

35. Effects of Temperature and Drought Stress on Physiological Processes Associated With Oak Decline

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Oak decline is a term used to describe a sequence of events (decline syndrome) which is typically triggered by an **abiotic** stress and subsequently involves other biotic and **abiotic** factors that cause the progressive deterioration and eventual death of a tree. Decline diseases lack a single causal agent, and in that way are different from diseases caused by one pathogen or by a single **abiotic** injury. Decline and premature death of oaks in the oak-dominated eastern deciduous forests have been documented in at least twenty-six separate reports over the past 140 years (Ammon et al., 1989).

Drought-induced stress appears to trigger or contribute to the decline syndrome in many of these reports for the eastern United States (Beal, 1926; Hursh and Haasis, 1931; McIntyre and Schnur, 1936; True and Tyron, 1956; Gillespie, 1956; Fergus and Ibberson, 1956; Staley, 1965; Lewis, 1981; Tainter et al., 1983; Law and Gott, 1987; Maass, 1989; Tainter et al., 1990; Myers and Killingsworth, 1992). Under environmental conditions in which water availability may limit growth, abnormally high temperatures can alter normal energy flows and can increase both respiration and transpiration. Temperature and water availability are among the most critical **abiotic** conditions that must remain within certain ranges for optimum growth of any species, and oaks are no exception. Temperature can influence, growth and development, metabolism, carbon translocation, enzyme action, water potential, and transpiration (Salisbury and Ross, 1978). Water probably provides the strongest influence on productivity of vegetation in forest ecosystems than any other **abiotic** factor (Whittaker, 1975; Kozlowski, 1982).

Concentrations of such greenhouse gases as carbon dioxide (CO₂), methane, and oxides of nitrogen in the atmosphere are predicted to double in the next 100 years (Edmonds, et al., 1984; Friedli et al., 1986), thereby increasing the greenhouse effect and leading to an estimated increase in global mean temperature of 1.5 to 4.5 °C (National Academy of Sciences, 1983). In addition to these increases of gases, summertime precipitation is predicted to decrease from 5 to 10%, and wintertime precipitation is predicted to increase from 0 to 15% (Karl et al., 1991). However, opposite responses of greater precipitation, lower maximum temperatures, and higher minimum temperatures have also been predicted (Idso and Balling, 1992).

Under the warmer and drier climate change scenario, normal ecosystem functions and energy flows could be altered as individual trees and species adapt to the predicted changes. This adaptation will depend on a number of such factors as the magnitude and rate of climate change and the extent to which increased CO₂ can offset the potential growth-limiting effects of elevated temperature and drought (Keller, 1984). Woodman and Furness (1988) predicted an increase in tree injury and death from insects and pathogens, acting as single agents, resulting from a warmer and drier climate. For instance, trees growing on suboptimum sites would be more susceptible to insect attacks (Miller et al., 1987). In general, pest problems would increase in stands containing less vigorous, stressed trees (Hedden, 1987) found in older, unmanaged, and denser forests. More than thirty years ago, Hepting (1963) described the potential for the incidence, severity, and northern ranges of diseases to increase should climate factors, which normally act as constraints against outbreaks, become altered. Climate modeling with regard to decline of evergreen oaks in the Mediterranean area predicts an increase in host range of the root pathogen *Phytophthora cinnamomi* Rands, in addition to increases in root disease severity and fungus survivability (Brasier and Scott, 1994). Tomlinson (1993) postulated that increased temperature and reduced rainfall led to nutrient deficiency, fine root mortality, and, eventually, crown dieback as nutrient cations were leached from soil by acids formed from mineralization and nitrification in excess of the tree's needs. An increased frequency of such stresses as drought and elevated temperature may trigger increasing numbers of decline events and therefore place a greater burden on present oak resources.

The southern United States produces 57% of the nation's hardwood lumber, 40% of its hardwood plywood, and 60% of its pulpwood, a large part of which is hardwood (Kronrad, 1993). Red and white oak lumber accounted for more than half the \$3.5 billion value of hardwood lumber in the eastern United States in 1990. Within the next fifty years, the U.S. Forest Service predicts an 80% increase in hardwood harvesting at the same time growth is declining as a result of several factors including 1) growth decline in some species (oaks), 2) increased death, 3) low regeneration rates, and 4) declines in acreage (Kronrad, 1993). The most recent Forest Inventory Analysis (FIA) data indicate that of the 42 million hectares (ha) of hardwood forest type occurring in the twelve southern states, 44% are vulnerable to oak decline, and of this area, 6% of bottomland and 10% of upland types are affected by oak decline (Hoffard et al., 1995). Furthermore, volume

losses resulting from oak death are about 1.4 times greater on affected areas compared to unaffected areas. Given that this important oak resource is declining in availability at a time of increasing demand while simultaneously facing the possibility of an increasingly stressful environment, it is imperative to understand the effects of such environmental stresses as a warmer average temperature and more frequent droughts on oak tree physiology and growth. Additional studies will also be needed to examine the effects of such stresses along with effects of insect attacks and disease occurrence.

