

## Growth, Allocation and Water Relations of Shade-grown *Quercus rubra* L. Saplings Exposed to a Late-season Canopy Gap

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For understory saplings to exploit canopy gaps successfully, carbon gain must increase in the gap environment. We predicted that total biomass of shade-grown red oak saplings would increase after exposure to a late-season canopy gap, and that increased water and nutrient demand within the canopy gap would drive changes in the allocation of this carbon. Shade-grown red oak saplings acclimated to gaps by increasing biomass during the season of gap formation and increasing the potential for carbon gain in the following summer. Within-season carbon gain did not result from greater production of leaf area, so it most likely arose from higher photosynthetic rates of existing shade-developed foliage, which may be linked to accumulation of leaf nitrogen. During the season of gap formation, shade-gap plants increased allocation to storage of total non-structural carbohydrates (TNC), and to root growth. The increase in TNC storage suggests that shade-developed saplings exposed to gaps were also primed for fast growth and carbon gain in the following summer. The increase in root growth suggests that higher nutrient and water demand drove allocation shifts to enhance the capacity for nutrient and water uptake in the gap. Plant hydraulic conductivity ( $K_a$ ) of shade-grown plants was limited upon exposure to the gap, possibly because of embolism formation resulting from the abrupt increase in water demand. Greater water potential gradients compensated for limitations to  $K_a$ , allowing saplings to maintain high transpiration rates, suggesting that actual water uptake of shade-gap plants was unaffected by gap exposure.

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**Key words:** Acclimation, canopy gaps, carbon allocation, hydraulic conductivity, nitrogen allocation, non-structural carbohydrates, *Quercus rubra* L., red oak, stomatal conductance, transpiration, water-relations.

### INTRODUCTION

Formation of late-season (post-leaf development) canopy gaps is common in temperate forests (Romme and Martin, 1982), and can produce substantial environmental changes for saplings persisting in the understory prior to gap formation. Such changes include abrupt and dramatic increases in irradiance (Canham *et al.*, 1990), and the greater input of radiation may drive large increases in leaf temperature (Bazzaz and Pickett, 1980). Together, these may result in higher plant-water demand. The ability to acclimate quickly to these changes is advantageous for long-lived trees, such as northern red oak (*Quercus rubra* L.), growing in the highly competitive environment of a canopy gap.

Acclimation is the process by which physiological or morphological changes increase the capacity for carbon gain in a new environment. Greater carbon gain can stimulate growth during the season of gap formation or in the following summer. For shade-tolerant species which rely primarily on one cohort of leaves for seasonal carbon gain, saplings must be able to overcome potential photoinhibition and also increase photosynthetic rates of existing, shade-developed foliage to increase carbon gain. This may be related to an ability to increase nitrogen content of existing foliage through reallocation of plant nitrogen or increased

nitrogen uptake from the soil (Naidu and DeLucia, 1997). Alternatively, production of new leaves in the gap can also lead to greater carbon gain, and provides the added advantage of increased height, which may be critical in avoiding overtopping by neighbours. The production of new tissues may also require an increase in plant nitrogen content.

At the whole-plant level, immediate changes in growth and carbon allocation may affect the ability of shade-grown plants to maximize carbon gain during the season of gap formation and beyond. However, much of the research to date on the response of shade-grown plants to increased irradiance has focused on leaf-level phenomena; few studies have examined whole-plant responses. Growth of above-ground tissues tends to increase in response to canopy gaps (Lorimer, 1983; Smith, 1983; Canham and Marks, 1985; Canham, 1988; Uhl *et al.*, 1988), and increased root:shoot ratios have been reported for some tropical species upon being moved from low to high light (Fetcher, Strain and Oberbauer, 1983; Osunkoya and Ash, 1991). However, potential shifts in allocation in response to increased irradiance for other species have yet to be investigated, and direct evidence of growth enhancement immediately following the increase in irradiance (during the same season) is limited (Webb, 1976; Fetcher *et al.*, 1983, Rice and Bazzaz, 1989; Osunkoya and Ash, 1991).

Allocation shifts in shade-grown plants exposed to canopy gaps may be driven partially by changes in plant water demand. Higher irradiance in gaps may cause higher leaf

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temperatures and lead to a steeper vapour-pressure gradient between the leaf and surrounding air. Such conditions would increase the water demand of saplings in the gap. Increased water demand may also result if new leaves are produced. To increase whole-plant water uptake, saplings may shift allocation towards water-conducting tissues in stems and roots. The ability of shade-grown plants to rapidly increase their capacity for water uptake may affect physiological acclimation of leaves during the season of gap formation.

Saplings exposed to late-season canopy gaps acclimate shade-developed leaves by increasing photosynthetic rates and also typically produce a new flush of leaves subsequent to gap exposure (Naidu, 1996; Naidu and DeLucia, 1997). Both processes greatly increase potential carbon gain during the season of gap formation, but the relative allocation of this carbon to shoot growth, root growth and storage reserves is unknown. For example, in the absence of within-season growth increases, allocation to carbohydrate storage reserves may allow saplings to rapidly proliferate roots and grow in height in the subsequent year.

To relate known leaf-level acclimation responses of shade-grown red oak saplings to whole-plant responses, we examined allocation of total biomass, nitrogen and non-structural carbohydrate reserves during the season of gap-exposure. We predicted that total biomass of shade-grown red oak saplings would increase after exposure to a late-season canopy gap, and that increased water and nutrient demand within the canopy gap would drive changes in the allocation of this carbon.

