Forest Ecology and Management 108 (1998) 127-134

Forest Ecology and Management

Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability

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Received 30 September 1997; accepted 10 December 1997

Abstract

Cherrybark oak (*Quercus pagoda* Raf.) seedlings were established and raised in the field under four light levels (100%, 53%, 27% or 8% of full sunlight) to study the effects of light availability on their shoot growth, biomass accumulation, and biomass distribution. After two growing seasons, greatest stem growth was observed on seedlings which received intermediate light levels, and this growth was associated to a greater accumulation of total seedling biomass and a distribution pattern which balanced accumulation of root and shoot biomass. In contrast, less biomass accumulation and a biomass distribution pattern that favored root growth over stem growth were characteristic of seedlings receiving full sunlight. These results suggest that regeneration of cherrybark oak on mesic sites may be limited by preferential root growth, but reproduction of this species may be amenable to silvicultural practices that improve the light environment through stand manipulation. Published by Elsevier Science B.V. All rights reserved.

Keywords: Bottomland hardwood; Regeneration; Root/stem ratio

1. Introduction

Throughout their range in North America and regions of Europe and Asia, natural regeneration of oaks (*Quercus* spp.) is often problematic (Evans, 1982; Crow, 1988; Tbadani and Ashton, 1995). Acorn and seedling herbivory, frost damage and flood damage to seedlings, severe moisture competition from herbaceous weeds, and low understory light levels are among the biotic and abiotic factors often cited as contributing to the oak regeneration problem (Racine, 1971; McGee, 1975; Adams et al., 1992; Lorimer et al., 1994; Angelov et al., 1996). Additionally, many oak systems have been subjected to antbropogenic activities which have intensified the adverse effects of some of these factors on reproduction. As examples, the exclusion of fire in mixed-oak forests of the upper Midwest and northeastern United States is thought to have placed oak reproduction at a competitive disadvantage among more shade tolerant, late-successional species (Reich et al., 1990; Abrams and Nowacki, 1992); introduced exotic weeds likely reduce soil moisture availability resulting in decreased oak seedling survival and growth in oak woodlands of the western United States (Gordon et al., 1989): and, creation of water impoundments for wildlife habitat has altered hydrologic regimes

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0378-1127/98/$19.00 Published by Elsevier Science B.V. All rights reserved.
PII S0378-1127(98)00220-5

sufficiently enough to preclude establishment and growth of flood-intolerant oak reproduction in some areas of bottomland hardwood forest in the southern United States (Young et al., 1995). As a result, regeneration pools are often stocked with reproduction of Insufficient size or distribution to successfully regenerate disturbed areas of oak-dominated forests (Johnson, 1993).

Of the limiting factors listed above, light availability in the understory of mixed-oak forests appears pervasively linked to oak seedling growth and morphology. Crow (1992), who studied northern red oak (*Quercus rubra* L.) seedlings grown under various overstory conditions in Wisconsin, USA, observed multiple flushing and subsequently height Increment was inversely related to overstory cover. A similar height growth:canopy cover relationship was observed by Johnson (1992) in two xeric oak ecosystems in Michigan, USA. In a central Himalayan forest, Thadani and Ashton (1995) found banj oak (*Quercus leucotrichophora* A. Camus) seedling morphology was altered by the prevailing light environment in stands of different tenurial practices. High height/diameter ratios of stems were observed on seedlings established in protected stands indicative of a low understory light environment, while seedlings established in moderately disturbed stands with greater light availability in the understory developed stems with lower height/diameter ratios (Thadani and Ashton, 1995). Once oak seedlings deplete cotyledon reserves, inadequate light generally reduces carbon gain and seedlings respond by altering biomass accumulation such that shoot growth is favored over root growth (Crow, 1988; Thadani and Ashton, 1995; Ashton and Larson, 1996). A relatively high leaf area and shoot/root ratio allows for more effective utilization of the limited light resource (Hodges and Gardiner, 1993).