Much of the bottomland oak resource, especially in the Lower Mississippi Alluvial Valley, has been removed for agriculture (Ford, 1994). The remaining bottomland hardwood forests, and the upland hardwood forests, will contribute greatly to the multiple resource needs of fiber, wildlife habitat, and recreation placed by society on the forests of the southern United States. Because decline diseases are triggered by stress, symptoms typically occur simultaneously over wide geographic regions and often affect a single species, or group of species. Therefore, it is essential to be able to predict how the bottomland and upland oak resources in the southern United States will respond to increased stress from elevated temperature and drought, and to determine whether oaks on better sites could become more susceptible to a decline-triggering stress.

During 1994, an experiment was conducted to examine the effects on seedling physiology and growth of three bottomland and three upland oak species from the combined stresses of elevated temperature and drought under a predicted 1.5 to 4.5 °C increase in average global temperature. The results of the first year are presented here and represent average responses of seedling oaks to the very low end of the predicted increases in global mean temperature and drought. Although studies of seedling physiology have limited application to mature trees and whole ecosystems, data from this experiment should be useful to process modelers interested in simulating effects of moderate temperature and drought stress on individual whole plants and in extrapolating the data to estimate effects at the ecosystem level.

Methods

Plant Culture

During May of 1993, seeds of the following four species in the red oak group were planted: 1) southern red (*Q. falcata* Michx.), 2) nuttall (*Q. nuttallii* E.J. Palmer), 3) willow (*Q. phellos* L.), and 4) scarlet (*Q. coccinea* Mtinchh.). Two species in the white oak group were also planted: 1) white (*Q. alba* L.), and 2) overcup (*Q. lyrata* Walter). All the seeds were planted in treepots (7.5 l; 41 x 15 x 15 cm) with fritted clay (van Bavel et al., 1978) as the potting medium. Acorns were collected in the fall of 1992 from the following sources: 1) nuttall, willow, and overcup from an area near Stoneville, Mississippi, southern red from near Redwood, Mississippi, 3) scarlet from near La Grange, Tennessee, and 4) white from near Cadiz, Kentucky. Seedlings were given 35 g of a controlled-release fertilizer

containing nitrogen-phosphorus-potassium (N-P-K) (17-6-10) and other minor nutrients (Sierra Blend, Grace-Sierra Co.) at the start of each growing season. Seedlings were exposed to similar temperature and shading during 1993, and subjected to three soil moisture and three air temperature shading treatments during 1994.

Temperature Shading and Soil-Moisture Treatments

Three greenhouses provided three distinct summertime temperatures for three similar sets of plants by using a combination of evaporative cooling and shading that was needed to reduce heat loads inside the greenhouses. Evaporative cooler thermostats and shade cloths were adjusted to produce the treatments employed, that reflect differences from actual average monthly maximum temperatures during June to October of 1994 against a baseline average monthly maximum temperature of 1) 27.4 °C (Base), 2) a baseline + 0.7 °C (Base + 0.7), and 3) a baseline + 1.7 °C (Base + 1.7) (Figure 35.1). To produce these temperatures, greenhouse roof areas were covered year round with 50% shade cloth in the following three manners: 1) 100%-covered for the Base, 2) 40%-covered for the Base + 0.7, and 3) 25% covered for the Base + 1.7 treatments. Average year-round temperatures, from the time acorns were planted until seedlings were harvested, were 26.0 °C, 26.4 °C, and 26.8 °C, respectively, for the Base, Base + 0.7, and Base + 1.7 summertime treatments. During winter, temperatures were prevented from falling below 0 °C in all greenhouses.

Soil-moisture regimes were started in mid-July 1994 with adequate water (A), intermediate water (B), and drought (C) treatments maintained at or above, 27%

