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Growth and Water Use Efficiency of *Quercus alba, Q. bicolor, Q. imbricaria* and *Q. palustris* Seedlings Under Conditions of Reduced Soil Water Availability and Solar Irradiance

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ABSTRACT

Growth and water use efficiency were determined for 2-year-old white oak (*Quercus alba*), swamp white oak (*Q. bicolor*), shingle oak (*Q. imbricaria*) and pin oak (*Q. palustris*) seedlings grown under three shade treatments (30, 55, and 73%) and two irrigation regimes (container capacity and mild drought). With species and water regimes combined, the dry weight increment, root, stem, leaf, shoot dry weight and water use efficiency of the oaks decreased significantly as shade level increased from 30 to 73%. Shade had no effect on height increment, while shoot/root dry weight ratio increased with increasing shade. White oak and swamp white oak closely followed this overall pattern, but the only response shingle oak and pin oak exhibited to increasing shade levels was an increase in shoot/root ratio of 24 and 26%, respectively.

With species and shade levels combined, experimentally imposed drought reduced the oak seedling dry weight increment, root, leaf, and shoot dry weights, caliper increment and water use efficiency. The drought treatment had no effect on seedling height increment, but increased the shoot/root dry weight ratio. Under the drought regime, white oak and shingle oak had the highest water use efficiency values (1.65 and 1.73 mg cm^{-3}) compared with values of 1.46 mg cm^{-3} for pin oak and 1.01 mg cm^{-3} for swamp white oak. White oak and shingle

oak also had the lowest shoot/root ratios (0.60 and 0.87) when compared with pin oak (0.96) and swamp white oak (1.08).

Upland white oak and shingle oak seedlings had the lowest specific leaf areas (158.7and 157.7 cm^2/g) while the bottomland pin oak (176.1 cm^2/g) and swamp white oak (174.8 cm^2/g) had the highest. Pin oak and shingle oak seedlings flushed more times (2.5 and 1.9) during the growing season than swamp white oak (1.6) and white oak (1.0). Drought reduced the number of flushes of all the tested oak species with the exception of white oak, while shade had no detectable effect on oak seedling flushing.

INTRODUCTION

The effects of shade on growth and development of oak seedlings have been examined in numerous studies by growing seedlings under shadecloth or similarly altering radiation levels (Shirley 1929, McGee 1968, Loach 1969, Musselman and Gatherum 1969, Phares 1971, Farmer 1975, Johnson 1984, Gottschalk 1985). The results of these studies have sometimes been inconsistent with one another. For example, in some cases height growth increased with increasing shade (Shirley 1929, Musselman and Gatherum 1969), in other cases it decreased with shade (McGee 1968, Johnson 1984). Others studies indicated that shade had no effect on oak height growth (Farmer 1975) or that peak growth occurred at intermediate irradiance levels with height decreases in both directions (Phares 1971, Shirley 1929). One reason for such inconsistencies may be the use of first year seedlings in most of these studies. Early survival and growth of oak seedlings are strongly influenced by the stored carbon and nutrient reserves of the hypocotyledons (Crow 1988). However, once seedlings establish root systems adequate for supplying water and nutrients to the plant, increased irradiance levels will usually result in increased growth rates. Another factor not considered in many of these studies is the possibility of interaction between irradiance and soil moisture. Together with shade, competition for water and nutrients in the understory of forest stands with an abundance of dominant tree roots in surficial soil can reduce seedling growth (Carvell and Tryon 1961, Ferrell 1953). Oak seedlings benefit from light shade because it moderates temperatures and water use (Kramer and Kozlowski 1979). Exposure to full solar irradiance can induce severe water stress in plants, especially during times of drought. Root growth of northern red oak (*Quercus rubra* L.) is particularly sensitive to even moderate drought. Red oak seedlings subject to various degrees of drought did not regenerate new roots at -0.6 MPa (-6 bars) (Larson and Whitmore 1970). However, white oak roots have been reported to be able to continue growth when the surrounding soil water potential was -1.2 MPa (Teskey et al. 1978). Farmer (1980) found that white oak seedlings have lower shoot/root ratios than northern red oak and it has been reported that white oak also has a deeper root system than northern red oak (Stout 1968, Hinckley et al. 1980).

Few studies of any oak species have examined the combined effects of shading and drought on growth and water use of seedlings (Gatherum et al. 1963, Musselman and Gatherum 1969). Consequently growth and water use of four oak species under varying shade and soil moisture conditions were examined in this study. Two of the oak species studied belong to the subgenus Leucobalanus, the white oaks [swamp white oak (*Quercus bicolor* Willd.) and white oak (*Q. alba* L.)] and two belong to the subgenus Erythrobalanus, the red oaks which include pin oak (*Q. palustris* Muenchh.) and shingle oak (*Q. imbricaria* Michx.) (Harlow et al. 1979). Within each subgenus a bottomland species (swamp white oak and pin oak) and an upland species (white oak and shingle oak) were included in this study. Shingle oak and swamp white oak were selected because they have been little studied to date.