Cherrybark oak (*Quercus* pagoda Raf.) is a common overstory species in bottomland hardwood forests throughout the southern United States where it is favored by managers for its superior form, excellent wood quality, and desirable hard mast production (Putnam et al., 1960; Krinard, 1990). Within its range, cherrybark oak is often found on very productive alluvial sites where it grows in association with several other hardwood tree species forming stands with multi-storied canopies (Krinard, 1990). Contrary to its relative overstory importance and favorable mast production. cherrybark oak advance reproduction is often lacking in the understory. Several factors, including seasonal flooding and competition from other vegetation. may limit establishment and growth of oak reproduction in bottomland hardwood forests. However, low understory light levels are characteristic of multi-storied bottomland hardwood stands (Jenkins and Chambers, 1989). and may be the most limiting factor on establishment and growth of shade intolerant species such as cherrybark oak (Hodges and Gardiner, 1993). In this experiment, cherrybark oak seedlings were raised in the field under four light levels to determine how light availability influences growth and biomass distribution during seedling establishment. We hypothesized that growth of cherrybark oak seedlings would be regulated by the influence of light availability on total carbon gain and biomass distribution patterns.

2. Methods

The study was conducted in an open field at Blackjack Research Farm located near Starkville, MS, USA (latitude = 33°26′N, longitude = 88°46′W). Soil in the field was classed as a Marietta series (fine-loamy, siliceous, thermic, Fluvaquentic Eutrochrepts) and has a site index of 29 m at 50 yr for cherrybark oak. In the field. several wooden frames (3.5 m wide × 3.5 m long × 2.0 m tall) were built to support neutral density shade fabric (Pak, Atlanta, GA, USA). Three fabric densities were draped over the frames to provide four levels of light availability, 100% of full sunlight (no fabric), 53% of full sunlight, 27% of full sunlight and 8% of full sunlight. Two replicates of each light regime were constructed in the field for a total of eight frames. It should be noted that the various light regimes likely created air temperature and humidity differences that may be a component of treatment results, but these environmental variables were not measured.

In the early spring of 1985, all vegetation was removed from within the eight frames with a rototiller. Two cherrybark oak acorns, randomly selected from a sample collected under several trees and graded for size uniformity, were sown 2.5 cm deep at 20 equally spaced (0.6 m × 0.6 m) planting spots in each frame. After germination. one seedling was removed if both acorns at a planting spot were viable. The oak seedlings were grown for 2 yr in their respective light environments, during which time soil moisture deficits were prevented by maintaining field capacity with drip irrigation and water sprinklers. Competing vegetation was kept out of the frames with garden hoes during the growing season, and insect herbivory to seedlings was curtailed with foliar applications of pesticides as needed. Fabric was removed from the frames after leaf senescence between the first and second growing seasons, and it was replaced on the frames shortly before bud break in the spring.

Near the end of both growing seasons, five randomly selected seedlings from each frame were measured for height to the nearest cm, and root-collar diameter to the nearest mm. Following stem measurements, these same five seedlings were harvested to determine seedling biomass accumulation and distribution. Leaves were removed from stems, stems were severed at the root-collar, and all roots were excavated from the soil by hand. Roots were rinsed free of soil, then all biomass components were oven-dried at 70°C before weighing with an analytical balance. Leaf weight ratio (leaf weight ÷ plant weight), stem weight ratio (stem weight ÷ plant weight), and root/stem ratio (root weight ÷ stem weight) were calculated for each seedling from dry weights of the biomass components.

The entire study was repeated in time with the second trial beginning in the spring of 1987 and ending in the fall of 1988. All methods were the same as those described for the first trial except acorns were sown 3 weeks earlier in 1987. Analysis of variance according to a completely randomized design was performed on means of seedling responses measured in each light regime frame. Significant effects were separated with Duncan's Multiple Range test ($\alpha = 0.05$). Additionally, a simple correlation analysis was performed to test for a relationship between seedling biomass and root/stem ratio.

