

Review article

Oak growth, development and carbon metabolism in response to water stress

RE Dickson, PT Tomlinson

USDA Forest Service, North Central Forest Experiment Station, Forestry Sciences Laboratory,
5985 Highway K, Rhinelander, WI 54501, USA

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Summary — The genus *Quercus* (Fagaceae) contains both deciduous and evergreen species adapted to a wide range of sites differing widely in moisture availability. Different oak species have developed both morphological and physiological adaptations to survive and grow on such sites. Morphological adaptations in leaves, stems and roots aid in both drought avoidance and drought tolerance. Physiological adaptations involve control of stomatal conductance, leaf water potential, osmotic adjustment and photosynthetic carbon fixation. Carbon fixation can be divided into stomatal and nonstomatal responses. Stomatal response is probably the most important factor controlling carbon fixation. The more drought-tolerant species control stomatal function to allow some carbon fixation with stress, thus improving water use efficiency, or open stomates rapidly when water stress is relieved. Nonstomatal responses of carbon fixation such as photosystem II light energy conversion and the dark reactions of Rubisco carbon fixation are quite resistant to water stress, although internal resistance to CO₂ movement may increase. With water stress, soluble sugar/starch ratios increase, new leaf development decreases or stops altogether, and carbon allocated to leaf development shifts to lower stem and root for growth or storage. Many oak species, genotypes and hybrids are available that may be adapted to difficult sites. Use of such genotypes could greatly improve current forest management systems and horticultural amenity plantings.

***Quercus* / water-stress tolerance / photosynthesis / stomatal response / nonstomatal response / Rubisco / carbon allocation / genotypes / hybrids**

Résumé — **Croissance, développement et métabolisme du carbone de chênes soumis à une sécheresse.** Le genre *Quercus* (Fagaceae) comporte à la fois des espèces décidues et des espèces sempervirentes adaptées à une large gamme de stations présentant des disponibilités en eau très diverses. Les chênes ont développé des adaptations morphologiques et physiologiques pour survivre et pousser dans ces stations. Des adaptations morphologiques dans les feuilles, les tiges et les racines permettent la fois la tolérance et l'évitement de la sécheresse. Les adaptations physiologiques impliquent à la fois le contrôle et la conductance stomatique du potentiel hydrique foliaire, du degré d'ajustement osmotique, et de la fixation photosynthétique de carbone. L'assimilation de carbone est contrôlée par des facteurs liés aux stomates ou d'origine non stomatique. La réponse des stomates est

sans doute la plus importante réponse de limitation de la fixation photosynthétique de carbone. Les espèces les plus tolérantes à la sécheresse limitent la fermeture des stomates de manière à permettre une assimilation substantielle de carbone en situation de contrainte, ce qui leur permet d'améliorer leur efficacité d'utilisation de l'eau ; ou alors, elles les rouvrent très rapidement, dès que les réserves hydriques ont été reconstituées, même partiellement. Les processus non stomatiques de la photosynthèse, tels que la conversion photochimique et les réactions biochimiques des cycles de carboxylation centrés sur la Rubisco, semblent particulièrement peu sensibles à la sécheresse, même s'il s'avère que des résistances localisées dans le mésophylle et s'opposant à l'influx de CO₂ vers les chloroplastes puissent augmenter. Le rapport sucres solubles/amidon augmente en cours de sécheresse, l'expansion foliaire est ralentie, voire bloquée, et le carbone destiné initialement au développement des feuilles est détourné vers la base de la tige et vers les racines, où il sert à maintenir une croissance minimale, ou au stockage de réserves. De nombreux génotypes de chênes (espèces, hybrides, provenances) sont disponibles et peuvent s'adapter à des stations médiocres. L'utilisation de tels génotypes pourrait significativement améliorer la sylviculture du chêne et les plantations d'ornement.

Quercus / tolérance à la sécheresse / photosynthèse / stomates / Rubisco / allocation de carbone / génotypes / hybrides

INTRODUCTION

The genus *Quercus* in the family Fagaceae contains some of our most valuable forest tree species and some of our most persistent forest weed species. Oaks are native to most continents with about 500 species worldwide (Little, 1979; Kleinschmit, 1993; Rushton, 1993) (table I). The number of native species decreases from southern to northern latitudes (table I) consistent with the tropical origin of the species (Nixon, 1993). The genus contains both deciduous

and evergreen species adapted to a wide range of sites from seasonally flooded wetlands to xeric uplands and deep sands. Given this wide variation, it should be no surprise that response to water stress by individual species varies widely.