## MATERIALS AND METHODS

### *Experimental design*

One-year-old red oak nursery stock (West Wisconsin Nursery, Sparta, WI, USA) was obtained in mid-May and stored with moist roots in a darkened cold-room ( $< 5^{\circ}\text{C}$ ) until planting (26 May 1994). Saplings were approx. 9 to 14-cm tall, and had been open-grown prior to lifting in late spring. Planting was delayed until after the forest canopy was established to ensure that plants placed in the understory developed under shade conditions. Before planting, roots were rinsed, blotted dry and saplings were weighed. The largest ( $> 7.5$  g) and smallest ( $< 2$  g) individuals were discarded, and the remaining 200 saplings were potted in soil:sand:clay (1:1:1 v/v) in  $23 \times 38$ -cm (15.8 l) pots. The soil mixture was chosen for ease of separating roots from soil during subsequent harvests. Initial dry weight at time of planting was calculated from a fresh-weight (f. wt) to dry-weight (d. wt) regression ( $\text{d. wt} = 0.4129 \times \text{f. wt} - 0.0479$ ,  $r^2 = 0.963$ ) created from the saplings that were not planted ( $n = 43$ ). At Trelease Woods, a University of Illinois ecological research area 8 km northeast of Urbana, Illinois, 135 arbitrarily-chosen saplings were placed in deep shade in the forest understory. The remaining 65 plants were placed in a nearby, naturally-occurring canopy gap (75 m<sup>2</sup>). Saplings were fertilized 1 week after planting with a top-dressing of 30 g per pot slow-release fertilizer (Osmocote, Sierra Chemical Co., Milpitas, California). Pots were mulched

with peat moss to reduce evaporation from the soil and were kept well-watered throughout the season by natural rainfall. Plants were sprayed with insecticide (Orthene, 327 PPM) twice during the growing season. Destruction by mammals was prevented by surrounding the plots with electric fencing.

Leaf expansion for this species in the understory was complete in 20 d (Naidu, 1996). We waited an additional 36 d after complete expansion to ensure complete leaf development in the shaded understory before moving 50 of the understory plants to the canopy gap (transfer: 21 Jul. 1994, 56 d from planting). This move simulated the occurrence of a late-season (relative to leaf development) canopy gap. The experimental design consisted of three treatments: fully shade-grown plants (shade); fully gap-grown plants (gap); and shade-grown plants moved to the canopy gap (shade-gap). Despite precautions, 15% of saplings in the shade environment died prior to the transfer date, mainly as a result of fungal pathogens and local herbivory (which tends to be high in fertilized plants), and after the transfer date 32% of saplings remaining in the understory died. Seasonal mortality of plants in the gap environment was less than 15%. Only healthy plants were selected for experimentation.

Previous measurements in the same gap and shade environments (Naidu, 1996) revealed that, on a typical sunny day, integrated daily irradiance in full sun was 37 mol m<sup>-2</sup> d<sup>-1</sup>, and was 4% of full sun in the shade and 40% of full sun in the gap. Maximum air, leaf and soil temperatures in full sun were 31, 37, and 29 °C, respectively, and were 1–2 °C lower than full sun in the gap. Maximum air and soil temperatures in the shade were 4–5 °C lower than full sun; however, midday leaf temperatures in the shade were as much as 10 °C cooler than full sun. Therefore, the move from shade to gap conditions represented a ten-fold increase in irradiance and an increase in midday leaf temperatures by as much as 8–9 °C.

Saplings were harvested on days 28, 56, 63, 84, 113 and 171 after planting. The first two harvests were made prior to transfer (the evening of day 56), when only shade and gap treatments existed. The remaining harvests included all three treatments with the exception that shade plants are missing from day 113 because of the low survival in the understory. The final harvest (13 Nov. 1994; day 171) was made after leaf senescence was complete, therefore leaf and physiological data are not reported for this harvest. For each treatment, ten plants were harvested except day 113 gap (nine), and day 171 gap (nine), shade-gap (11) and shade (four).

In the evening prior to a harvest, plants were arbitrarily selected and moved to a growth chamber with environmental conditions similar to the shade or gap area from which they came. Measurements were made in growth chambers to control for day-to-day variability in environmental conditions. Relative humidity (RH) was 60–65% in both chambers; this was similar to values measured in the field, which were similar for both the gap and understory areas used in this experiment. Irradiance was 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for shade plants and 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for gap and shade-gap plants. To determine transpiration under maximal evaporative demand, light levels corresponded to peak irradiances

found in understory and gap environments. Pots were watered to field-capacity and plants allowed to equilibrate with soil water overnight. Soil water potential ( $\Psi_{\text{soil}}$ ) was thus assumed to be zero, and was equal across treatments since all plants were potted in the same soil type. After 2–3 h of exposure to light the following day, leaf conductance was measured. After subsequent determination of stem water potential, plants were harvested.