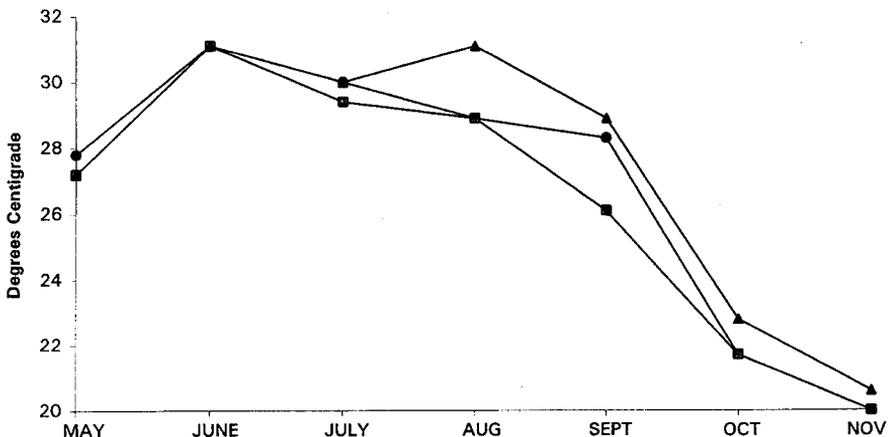


Figure 35.1. Average monthly maximum temperatures for the 1994 growing season; differences are described in the text. ■ = Base, ● = Base + 0.7 °C, ▲ = Base + 1.7 °C. Differences in temperatures of 0.7 °C and 1.7 °C above Base were achieved as averages from May to October.

(-0.3 MPa), 22% (-0.6 MPa), and 17% (-1.2 MPa) volumetric soil moisture (soil-moisture potential), respectively. Soil moisture was measured regularly by time-domain reflectometry (Soil Moisture Equipment Corp.), and seedlings were watered to field capacity with deionized water each time the predetermined minimum volumetric soil moisture was attained. On the warmest days, A seedlings were watered every 24 hours, and C seedlings were watered approximately every 36 to 48 hours.

Experimental Design and Biological Measurements

A randomized complete block design was used in which three replicates of each species \times moisture regime combination were distributed in thirty-six positions on each of three benches per greenhouse. Each bench was a block with the first being closest to the evaporative cooler so that air in this block was presumably cooler and more humid than air in block three, which was farthest from the cooler and next to the exhaust fans. Half the number of seedlings per bench (eighteen) were harvested after the first year, and the remaining seedlings were harvested after the 1995 growing season. Analysis of variance (ANOVA), using SAS software was performed on values of net photosynthesis (P_{net}), stomatal conductance (g_s), transpiration rate (TR), leaf pigment concentrations (chlorophylls a and b, and carotenoids and xanthophylls), and predawn leaf xylem water potential (ψ) measured during the first, sixth, tenth, and fourteenth weeks (July to October) following the start of different soil-moisture regimes. Heights and diameters, biomass (leaves, stems, and roots), and foliar concentrations of calcium (Ca), magnesium (Mg), K, and P were measured at the end of the growing season. All variables were analyzed in a two-way analysis of variance (six species \times three soil-moisture regimes) for different responses in species and soil-moisture treatments within each greenhouse.

Stomatal conductance and photosynthetic and transpiration rates were measured on fully expanded leaves with a LI-6250 portable photosynthesis system (LiCor, Inc.) and a 1-l cuvette. Measurements were made during the day with photosynthetic photon flux densities (PPFD; \pm standard error) between 1100 and 1300 ± 2 to $5 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean leaf temperatures (\pm standard error) in the cuvette from 23 to 33 ± 0.1 to 0.2 °C depending on the month, and relative humidities (\pm standard error) in the cuvette from 61 to 83 ± 0.2 to 1.2%. Photosynthetic photon flux densities were generated by a quartz halogen projection lamp (GE-ESD, General Electric Co.) for consistency. Using a pressure chamber, predawn leaf-water potentials were measured on the same leaf of each seedling used to measure gas exchange nine to eighteen hours earlier. Chlorophyll, carotenoids, and xanthophylls were extracted in 10 ml of dimethyl sulfoxide (Hiscox and Israelstam, 1979) from two 0.78 cm^2 disks removed from the portion of each leaf that was in the cuvette for gas exchange measurements. Pigment absorbencies were measured following extraction in the dark at 65 °C for fifteen to eighteen hours, and pigment concentrations were estimated according to the equations of Lichtenthaler and Wellburn (1983) for 100% acetone. For biomass determinations, leaves, stems, and roots of seedlings were dried to a constant

Table 35.1. Data Quality Objectives and Achievements for the Response Variables¹

Response variable	Precision (%)	Completeness (%)
Leaf xylem water potential	10 6.2	99 100
Net photosynthesis	10 4.6	99 99
Stomatal conductance	10 7.0	99 99
Transpiration	10 6.2	99 99
Chlorophyll a	10 5.3	99 98
Chlorophyll b	10 9.0	99 98
Carotenoids & xanthophylls	10 4.8	99 98
Leaf biomass	15 12.3	99 99
Stem biomass	15 16.2	99 99
Root biomass	1.5 10.6	99 99
Stem height	15 8.0	99 100
Stem diameter	10 4.9	99 100

¹ Precision was expressed as a coefficient of variation for the reduced data. Completeness was measured as the ratio of actual measurements recorded to the total number of possible measurements. The first value in each category was the objective, the second value was the achievement.

weight at 70 °C and then were weighed. Stem heights were measured to the nearest mm from 2.54 cm above the soil line to the tip of the dominant leader; stem diameters were measured to the nearest 0.01 mm at 2.54 cm above the soil line. Samples of dried leaf tissue were analyzed for Ca, Mg, and K concentrations using atomic absorption spectrophotometry, and for P concentrations using acid extraction and a colorimetric technique.