Because there have been several recent reviews about various aspects of plant response to water stress (Hsiao, 1973; Hinckley et al, 1978b, 1991; Kozlowski, 1982 a,b; Tyree and Ewers, 1991), we will confine this work largely to oaks, and if information is available, to individual species response to water stress. Special emphasis will be placed on the physiological sequences involved in carbon fixation, and carbon allocation in response to water stress. Species differences in response to water stress will be briefly reviewed to include recent comparisons of various American and European species not covered by Abrams (1990), and to provide background for the discussion of physiological responses. Similarly, morphological adaptations are briefly reviewed to emphasize characteristics of drought tolerance and drought avoidance and to provide additional background for physiological responses. Morphological and physiological adaptations must be considered together because both are involved to

Table I. Worldwide and regional distribution of native oak species (*Quercus* spp, Fagaceae).

	<i>No of species</i>
Worldwide	500
North and South America	200
Mexico	125
United States	60
Europe	25
France	8
Wisconsin-Minnesota	7

Little, 1979; Kleinschmit, 1993; Rushton, 1993.

varying degrees in the strategies different oak species have developed to tolerate water stress.

Species differences in response to water stress

The adaptability of different oak species to water stress varies widely. A recent review by Abrams (1990) discusses the morphological and physiological adaptations of North American *Quercus* species in considerable detail.

Differences in rooting depth, leaf morphology, leaf water potential, osmotic potential, photosynthesis and stomatal conductance are involved in varying degrees in drought response. Both drought avoidance (deep rooting, leaf curling, leaf loss, etc) and drought tolerance (osmotic adjustment, stomatal control to maintain moderate photosynthetic rates, etc) are strategies used in varying degrees by different oak species (Pallardy and Rhoads, 1993). Nevertheless, because of the wide range of sites occupied by different oak species and the resulting extremes in moisture stress encoun-

tered, there is no common oak strategy in response to water stress.

Different oak species may be placed in rather broad categories of moisture stress tolerance, based primarily on the sites they commonly occupy (table II, also see Wuenschel and Kozlowski, 1971; Hinckley et al, 1978a). Although most ecophysiological comparisons have been between oaks and other associated species (Abrams and Knapp, 1986; Kubiske and Abrams, 1993), some direct comparisons between different co-occurring oak species have been made. For example, black oak (*Q. velutina*) had greater water use efficiency than bur oak (*Q. macrocarpa*), white oak (*Q. alba*), and red oak (*Q. rubra*) (Wuenschel and Kozlowski, 1971; Bahari et al, 1985), while chestnut oak (*Q. prinus*) was more drought tolerant than red oak (*Q. rubra*) (Abrams et al, 1990; Kleiner et al, 1992) (see Abrams 1990 and references therein for other direct comparisons). *Q. rubra* and *Q. robur* are quite sensitive to moisture stress and are found primarily on the best mesic to dry-mesic sites, although *Q. rubra* may be found on certain xeric sites (Kubiske and Abrams, 1992). *Q. petraea* is often associated with *Q. robur* in

Table II. Relative tolerance classification of *Quercus* species to water stress based on sites commonly occupied by the species.

<i>Species name</i>	<i>Common name</i>	<i>Water stress</i>
<i>Q. rubra</i>	Northern red oak	Sensitive
<i>Q. shumardii</i>	Shumard oak	Sensitive
<i>Q. robur</i>	Pedunculata oak	Sensitive
<i>Q. petraea</i>	Sessile oak	Intermediate
<i>Q. velutina</i>	Black oak	Intermediate
<i>Q. coccinea</i>	Scarlet oak	Intermediate
<i>Q. macrocarpa</i>	Bur oak	Intermediate
<i>Q. muehlenbergii</i>	Chinkapin oak	Intermediate
<i>Q. marilandica</i>	Blackjack oak	Tolerant
<i>Q. stellata</i>	Post oak	Tolerant
<i>Q. laevis</i>	Turkey oak	Tolerant
<i>Q. gambelii</i>	Gambel oak	Tolerant

forest stands, but *Q. petraea* is considered more drought tolerant (Levy et al, 1992; Breda et al, 1993). A direct comparison between *Q. petraea*, *Q. robur* and *Q. rubra* indicated that *Q. petraea* was more drought tolerant than the other two species (Vivin et al, 1993). *Q. velutina*, *Q. coccinea* and *Q. macrocarpa* are examples of species with intermediate to quite drought-tolerant characteristics. The upland variety of *Q. macrocarpa* is considered one of the most drought tolerant of the eastern North American oaks (Johnson, 1990). In the northwestern part of its range, *Q. macrocarpa* can grow in areas with less than 38 cm of rain per year. However, co-occurring *Q. stellata* and *Q. muehlenbergii* may be equally or more tolerant of water stress. In a competitive situation where both *Q. macrocarpa* and *Q. muehlenbergii* were growing on the same site, *Q. muehlenbergii* appeared more drought tolerant (Abrams and Knapp, 1986; Bragg et al, 1993). *Q. marilandica* and *Q. stellata* are common associates on nutrient-poor and droughty sites throughout the Missouri and Oklahoma Ozarks.