Because various silvicultural methods call for the reduction of overstory canopy to stimulate oak reproduction, there is a need to determine more precisely which irradiance levels provide the best survival and growth conditions for seedlings of a given oak species. Since competition by roots for soil moisture is often severe in the understory of forest stands, and since this competition also limits the ability of plants to tolerate understory conditions, this study was designed to determine the combined effects of reduced irradiance and soil moisture on growth and development of oak seedlings. The objectives of this study were to determine if there are differences in growth and water use efficiency (mg/cm^{-3}) within each oak species among three shade levels and two soil water regimes and to determine if differences are associated with oak species, oak subgenus, or ecological niche of a species.

METHODS

The study was conducted during the summer of 1989 in a greenhouse constructed with iron-free glass located at the University of Illinois in Urbana-Champaign. Iron-free glass allows penetration of solar radiation of a spectral quality more similar to natural radiation in comparison with the glass normally used in greenhouses. Temperatures in the greenhouse ranged from 23-26°C during the day and 20-23°C during the night. The seedlings were grown under natural light and photoperiod between May 22 and October 16. One hundred 2-0 bare-root dormant seedlings each of white oak, swamp white oak, pin oak, and shingle oak were obtained from commercial nurseries in the midwestern U. S. All seedlings were in the 15-30 cm shoot height class, with the exception of white oaks which ranged from 30-46 cm in shoot height. The seedlings were measured for initial stem height and caliper (diameter) at 1 cm above the root collar and then planted in a steam pasteurized 1:1:1 fertile loamy soil: perlite: sphagnum peat moss mixture (pH of 5.5) in 60 cm tall by 10 cm diameter cylindrical pots. The pH did not change appreciably during the course of this study. No fertilizers were added to the soil mixture. The initial fresh weights of all seedlings and pot weights were determined. In each pot, a seedling was planted in 2.6 kg of the air dry soil mixture. The seedlings then were watered daily with tap water and allowed to break bud and grow for five weeks. After five weeks, 30 seedlings of white oak, 25 seedlings of swamp white oak, and 20 seedlings of pin oak and shingle oak (unequal replicates due to mortality) were placed under each of three shade tents with advertised shade values of 30%, 55%, and 73% of incident light. The advertised shade percentages of these tents were found to correspond exactly with the percentage reductions in photosynthetically active radiation (PAR) (±1%) measured with a Li-Cor Integrating Photometer at noon and 4 p.m. (Model LI-188B with quantum sensor, Li Cor Inc., Lincoln, Nebraska). The shade tents were 1.33 m wide x 1.67 m long and had 1.33 m walls on each of four sides. An additional three seedlings per species were destructively measured to obtain an estimate of total, root, stem, leaf and shoot (sum of leaf and stem) fresh and dry mass. These ratios of initial dry weight to fresh weight measurements were used to obtain a value of seedling dry weight at this stage of the study. Dry weight increments were estimated by difference from the dry seedling weights at the end of the study. The proportions of dry to fresh weight obtained for the three seedlings per species were highly consistent, differing by no more than 5% in any case. The estimated initial dry weight means and standard deviations were 33.34 ± 9.76 g for white oak, 8.13 ± 2.20 g for swamp white oak, 7.48 ± 3.33 g for shingle oak, and 7.51 ± 1.82 g for pin oak seedlings.

The seedlings were grown for 2-3 weeks with regular watering to allow them to acclimate to the shade. Then all pots were watered to the drip point, allowed to drain for 24 h, and weighed to determine container water capacity, (the difference between total pot weight 24 h after watering and the sum of container, dry soil mixture, and initial plant fresh weights). Half of the seedlings of each species under each shade treatment were maintained at 90-95% of container water capacity while the remaining seedlings had drought imposed by withholding watering.

Three pots with seedlings maintained at container water capacity for each shade and species combination were sampled randomly every 2-5 days and weighed to monitor the water lost from the pots. All pots were then watered accordingly to restore container-capacity weight and the amount of water added at each watering was recorded. Three pots without seedlings for each shade treatment and watering regime were mixed in with the other seedling pots, weighed, and watered periodically in the same manner as the respective pots containing seedlings in order to estimate pot evaporation. Water use for each plant between bimonthly weighings was calculated as the change from initial weight of watered pots containing seedlings plus the amount of water added during the interval minus the water loss of the corresponding check pots lacking seedlings. The water in the system due to increasing seedling weight was not considered because it constituted an insignificant proportion of transpired water.