Data quality objectives of precision and completeness for measurement variables were met, or exceeded, in most cases (Table 35.1). Accuracy of data could not be measured for all variables but was ensured by calibrating all instruments according to manufacturers' specifications and by adhering to published standard operating procedures.

Results

Average ψ for the six species showed some differences (Base + 0.7), and general trends resulting from differences in soil-moisture treatments six weeks after treatments were in place (Table 35.2). Differences continued to be evident in Weeks 10 (Base + 1.7) and 14 (Base and Base + 0.7). Throughout the experiment, ψ tended to be more negative for the majority of seedlings in the warmer and drier air environment of block 3 in each greenhouse; **nuttall** oak tended to have greater negative ψ values (data not shown). The values of predawn ψ measured in this study are about seven to ten times less than those reported for sapling and mature *Q. alba* L. (Hinckley et al., 1978; Dougherty and Hinckley, 1981) under prolonged drought that caused soil-moisture potentials from - 2.0 to - 4.5 MPa. The drought stress treatment (- 1.2 MPa) in the present study, although moderate in severity, could not be sustained in container-grown seedlings of this size for more

Table 35.2. Average Predawn Leaf Xylem Water Potentials (ψ) of Six Species of Two-Year-Old Oak Seedlings Exposed to Three Temperature Shade Treatments and Three Soil-Moisture Regimes¹

Temp.	Moist.	Ψ (-MPa)			
		Wk. 1	Wk. 6	Wk. 10	Wk. 14
Base	A	.24 ± .01	.28 ± .02	.29 ± .02	.22 ^b ± .01
	B	.24 ± .02	.30 ± .02	.29 ± .02	.27 ^a ± .02
	C	.24 ± .01	.30 ± .02	.32 ± .02	.26 ^{ab} ± .02
Base + 0.7	A	.26 ± .02	.27 ^b ± .02	.27 ± .01	.18 ^b ± .01
	B	.22 ± .02	.32 ^a ± .01	.27 ± .01	.21 ^{ab} ± .01
	C	.23 ± .02	.33 ^a ± .01	.29 ± .02	.23 ^a ± .01
Base + 1.7	A	.26 ^a ± .02	.26 ± .02	.30 ^b ± .02	.22 ± .02
	B	.22 ^b ± .01	.29 ± .02	.31 ^b ± .02	.19 ± .01
	C	.27 ^a ± .01	.29 ± .02	.38 ^a ± .02	.22 ± .02

¹ Data are means of eighteen samples ± SE. Also, means with different letters between soil-moisture regimes, and within the same temperature treatment and time interval combinations, are different as determined by Duncan's Multiple Range Test ($P = 0.05$)

than forty-eight hours without inducing severe wilting and risking the possibility of branch dieback.

Mean P_{net} (Table 35.3) of all species without regard to soil-moisture regimes was greater in Base + 0.7 ($8.2 \pm 0.3 \mu\text{molm}^{-2}\text{s}^{-1}$) and Base + 1.7 ($7.8 \pm 0.4 \mu\text{molm}^{-2}\text{s}^{-1}$) temperatures than in the Base temperature ($6.4 \pm 0.3 \mu\text{molm}^{-2}\text{s}^{-1}$). Furthermore, P_{net} was significantly greater ($P = 0.05$) in block 3 than in block 1 of each greenhouse at 6, 10, and 14 weeks (data not shown) probably because the air surrounding block 3 was warmer than that of block 1 because of its greater distance from the evaporative cooler pads. However, within temperature treatments, there was little relationship between mean P_{net} of all species and soil-moisture treatments. Mean P_{net} values averaged across temperature treatments were $7.3 \pm 0.3 \mu\text{molm}^{-2}\text{s}^{-1}$ for soil-moisture regime A, $7.6 \pm 0.4 \mu\text{molm}^{-2}\text{s}^{-1}$ for regime B, and $7.5 \pm 0.4 \mu\text{molm}^{-2}\text{s}^{-1}$ for regime C, again indicating little response to soil-moisture treatments. These same trends of an apparent greater response to warmer temperatures and little response to soil-moisture regime were evident for g_s and TR although individual analyses of g_s and TR responses to soil-moisture regimes within temperature regimes were generally inconclusive (Table 35.3).