In eastern and central Oklahoma, these species form extensive low grade stands of "scrub oak". Other drought-tolerant species such as *Q. laevis* also are commonly found on nutrient-poor sites such as the sand hills and ridges of the southeastern United States (Berg and Hamrick, 1993). *Quercus gambellii*, found in the western and southwestern United States, is extremely modified morphologically to resist drought and fire. Over 50% of the plant biomass is commonly found underground in an extensive root system of rhizomes and lignotubers (Harrington, 1985; Clary and Tiedemann, 1986). In addition to large differences among species in drought tolerance, there are also large differences within species. Such genetic variation is commonly found in rangewide studies where western sources are more drought tolerant than eastern sources (Kriebel et al, 1976; Kuhns et al, 1993). Rainfall decreases

from east to west in the United States. Genetic variation in drought tolerance may also be found within a species from a restricted geographic area. A study in central Pennsylvania showed that *Q. rubra* ecotypes from xeric sites had both physiological and morphological modifications that increased drought tolerance compared to ecotypes from mesic sites (Kubiske and Abrams, 1992). In a similar study, ridge-top trees of *Q. ilex* were more drought resistant than valley-bottom trees (Sala and Tenhunen, 1994).

Morphological adaptations

Leaves of different oak species have many morphological and anatomical characteristics that improve their ability to resist or tolerate moisture stress or drought episodes. Such features are not exclusive to oaks, but also are found in other species adapted to xeric sites and high light environments. Characteristics such as smaller leaf size, increased leaf thickness, increased cutical thickness, increased stomatal density and decreased stomatal size are all features that improve drought resistance, decrease leaf heat load and photochemical damage and help maintain some minimum rate of photosynthesis under water stress (Matsuda et al, 1989; Abrams, 1990; Abrams et al, 1994). In addition, the more drought-tolerant species often exhibit greater leaf anatomical plasticity (the ability to change anatomically in response to environmental stresses) than drought-intolerant species (Abrams and Kubiske, 1990; Ashton and Berlyn, 1994). Deep rooting also is an adaptation to resist site moisture stress by drought avoidance.

Oaks are commonly tap-rooted, and the more drought-tolerant species often produce greater root length per unit of leaf area than companion species (Pallardy and Rhoads, 1993). Oak tap roots, or sinker roots from lateral roots, commonly pene-

trate 3 to 5 m in depth and may penetrate to 25 m or more (Stone and Kalisz, 1991). Tap-rooted or deep-rooted species may obtain most of their water requirements from the water table or deep groundwater sources and do not depend on uncertain rains and surface water (Ehleringer and Dawson, 1992). Predawn leaf water potential may be useful for estimating effective rooting depth. Both Hackberry (*Celtis occidentalis* L) and *Q muehlenbergii* leaf water potential increased after a brief fall rain while *Q macrocarpa* leaf water potential continued to decrease, indicating that *Q macrocarpa* could not utilize rain water in the upper soil layers (Abrams and Knapp, 1986). The ability to increase root growth into and to increase root proliferation within enriched microsites is important for nutrient uptake (Eissenstat and Caldwell, 1988b; Black et al, 1994) and also may be a factor in drought tolerance (Fitter, 1986; Eissenstat and Caldwell 1988a). When tap-root growth was inhibited by dry soil, *Q agrifolia* did not expand lateral roots into adjacent moist soil. In contrast, *Q lobata* and *Q douglasii* increased lateral root growth in the moist soil by 70 and 80%, respectively (Callaway, 1990).

CARBON FIXATION AND WATER STRESS

Physiological responses to moisture stress associated with carbon fixation can be conveniently divided into stomatal and non-stomatal responses. Trees under moisture stress face the conflicting problem of maintaining some degree of photosynthesis while minimizing water loss. Stomatal control in response to varying moisture stress is the first and perhaps the most important step in this process. However, nonstomatal response, such as mesophyll resistance or photosynthetic mechanisms, also may be important aspects of stress tolerance (Kubiske and Abrams, 1993). The perceived

relative importance of stomatal and non-stomatal response for control of photosynthetic carbon fixation has changed over the years as new evidence and new techniques have become available (Sharkey, 1990). The problem in determining control mechanisms lies in the fact that these are very complex systems, with many feedforward and feedback reactions, and with multiple control points that respond in different ways to environmental stress (Raschke, 1975; Chaves, 1991; Kelly and Latzko, 1991; Stitt and Schulze, 1994).