The dry weights of seedlings at the beginning of the treatment period were estimated by destructively sampling a second set of three seedlings of each species just prior to treatment initiation. Initial estimated dry weights of seedlings were increased according to mean proportionate increase in dry weight calculated for the samples of the respective oak species. The proportionate increase in dry weight for a species did not vary by more than 4% from the mean proportion. A change in whole plant dry weight for the final two-month treatment period was estimated by subtracting the estimated dry weights of seedlings at the beginning of the treatment period from the final dry weights. A water use efficiency value was calculated from the estimated change in whole plant dry weight divided by the estimated water use over the final 2 month treatment period.

The pots that were allowed to dry for the drought regime were weighed every 2-3 weeks after the initial 2-week acclimation period and watered with measured amounts of tap water when needed to maintain 25-30% relative water capacity (RWC), which was found to be at or just above that which caused partial stomatal closure in red, white and bur oak seedlings grown under the same conditions (unpublished data). This range also corresponds to predawn leaf water potentials of the same red, white, and bur oak seedlings, of -1.0 ± 0.3 MPa determined with the use of a pressure bomb (Soilmoisture Plant Water Status Console Model 3005, Santa Barbara, California).

The artificially imposed drought regime lasted for two months. Approximately 1 month was necessary to reach 25-30% RWC and seedlings were maintained for an additional month under mild drought conditions of -1.0 ± 0.3 MPa predawn seedling water potentials. The final seedling heights and calipers were also measured at this time. Then all seedlings were harvested by gently washing the soil mixture from the roots in water and root, shoot, and foliage fresh and oven-dry (70°C for 24 h) weights were determined.

Analysis of variance was used to determine variation due to species, shade and irrigation regimes in a 4x3x2 factorial treatment design with the use of the General Linear Models procedure of SAS (SAS Institute 1982). The experimental design was a systematic split-split plot with shade as main plots and species and irrigation as subunits and sub-subunits respectively. Individual seedlings were randomly assigned to sub-subunits and rerandomized twice during the treatment period. Interactions between these three variables were also included in the model. Scheffe's multiple-comparison procedure was used to determine differences of all main effects (Steel and Torrie 1980).

The number of flushes (foliar growth and expansion between periods of bud set) per tree were also tabulated throughout the study. Specific leaf area was determined at the end of this study by cutting a total of 60 leaf discs 1-cm in diameter (from fully expanded leaves randomly selected from seedlings in each of six shade x drought treatments) for each species and determining the oven-dry weights. The total area of the leaf discs was then divided by the total dry weight to obtain the specific leaf area (cm^2/g).

RESULTS

<u>Irradiance</u>

Growth of oak seedlings of all species combined varied significantly with irradiance levels (Tables 1 and 2). Mean dry weight increment, caliper increment, root and shoot dry weights, and water use efficiency decreased significantly as shade levels increased from 30% to 73%. The shoot/root ratio increased as shade levels increased from 55% to 73%. The caliper increments were similar for the 55% and 73% shade levels and were 20 percent less than those at the 30% shade level. The mean dry weight increment at the 73% shade level was 56 and 42 percent less than at the 30% and 55% shade levels respectively. The water use efficiency declined 42 percent between the 30% and 73% shade levels. Shading had no significant effect on leaf dry weight or height increment.

The effect of irradiance, or shade levels, on white oak followed the same trends as for the regression model with species and irrigation levels pooled, except that shading did not affect the shoot/root ratio (Table 3). The dry weight increment for white oak was 83% less at the 73% shade level compared with the 30% shade level. There were consistent increases at the 55% shade level for shoot, root and stem dry weight. The increases were not statistically significant, however, but may have been due to an intermediate-shade reduction of evapotranspiration.

The effect of irradiance on the growth and water use of swamp white oak differed from the overall pattern for all oak species combined in that only mean dry weight increment, root dry weight and shoot dry weight were affected. The mean dry weight increment declined 52 percent from the 30% to the 73% shade level. The root and shoot dry weights were least, though not significantly so, at the intermediate (55%) shade level (Table 4).

The shoot/root ratio was the only growth variable significantly affected by shading in pin oak and shingle oak seedlings. The shoot/root ratio increased 25 percent from the 55 to 73% shade level for both pin and shingle oak (Tables 5 and 6).

Irrigation

Mean growth values for all oak seedlings combined (Table 1) and individual oak species (Table 7) varied significantly with irrigation regimes. Experimentally-imposed drought reduced the mean dry weight increment, root, leaf and shoot dry weights, caliper increment and water use efficiency, while it increased the shoot/root ratio. There were reductions of 65 percent in mean dry weight increment, 42 percent in water use efficiency and 31 percent in caliper increment for all oak species combined over the course of this study. The combined shoot/root ratio mean increased by 22 percent in the drought stressed oak seedlings compared with those at container capacity. Oak height increment was not significantly affected by drought in this study.

Drought decreased the mean dry weight increment of white oak by 67 percent and the dry root weight 25 percent, while it increased the shoot/root ratio by 17 percent relative to seedlings grown with an adequate water supply (Table 7). Drought had no statistically significant effect on water use efficiency, caliper increment, stem, leaf and shoot dry weight, although the values for these variables decreased due to drought at each shade level (Table 3).