Taken as a whole, these results suggest that exposing these oak seedlings to warmer air temperatures tended to increase rates of net photosynthesis and transpiration, and increase stomatal conductance. Seedlings of *Q. rubra* L. exposed to warmer temperatures and greater PPF in an ozone-exposure study had greater stomatal conductances and greater rates of net photosynthesis than seedlings in a cooler environment with a lesser rate of PPF (Samuelson, 1994). However, results of the present study are in contrast to reports in which prolonged drought conditions caused marked decreases in P_{net} of *Q. alba* (Hinckley et al., 1979; Dougherty and Hinckley, 1981), and in *Q. petraea* Matt. Liebl. prolonged drought

Table 35.3. Average Net Photosynthesis (P_{net}), Stomatal Conductance (g_s), and Transpiration Rates (TR) for Six Species of Two-Year-Old Seedlings Exposed to Three Temperature and Shade Treatments and Three Soil Moisture Regimes¹

Temp	Moist	P_{net} ($\mu\text{molm}^{-2}\text{s}^{-1}$)				g_s ($\text{molm}^{-2}\text{s}^{-1}$)				TR ($\text{mmolm}^{-2}\text{s}^{-1}$)		
		Wk. 1	Wk. 6	Wk. 10	Wk. 14	Wk. 1	Wk. 6	Wk. 10	Wk. 14	Wk. 1	Wk. 6	Wk. 10
Base	A	7.1 ± .2	5.6 ± .3	5.3 ^b ± .3	6.7 ± .2	.21 ± .01	.12 ^b ± .01	.10 ^b ± .01	.17 ^b ± .01	2.9 ± .13	1.7 ± .12	1.3 ^b ± .10
	B	8.2 ± .4	6.1 ± .3	5.3 ^b ± .3	6.6 ± .3	.24 ± .01	.14 ^a ± .01	.11 ^{ab} ± .01	.18 ^b ± .01	3.1 ± .11	1.8 ± .12	1.4 ^{ab} ± .11
	C	8.0 ± .6	5.6 ± .3	6.0 ^c ± .3	7.0 ± .4	.28 ± .04	.12 ^b ± .01	.12 ^a ± .01	.22 ^a ± .02	3.3 ± .28	1.7 ± .11	1.6 ^c ± .10
Base + 0.7	A	7.9 ^b ± .4	8.3 ^c ± .3	7.9 ± .4	9.4 ± .4	.22 ± .02	.22 ^a ± .02	.15 ^{ab} ± .01	.28 ± .02	3.1 ± .21	3.5 ^a ± .20	2.4 ± .17
	B	8.9 ^a ± .3	8.4 ^a ± .3	7.5 ± .5	8.9 ± .4	.23 ± .01	.23 ^a ± .01	.17 ^a ± .01	.29 ± .02	3.3 ± .13	3.6 ^a ± .18	2.4 ± .18
	C	7.7 ^b ± .2	7.3 ^b ± .4	7.0 ± .4	8.7 ± .4	.24 ± .02	.17 ^b ± .01	.13 ^b ± .01	.30 ± .02	3.3 ± .18	2.8 ^b ± .21	2.2 ± .14
Base + 1.7	A	7.2 ^b ± .3	6.9 ^b ± .4	8.3 ^{ab} ± .3	6.8 ^{ab} ± .3	.23 ^b ± .01	.14 ^b ± .01	.17 ± .01	.16 ^b ± .01	2.2 ^b ± .11	2.5 ^b ± .23	2.1 ± .11
	B	8.3 ^a ± .4	9.0 ^a ± .4	7.9 ^b ± .4	6.7 ^b ± .4	.34 ^a ± .02	.23 ^a ± .02	.20 ± .02	.20 ^a ± .02	3.2 ^a ± .20	3.5 ^a ± .21	2.0 ± .12
	C	8.9 ^a ± .3	7.5 ^b ± .3	8.8 ^c ± .3	7.4 ^a ± .4	.30 ^a ± .02	.17 ^b ± .02	.17 ± .01	.21 ^a ± .02	2.9 ^a ± .15	3.2 ^a ± .26	2.3 ± .13

Data are means of eighteen samples ± SE. Also, means with different letters between soil-moisture regimes, and within the same temperature treatment and time interval co differ as determined by Duncan's Multiple Range Test ($P = 0.05$)

Table 35.4. Average Heights and Diameters of Six Species of Two-Year-Old Oak Seedlings Exposed to Three Temperature and Shade Treatments, and Three Soil-Moisture Regimes¹

Temp	Moisture	Height (cm)	Diameter (mm)
Base	A	156.6 ± 13.2	13.5 ± .7
	B	146.8 ± 13.6	12.8 ± .9
	C	147.8 ± 12.6	13.0 ± .8
Base + 0.7	A	139.1 ± 10.2	12.8 ± .5
	B	128.7 ± 10.6	12.3 ± .5
	C	138.6 ± 9.1	12.4 ± .5
Base + 1.7	A	127.7 ± 10.4	11.9 ± .5
	B	124.1 ± 9.7	11.3 ± .5
	C	142.0 ± 10.3	11.8 ± .6

¹ Data are means of thirty-six samples ± SE.

conditions caused marked decreases in P_{net} and g_s when predawn ψ dropped below -1.0 MPa (Epron and Dreyer, 1993). Similarly, P_{net} and g_s were reduced in *Q. robur* L., *Q. rubra*, and *Q. petraea* with predawn ψ as low as -3.5 MPa (Vivian et al., 1993).