#### Water relations

Leaf conductance, leaf temperature ( $T_L$ ), and leaf width (for calculation of leaf boundary layer) were measured on two to five leaves from the first flush of each plant. Plants in shade and gap environments flushed at about the same time; therefore, at a given harvest, all leaves measured were approximately the same age. Conductance and temperature were measured with a null-balance porometer (Li-1600M, Li-Cor, Lincoln, Nebraska) after conductance stabilized (10–30 s after clamping on the leaf). The porometer was also used to measure air temperature ( $T_A$ ) and RH near each plant in the growth chamber. ‘Wind’ speed in the growth chamber was measured near leaves with an anemometer (Turbo-Meter, Davis Instruments, Hayward, California) and was rarely above the detection threshold of the instrument ( $< 0.1 \text{ m s}^{-1}$ ). Similar low values of wind speed were measured in the field and were consistent with low values measured in tropical canopy gaps (Meinzer *et al.*, 1995). For subsequent calculations, average wind speed was taken as  $0.05 \text{ m s}^{-1}$ .

Stomatal conductance ( $g_s$ ) was calculated from porometer conductance values and boundary layer conductance in the cuvette via Ohms law analogy. Total leaf conductance under field conditions was estimated from  $g_s$  and boundary layer conductance ( $g_{bl}$ ) in the field (calculated from wind speed and leaf width, McDermitt, 1990). Total leaf conductance was then used to calculate leaf transpiration rate ( $E_L$ ) using RH,  $T_A$ ,  $T_L$ ; and atmospheric pressure to calculate the vapour pressure gradient according to Pearcy, Schulze and Zimmermann (1989). Leaf temperature during measurements was typically  $30 \text{ }^\circ\text{C}$  for gap and shade-gap plants, and  $28 \text{ }^\circ\text{C}$  for shade plants. The average conductance of two to five leaves per plant was taken as  $E_L$  for that plant. Self-shading is minimal for these small saplings; therefore, whole-plant transpiration rates ( $E_T$ ) were calculated by multiplying  $E_L$  by total plant leaf area. Since most gap plants produced a second flush of leaves, physiological measurements were made on only the first flush of leaves in each treatment to eliminate leaf age effects. Consequently,  $E_T$  may be somewhat underestimated for gap plants if the second flush of leaves had greater  $E_L$  rates. However, this error is likely to be small because a comparison of  $g_s$  for different leaf flushes in red oak saplings revealed that  $g_s$  of second flush leaves was only about 20% greater than that of first flush leaves (Ren and Sucoff, 1995).

Subsequent to conductance measurements, water potential was measured on the stem of each sapling ( $\Psi_{\text{stem}}$ ) using a pressure chamber (Plant Water Status Console, Model 3005, Soilmoisture Equipment Corp., Santa Barbara,

California). The stem was enclosed in a plastic bag, excised 1-cm above the base of the bottom-most leaf, and immediately placed in the pressure chamber. Pressure was applied at a rate of  $0.02 \text{ MPa s}^{-1}$ .

As a measure of the capacity for water transport, apparent hydraulic conductivity ( $K_a$ ; Meinzer and Grantz, 1990) was calculated as whole-plant transpiration divided by the difference between  $\Psi_{\text{stem}}$  and  $\Psi_{\text{soil}}$  (assumed to be zero, see above):  $K_a = E_T / (\Psi_{\text{stem}} - \Psi_{\text{soil}})$ . This estimate of  $K_a$  represents a majority of the resistance to water flow from the soil to the leaves, since the amount of stem tissue above the point of excision was a small fraction of total conducting length. Even in gap plants, the added resistance of the upper stem segment was likely to be negligible.

#### Biomass

Following water potential measurements, leaf area was measured using a leaf-area meter ( $\Delta T$  Area Meter, Delta-T Devices LTD, Cambridge, England). Pots were stored in a cold room ( $< 5 \text{ }^\circ\text{C}$ ) for 1–2 d, then roots were gently separated from the soil by shaking and rinsing under a slow stream of water. Roots rarely reached the bottom or sides of the pots and exploited only a small fraction of the total pot volume. For each harvest, root biomass includes only harvestable roots and does not account for fine roots or root turnover between harvests. Leaf, stem and root material were dried in a forced-air oven at  $100 \text{ }^\circ\text{C}$  for 1 h immediately following harvest of each component. The temperature was then reduced to  $70 \text{ }^\circ\text{C}$  and tissue was dried to a constant mass. The initial hour of high temperature was delivered to denature respiratory enzymes that may consume carbohydrates. Although long-term drying of plant tissue at greater than  $70 \text{ }^\circ\text{C}$  can cause nitrogen to volatilize, the drying regime used did not produce significant differences from constant drying at  $70 \text{ }^\circ\text{C}$  in nitrogen content of leaves, stems, or roots in shade or gap plants ( $P > 0.05$ , data not shown).

#### Nitrogen and carbohydrate content

Dried leaves, stems and roots were ground to pass a 40 mesh screen (Thomas-Wiley Mill, Thomas Scientific, Swedesboro, NJ), and total Kjeldahl nitrogen was then determined with an auto-analyzer (Traacs 800, Bran and Luebbe, Buffalo Grove, Illinois) following acid digestion (Lowther, 1980). Starch and soluble sugar content was determined as glucose equivalents using ethanol and perchloric acid extraction, respectively, on ground samples according to Tissue and Wright (1995). Starch and soluble sugars in each plant component were added together to determine total non-structural carbohydrate content (TNC) as glucose equivalents, and TNC was calculated as a percentage (%TNC) of root, stem and leaf biomass. Variation in response to diurnal fluctuation of carbohydrate pools was minimized by collecting all samples at the same time of day (midday) and refrigerating samples until they could be dried (see above).