The effect of drought on swamp white oak (Table 7) followed the pattern for all oak species combined with the exception that drought did not significantly affect the stem, leaf, and shoot dry weights. Declines were 66 percent in mean dry weight increment, 43 percent in water use efficiency and 87 percent in caliper increment. The root dry weight declined 37 percent and the shoot/root ratio increased 42 percent relative to well-watered swamp white oak seedlings. Growth and water use values declined with drought, while shoot/root ratio increased with drought for all shade levels and stem dry weight increased with drought at the 73% shade level (Table 4). Under the drought regime, water use efficiency increased with shade, but this interaction was not significant.

For pin oak, drought had no detectable effect on stem, leaf, and shoot dry weights (Table 7). Reductions of 67 percent in mean dry weight increment, 42 percent in water use efficiency, 27 percent in caliper increment and 41 percent in root dry weight occurred relative to well watered pin oak seedlings. The mean shoot/root ratio increased 30 percent overall due to drought.

The effect of drought on shingle oak (Table 7) was to decrease the mean dry weight increment by 57 percent and water use efficiency by 59 percent. The dry root weight declined 30 percent and the shoot/root ratio increased 21 percent with drought. Decreases in all variables except shoot/root ratio were found due to drought at all shade levels (Table 6). Shoot/root ratio increased due to drought at each shade level.

A shade x irrigation interaction occurred for the mean dry weight increment of swamp white oak. The mean dry weight increment decreased with shade at container pot capacity, but increased (non-significant) with shade under the drought regime (Table 8).

There is a possibility that size and shoot/root ratio may be correlated and that treatments influencing seedling size influenced this ratio. However, the slopes and intercepts of linear regressions of final dry weight and shoot/root ratio were different for irrigation compared with shade treatments. This indicates that the treatments influenced shoot/root ratios independently from any total plant dry weight relationship.

Other variables measured were number of flushes and specific leaf area. Pin oak flushed the most with an average of 2.5, followed by shingle oak (1.9), swamp white oak (1.6), and white oak (1.0) (Table 9). The specific leaf area was greatest in bottomland pin oak (176.1 cm^2/g) and swamp white oak (174.8 cm^2/g) and lowest for the upland shingle oak (157.7 cm^2/g) and white oak (158.7 cm^2/g).

DISCUSSION

The results of this study are consistent, for the most part, with the findings of Musselman and Gatherum (1969), who found that stem, leaf, shoot, and root dry weight decreased with shade and with reductions in available soil moisture for northern red oak seedlings. In contrast with the Musselman and Gatherum results, we did not find any significant increase in height of four oak species with increased shade. Increases in shoot/root ratio with decreases in soil moisture were also reported by Gatherum et al. (1963) for species of two hardwood and three coniferous seedlings. Norby and O'Neill (1989) reported a greater water use efficiency for white oak (6.3 mg cm^{-3}) than our overall mean (1.81 mg cm^{--3}). However, this discrepancy may be due to their use of first year seedlings rather than third year seedlings from bare-root nursery stock as employed in this study.

White oak is generally considered intermediate in shade tolerance and is more tolerant than the red oaks (Fowells 1965). Swamp white oak, a member of the white oak group, is also considered intermediate in shade tolerance (Fowells 1965). Pin oak, in the red oak group, is a common associate of swamp white oak. However, pin oak is considered to be intolerant of shade and it is recommended that pin oak receive at least 2/3 of full solar irradiance for successful regeneration

(Fowells 1965). Shingle oak, another member of the red oak group, occurs on a variety of sites, from dry upland ridges to rich and moist river bank soils (Iles 1988). Although there is little published research on the biology of shingle oak, it is considered to be somewhat intolerant of shade (Elias 1980).

In this study (Tables 3 and 4), 55% shade did not markedly reduce growth or water use efficiency of the white oaks relative to 30% shade. However, reduction in irradiance caused by the 73% shading did reduce growth and water use efficiency significantly in comparison with lower shade levels. Hence, increases in solar irradiance above 45% will probably not benefit growth as markedly as decreases in solar irradiance below 45% will inhibit growth. This study revealed few differences among shade levels between 30 and 73% on growth and water use efficiency of shingle and pin oak (Tables 5 and 6) in comparison to the white oaks.