The pattern of increasing carbon assimilation as temperature increased was not immediately evident in either the height and diameter data (Table 35.4) or the biomass data (Table 35.5) resulting primarily from a plant culture artifact during seedling establishment that resulted in larger seedlings in the Base temperature treatment than in Base + 0.7 and Base + 1.7 treatments. The effect of greater carbon uptake in warmer temperatures was evident as greater increases in average heights (Base = 124%, Base + 0.7 = 318%, Base + 1.7 = 283%) and average diameters (Base = 82%, Base + 0.7 = 184%, Base + 1.7 = 149%) expressed as percentages of pretreatment heights and diameters for all species across soil-moisture treatments. Drought-stressed seedlings exposed to the Base + 1.7 temperature treatment had greater leaf and total shoot biomass than seedlings in the intermediate or adequately watered treatments, although means separations for stem and root biomass between water regime treatments were inconclusive (Table 35.5). Root/shoot ratios indicate that in the Base + 0.7 and Base + 1.7 temperature treatments, carbon allocation favors roots at the expense of shoots. Within Base and Base + 0.7 treatments, root/shoot ratios tend to increase as soil moisture decreases. This allocation pattern would facilitate greater root growth for attaining more water under drought conditions. Seedlings in the A and B soil-moisture regimes exposed to the Base temperature had a near 1:1 carbon allocation balance between roots and shoots.

Comparisons of concentrations of chlorophylls a and b, and carotenoids and xanthophylls on a weight per area basis and a weight per weight basis between soil-moisture treatments at the various combinations of time and temperature treatments either did not differ or the comparisons were inconclusive (Table 35.6). White oaks tended to have the highest concentrations of all pigments on the basis of area; overcup oaks had the highest concentrations of chlorophylls a and b on a weight basis (data not shown). The effects of drought and elevated temperature on

Table 35.5. Average Dry Weights of Leaves, Stems, Shoots (Leaves and Stems), Roots, and Root/Shoot Ratios (R/S) of Six Species of Two-Year-Old Oak Seedlings Exposed to Three Temperatures and Shade Treatments, and Three Soil-Moisture Regimes¹

Temp.	Moist.	Leaves (g)	Stems (g)	Shoots (g)	Roots (g)	R/S
Base	A	35.7 ± 4.5	91.4 ± 16.9	127.1 ± 20.7	133.1 ± 13.0	1.05
	B	32.9 ± 5.0	89.0 ± 18.2	121.9 ± 22.7	124.2 ± 21.5	1.02
	C	29.6 ± 4.1	81.2 ± 14.8	110.8 ± 18.3	125.7 ± 14.6	1.13
Base + 0.7	A	29.6 ± 3.1	62.5 ± 7.4	92.0 ± 10.1	116.2 ± 9.9	1.26
	B	27.2 ± 4.1	51.6 ± 10.7	78.7 ± 14.5	120.4 ± 14.2	1.53
	C	28.0 ± 2.8	54.0 ± 6.0	82.0 ± 8.3	113.4 ± 8.7	1.38
Base + 1.7	A	24.6 ^b ± 2.7	55.0 ^{ab} ± 7.7	77.8 ^b ± 9.0	95.9 ^{ab} ± 9.3	1.23
	B	21.3 ^b ± 3.2	41.3 ^b ± 6.1	62.5 ^b ± 9.1	75.6 ^b ± 8.7	1.21
	C	33.1 ^a ± 2.6	65.5 ^a ± 7.9	98.6 ^a ± 8.8	112.1 ^a ± 7.9	1.14

¹ Data are means of eighteen samples ± SE. Also, means separation (P = 0.05) between moisture regimes within temperature treatments are indicated by different letters as determined by Duncan's Multiple Range Test.