Stomatal responses

Stomatal closure decreases internal carbon dioxide concentration (C_i), which in turn alters photosynthetic mechanisms. These same photosynthetic mechanisms also may be independently influenced by water stress; therefore, it is very difficult to determine the exact sequence of events. Nevertheless, stomates do close with mild water stress, and this closure increases resistance to carbon dioxide diffusion into the leaf and water diffusion out of the leaf. Ideally, plants should maintain some level of internal CO_2 concentration and carbon fixation and, at the same time, minimize water loss. Oaks are quite adept at this, particularly when compared to other associated tree species (Bahari et al, 1985; Kloeppel et al, 1993; Kubiske and Abrams, 1993). Differences in stomatal response, resistance to water stress and increased water-use efficiency also are found when xeric and mesic oak species are compared and when xeric and mesic ecotypes of the same species are compared (Kubiske and Abrams, 1992). In a study comparing ridge-top trees of *Q illex* to valley-bottom trees during a severe drought, the ridge-top trees regulated stomatal conductance to more closely match available soil moisture, maintained higher shoot water potential and suffered less

severe moisture stress (Sala and Tenhunen, 1994).

The mechanisms that control stomatal opening and closing have been studied for many years (Raschke, 1975; Outlaw, 1983; Raschke et al, 1988). Many factors are involved such as K^+ movement, internal CO_2 concentration, light intensity, cell water potential and hormones. Such studies are complicated because there are both short-term (within minutes) and long-term (days to weeks) responses that probably have different control systems. In addition, there may well be multiple sensors for different environmental stresses. Here, we are concerned with the long-term effects of water stress on oak physiology. Response that takes place over days or weeks certainly requires exchange of information between shoots and roots, and such long-distance signaling usually requires a hormone (Goljan et al, 1989). Work in recent years has shown that abscisic acid (ABA) is probably the hormone involved (Davies and Zhang, 1991; Khalil and Grace, 1993; Davies et al, 1994), although other root-produced hormones and hormone precursors also may be involved (Smit et al, 1990; Jackson, 1994). Roots in drying soil respond to this local water stress by producing ABA. This root-produced ABA is transported to leaves in the xylem sap where it decreases leaf expansion and stomatal conductance. Studies have shown that root production of ABA, xylem transport of ABA and stomatal conductance are closely correlated without any measurable change in leaf water potential. For example, split root studies have shown that stomatal conductance responded to soil drying in one part of the root system with no effect on plant water status. Rewatering or severing the roots in drying soil restored stomatal conductance to well-watered conditions (Davies et al, 1994).

Trees also respond to other long-distance metabolic, hydraulic and perhaps electrical signals (Hewett and Wareing, 1973; Alvin

et al, 1976; Mozes and Altman, 1977; Smit et al, 1990; Hinckley et al, 1991), but the relative importance of hormones or other potential signals to any particular species or particular environmental stress is unknown. Perhaps part of the advantage oaks have over other associated species is that they have better control of stomatal conductance, and thus carbon fixation by careful regulation of ABA or some other signal produced in the roots.

Stomatal and nonstomatal responses to water stress are usually defined by calculations of internal CO_2 concentrations from gas exchange measurements (Farquhar and Sharkey, 1982; Jones, 1985). However, such calculations may introduce considerable error if stomatal closure is not uniform across the leaf. Patchy stomatal closure may lead to calculated decreases in photosynthesis, mean stomatal conductance, internal CO_2 concentration, quantum yield and mesophyll conductance that may not be valid (Olsson and Leverenz, 1994). In addition, the degree of patchiness cannot be predicted because it varies with species, rate of drying and total imposed stress (Ni and Pallardy, 1992). Determinations of stomatal and nonstomatal responses require direct measurement of the various components of nonstomatal responses to differentiate the relative importance of these responses to stress (Epron and Dreyer, 1993a).

Nonstomatal photosynthetic mechanisms

Photosynthetic rates of *Q rubra* rapidly decrease as water stress increases and often drop to zero under severe water stress (Weber and Gates, 1990). Such photosynthetic rates measured as carbon exchange rates do not provide much information about control mechanisms. Measurements of changes in stomatal conductance and pho-

tosynthetic rates can divide photosynthetic response into stomatal and nonstomatal responses. Various nonstomatal responses, such as light energy reactions, mesophyll resistance to CO₂ diffusion, Rubisco carbon fixation and other enzyme reactions, may be affected by water stress and decrease photosynthetic rates. Photosynthetic light response curves and CO₂ response curves (A/C_i curves) can provide considerable information about the various physical and biochemical factors that control photosynthetic rates, such as quantum yield and other light energy reactions, and Rubisco activity or carboxylation efficiency. However, such response curves will not completely define the biochemical effects because many biochemical reactions are involved in photosynthesis control (Stitt, 1991; Stitt and Schulze, 1994).