Although shingle oak and pin oak are considered shade intolerant, the only response these species exhibited to the tested shade levels was to increase shoot/root ratio with shade (Tables 5 and 6). This response is indicative of shade intolerant trees such as jack pine (*Pinus banksiana*)(Kimmins 1987) and yellow poplar (*Liriodendron tulipifera*)(Loach 1970). Shade intolerant trees show a greater increase in shoot/root ratio as shade increases than do more tolerant species. Newhouse and Madgewick (1968) have found that rapid shoot growth in tree species is associated with intolerance of shade. Other authors have noted that the more tolerant tree species are characterized by the maintenence of a uniform pattern of growth over a wide range of shade (Baker 1945, Loach 1967 and Loach 1970). Consistent with these patterns, shingle oak and pin oak (Tables 5 and 6) showed an increase in shoot/root ratio with increasing shade while the more tolerant white oak and swamp white oak did not (Tables 3 and 4). Additionally, shade intolerant and faster growing shingle oak and pin oak flushed more times than the more tolerant white oak and swamp white oak seedlings. Reich et al. (1980) stated that multiple flushes occur in white, bur and post oak seedlings during the spring under conditions of favorable light and moisture, while single flushes occur when unfavorable conditions are present. Shingle oak and pin oak seem to be able to flush repeatedly, and more times than the white oaks, even when conditions are only marginally favorable for growth.

White oak and shingle oak seedlings seem to be more drought tolerant than pin oak and swamp white oak seedlings. Four important characteristics that can be used to help indicate drought tolerance in a tree species are higher water use efficiency, lower shoot/root ratio, lower specific leaf area, and less stem diameter inhibition than drought intolerant species (Gottschalk 1985, Larcher 1980). White oak alone exhibited an ability to maintain similar water use efficiency values under either irrigation regime (Table 7). Under the drought regime, rankings for water use efficiency from highest to lowest were: shingle oak (1.73 mg cm^{-3}), white oak (1.65 mg cm^{-3}), pin oak (1.46 mg cm^{-3}) and swamp white oak (1.01 mg cm^{-3}). The rankings for shoot/root ratio under drought from lowest (most advantageous) to highest were: white oak (0.60), shingle oak (0.87), pin oak (0.96), and swamp white oak (1.08). With moisture and shade treatments combined (no significant differences among them in area to weight ratio), the upland white oak and shingle oak had the lowest specific leaf areas. Such low specific leaf areas are characteristic of drought avoiders (Larcher 1980). Caliper increment (radial stem growth) of oaks is much more sensitive to stress and limiting factors than other variables such as height growth (Gottschalk 1985). The bottomland species, pin oak and swamp white oak, were the only species that showed a significant decrease in caliper increment due to drought. Swamp white oak was the most sensitive of the two as its caliper increment declined 86 percent, while pin oak's declined only 35 percent relative to the radial stem growth increments of well watered seedlings.

Under drought conditions, species that maintain a low shoot/root ratio are able to maximize water uptake by having a greater root surface to exploit scarce soil water and minimize evapotranspiration through reduced foliage quantity. Plants with a high water use efficiency under dry soil conditions can more efficiently use available water in producing phytomass (Larcher 1980). The two upland species, white oak and shingle oak, differed in their physiological responses to drought. Overall, white oak had a lower shoot/root ratio (0.56) than shingle oak (0.80), while shingle oak had a greater water use efficiency than white oak (Table 10). These differences may reflect different adaptive strategies to drought of these two upland oak species. The more shade intolerant shingle oak, with its high water use efficiency and high shoot/root ratio, is better equipped to compete both on droughty soils and on fertile sites where both soil moisture and irradiance may be limited due to competition from fast growing plants.

The two white oak species in this experiment exhibited higher shade tolerance and lower water use efficiencies than the two red oak species studied.

Pin oak and shingle oak are species which inhabit sites that may experience flooding and drought during the same growing season. Thus high water use efficiencies may be a physiological adaptation allowing pin and shingle oaks to grow on sites with alternating wet and dry periods. High water use efficiencies and high shoot/root ratios together allow a tree to compete well for solar radiation while at the same time efficiently using limited soil water resources on good sites where vegetative competition is great. Our results indicate that shingle oak is better able to maintain a high water use efficiency under drought conditions in comparison with pin oak. Furthermore, shingle oak does not drastically increase its shoot/root ratio in response to drought as does pin oak. This may be due in part to the coarse root system of shingle oak which is more sensitive to stress than the highly fibrous root system of pin oak (Struve and Moser 1984). Shingle oak is found more on dry upland sites than is pin oak, perhaps owing to the noted differences in functional and structural response to drought between these two species.

Of the white oaks, swamp white oak seems to be the most site specific. It had the lowest water use efficiency and highest shoot/root ratio for any of the oak species in this study (Table 10). This is consistent with its natural occurrence on poorly drained-upland depressions, swamp margins, stream banks and moist, peaty flats (Fowells 1965), sites which rarely undergo drought. Swamp white oak exhibited an irradiance x drought interaction (Table 8) in that at container water capacity the dry weight increment decreased with shade, but increased with shade under drought conditions. This interaction is probably due to a reduction in evapotranspiration of this midtolerant oak species caused by shade under drought conditions.