Statistical analysis

Because of the small sample size, differences among treatments at each harvest date were determined using a Kruskal-Wallis (rank sum) non-parametric test. Data were analyzed with SAS statistical software (version 6.10, SAS Institute Inc., Cary, NC).

RESULTS

Biomass

The mean dry weight at time of planting (day 0) of all subsequently harvested saplings was 2.089 g (s. d. = 0.731). At the time of transfer (day 56), shade and gap plants had increased total dry weight by 3 and 19%, respectively. Following the initial leaf flush, there was no increase in growth of red oak saplings grown throughout the season in the shaded understory; however, saplings grown in the canopy gap began to significantly increase total biomass by day 63, levelling off by day 113 (Fig. 1). Biomass accumulation in gap plants was mainly a result of increased

root biomass, although smaller increases in leaf and stem biomass, from a second flush of leaves, also contributed. Shade-gap saplings increased total biomass within 56 d (day 113 from planting) of exposure to a canopy gap. As in gap plants, this was primarily a result of an increase in root biomass which was 164% greater than shade plants by the end of the season. Stem biomass also increased by 73% by the end of the season, but contributed very little to the increase in total biomass. In contrast to previous studies (Naidu, 1996), shade-gap plants did not produce new leaves after transfer to the gap; therefore, leaf biomass and leaf area (data not shown) did not differ between shade and shade-gap plants. The substantial increase in root biomass also resulted in a 52% greater root:shoot ratio of shade-gap plants relative to shade plants by the end of the season (data not shown).

Nitrogen content

Shade-grown plants also changed nitrogen allocation patterns in response to gap conditions. Gap plants had lower percentage nitrogen (% N) than shade plants in roots,

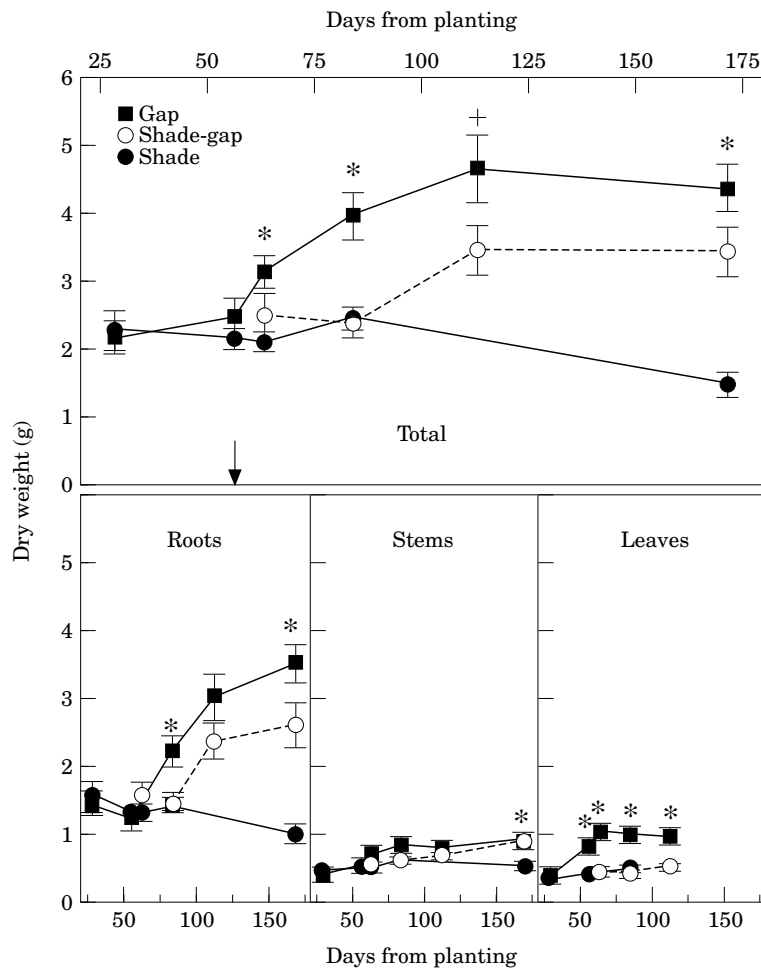


FIG. 1. Total and component (root, stem and leaf) biomass during the growing season of *Quercus rubra* saplings grown in a canopy gap (gap) or the forest understory (shade) or grown in the forest understory and transferred to a canopy gap (shade-gap). Dry weight on day 0 for these saplings was 2.089 g (s.e. = 0.064). The shade-gap plants were transferred to the gap (arrow in the upper panel) after cessation of leaf expansion and height growth in the understory. Error bars ( $\pm$ s.e.m.) are shown, except when smaller than the symbol size. Significant differences among treatments at each sample date are indicated above the points. \*,  $P < 0.05$ ; +,  $P < 0.10$ .