Measurement of several metabolites and enzyme systems would be necessary to more completely define response controls. In addition, stomatal closure usually decreases internal CO₂ concentration, which in turn influences both light energy reactions and photosynthetic biochemical reactions. Such physiological responses may result from either water stress or a decrease in internal CO₂ concentration.

In recent years, several techniques applicable to field situations have become available for measuring both light energy reactions and photosynthetic mechanisms. With these techniques, such as in situ chlorophyll a fluorescence, net CO₂ assimilation rates and stomatal conductances, considerable information on nonstomatal responses can be obtained. Studies with several oak species (*Q rubra*, *Q petraea*, *Q pubescens*, *Q cerris* and *Q ilex*) have shown that photosynthesis and stomatal conductance decreased rapidly with increasing water stress (Epron and Dreyer, 1990, 1993b; Epron et al, 1993). Carbon dioxide response curves (A/C_i response curves) indicated that both stomatal and nonstom-

atal factors were involved in decreased carbon fixation. However, fluorescence measurements showed that light energy conversion, light-driven electron transport and ATP and nicotinamide adenine dinucleotide phosphate (NADPH) production associated with photosystem II were not affected (Epron and Dreyer, 1990, 1993b; Epron et al, 1992, 1993). Similarly, the chemical production of ATP and NADPH was not affected by water stress in sunflower (*Helianthus annuus*) (Ortiz-Lopez et al, 1991).

Decreases in photosystem II (PS II) activity were found only with high light and severe drought conditions with no CO₂ fixation. Such conditions can lead to damage in PS II reaction centers and photochemical bleaching when there is no outlet for the light energy and electron flow in the system (Epron et al, 1993). These studies showed that photochemistry and quantum yield remained stable with increasing water stress and thus could not explain the nonstomatal response indicated by analysis of the A/C_i curves.

Nonstomatal response to water stress may not be associated with the mechanisms of light energy transfer or carbon fixation. Studies have shown that internal CO₂ concentration may remain constant or actually increase as stomates close while PS II activity did not decrease (Epron and Dreyer, 1993a). Decreases in photosynthetic rates indicated that the internal resistance to CO₂ movement (movement of CO₂ from the stomatal cavity to the site of fixation in the chloroplast) increased (Epron and Dreyer, 1993a; Epron et al, 1995). Unfortunately, the amount and activity of Rubisco carbon fixation and other associated enzyme systems were not measured simultaneously. Additional studies with *Q petraea* and ¹⁴C autoradiography showed that this species responded to water stress with patchy stomatal closure and CO₂ fixation. Thus, the nonstomatal response may be an artifact of the calculations involved from patchy stomatal

closure and the decrease in photosynthetic carbon fixation was largely the result of stomatal closure (Epron and Dreyer 1993b).

Rubisco carbon fixation may or may not be directly affected by water stress. Although the evidence is conflicting, most studies indicate no significant water-stress effect on Rubisco activity (Gimenez et al, 1992). Studies that do show decreasing activity with water stress may not adequately evaluate other metabolites or metabolic activity that can indirectly influence Rubisco activity (Kicheva et al, 1994). In a recent study with tobacco plants transformed to contain different concentrations of functional Rubisco, the percentage decrease in photosynthesis with water stress was the same in all plants (Gunasekera and Berkowitz, 1993). In other words, the total amount of Rubisco activity available had no effect on the water stress-induced decrease in carbon fixation. Decreases in stomatal conductance and internal CO₂ concentration were also similar among the transformed plants, and internal CO₂ concentration remained well above the compensation point. If Rubisco activity decreased with water stress, steady-state concentrations of ribulose-1,5-bisphosphate (RuBP) should increase, barring changes in other enzyme systems. Instead, concentrations of RuBP decreased with increasing water stress, indicating a water-stress effect on the enzymatic regeneration of RuBP, which in turn inhibited Rubisco carbon fixation. Other enzyme systems, such as sucrose phosphate synthase and nitrate reductase, decrease in activity with water stress (Sharkey, 1990; Stitt and Schulze, 1994). However, such decreases in enzyme activity are probably the result of low internal CO₂ concentration in water-stressed plants because activity recovers if these water-stressed plants are placed in high CO₂.

Determining which enzyme system and control functions change with water stress will require carefully designed studies that

examine several such functional systems at the same time. Stomatal and nonstomatal effects of water stress vary with species, rate and degree of water stress imposed, and with many other factors. However, carefully designed studies that examine several such aspects have already clarified differences in drought response among oak species, such as *Q rubra*, *Q petraea* and *Q cerris* that potentially differ widely in drought tolerance (Epron et al, 1993).