3. Results

Germination and survival were excellent for both replications in time, as nearly 100% of all seed spots were occupied by a seedling. Perhaps because of the earlier sowing date and milder growing conditions, seedlings from the second trial were generally larger than those from the first trial. For example, seedling biomass in the 1985–1986 trial averaged 17.5 g, while seedling biomass in the 1987–1988 trial averaged 156.3 g ($P < 0.0001$). However. treatment x trial interactions were not detected for any of the studied variables, so treatment results presented are inclusive of both trials.

3.1. *Stem growth*

Light availability did not strongly influence seedling height growth during the first growing season (Fig. 1). All seedlings averaged about 23 cm tall except for those raised under 53% light which were about 48% taller ($P = 0.0037$). Greatest differences in stem height were observed at the end of the second growing season. At that time, seedlings

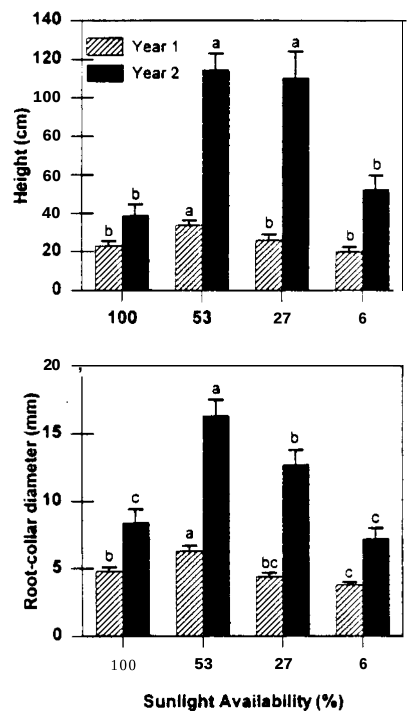

Fig. 1. Height and root-collar diameter ocherrybark oak seedlings established and raised for 2 yr in the field under four light levels. Letters signify difference at an a level of 0.05, and bars represent ± standard error of the mean.

showed a quadratic response to light availability as seedlings raised under moderate light levels averaged 146% railer than seedlings which received 100% or 8% sunlight ($P < 0.0001$).

Root-collar growth initially responded to light availability in the first growing season (Fig. 1). As with stem height, largest root-collars were measured on seedlings which received 53% light ($P < 0.0001$). However, a strong treatment effect on root-collar diameter was observed after the second growing season when root-collar growth exhibited a quadratic response to light availability. Seedlings raised under 53% sunlight maintained the largest root-collars two years after germination, while seedlings raised under 8% or 100% sunlight developed root-collars half the size of those measured on the largest seedlings ($P < 0.0001$).

3.2. *Biomass accumulation*

Light availability had a strong effect on the amount of biomass accumulated by cherrybark oak seedlings,

