass accumulation patterns of other oak species established

Table 1—Residual stand conditions following three levels of overstory removal in a mixed-species bottomland hardwood stand, Sharkey County, MS

	Target stocking level		
Variable[a]	0 %	25 %	50 %
Trees per hectare	0	39	89
Mean stem diameter (cm)	-	48.8	46.8
Basal Area (m^2 ha^{-1})	0	7.6	15.37
Stocking per hectare (%)	0	26	53

[a] Residual stand data cited from Ware and Gardiner (2004).

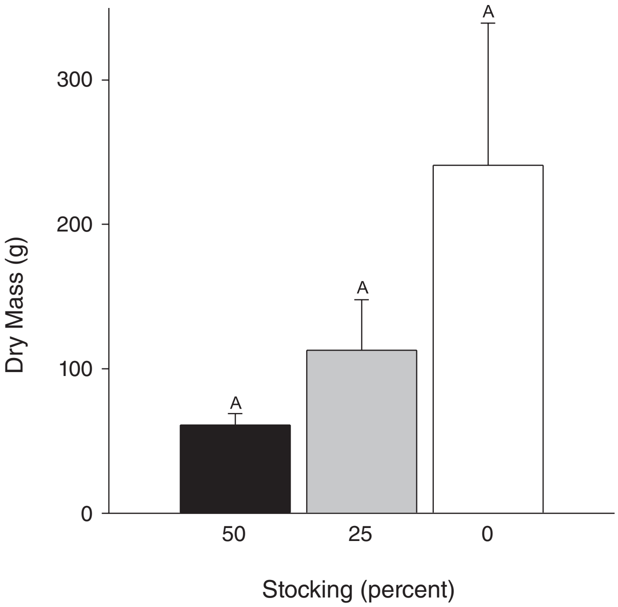

Figure 1—Mean dry mass of Nuttall oak seedlings 3 years after outplanting under 0, 25, or 50 percent stocking, Sharkey County, MS. Standard error bars with the same letter are not significant at the 0.05 probability level.

under environments of partial sunlight. Research on cherrybark oak seedlings illustrates that this species exhibits a quadratic response to light availability, such that the greatest biomass accumulation occurs under moderate light levels, whereas extremely low or high light availability results in diminished biomass accumulation (Gardiner and Hodges 1998, Guo and others 2001). Ziegenhagen and Kausch (1995) reported a similar growth response by pedunculate oak (*Quercus robur* L.) grown under neutral density shade cloth in Germany. Based on the findings reported for these other oak species, we expected Nuttall oak to exhibit greatest

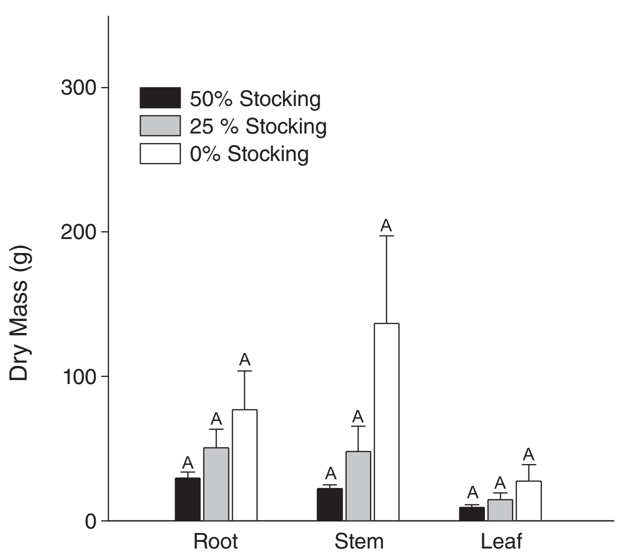

Figure 2—Mean dry mass of root, stem and leaf tissues for Nuttall oak seedlings 3 years after outplanting under 0, 25, or 50 percent stocking, Sharkey County, MS. Mean comparisons are for a given tissue type, and standard error bars with the same letter are not significant at the 0.05 probability level.