CARBON ALLOCATION AND WATER STRESS

Water stress and leaf development

Leaf development is probably the most sensitive plant response to water stress. Leaf expansion rates decrease in response to soil moisture stress well before measurable effects on shoot-water relations are found (Davies and Zhang, 1991; Davies et al, 1994). In addition, leaf expansion decreases well before root growth decreases with water stress (Ball et al, 1994). As with stomatal conductance, some long-distance signal from roots decreases leaf growth, thus maintaining a balance between shoot and root growth and permitting a shift of carbon allocation to roots for continual growth. The mechanisms that control leaf expansion in response to changing plant water status are not clear, and the interactions between roots and leaf cell turgor change are largely unknown (Borchert, 1991), but may involve transmission of pressure changes, electrical, or hormonal signals (Daie, 1988; Smit et al, 1990).

Leaf development is particularly important to flushing species such as oak because the total leaf area of the expanding flush is critical for cumulative carbon fixation. Indeterminate species may continue production of smaller leaves under mild water stress

(Metcalf et al, 1989) while flushing may be completely stopped in oak. The control of episodic growth flushes in oak is unknown (Dickson, 1994), but oaks have a conservative growth strategy in which flushing and new leaf production cease or are severely depressed with various environmental stresses and photosynthate is redirected to root growth and storage (Gordon et al, 1989; Dickson, 1991b). Water stress in oak and other flushing species decreases the rate of leaf expansion, decreases final leaf size and decreases the number of leaves in a flush (Gordon et al, 1989). Severe soil moisture stress is not required to significantly decrease leaf area and dry weight of northern red oak seedlings (table III). Similar results were found for cacao (*Theobroma cacao* L), a flushing species like oak, where an increase in water stress caused a rapid decrease in leaf expansion of the developing flush and redirection of photoassimilate from the developing flush to lower stem and roots (Deng et al, 1990). The decrease in total leaf area, associated with decreases in stomatal conductance and photosynthesis, significantly decreases total carbon fixation.

Water stress and carbon partitioning within the leaf

Carbon partitioning to different chemical fractions within the leaf is the result of a number of alternative enzyme reactions, cofactors and interacting control points all dependent in turn on genotype, developmental stage of the plant and environmental factors (Daie, 1988; Stitt and Quick, 1989; Stitt and Schulze, 1994). Thus, it is not surprising that carbon partitioning is influenced by water stress. A common response to water stress is a shift in carbon flow to sucrose and other low molecular weight compounds. Such shifts aid in the maintenance of turgor and increase transportable

Table III. Effect of drought stress timing on leaf growth of northern red oak seedlings.

<i>Timing of stress</i>	<i>Leaf area (cm²)</i>	<i>Leaf dry weight (g)</i>
Flush ²		
Control ¹	807 a ²	4.50 a
Early	101 c	0.55 c
Mid	345 b	1.83 b
Late	497 b	2.83 b
Flush ³		
Control	1 402 a	7.06 a
Early	237 b	1.12 b
Mid	412 b	1.64 b
Late	579 b	3.10 b

¹ Control plants were well watered throughout the experiment and experienced no water stress. The early, mid and late treatments were water-stress cycles started at acorn planting, after 2 and 4 weeks, respectively. These treatments produced 3, 2, and 1 dry-down cycles by the time plants reached 3 lag and were harvested (see Dickson, 1991b for explanation of the *Quercus* morphological index [QMI] system). The plants were rewatered after the soil reached 12% soil moisture as measured with time domain reflectometry (TDR). At 12% moisture content, plant water potential increased to about -1.0 to -1.2 MPa. ² Data are the mean of at least five replicates. Letters indicate significant differences ($P = 0.01$) as determined with Duncan's multiple range test.

compounds (Morgan, 1984; Chaves, 1991). The sucrose/starch ratio usually increases with water stress as a result of increased flow of carbon to sucrose and, in some cases, an increase in starch breakdown. A shift from starch storage to sucrose has adaptive value because it enables osmotic adjustment and sustains export during stress events. The exact mechanism(s) of the shift in sucrose production is unknown. Starch is often considered a storage or "overflow" carbohydrate pool for excess carbon fixed during periods of high photosynthetic rates. In contrast, it is more likely that starch and sucrose production are independently controlled to provide an integrated response to

changing environmental conditions (see Daie, 1988 and references therein). In addition, starch is synthesized in the chloroplast and sucrose is synthesized in the cytosol, and their relative rates of synthesis are controlled by a number of transmembrane carriers and enzyme systems (Dickson, 1991a). These systems are adaptive; adjusting to different environmental requirements; and they also are interactive, responding to changing requirements of the whole plant. These multiple enzyme systems and alternative pathways for carbon flow provide redundancy so that the plant can adapt to changing environmental conditions.