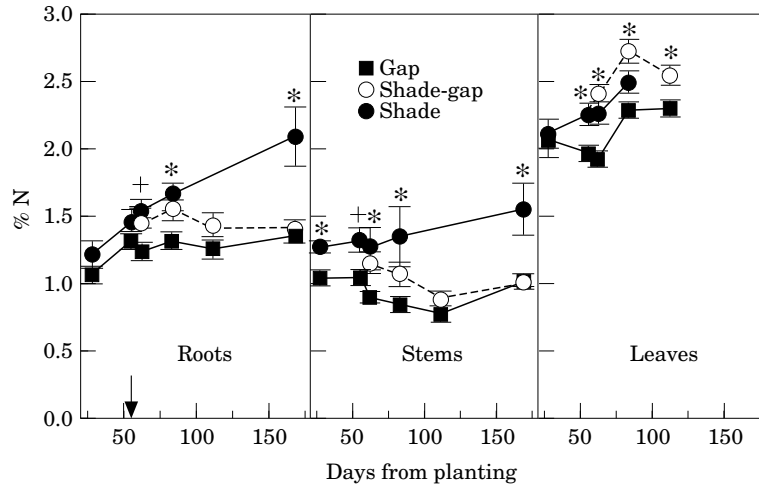


FIG. 2. Nitrogen content as a percentage of root, stem and leaf biomass during the growing season of *Quercus rubra* saplings grown in a canopy gap (gap) or the forest understory (shade) or grown in the forest understory and transferred to a canopy gap (shade-gap). The arrow in the left panel indicates the transfer date. Error bars ( $\pm$ s.e.m.) are shown, except when smaller than the symbol size. Significant differences among treatments at each sample date are indicated above the points. \*,  $P < 0.05$ ; +,  $P < 0.10$ .

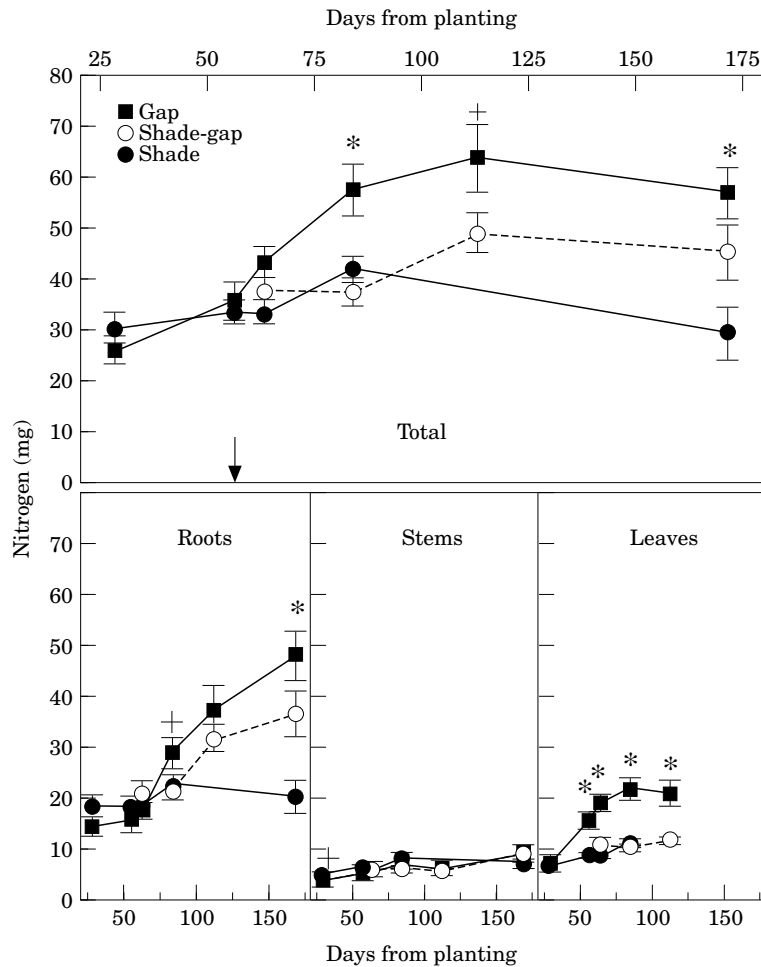


FIG. 3. Total and component (root, stem and leaf) nitrogen content during the growing season of *Quercus rubra* saplings grown in a canopy gap (gap) or the forest understory (shade) or grown in the forest understory and transferred to a canopy gap (shade-gap). The arrow in the upper panel indicates the transfer date. Error bars ( $\pm$ s.e.m.) are shown, except when smaller than the symbol size. Significant differences among treatments at each sample date are indicated above the points. \*,  $P < 0.05$ ; +,  $P < 0.10$ .

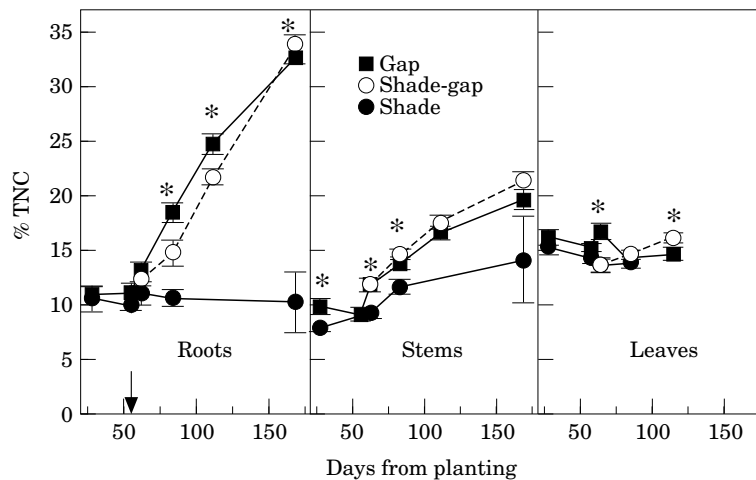


FIG. 4. Total non-structural carbohydrate (TNC) content in glucose equivalents as a percentage of root, stem and leaf biomass during the growing season of *Quercus rubra* saplings grown in a canopy gap (gap) or the forest understory (shade) or grown in the forest understory and transferred to a canopy gap (shade-gap). The arrow in the left panel indicates the transfer date. Error bars ( $\pm$  s.e.m.) are shown, except when smaller than the symbol size. Significant differences among treatments at each sample date are indicated above the points. \*,  $P < 0.05$ .