Table 35.6. Average Content of Chlorophyll A, Chlorophyll B, and Carotenoids and Xanthophylls, on a Weight/Weight and Weight/Area Basis, of Six Species of Two-Year-Old Oak Seedlings Exposed to Three Temperature and Shade Treatments and Three Soil-Moisture Regimes

Temp.	Moist	Chlorophyll a ($\mu\text{g cm}^{-2}$)				Chlorophyll b ($\mu\text{g cm}^{-2}$)				Car + Xan ($\mu\text{g cm}^{-2}$)			
		Wk. 1	Wk. 6	Wk. 10	Wk. 14	Wk. 1	Wk. 6	Wk. 10	Wk. 14	Wk. 1	Wk. 6	Wk. 10	Wk. 14
Base	A	48 \pm 2	46 \pm 2	45 ^{ab} \pm 2	42 \pm 2	27 \pm 2	30 \pm 2	26 ^{ab} \pm 1	23 \pm 2	8.7 \pm .3	9.0 \pm .3	9.9 ^{ab} \pm .4	8.9 \pm .4
	B	45 \pm 2	46 \pm 2	43 ^b \pm 2	42 \pm 2	26 \pm 2	29 \pm 2	24 ^b \pm 1	23 \pm 1	8.2 \pm .4	9.0 \pm .3	9.1 ^b \pm .4	8.6 \pm .6
	C	46 \pm 2	45 \pm 2	49 ^a \pm 2	50 \pm 7	27 \pm 2	30 \pm 2	27 ^a \pm 2	37 \pm 13	8.3 \pm .3	8.6 \pm .3	11 ^a \pm .3	1.6 \pm .2
Base + 0.7	A	41 \pm 2	39 \pm 2	41 \pm 2	44 \pm 2	29 \pm 2	22 \pm 2	21 \pm 1	21 \pm 2	7.7 \pm .4	8.8 \pm .4	9.3 \pm .2	9.7 ^a \pm .4
	B	41 \pm 2	41 \pm 2	37 \pm 2	39 \pm 3	29 \pm 2	24 \pm 2	20 \pm 1	21 \pm 2	7.8 \pm .4	9.0 \pm .3	9.6 \pm .5	8.1 ^b \pm .6
	C	40 \pm 2	37 \pm 2	39 \pm 1	39 \pm 2	27 \pm 2	24 \pm 2	21 \pm 1	23 \pm 2	8.2 \pm .4	8.3 \pm .4	10 \pm .4	8.1 ^b \pm .5
Base + 1.7	A	41 \pm 3	40 \pm 3	42 \pm 2	42 \pm 3	27 \pm 2	29 \pm 3	24 \pm 2	25 \pm 2	7.3 \pm .5	8.2 \pm .7	9.9 \pm .5	8.4 \pm .7
	B	43 \pm 2	43 \pm 2	44 \pm 2	44 \pm 3	26 \pm 2	29 \pm 2	24 \pm 1	25 \pm 2	7.5 \pm .5	8.0 \pm .5	9.9 \pm .5	8.7 \pm .6
	C	43 \pm 2	41 \pm 2	42 \pm 2	44 \pm 2	27 \pm 2	28 \pm 3	24 \pm 2	25 \pm 2	7.7 \pm .4	8.1 \pm .3	9.8 \pm .5	8.8 \pm .4

		Chlorophyll a ($\mu\text{g mg}^{-1}$)				Chlorophyll b ($\mu\text{g mg}^{-1}$)				Car+ Xan ($\mu\text{g mg}^{-1}$)			
		Wk. 1	Wk. 6	Wk. 10	Wk. 14	Wk. 1	Wk. 6	Wk. 10	Wk. 14	Wk. 1	Wk. 6	Wk. 10	Wk. 14
Base	A	11.9 \pm 1.8	10.7 \pm .8	8.9 \pm .7	7.6 ^{ab} \pm .6	7.0 \pm 1	7.1 \pm .7	5.1 \pm .5	4.3 \pm .4	2.4 \pm .3	2.3 \pm .1	2.1 \pm .1	1.7 \pm .1
	B	11.5 \pm 1.2	10.1 \pm .4	8.3 \pm .6	6.8 ^b \pm .5	6.8 \pm .9	6.4 \pm .4	4.8 \pm .5	3.8 \pm .3	2.3 \pm .2	2.2 \pm .1	1.9 \pm .2	1.5 \pm .1
	C	12.4 \pm 1.3	10.6 \pm .6	8.9 \pm .6	9.8 ^a \pm 1.6	7.5 \pm .9	7.0 \pm .6	5.0 \pm .4	7.4 \pm 2.9	2.4 \pm .2	2.2 \pm .1	2.1 \pm .1	1.5 \pm .4
Base + 0.7	A	8.8 \pm .7	8.3 \pm .2	8.6 \pm .5	7.6 \pm .4	5.9 \pm .6	4.1 \pm .5	4.5 \pm .3	4.0 \pm .4	1.9 \pm .2	2.0 \pm .1	2.3 \pm .1	1.8 ^a \pm .1
	B	8.6 \pm .6	8.4 \pm .6	7.7 \pm .4	6.5 \pm .5	5.9 \pm .6	5.0 \pm .5	4.2 \pm .3	3.6 \pm .4	1.8 \pm .1	2.0 \pm .2	2.2 \pm .1	1.5 ^b \pm .1
	C	8.9 \pm .6	8.3 \pm .6	8.7 \pm .5	7.0 \pm .4	6.4 \pm .6	5.3 \pm .5	4.8 \pm .4	3.8 \pm .3	1.9 \pm .1	2.0 \pm .1	2.3 \pm .1	1.6 ^{ab} \pm .1
Base + 1.7	A	7.9 \pm .6	9.0 ^b \pm .7	9.9 \pm .8	7.1 \pm .8	5.3 \pm .6	6.6 \pm .7	5.8 \pm .5	4.3 \pm .5	1.5 \pm .1	2.0 \pm .2	2.5 \pm .2	1.5 \pm .2
	B	8.9 \pm .6	10.7 ^a \pm .7	11.2 \pm .7	7.7 \pm .5	5.7 \pm .5	1.3 \pm .8	6.4 \pm .7	4.3 \pm .3	1.7 \pm .1	2.1 \pm .1	2.8 \pm .2	1.6 \pm .1
	C	8.6 \pm .6	9.0 ^b \pm .5	9.1 \pm .6	7.8 \pm .4	5.6 \pm .6	6.3 \pm .6	5.5 \pm .4	4.5 \pm .3	1.7 \pm .1	1.9 \pm .1	2.5 \pm .2	1.7 \pm .1