The extension of these data to ecological behavior of these oak species requires caution. In a forest not only is the quantity of light changed, but also the quality of light as the overstory canopy differentially absorbs and transmits various wavelengths of PAR and other solar radiation. Also, frequent dieback or browsing of advance oak regeneration will influence shoot/root ratios in the field. Hence the results of this study relate more to early establishment and growth of oak seedlings in forest understories than to the longer-term patterns of growth and development of advance oak regeneration, and should be extrapolated to field conditions with caution until confirmed by field studies.

SUMMARY

This study has shown that both increasing shade and drought decrease the growth and water use efficiency of four oak species of the central United States. Overall, the red oaks (shingle and pin oak) had the highest water use efficiencies and flushed more than white oak and swamp white oak, consistent with the generally faster juvenile growth rates of intolerant species. Shingle and pin oak also increased markedly in shoot/root ratio in response to shade, which is a characteristic of shade intolerant trees. Swamp white oak and white oak have the characteristics of midtolerant species, maintaining similar shoot/root ratios under a range of intermediate shade levels, exhibiting fewer flushes and smaller caliper increments overall in comparison with the two red oaks.

Under drought conditions, white oak and shingle oak had the lowest shoot/root ratios, highest water use efficiencies and smallest specific leaf areas, appropriate to their observed ability to grow on dry sites. However, both white and shingle oaks seem to have broad ecological amplitudes with respect to soil water availability, growing on mesic sites and, in the case of shingle oak, also on moist soils and on poorly drained flats with pin oak and post oak. Pin oak, which was between white oak and swamp white oak in shoot/root ratio and water use efficiency values under drought conditions, and similar to swamp white oak in specific leaf area, occurs in bottomland areas subject to flooding and in pin oak -post oak flats with a fragipan creating alternating wet and dry conditions. Swamp white oak and pin oak, the bottomland species, were the only ones to exhibit a significant decrease in caliper increment with drought. Swamp white oak was the most sensitive of the four oak species to drought, consistent with its ecologically narrow niche of moist sites.

This study examined two of the most important factors influencing forest regeneration, irradiance and soil moisture. The results indicate that the two white oaks were more shade tolerant than the two red oaks and will, therefore, more successfully survive in smaller openings and under denser canopies than pin and shingle oak. The data show a tendency suggesting that on sites where soil moisture may be limiting part of the season, shade levels from 55-73% may reduce evapotranspiration and increase growth of swamp white oak seedlings compared with more open conditions on the same site. Shingle oak may be a suitable native tree for minespoil reclamation and urban planting due to its drought tolerance and high water use efficiency described in this study combined with its moderately fast growth rate, mast production for wildlife and tolerance of wide pH ranges (Iles 1968).

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Table 1. Analysis of variance for growth and water use variables of four oak species grown under wet and dry irrigation regimes and three shade levels.

Source of variation	Degrees of freedom	Mean squares for					
		Dry Wt. Increment	Water Use Efficiency	Root Dry Wt.	Stem Dry Wt.	Leaf Dry Wt.	Top Dry Wt.
Oak Species	3	87.76*	27.90**	6144.32**	583.94**	108.56**	1176.32**
Shade Regime	2	288.67**	25.25**	358.49**	30.40**	15.57	70.52*
Spec. x Shade.	6	70.95*	7.12	214.96**	24.60*	10.79	62.90**
Irrigation Regime	1	1331.51**	78.48**	1131.52**	9.78	43.29**	94.21*
Spec. x Irr.	3	26.61	14.43**	75.55	0.64	1.50	3.20
Shade x Irr.	2	149.76**	4.52	45.40	5.20	4.81	18.53
Spec. x Shd. x Irr.	6	21.73	0.90	24.27	2.73	2.63	9.87
Error	256	29.77	3.68	44.65	4.46	5.51	16.66

Source of variation	Mean squares for		
	Shoot/Root Ratio	Caliper Increment (x1000)	Height Increment
Oak Species	1.91**	18.54**	79.01
Shade Regime	0.23*	1.73**	60.89
Spec. x Shade.	0.17*	1.36**	79.65
Irrigation Regime	2.66**	7.81**	16.78
Spec. x Irr.	0.20*	1.10	77.60
Shade x Irr.	0.05	0.19	89.49
Spec. x Shd. x Irr.	0.06	0.28	54.47
Error	0.06	0.32	55.61

* Significant at the 0.05 level
** Significant at the 0.01 level

Table 2. Mean growth and water use values for oak seedlings grown at three shade levels, with four oak species and two soil moisture levels pooled.