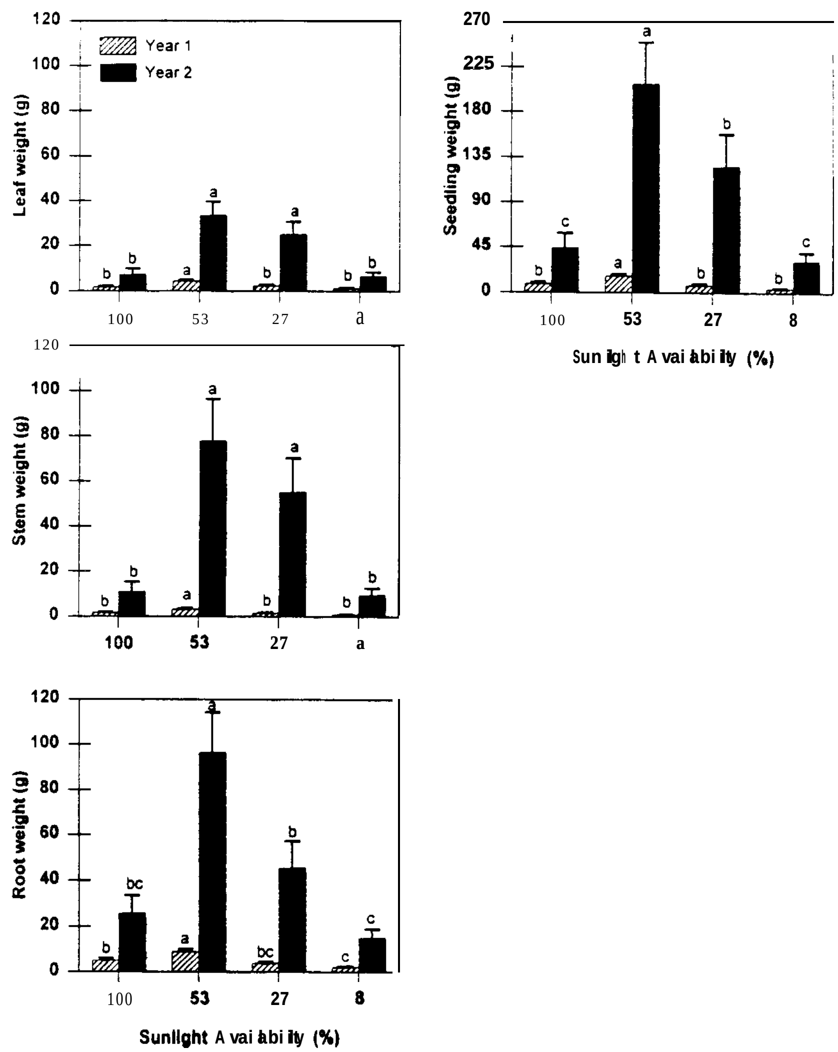

Fig. 2. Leaf weight, stem weight, root weight and total weight of cherrybark oak seedlings established and raised for 2 yr in the field under four light levels. Letters signify difference at an a level of 0.05, and bars represent ± standard error of the mean.

but this treatment effect was most prominent after the second growing season (Fig. 2). In the first growing season, greatest carbon gain was observed on seedlings raised under 53% sunlight, and this trend was maintained through the second growing season (Year I. $P < 0.0001$; Year 2, $P < 0.0001$). Through two years of growth, seedling biomass accumulation was lowest in environments of 100% and 8% sunlight such that seedlings grown under those light regimes were about 170 g lighter than the best seedlings (Fig. 2).

Biomass accumulation in leaves, stems and roots showed a quadratic response to light availability after two growing seasons. Seedlings raised under moderate light levels yielded the greatest quantities of leaf and stem biomass (Fig. 2). Lowest yields of leaf and stem biomass occurred on seedlings receiving 100% or 8% sunlight (Leaf, $P < 0.0001$; Stem, $P < 0.0001$). After two growing seasons, root biomass of seedlings receiving 53% sunlight was over 3.5 times greater than root biomass of seedlings which received 100% or 8% sunlight ($P < 0.0001$) (Fig. 2).

3.3. *Biomass distribution*

In addition to differences in growth and biomass accumulation, biomass distribution within cherrybark oak seedlings was strongly controlled by light availability (Fig. 3). Seedlings grown under full sunlight accumulated the smallest proportion of leaf dry matter during the first growing season ($P = 0.0005$) (Fig. 3). A similar trend was maintained through the second growing season as plants grown under 27 or 8% sunlight favored leaf tissue production more than seedlings grown in full sunlight ($P = 0.0035$). All first year seedlings accumulated similar percentages of stem tissue ($P = 0.8755$) (Fig. 3). Cherrybark oak seedlings developed the greatest proportion of stem biomass when grown under 27% sunlight for two years, while smallest percentages of stem biomass were produced on open-grown seedlings ($P < 0.0001$).