Data are means of eighteen samples \pm SE. Also, means with different letters between soil moisture regimes, and within the same temperature treatment and time interval combinations, are different as determined by Duncan's multiple range test ($P = 0.05$).

pigment content are inconclusive and do not indicate any shift in resources to increase light-harvesting ability and thereby optimize the balance between carbon fixation and water lost through open stomata in plants exposed to drier soils or warmer air conditions within temperature treatments.

There were no differences in year-end foliar concentrations of K, Mg, Ca, and P between drought treatments in any of the temperature treatments (data not shown). At all three temperatures, white oak had greater foliar Ca concentrations ($P = 0.05$) than the other species (data not shown).

Discussion

On average, the oak seedlings in this experiment exhibited moderate increases in P_{net} , g_s , and TR, as well as corresponding increases in height and diameter growth as air temperature increased. However, P_{net} , g_s , TR, and height and diameter growth were all less in the Base + 1.7 temperature treatment compared to the Base + 0.7 treatment. Under these conditions, oak seedlings responded to increased temperature by increasing carbon uptake to a point at which greater respiration and general physiological stress began to have a damping effect on carbon uptake and growth.

There are no clear cut answers for predicting the climate of the future. If future regional climates produce warmer temperatures accompanied by short-term droughts, growth patterns similar to those in this present study might occur. In that climate scenario, oaks might benefit from warmer temperatures through increased carbon uptake and might exhibit some level of photosynthetic tolerance to drought thereby outperforming oaks in more mesic environments. This response could be detrimental to an oak species that becomes established on a site for which it is not well-suited in the long term. In this manner, an individual oak, a species of oak, or a group of oak species over a wide geographic region would be susceptible to decline initiated by a sudden and prolonged drought. Changes in soil-moisture availability, evapotranspiration, and the length of the growing season have been hypothesized with climate alterations of the magnitude predicted (Jones et al., 1994). It is clear that prolonged drought stress decreases gas exchange and net carbon assimilation in oaks (Hinckley et al., 1978; 1979), which if severe enough can reduce a tree's vigor and natural defenses. Severe drought can also cause embolisms in oak xylem vessels through cavitation (Tyree et al., 1992; Sperry and Sullivan, 1992; Tyree and Sperry, 1989). A large number of embolisms will limit growth by reducing water conductivity in the xylem (Schultze and Matthews, 1988). Drought stress, accompanied by elevated temperatures, can alter any number of normal physiological functions in oaks. Many reports relate oak decline to drought sites (relatively thin, rocky soils) on warmer, southern or western exposures to the extent that these conditions tend to define sites at high risk for increased oak mortality (Starkey et al., 1989). The probability of oak decline occurring on this type of site can be increased by an acute summer drought, a recent spring defoliation, or by the fact that oaks are physiologically mature.

Predicted changes in climate patterns over the next fifty years hold the potential to severely alter normal oak physiology and growth through increased drought and temperature stress in the southern United States. After a healthy tree has been stressed one or more times, its defense systems can become impaired making it vulnerable to attack by insects and diseases (Wargo and Haack, 1991), and the oak decline syndrome is fully expressed. Bottomland and upland oak resources are increasing in value and therefore it is critical to be able to predict how individual oak species, and groups of oak species, will respond to oak decline syndrome in a given region. Studies will continue to examine the many abiotic and biotic stresses that could be part of oak decline in the South.

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