Most of the information given here on carbon partitioning was developed with research on crop plants such as sugar beet and soybean because of their agricultural importance, genetic uniformity and growth uniformity. However, much information is available from work on hardwoods and conifers (Dickson, 1991a; Gower et al, 1995), and more could be developed for oaks grown with various environmental stresses. Because oaks are flushing species with cyclic leaf development, it is very important to use a developmental index such as the *Quercus* morphological index (QMI) (Dickson, 1991b) to study plants at the same developmental stage. Current studies on *Q. rubra* indicate that the major carbon metabolic pathways in leaves do not differ from those described for other plants (Dickson et al, 1990).

Water stress and carbon allocation within the plants

A common short-term response to water stress is the retention of current photosynthate in source leaves (Kuhns and Gjerstad, 1988; Deng et al, 1990). Water-stressed (leaf water potential -1.8 MPa) cacao seedlings retained 86% of photosynthetically fixed ^{14}C in source leaves 72 h after labeling, compared to 14% for nonstressed seedlings

(Deng et al, 1990). This retention of sucrose or other low molecular weight compounds in source leaves may be caused by a shift from export pools to vacuole storage and other leaf pools. Export processes are probably not the cause of the retention of recently fixed carbon because export capacity or translocation processes are relatively insensitive to water stress (Daie, 1988). Although the total amount of recently fixed carbon available for export usually declines because of decreases in carbon fixation or shifts in carbon pools, starch hydrolysis and efficiency of sucrose loading into the phloem may increase to maintain transport.

Long-term control of carbon allocation within the plant is regulated by source-sink interactions. The major sources in vegetative plants are mature leaves. The major sinks in vegetative plants are young developing leaves and stems, growing roots and stem and root storage pools (Dickson, 1991a). Under normal conditions or mild water stress, source leaves fix enough carbon for their own maintenance and for export to different sinks. Allocation of carbon to different sinks is largely independent of assimilate production, but is related to sink strength. Sink strength is related to size, growth rate, metabolic activity and respiration rate (Farrar et al, 1993). Developing leaves are strong sinks; stem and root storage pools are weak sinks in actively growing plants (Chapin et al, 1990). Perennial plants have developed elaborate sensing and control systems designed to maximize growth and to minimize damage in response to environmental stresses. Control of leaf expansion is one such system. As water stress increases, leaf expansion rates decrease (Joly and Hahn, 1989). When developing leaf growth slows, the relative sink strength decreases and more assimilate is available for transport to lower stem and roots. An increase in root growth or a decrease in shoot/root ratio is a common response to water stress. In a study with alfalfa (*Med-*

icago sativa L.), mild water stress decreased leaf growth but increased root dry weight (Hall et al, 1988). Roots of stressed plants contained twice as much translocated ^{14}C , and starch content increased by 20 to 30% compared to control plants. Oaks have a semideterminate growth habit with episodic flushes of new leaf and stem growth. Because all of the leaves are expanding at the same time, the new flush is a major sink for photosynthate. Our studies have shown that over 90% of the photosynthate from first-flush leaves was allocated to this new shoot growth (Isebrands et al, 1994). After leaf expansion, 95% of the current photosynthate was allocated to the lower stem and root for growth and storage (fig 1). Any change in this flushing growth pattern that decreases leaf growth or stops flushing would increase carbon allocation downward to the root system.

SILVICULTURAL AND ECOLOGICAL CONSIDERATIONS

Given the considerable amount of information available concerning biological attributes

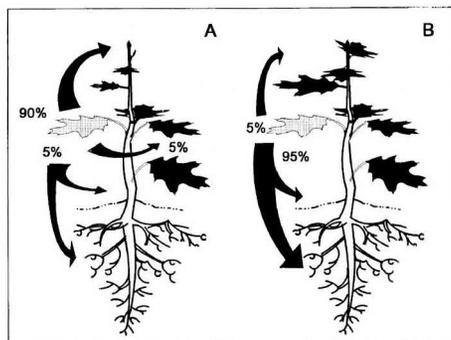


Fig 1. Upward and downward transport of ^{14}C photosynthate from first-flush leaves of northern red oak. Percentage values indicate within plant allocation of ^{14}C 48 h after photosynthetic exposure to $^{14}\text{CO}_2$. **A.** Representative plant at 2-leaf linear. **B.** Representative plant at 2-lag (from Dickson 1991b).

of different oak species and their response to water and other environmental stresses, how could such information be used to improve oak regeneration and subsequent stand growth? Nursery production of high-quality seedlings capable of acceptable survival and rapid growth after planting is possible with a few improved management techniques. Seed selection from superior stands or trees, mulching, optimum nursery-bed seed spacing, fertilization and irrigation regimes could significantly increase seedling quality. Such seedlings, planted in stands manipulated to favor oak growth, should survive and grow to be a significant component of future stands (Crow, 1988; Teclaw and Isebrands, 1993; Johnson, 1994). With current management practices, many oak stands in the United States will not maintain adequate numbers of oak after harvest (Crow, 1988; Abrams, 1992). This oak regeneration problem is widespread. Most universal prescriptions developed in one region have failed when used in different parts of the country because each region has its own distinct set of problems associated with oak regeneration. Regional, local and perhaps site-specific alternatives are needed (Teclaw and Isebrands, 1993). Biological and ecological information concerning seedling growth and response to water stress or other environmental stresses could be combined with information on regional climate and site-specific microclimate to design scientifically based silvicultural management systems.

