

Influence of overstory density on ecophysiology of red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*) seedlings in central Ontario shelterwoods

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Summary A field experiment was established in a second-growth hardwood forest dominated by red oak (*Quercus rubra* L.) to examine the effects of shelterwood overstory density on leaf gas exchange and seedling water status of planted red oak, naturally regenerated red oak and sugar maple (*Acer saccharum* Marsh.) seedlings during the first growing season following harvest. Canopy cover of uncut control stands and moderate and light shelterwoods averaged 97, 80 and 49%, respectively. Understory light and vapor pressure deficit (VPD) strongly influenced gas exchange responses to overstory reduction. Increased irradiance beneath the shelterwoods significantly increased net photosynthesis (P_n) and leaf conductance to water vapor (G_{wv}) of red oak and maple seedlings; however, P_n and G_{wv} of planted and naturally regenerated red oak seedlings were two to three times higher than those of sugar maple seedlings in both partial harvest treatments, due in large part to decreased stomatal limitation of gas exchange in red oak as a result of increased VPD in the shelterwoods. In both species, seedling water status was higher in the partial harvest treatments, as reflected by the higher predawn leaf water potential and seedling water-use efficiency in seedlings in shelterwoods than in uncut stands. Within a treatment, planted and natural red oak seedlings exhibited similar leaf gas exchange rates and water status, indicating little adverse physiological effect of transplanting. We conclude that the use of shelterwoods favors photosynthetic potential of red oak over sugar maple, and should improve red oak regeneration in Ontario.

Keywords: carbon isotope ratio, leaf conductance, oak regeneration, photosynthesis, water relations.

Introduction

Hardwood forests dominated by red oak (*Quercus rubra* L.) (> 31% of stand basal area) presently occur on more than 360,000 ha in the Great Lakes–St. Lawrence forest region of Ontario, providing timber, wildlife habitat and other economic and ecological values (Dey and Parker 1996, OMNR 2006).

As for most upland oak forest ecosystems of North America, fire is believed to have played a major role in the development and persistence of Ontario's red oak forests before European settlement. Fire reduces both overstory density and the abundance of shade-tolerant fire-sensitive species in the understory, thereby creating an environment conducive to the establishment, growth and successful canopy recruitment of red oak (Abrams 1992, 2005, Dey and Guyette 2000, Dey 2002). Widespread clearcut logging, land clearing for agriculture and other human disturbances beginning in the 19th Century further increased the prevalence of red oak by promoting the sprouting and release of oak advance regeneration (Dey and Guyette 2000, Johnson et al. 2002, Abrams 2005). Over the past 100 years, however, coordinated fire suppression, selective logging for oak timber and deer browsing, coupled with the intermediate shade tolerance and relatively slow initial shoot growth of red oak, have resulted in successional replacement of these ecosystems by forests largely composed of sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.) and other shade-tolerant species, particularly on more mesic sites (Abrams 1992, 2005, Loftis and McGee 1993, Dey 2002, Johnson et al. 2002).

Current management practices for upland oak species in Ontario, and elsewhere in eastern North America, focus on a combination of partial harvesting systems, some form of understory disturbance and underplanting to improve understory irradiance, reduce competition and increase stocking of oak regeneration (Loftis and McGee 1993, Dey and Parker 1997, Johnson et al. 2002). However, these approaches have not been adequately tested or calibrated for use in Ontario (Gordon et al. 1995, Dey and Parker 1996, 1997), and our knowledge of shelterwood effects on the ecophysiology of red oak and competing woody species is limited (Crunkilton et al. 1992, Buckley et al. 1998).

In an effort to improve provincial silvicultural guidelines for red oak, a large field study was established to investigate the effects of different shelterwood overstory densities and post-harvest understory release treatments on the regeneration of

red oak and associated hardwood species. A smaller supplemental study was established to examine the effects of shelterwoods on the ecophysiology of red oak and sugar maple, its primary woody competitor on mesic sites in Ontario. This study focused on two questions relevant to more successful red oak regeneration. (1) How do changes in overstory density affect gas exchange and water relations of red oak and sugar maple seedlings? (2) Do naturally regenerated red oak seedlings differ from planted seedlings in their ecophysiological response to partial harvesting treatments?

Materials and methods

Study site

The study was established in an 80- to 120-year-old, red-oak-dominated, second-growth hardwood forest classified as Eco-site 24.1 (sugar maple–red oak–basswood (*Tilia americana* L.)-dominated stand) (Chambers et al. 1997) located in Brudenell township near Foymount, Ontario (45°37'21" N, 77°35'71" W, 1250 m a.s.l.). The climate at the study site is cool and continental with a mean annual air temperature (T_a) of 4.3 °C and January and June mean T_a of –12.5 and 16.1 °C, respectively. Mean annual precipitation is 824.9 mm, with 391.5 mm of rainfall occurring during the growing season (May to September). Soils are generally shallow stony Sherbourne tills and sandy loam in texture.