Root/stem ratios were not influenced by light availability in the first growing season, but were strongly controlled by light availability in the second year (Year 1, $P = 0.4246$; Year 2, $P < 0.0001$) (Fig. 3). During the second growing season, cherrybark oak seedlings raised in full sunlight favored root growth more than stem growth such that 3.5 units of root tissue were produced for each unit of stem tissue. Lowest root/stem ratios were recorded for seedlings grown under moderate levels of light availability, as these seedlings accumulated near equal proportions of biomass in roots and stems (Fig. 3). Correlation analysis revealed that root/stem ratio and seedling biomass were not independent ($P < 0.0001$). However, the coefficient for this relation-

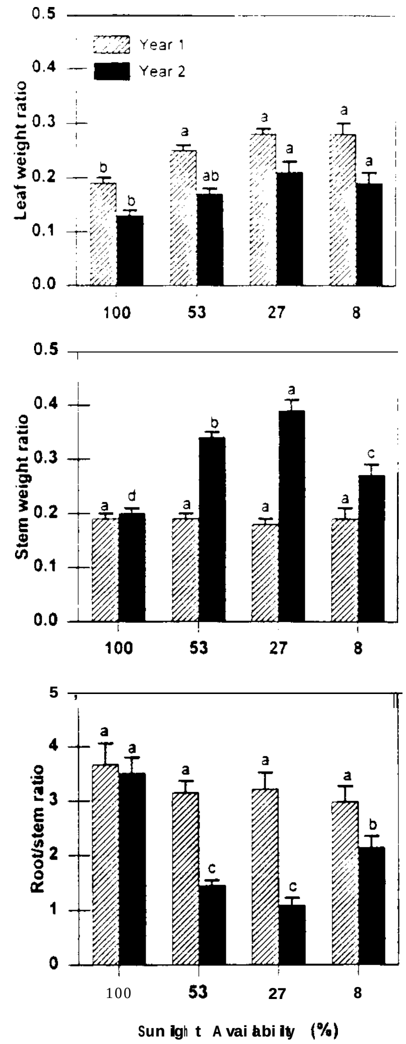

Fig. 3. Leaf weight ratio, stem weight ratio and root/stem ratio of cherrybark oak seedlings established and raised for 2 yr in the field under four light levels. Letters signify difference at an α level of 0.05, and bars represent ± standard error of the mean.

ship was rather low ($r = -0.44$), indicating only 19% of the variation in root/stem ratio was explained by seedling biomass.

4. Discussion

In agreement with previously reported results for other oak species (Carvell and Tryon, 1961; Jarvis, 1964; Callaway, 1992; Gottschalk, 1994; Ziegenhagen and Kausch, 1995), light availability had a strong effect on the development of chenybark oak seedlings. Yet, greatest effects of light availability on shoot growth, biomass accumulation and biomass distribution were not realized until the second growing season. It is generally believed that light availability probably does not limit oak seedling growth until cotyledon reserves are depleted (Crow, 1988). Working with northern red oak natural reproduction, Crow (1992) found that seedlings responded to light availability during the first growing season, but as in this study the response appeared to increase with time (Crow, 1992). The strong treatment response in the second growing season of this study indicated that cotyledon reserves were depleted and growth and biomass accumulation were determined by the seedling's capacity to harvest energy and produce photosynthates in their respective light environments.

Height and diameter growth of the studied seedlings responded quadratically to light availability suggesting that there may be a light optima for stem development of cherrybark oak reproduction. This finding is not universally supported by similar research conducted on other oak species. For example, Holmes (1995), who studied the effects of light availability on valley oak (*Quercus lobata* Nee), reported an increase in seedling height with an increase in light availability. Conversely, Jarvis (1964) noted that sessile oak (*Quercus petraea* (Matt.) Liebl.) seedlings increased in height with decreasing light availability. However, in close agreement with observations made by Ziegenhagen and Kausch (1995) on the development of pedunculate oak (Quercus *robur* L.) in response to light availability, greatest stem growth in this study was observed on seedlings receiving intermediate light levels. The superior stem growth observed under moderate light levels in this study was associated to a greater accumulation of total biomass and a biomass distribution pattern which balanced accumulation of root and shoot biomass. In contrast, reduced shoot growth of seedlings receiving full sunlight was associated to a lower level of biomass accumulation and a biomass distribution pattern which favored accumulation of root biomass over stem biomass.