Each tree species has a different strategy or inherent response to the many stresses encountered in its ecological community (Kolb et al, 1990). In addition, response to short-term stress is often quite different from response to long-term stress, and trees have the ability to acclimate to stress over time (Hinckley et al, 1978b, 1991). Considerable genetic variability exists within our most important commercial oak species (Kolb and Steiner, 1989; Kriebel, 1993), and this

genetic potential could be exploited to select genotypes more suitable for specific sites. Such genetic differentiation has taken place in natural stands (Kubiske and Abrams, 1992; Sala and Tenhunen, 1994) and in introduced populations (Daubree and Kremer, 1993). In addition, there are empirical observations about a large number of less well known oak species and hybrids (Sternberg, 1990). This empirical information could provide insight concerning the growth of these species or genotypes, and site interactions. Northern red oak is a fast growing, highly desirable, commercial and landscape species, but it produces its best growth only on the best mesic sites. Other species are better adapted to wet sites (*Q shumardii*, *Q nuttallii*, *Q phellos* or *Q palustris*), to calcareous sites (*Q imbricaria*, *Q alba*, *Q muehlenbergii*) and to xeric sites (*Q velutina*, *Q petraea*, *Q macrocarpa*). Given the large number of species and hybrids available, we believe more attention should be given to the introduction and testing of these less conventional species or hybrids in both forestry and urban landscape settings. Why not take advantage of the great potential found within the genus and within each species to improve production on the best sites and to reforest problem sites?

Oak hybrids have great potential to combine the best qualities of both species to improve growth or drought tolerance. The greatest use of oak hybrids is in landscape and horticultural plantings (Sternberg, 1990). Unfortunately, the use of genetically improved or hybrid stock by silvicultural practitioners is not promising (Steiner, 1993). Hybridization among the red oaks (*Erythrobalanus*) and among the white oaks (*Lepidobalanus*) is common (Jensen et al, 1993), and many natural and artificial hybrids are available or could be produced that tolerate wet or dry sites and acid or calcareous soils. In addition, hybrids may exhibit hybrid vigor with increased growth rates (Sternberg, 1990). Hybrids have the

potential to produce strong adaptable plants for silvicultural and horticultural applications, if we can overcome our conservative approaches and think like long-term agricultural crop breeders. With appropriate seedling quality, genetic selection and stand management, it should be possible to take advantage of the drought resistance and xeric traits of oaks in forest management.

CONCLUSION

There is no common oak strategy for response to moisture stress. Deep rooting, adaptive leaf morphology, changes in osmotic potential, control of stomatal conductance, drought-resistant energy transfer, drought-resistant carbon fixation-enzyme systems and conservative growth and carbon allocation patterns are all used in varying degrees by different oak species and different ecotypes within species.

Stomatal gas exchange is carefully controlled in most oak species. Oaks, when compared to other associated tree species, maintain some degree of stomatal conductance with increasing water stress. If completely closed by severe water stress, stomates will rapidly reopen when the stress is removed. Such stomatal control leads to increased water-use efficiency and maintains some carbon fixation during drought episodes.

Nonstomatal responses are quite resistant to water stress in oaks. Photosystem II activities of light energy conversion, electron transport and reductant production are not affected by water stress except under severe drought conditions and high temperatures with no CO₂ fixation. The enzyme systems of the dark reactions of carbon fixation also are quite resistant to moisture stress. However, some systems such as the regeneration of ribulose-1,5-bisphosphate may be sensitive to water stress and limit overall carbon fixation.

Carbon allocation patterns are predictable and dependent on the particular stage of the flush cycle. Carbon flow between starch and sucrose may change during water stress and more carbohydrate may be retained in leaves. However, the major impact of water stress is on leaf development. Water stress imposed during a flush decreases leaf size and number of leaves, may stop flushing altogether and increases carbon allocation to the root system.

There is currently enough information available concerning ecological characteristics and stress response of many oak species to make significant improvements in management practices. Nursery practices such as seed selection, irrigation and fertilization regimes can be designed to produce high-quality oak seedlings. Silvicultural practices could be designed to take advantage of the physiological information and growth strategies of different oak species. More consideration should be given to exotic species and hybrids that are inherently adapted to either highly productive or difficult sites.

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