Overstory (trees > 2.5 cm diameter at breast height (DBH)) basal area, density and DBH averaged 33.1 m² ha⁻¹, 1630 stems ha⁻¹ and 12.1 cm, respectively. Roughly 35% of the basal area (11.7 m² ha⁻¹) and 9% of density (141 stems ha⁻¹) were comprised of red oak, which averaged 30.7 cm DBH. Other major components of the forest overstory were sugar maple (9.7 m² ha⁻¹, 610 stems ha⁻¹, 11.7 cm DBH) and basswood (3.8 m² ha⁻¹, 83 stems ha⁻¹, 21.6 cm DBH). Sugar maple advance regeneration dominated the understory with more than 328,000 stems ha⁻¹ that averaged 3.3 mm in basal diameter and 24.1 cm in height. Red oak regeneration numbered about 15,200 stems ha⁻¹ and was uniformly small with mean basal diameter and height of 2.7 mm and 18.0 cm, respectively.

Overstory treatments

The larger red oak study comprised a complete randomized experimental design. In the spring of 1994, 54 adjacent 0.40-ha (60 × 60 m) treatment plots were established. In early May 1994, 130 bareroot 2-year-old red oak seedlings (Orono Nursery, Orono, ON) averaging 9.0 cm in height and 3.7 mm in basal diameter were underplanted in each treatment stand at 2 × 2 m spacing. The following winter, 18 stands were harvested by 1 of 3 randomly assigned overstory treatments: light (low density) shelterwood (L), moderate (medium density) shelterwood (M) or left untreated as uncut (high density) (U) controls. The shelterwood harvests focused on removal of small, inferior non-oak trees from the lower crown classes to create a uniform residual overstory (Loftis 1990). Overstory basal area was reduced by roughly 55% to 16.1 m² ha⁻¹ in the

M shelterwoods and by 85% to 5.3 m² ha⁻¹ in the L shelterwoods. Overstory crown cover, measured with a spherical densiometer, averaged 80% in the M shelterwood stands and 49% on the L shelterwoods, compared with nearly full canopy closure (97%) in the U stands.

Seedling ecophysiology

Four stands of each of the three overstory treatments were selected for periodic assessment of seedling ecophysiology in the post-harvest growing season. This growing season was characterized by near normal T_a and below normal precipitation (relative to the 35-year climatic average for the study area) (–34%), with total rainfall of 141.7 mm. Leaf gas exchange and water status were measured on three randomly selected seedlings of naturally established sugar maple and red oak, and planted red oak per treatment stand on June 16, July 19, August 2 and September 6. With the exception of August 2, which was uniformly overcast for most of the day, the sky was clear on all sampling days. Different seedlings within a centrally located 0.06-ha circular subplot in each treatment stand were measured on each sampling date. Almost all seedlings of both study species exhibited a single shoot flush, and sampling was confined to the youngest, fully expanded leaf to minimize physiological differences due to leaf age among species and overstory treatments (Hanson et al. 1986). Seedlings 10 to 30 cm in height were sampled to minimize the potential confounding influence of seedling size on ecophysiology and to ensure similar seedling crown exposure to understory light.

Seedling gas exchange

Seedling gas exchange was measured with an LI-6200 portable photosynthesis meter (Li-Cor, Lincoln, NE) equipped with a 0.25-l cuvette. Sampling began after complete evaporation of dew from leaf surfaces, with measurement occurring between 1000 and 1400 h. The sequence of stands sampled differed on each date to minimize diurnal effects on measured variables. Care was taken to ensure leaf orientation was unchanged and that the leaf and quantum sensor attached to the cuvette were exposed to the same light environment during measurements. Gas exchange values from two consecutive 10-s measurements were averaged, and net photosynthesis (P_n), leaf conductance to water vapor (G_{wv}) and the ratio of intercellular (C_i) to ambient (C_a) CO₂ concentration (C_i/C_a) were estimated by the method of von Caemmerer and Farquhar (1981). Steady-state rates of leaf gas exchange were typically attained within 30 to 45 s of sealing foliage in the cuvette, minimizing error associated with cuvette heating during prolonged sampling under high irradiance conditions. Gas exchange was measured when CO₂ concentration in the cuvette ranged between 340 and 360 ppm. The portable photosynthesis meter monitored leaf-incident photosynthetic photon flux (PPF), T_a and vapor pressure deficit (VPD) during the gas exchange determinations.

Sampled foliage was collected to determine leaf area and dry mass enclosed in the cuvette and calculate leaf mass per area (LMA). Leaf area was measured with a Li-Cor LI-1000 leaf area meter, and leaf dry mass was determined after oven

drying to constant mass at 65 °C. Because both study species are hypostomatous, gas exchange was expressed on a projected (i.e., one-sided) leaf area basis.