stems and leaves throughout most of the season (Fig. 2). After the move to the canopy gap, shade-grown plants decreased %N of roots and stems and increased %N in leaves. Total nitrogen was calculated by multiplying %N and biomass. Total nitrogen content of stems differed very little between treatments or over the growing season (Fig. 3). However, greater biomass of roots and leaves in gap plants resulted in a higher total nitrogen content in these organs and, consequently, total plant nitrogen was greater in gap than shade plants by the end of the season. Similarly, the total nitrogen content of shade-gap plants increased after transfer, solely because of the increased nitrogen content in roots resulting from increased root biomass.

#### Carbohydrate content

Total non-structural carbohydrates represent storage reserves for future growth. In leaves, TNC as a percent of biomass (% TNC) remained relatively constant across the season and among treatments (Fig. 4). However, % TNC in stems of gap plants was higher than shade plants for most of the season and % TNC of roots was substantially greater. Shade-gap plants increased %TNC in roots and stems almost immediately upon exposure to gap conditions and thereafter paralleled seasonal patterns seen in gap controls.

#### Water relations

Gap plants had higher leaf stomatal conductance ( $g_s$ ), leaf transpiration rate ( $E_L$ , not shown), and whole-plant transpiration rate ( $E_T$ ) throughout the season than shade controls (Fig. 5). Because of missing shade controls from the day 113 harvest, it is difficult to compare shade-gap and shade plants (Fig. 5); however,  $g_s$  and  $E_L$  of shade-gap plants were not significantly different from gap controls by day 113 (56 d after transfer). Stem water potential ( $\Psi_{stem}$ ) and apparent hydraulic conductivity ( $K_a$ ) of gap plants were higher than shade plants throughout the season. Stomatal conductance,  $E_T$ ,  $\Psi_{stem}$ , and  $K_a$  values increased in the early

part of the season for both shade and gap controls before levelling off mid-season. Upon exposure to the canopy gap, shade-grown plants decreased  $\Psi_{stem}$  and did not recover until day 113. Although  $K_a$  did not decrease upon transfer, seasonal increases lagged behind increases in both shade and gap controls.

## DISCUSSION

Upon formation of canopy gaps, shade-developed saplings persisting in the understory are exposed to a dramatic increase in light and temperature, with a corresponding increase in water and nutrient demand. Red oak saplings acclimate to canopy gaps via increases in photosynthetic rates of existing leaves and production of new leaves in the new light environment (Naidu, 1996; Naidu and DeLucia, 1997). The resultant increase in carbon gain has implications for whole-plant growth and allocation, which is the emphasis of the current study. Consistent with our prediction, results indicate that whole-plant biomass accumulation and carbon allocation patterns of shade-grown red oak saplings change during the season of gap formation. Total biomass of shade-gap plants increased within 56 d of exposure to the canopy gap, and this was mainly a result of increased root biomass (Fig. 1). Rapid increases in root growth of shade-grown plants upon exposure to increased irradiance has also been observed in sugar maple saplings (unpubl. res.; Webb, 1976), suggesting that rapid root growth may be a common acclimation response of saplings to canopy gap formation. Although stem biomass of shade-gap red oak saplings was also significantly greater than shade controls by the end of the experiment (Fig. 1), proportionally greater allocation to roots resulted in higher root:shoot ratios of shade-gap plants. Preferential allocation to roots has been previously documented for red oak seedlings (Walters, Kruger and Reich, 1993a, b) and may represent a storage strategy for surviving disturbances such as fire (Crown, 1988).

The lack of new leaf production in shade-gap plants in the year of this study contrasts with results of three previous