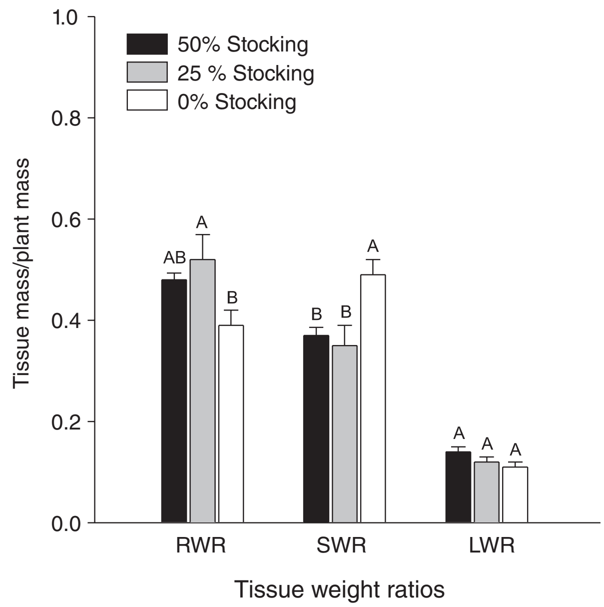

Figure 3—Mean root weight ratios (RWR), stem weight ratios (SWR) and leaf weight ratios (LWR) for Nuttall oak seedlings 3 years after outplanting under 0, 25, or 50 percent stocking, Sharkey County, MS. Mean comparisons are for a given tissue type, and standard error bars with the same letter are not significant at the 0.05 probability level.

biomass accumulation and a relatively balanced distribution of root and stem tissues in treatments that retained residual stocking. These were not our observations, and our diverging results may have arisen from at least three different factors.

A fundamental difference between the light environment in the understory of a natural bottomland hardwood stand and the light environment in the controlled studies of Gardiner and Hodges (1998) and Ziegenhagen and Kausch (1995) is light quality. In addition to reducing the quantity of photosynthetically active radiation incident in the understory, hardwood forest canopies alter light quality by reducing the red:far-red ratio of the spectrum (Kozlowski and others 1991). Neutral density shade cloth, such as used by researchers in controlled experiments, effectively reduces light quantity, but does not impact light quality. Thus, it is possible that growth of seedlings established in the partially harvested plots in this study was impacted by the decrease in light availability as well as altered light quality.

However, altered light quality may not sufficiently explain the results we observed. First, the partially harvested plots in this study, particularly plots that retained 25 percent residual stocking, had canopies that were sparse enough to allow direct sunlight to comprise a substantial proportion of the radiation received by underplanted seedlings. Additionally, a reduced red:far-red ratio, which is typical of deep shade environments, generally induces a shift in carbon allocation away from the root system in favor of the shoot. This was not observed in our study, as Nuttall oak seedlings established under partial canopies showed a preference for biomass accumulation in root tissue.

Secondly, light availability may impact carbon allocation in Nuttall oak differently than other bottomland oaks. Earlier research illustrated that Nuttall oak leaf physiology responds markedly different to light availability than does cherrybark oak and overcup oak (*Quercus lyrata* Walt.) (Gardiner 2002). As differences in leaf physiology among species have been identified, it is reasonable to conclude that various oak species may exhibit a range of developmental strategies that lead to differing morphologies relative to light availability. In support of this argument, Long and Jones (1996) reported that oak species endemic to the southern United States showed inherently different growth strategies that led to contrasting morphologies during the establishment year.

Finally, factors other than light availability, particularly moisture stress, may have limited carbon assimilation and altered biomass accumulation patterns of the underplanted oak seedlings. Evidence for this explanation is provided by our observations of the SWRs and RWRs of seedlings we sampled. Our results indicate that seedlings established beneath 25 and 50 percent stocking favored root growth over stem growth. Favoring biomass accumulation in roots over shoots has been attributed to moisture stress in seedlings of other oak species (Canadell and Rodà 1991, Kolb and Steiner 1990). We expected the residual overstory in partially harvested plots to moderate understory vapor pressure deficits and reduce transpiration of underplanted seedlings. However, it is possible that the residual trees in partially harvested plots provided substantial below-ground competition which could have resulted in high moisture stress of the underplanted seedlings.

CONCLUSIONS

Reliable practices for reproducing bottomland oaks in existing hardwood stands currently are not available. While a range of practices can be applied to increase understory light availability, appropriate stand structures for improving growth of bottomland hardwood reproduction have not been identified. We examined biomass accumulation of Nuttall oak seedlings artificially established beneath three levels of residual stand stocking. Based on our findings, stand stocking level did not influence Nuttall oak seedling establishment or biomass accumulation. An earlier report from this study site indicated that Nuttall oak could be successfully underplanted beneath a range of stand densities (Ware and Gardiner 2004). Findings from this research are generally in agreement with the findings of Ware and Gardiner (2004).

However, high error terms associated with treatment means in this study may have masked differences, and trends observed in the data may become more prominent over time. We did observe that stand stocking altered the proportional distribution of biomass among root and stem tissues. Seedlings established under zero percent stocking showed the greatest proportion of biomass accumulated in stem tissue, while seedlings raised under 25 percent stocking showed the greatest proportion of biomass accumulated in root tissue. These findings suggest that Nuttall oak seedlings planted in the understory of partially harvested stands may have experienced substantial moisture stress.

Notably, our field observations for Nuttall oak contrast with previously reported biomass distribution patterns for other oak species raised under more controlled light environments. Our findings warrant additional research investigating interactions between light availability and competition associated with stand structure in bottomland hardwood forests.

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