GROWTH VARIABLE	PERCENT SHADE		
	30	55	77
Observations (n)	95	92	93
Dry Weight Increment (g)	6.23 a*	4.66 a	2.72 b
Water Use Efficiency (mg cm^{-3})	2.45 a	2.11 a	1.42 b
Root Dry Weight (g)	12.80 a	13.30 a	9.42 b
Stem Dry Weight (g)	3.79 a	4.02 a	2.86 b
Leaf Dry Weight (g)	4.47 ns	3.91	3.64
Shoot Dry Weight (g)	8.26 a	7.94 ab	6.51 b
Shoot/Root Ratio (dry weight)	0.75 ab	0.72 b	0.82 a
Caliper Increment (mm)	0.34 a	0.27 b	0.26 b
Height Increment (cm)	15.02 ns	13.72	13.57

* Means within a row followed by the same letter are not significantly different at 0.05 level according to Scheffe's test.

Table 3. The effects of shade on growth and water use variable means of white oak.

WHITE OAK

Percent Shade	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)
30	CC#	15	2.78	28.91	7.89	7.12	15.02
	DR	15	2.27	20.61	6.82	5.41	12.23
	Mean+	30	2.53a*	24.76a	7.36a	6.27ns	13.62a
55	CC	14	2.51	33.92	9.74	6.99	16.74
	DR	15	2.34	24.64	8.41	5.31	13.72
	Mean	29	2.42a*	29.28a	9.08a	6.15	15.23a
73	CC	13	0.60	18.82	4.83	4.34	9.17
	DR	15	0.34	16.64	5.71	4.32	10.03
	Mean	28	0.47b	17.73b	5.27b	4.33	9.60b

Percent Shade	Irrigation Level	N	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC	15	13.43	0.52	0.38	13.73
	DR	15	4.17	0.63	0.038	15.20
	Mean	30	8.80a	0.57ns	0.38a	14.47ns
55	CC	14	10.64	0.50	0.24	13.79
	DR	15	4.09	0.57	0.17	13.63
	Mean	29	7.36a	0.54	0.20 b	13.71
73	CC	13	2.32	0.53	0.15	10.74
	DR	15	0.75	0.60	0.09	10.20
	Mean	28	1.53 b	0.57	0.12 b	10.47

CC is the 90-95% container capacity regime. DR is the drought regime (20-25% container capacity).
+ Mean is for the pooled irrigation values at the given shade level.
* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.
ns Not significant.

Table 4. The effects of shade on growth and water use variable means of swamp white oak.

SWAMP WHITE OAK

Shade Level	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)
30	CC[#]	12	2.55	9.23	2.61	4.54	7.15
	DR	13	0.98	5.42	2.28	3.12	5.40
	Mean[+]	25	1.76ns	7.33a*	2.44ns	3.83ns	6.28ns
55	CC	11	1.43	6.55	2.12	2.77	4.89
	DR	12	0.93	4.07	1.81	2.78	4.59
	Mean	23	1.18	5.31 b	1.97	2.78	4.74
73	CC	14	1.44	7.06	2.06	3.21	5.27
	DR	11	1.14	4.86	2.76	2.76	4.94
	Mean	25	1.29	5.96ab	2.12	2.98	5.10

Shade Level	Irrigation Level	N	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC	12	8.81	0.79	0.27	19.29
	DR	13	1.63	1.01	0.03	16.65
	Mean	25	5.22a	0.90ns	0.15ns	17.97ns
55	CC	11	3.89	0.75	0.14	9.86
	DR	12	1.70	1.16	0.05	17.12
	Mean	23	2.79ab	0.96	0.10	13.49
73	CC	14	3.05	0.75	0.24	13.78
	DR	11	1.93	1.08	0.01	14.95
	Mean	25	2.49 b	0.91	0.12	14.37

\# CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).
\+ Mean is for the pooled irrigation values at the given shade level.
* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.
ns Not significant.

Table 5. The effects of shade on growth and water use variable means of pin oak.

PIN OAK

Percent Shade	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)
30	CC[#]	10	2.88	9.67	2.99	3.52	6.52
	DR	10	1.57	5.05	1.76	2.42	4.18
	Mean[+]	20	2.22ns	7.36ns	2.38ns	2.98ns	5.35ns
55	CC	10	2.47	8.12	2.07	3.28	5.36
	DR	10	1.14	5.02	1.67	2.62	4.29
	Mean	20	1.81	6.57	1.87	2.95	4.82
73	CC	10	2.14	6.66	1.84	3.28	5.12
	DR	10	1.67	4.35	1.88	3.36	5.24
	Mean	20	1.91	5.50	. 1.86	3.32	5.18

Percent Shade	Irrigation Level	N	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC	10	8.42	0.68	0.56	15.85
	DR	10	2.11	0.82	0.51	10.25
	Mean	20	5.26ns	0.75 b*	0.54ns	13.05ns
55	CC	10	6.23	0.66	0.60	14.60
	DR	10	1.70	0.82	0.36	13.05
	Mean	20	3.96	0.74 b	0.42	13.82
73	CC	10	4.40	0.77	0.63	14.40
	DR	10	2.55	1.22	0.44	16.30
	Mean	20	3.48	1.00a	0.54	15.35

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).

+ Mean is for the pooled irrigation values at the given shade level.

* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.

ns Not significant.