A likely explanation for the reduced stem growth, low biomass accumulation, and the biomass distribution pattern that favored root growth observed on open-grown seedlings in this study involves moisture stress. In spite of a watering regime that maintained soil at field capacity, air temperature and consequently vapor pressure deficit are generally much higher in full sunlight than under partial sunlight. Under full sunlight, the high vapor pressure deficit would typically lead to a high transpiration rate and eventually a greater likelihood of seedling moisture stress. If open-grown seedlings experienced greater moisture stress than seedlings receiving partial sunlight, we would expect stomatal or internal plant resistances to limit photosynthesis which would eventually limit biomass production (Hodges, 1967; Weber and Gates, 1990). Moisture stress may also explain the biomass distribution pattern observed on the open-grown seedlings. In accord with root/stem ratio values for open grown seedlings in this study, moisture-stressed oaks typically increase their water absorbing capacity by favoring root growth (Kolb and Steiner, 1990; Canadell and Rodà, 1991).

The above findings not only suggest reasons for the difficulty in regenerating cherrybark oak, but also are in good agreement with what is known about the ecology of this species. Cherrybark oak occurs naturally on a range of sites varying from dry-mesic to wet-mesic; regeneration of this species is typically more of a problem on mesic and wet-mesic sites than on drier sites (Hodges and Gardiner, 1993). Though favoring root growth more than shoot growth (higher root/stem ratio) is beneficial to survival and growth on dry sites after disturbance (Rice and Bazzaz, 1989; Walters et al., 1993), the tendency of chenybark oak to favor root growth in open environments may be a detriment on more mesic sites were competition is typically greater.

Though light availability appeared to have a dramatic effect on biomass distribution of cherrybark oak seedlings, several authors have raised caution about compannp allometric relationships of plants of different sizes (Hunt and Lloyd, 1987; Kuppers et al.,1988; Rice and Bazzaz, 1989; and Walters et al., 1993). In the present study, plant size varied greatly between treatments and trials, but size differences did not appear to alter treatment effects on allometric relationships. That size differences were not a factor is seen most easily by a comparison of root/stem ratios. First, the correlation between root/stem ratio and seedling biomass was rather low (see Section 3). Additionally, seedling size in all light regimes was much higher in the second trial, but analysis of root/stem ratios did not reveal any treatment *x* trial interaction. Thus, allometric relationships of seedlings in this study appear to have been determined primarily by light availability rather than seedling size.

5. Management implications

Several management implications for cherrybark oak are apparent from this research. First, effects of light availability on seedling growth, biomass accumulation, and biomass distribution were by and large not realized until the second growing season. Under field conditions, acorn reserves appeared to determine seedling growth potentials during the first growing season. Thus, development of larger, advance cherrybark oak reproduction will require time regardless of the light regime.

Secondly, best growth and biomass accumulation in cherrybark oak seedlings were found under moderate light levels. Adequate light is supplied and perhaps other benefits such as reduced moisture stress are realized under partial sunlight. Hence, this species may be amenable to development of silvicultural practices that increase growth by improving the light environment with canopy or midstory manipulations.

Finally, the distribution of seedling biomass was dramatically influenced by light availability. Seedlings grown under even moderate light levels may have to undergo significant morphological acclimation to function well in high light environments once released. Yet, it is assumed that a large, vigorous seedling will not lose much of its competitive advantage during an acclimation period.

Acknowledgements

The authors sincerely thank R. Tim Deen and Greg C. Janzen who were responsible for installing and maintaining the experiment in the field. Ken W. Krauss provided a critical review of an earlier draft of this manuscript.

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