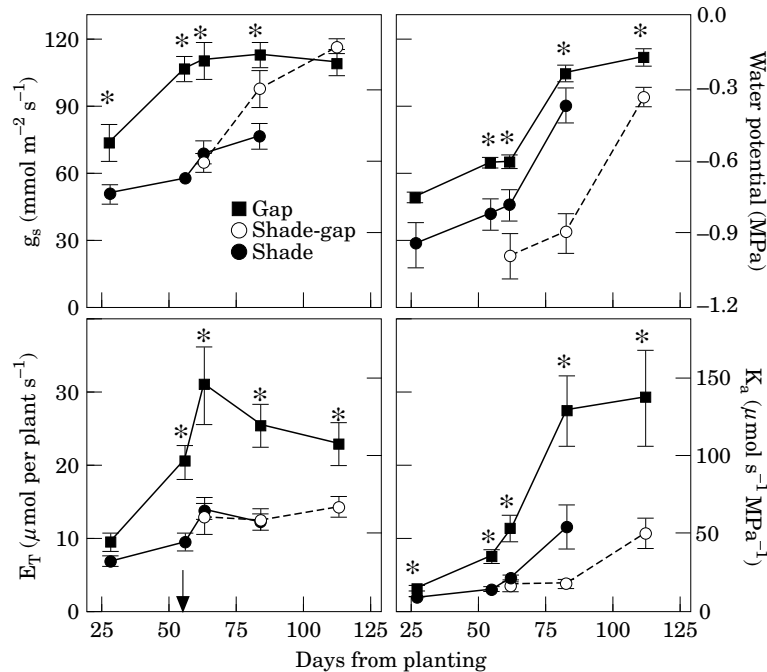


FIG. 5. Stomatal conductance ( $g_s$ ), whole-plant transpiration ( $E_T$ ), stem water potential, and apparent hydraulic conductivity ( $K_a$ ) during the growing season of *Quercus rubra* saplings grown in a canopy gap (gap) or the forest understory (shade) or grown in the forest understory and transferred to a canopy gap (shade-gap). The arrow in the lower left panel indicates the transfer date. Error bars ( $\pm$  s.e.m.) are shown, except when smaller than the symbol size. Significant differences among treatments at each sample date are indicated above the points. \*,  $P < 0.05$ .

studies (Naidu, 1996), and suggests that year-to-year variation in environmental conditions (such as amounts of rainfall) may influence allocation patterns of acclimating saplings. It is unclear whether allocation to leaf production would have resulted in less accumulation of root biomass in the current study. However, since relative growth rate is positively correlated with leaf allocation in red oak seedlings (Walters *et al.*, 1993b), investment in leaf production is likely to have increased biomass accumulation even more dramatically, and may have allowed shade-gap plants to reach the size of gap plants. Further growth enhancement is unlikely since dry weight of red oak seedlings reaches maximal levels around 30% of full sun (Phares, 1971) and gap irradiance in the current study was 40% of full sun.

The increase in root and stem biomass of shade-gap plants was partially a result of increased accumulation of total non-structural carbohydrates, which accounted for a maximum of 34 and 22% of root and stem biomass, respectively, at the end of the season (Fig. 4). This supports previous evidence that roots and stems are the major sinks for carbon in single-flush red oak seedlings (Dickson, Isebrands and Tomlinson, 1990). Most of the TNC found in roots and stems was starch (soluble sugars were never more than 5.5% of root or stem biomass), although soluble sugars accounted for almost half of TNC in leaves (data not shown). Because nitrogen accounted for less than 2.5% of total root or stem biomass at the end of the season (Fig. 3), most of the remaining biomass accumulation must be attributable to structural compounds, i.e. growth of roots and stems. Maximum rooting depth of shade-gap plants was greater than that of shade plants (unpubl. res.); however, increased stem growth was in girth and not height,

since these plants did not produce a new growth flush in the gap.

The increase in % TNC of shade-gap plants was initiated almost immediately upon exposure to the gap conditions (Fig. 4). This suggests that photosynthetic rates of the existing, shade-developed leaves began to increase quickly as well, and that this increase is far in excess of that needed for current growth. Significant increases (40–110%) in maximum photosynthetic rates of shade-gap red oak leaves (measured 4 weeks after exposure to a canopy gap) have been documented in three previous studies (Naidu, 1996). These increases were probably a result of both higher irradiance within the gap and a shift in the shape of the light response curve (Naidu, 1996; Naidu and DeLucia, 1997). The lack of investment in new leaf tissue in the current study indicates that within-season carbon gain was mainly a result of this physiological acclimation of existing, shade-developed leaves. Furthermore, shifts in carbon allocation towards increased root production probably enhanced physiological acclimation of leaves by increasing availability of water and nutrients. These data suggest that physiological and structural acclimation are tightly integrated in this species. The substantial increase in % TNC by the end of the season (shade-gap and gap plants are very similar), indicates that these saplings were primed for initiating a large growth flush in the following year. This suggests that greater allocation to carbohydrate storage in shade-gap plants increased the potential for carbon gain in the season following gap formation.

Greater accumulation of nitrogen in shade-gap plants supports the idea that acclimation potential may be coupled to an ability to increase nitrogen uptake to enable higher

photosynthetic rates in leaves (Naidu, 1996; Naidu and DeLucia, 1997). This is further supported by the increase in % N of leaves in shade-gap plants. Increased leaf % N could also be attributable to greater allocation towards compounds associated with protection from excess light or herbivory. However, the excess nitrogen in shade-gap (and gap) plants was primarily located in roots (Fig. 2), a portion of which may be complexed in storage proteins which can serve as a nitrogen pool for future growth (for a review see Stepien, Sauter and Martin, 1994). The decrease in % N of roots and stems (Fig. 3), despite greater biomass accumulation, is partially a dilution effect resulting from increased % TNC, and suggests that nitrogen contents exceeded amounts needed for growth. Since leaf biomass and leaf area (data not shown) did not change, the less than 1 % increase in leaf % N did not result in a significant increase in total leaf nitrogen (Fig. 3). Previous shorter term studies of other tree species saw either no change (Nunes, Ramalho and Dias, 1993) or a decrease (Syvertsen and Smith, 1984) in leaf nitrogen. Since the saplings in this study were fertilized, patterns of nitrogen allocation may vary for saplings grown under field conditions. If nitrogen supply is severely limited, photosynthetic acclimation of leaves, and consequently rapid growth responses, may be limited as well.