Table 6. The effects of shade on growth and water use variable means of shingle oak.

SHINGLE OAK

Shade Level	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)
30	CC#	10	5.08	8.33	1.53	4.39	5.92
	DR	10	1.79	6.14	1.54	3.82	5.35
	Mean+	20	3.44ns	7.24ns	1.54ns	4.10ns	5.63ns
55	CC	10	3.91	7.22	1.31	3.09	4.40
	DR	10	2.09	5.44	1.21	2.86	4.07
	Mean	20	3.00	6.33	1.26	2.98	4.24
73	CC	10	3.61	7.42	1.70	4.38	6.08
	DR	10	1.29	4.48	1.10	3.23	4.33
	Mean	20	2.45	5.98	1.40	3.80	5.20

Shade Level	Irrigation Level	N	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC	10	7.17	0.74	0.33	17.05
	DR	10	2.70	0.89	0.32	11.35
	Mean	20	4.94ns	0.81ab*	0.33ns	14.20ns
55	CC	10	4.26	0.62	0.40	14.40
	DR	10	3.00	0.74	0.34	13.00
	Mean	20	3.63	0.68 b	0.37	13.70
73	CC	10	6.03	0.81	0.38	16.35
	DR	10	1.86	0.99	0.34	14.15
	Mean	20	3.93	0.90a	0.36	15.25

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).
+ Mean is for the pooled irrigation values at the given shade level.
* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.
ns Not significant.

Table 7. The effects of drought on the growth and water use of white (WO), swamp white oak (SWO), pin oak (PO) and shingle oak (SO).

Species	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)
WO	CC#	42	1.96ns	27.45*	7.56ns	6.22ns	13.78ns
	DR	45	1.65	20.63	6.98	5.01	11.99
SWO	CC	37	1.79*	7.61*	2.26ns	3.51ns	5.77ns
	DR	36	1.01	4.80	2.09	2.90	4.99
PO	CC	30	2.50*	8.15*	2.30ns	3.36ns	5.66ns
	DR	30	1.46	4.81	1.77	2.80	4.57
SO	CC	30	4.20*	7.68*	1.51ns	3.95ns	5.46ns
	DR	30	1.73	5.35	1.28	3.30	4.58
MEAN	CC	139	2.53*	13.74*	3.71ns	4.39*	8.10*
	DR	141	1.46	9.97	3.41	3.64	7.05

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).
* Means within the column pair for an oak species are significantly different at 0.05 level according to the F-test.
ns Not significant.

Table 7 (Cont'd). The effects of drought on the growth and water use of white (WO), swamp white oak (SWO), pin oak (PO) and shingle oak (SO).

Species	Irrigation Level	N	Dry Wt. Increment (g)	Shoot Root Ratio	Caliper Increment (mm)	Height Increment
WO	CC#	42	9.06*	0.52*	0.30ns	12.82ns
	DR	45	3.00	0.60	0.21	13.01
SWO	CC	37	5.17*	0.76*	0.22*	14.40ns
	DR	36	1.74	1.08	0.03	16.29
PO	CC	30	6.35*	0.70*	0.59*	14.95ns
	DR	30	2.12	0.96	0.44	13.20
SO	CC	30	5.82*	0.72*	0.37ns	15.93ns
	DR	30	2.52	0.87	0.33	12.83
MEAN	CC	139	6.74*	0.67*	0.35*	14.37ns
	DR	141	2.39	0.87	0.24	13.85

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).
* Means within the column pair for an oak species are significantly different at 0.05 level according to the F-test.
ns Not significant.

Table 8. Interaction of shade and drought on the dry weight increment (g) of swamp white oak.

	Shade Percentage			
Irrigation	30	55	73	Mean
Container Capacity	8.81 n=12	3.89 n=11	3.05 n=14	5.17**
Drought Regime	1.63 n=13	1.70 n=12	1.93 n=11	1.74
Mean	5.22 a	2.79 ab	2.49 b*	

* Means within a row followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.
** Means in the column are significantly different at 0.05 level according to the F test.

Table 9. The effect of irrigation regime on the observed number of flushes of four oak species.

	Observed Flushes			
Species	Container Capacity	Drought Regime	Mean	Range
White oak	1.00	1.01	1.00	1-2
Swamp white oak	1.68	1.61	1.64	1-3
Pin oak	2.70	2.30	2.50	1-4
Shingle oak	2.00	1.77	1.90	1-3

Table 10. Sources of variation among species, with shade and irrigation levels pooled.

Species	Water Use Efficiency ($mg\ cm^{-3}$)	Shoot/Root Ratio	Caliper Increment (mm)
White oak	1.81 b*	0.56 c	0.24 c
Swamp white oak	1.41 b	0.92a	0.12 d
Pin oak	1.98ab	0.83ab	0.52a
Shingle oak	2.96a	0.80 b	0.35 b

* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.