The dramatic increase in root biomass of shade-gap plants may have been driven by an increased demand for nutrients, particularly nitrogen; however, it may also have been driven by the increase in plant water demand associated with the higher irradiance and temperature regime of the canopy gap. The effects of the transition to a gap environment on plant water relations were examined in more detail through measurements of stomatal conductance and stem water potential. The increase in stomatal conductance ( $g_s$ ; Fig. 5) and transpiration per unit leaf area ( $E_L$ ; not shown) of shade-gap plants is consistent with previous results in which stomatal conductance of shade-gap red oak and white ash (*Fraxinus americana* L.) leaves significantly increased over that of shade leaves and was not significantly different from gap leaves 28 d after transfer to a canopy gap (Naidu, 1996). However, increases in stomatal conductance (Naidu, 1996) or transpiration (Syvertsen, 1984) were not seen for other tree species, indicating that this response is species-specific.

Seasonal increases in  $E_T$  occurred in all plants (particularly gap controls), indicating increased water uptake over the season (Fig. 5). This appears to be related to a seasonal increase in the capacity for water transport through the plant (apparent hydraulic conductivity,  $K_a$ ) and a concurrent increase (values closer to zero) in stem water potential ( $\Psi_{stem}$ ; Fig. 5). These data support previous evidence of a positive relationship between seedling leaf-water potential and conductivity in red oak (Ren and Sucoff, 1995). Initial low (more negative) stem water potentials at the beginning of the season were required to overcome high resistances which were probably a result of winter emboli and damaged root systems of transplanted saplings. As conductivity increased over the season, lower water potential gradients were required to maintain steady or increasing transpiration rates. Seasonal increases in  $K_a$  can result from increased allocation to conducting organs (roots and stems) relative to

leaf area or conducting tissue in roots and stem, or from changes in anatomical properties of xylem (e.g. larger diameter xylem vessels or fewer emboli). Increased allocation to roots and stems (Fig. 1) occurred in gap and shade-gap plants, but was not evident in shade plants. Thus seasonal increases in  $K_a$  for shade plants must have resulted from changes in xylem properties, e.g. re-filling of winter emboli (Sperry, Donnelly and Tyree, 1988; Sperry *et al.*, 1994; Magnani and Borghetti, 1995) or increased xylem production in stems or roots (Sperry *et al.*, 1994).

After 28 d of exposure to the gap (day 84),  $K_a$  of shade-gap plants was less than that of shade plants, and subsequent seasonal increases in  $K_a$  appeared to lag behind those of shade and gap controls. This suggests damage to conducting tissues from embolism induction upon exposure of shade-grown plants to higher evaporative demands in the gap. The subsequent increase in  $K_a$  of shade-gap plants (day 113, Fig. 5) suggests that this damage was either repaired via refilling of emboli, or offset by increased allocation to root and stem xylem. The latter is supported by increases in structural allocation to roots and stems of shade-gap plants (see above). Despite the lag in seasonal  $K_a$  increase, shade-gap plants were able to maintain rates of whole plant transpiration during the 4 weeks following gap exposure by operating at lower stem water potentials (Fig. 5). This lack of change in  $E_T$  of shade-gap saplings was evident despite an increase in leaf-level transpiration rate because total leaf area did not change and this variable was more influential in determining whole plant transpiration than  $E_L$ . This suggests that actual water uptake of shade-gap plants did not increase over that of shade controls.

We predicted that increased plant water demand, resulting from higher irradiance and temperatures, and increased nutrient demand, resulting from greater leaf production or acclimation of existing leaves, would drive carbon allocation changes in shade-grown saplings exposed to canopy gaps. Greater investment of biomass towards root production suggests that the capacity for water and nutrient uptake did increase in response to the gap environment, which supports this prediction.

Although an increase in the capacity for water uptake in shade-gap plants is suggested by the increase in root growth, data indicate that actual water uptake did not change in response to gap formation. Whole-plant transpiration and hydraulic conductivity of shade-gap saplings did not increase over that of shade controls. Transpiration rates of red oak saplings were maintained at sufficient levels without substantial changes in hydraulic conductivity through maintenance of greater water potential gradients in shade-gap plants. This may be related to other drought-avoidance and drought-tolerance characteristics in this species (Hinckley *et al.*, 1978; Parker *et al.*, 1982; Bahari, Pallardy and Parker, 1985). However, saplings in this study were well-watered, and competition for water under field conditions may result in lower transpiration rates if conductivity does not adjust in natural gaps. Since actual uptake of nitrogen did increase, but water uptake did not, the increase in root growth may have been driven more by an increase in nutrient than in water demand.

Under the high water and nitrogen conditions of this



experiment, shade-grown red oak saplings acclimated to canopy gaps via increased carbon gain during the season of gap formation and increased potential for greater carbon gain in the subsequent season. Increases in within-season carbon gain appeared to result mainly from higher photosynthetic rates of existing shade-developed foliage, and did not result from increased production of photosynthetic surface area, although the latter has been seen previously (Naidu, 1996). The increase in photosynthetic rates may be linked to accumulation of nitrogen reserves. Increased allocation to storage of non-structural carbohydrate is evidence that shade-gap plants are primed for fast growth and carbon gain during the following season. Increased allocation to roots also suggests that higher nutrient and, perhaps, water demand drives allocation shifts which enhance the ability for nutrient and water uptake in the gap. Greater water potential gradients compensated for limitations to hydraulic conductivity, thus allowing saplings to maintain high transpiration rates; however, more water-limited conditions in natural gaps could affect this relationship.

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