Seedling water status

Predawn (Ψ_{pd}) and midday (Ψ_{md}) water potentials were estimated from xylem pressure potential (Ψ_x) measurements obtained with a pressure chamber, before sunrise and at the time of gas exchange measurements, respectively (Ritchie and Hinckley 1975). A single leaf was used for Ψ_x measurements of oak. Shoots supporting two leaves were used for sugar maple to avoid confusion with balance pressure recognition caused by phloem exudation from leaf petioles (Bahari et al. 1985). Leaf tissues sampled for gas exchange measurements were used to determine Ψ_{md} . Tissue samples were sealed in humidified plastic bags and stored on ice to avoid dehydration between collection and Ψ_x measurement.

Water-use efficiency

Water-use efficiency (WUE) in the post-harvest growing season was estimated from stable carbon isotope ratios ($\delta^{13}C$) of leaf tissues collected in September 1995, according to the same sampling scheme as that used for seedling ecophysiology ($n = 108$). Leaf $\delta^{13}C$ was determined with an isotope ratio mass spectrometer (Delta S, Finnigan MAT, San Jose, CA) at the Stable Isotope Ratio Facility for Environmental Research at University of Utah, Salt Lake City, UT, USA. The overall measurement precision was $\pm 0.11\text{‰}$. The $\delta^{13}C$ (‰) of foliage was calculated as:

$$\delta^{13}C = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) 1000$$

where R_{sample} and R_{standard} are the $^{13}C/^{12}C$ of the plant sample and PeeDee belemnite standard for source air, respectively (Farquhar et al. 1989, Ehleringer et al. 1993). This approach provides seasonally integrated measures of WUE that are preferable to those derived from periodic, instantaneous leaf gas exchange measurements (Ehleringer et al. 1993).

Statistical analyses

This study comprised a completely randomized experimental design with the 12 adjacent stands sampled. The effects of overstory treatment (T), species (S) and their interaction ($T \times S$) on seasonal mean values of seedling gas exchange, water status and leaf $\delta^{13}C$ were tested by analysis of variance (ANOVA) with the following mixed general linear model:

$$Y_{ijk} = \mu + b_0 + b_1 T_i + b_2 P_{ij} + b_3 S_k + b_4 TS_{ik} + b_5 PS_{ijk} + \epsilon_{ijk}$$

where P is plot within treatment, defined as a random effect. In all cases, descriptive statistics of variables were examined before analysis to ensure that they were normally distributed. Examination of residual plots indicated that the variances of the error terms for G_{wv} were proportional to the mean. Variance

was stabilized by a natural logarithmic transformation, and ANOVA was applied to the transformed data. Overstory treatment effects were tested with the P type III mean square as an error term, and S and $T \times S$ interaction treatments were tested with the type III mean square of the $P \times S$ treatment. Mean comparison tests for S and T effects were made with an LSD test and type III mean squares only when F tests for these effects were significant ($P < 0.05$).

The relationships of leaf gas exchange and leaf $\delta^{13}C$ with leaf microclimatic variables and plant factors were determined by linear regression analysis. Values of statistical significance are identified by asterisks as: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$. Correlation analyses were made only on those measurements obtained when $PPF \geq 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($n = 43-50$), the photosynthetic light saturation point identified for both species by boundary line analysis (Webb 1972, Hinckley et al. 1978).

Results and discussion

Leaf gas exchange

Leaf gas exchange of both species was light-limited and did not differ in the heavy shade of the U stands where mean PPF was close to the photosynthetic light compensation points for red oak and sugar maple (Hinckley et al. 1978, Hanson et al. 1988, Ellsworth and Reich 1992a; Figure 1). Leaf-incident PPF in the U stands averaged 1–2% of full sunlight ($PPF = 23 \pm 2 \mu\text{mol m}^{-2} \text{s}^{-1}$; mean ± 1 standard error), which is similar to that reported for other undisturbed northern hardwood stands (Jurik 1986a, Canham et al. 1990). As a result, P_n and G_{wv} were low and C_i/C_a was high in both species.

Partial harvesting modified understory microclimate and significantly increased mean leaf-incident PPF to 25% ($PPF = 508 \pm 41 \mu\text{mol m}^{-2} \text{s}^{-1}$) and 41% sunlight ($PPF = 825 \pm 51 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the L and M shelterwoods, respectively, roughly proportional to the extent of canopy disturbance (Buckley et al. 1998, Aussenac 2000, Gray et al. 2002). The higher PPF in the shelterwoods than in the U stands significantly increased rates of leaf gas exchange, and this response differed between species (Figure 1). Mean P_n of sugar maple seedlings increased threefold in both shelterwood treatments relative to U stands. By comparison, P_n of red oak seedlings increased four to five times in the M shelterwood, and more than six times in L shelterwoods, and the difference between the M and L stands was statistically significant. Leaf G_{wv} increased by 50 to 70% in sugar maple, and 100 to 200% in red oak in response to overstory reduction, but G_{wv} did not differ significantly between shelterwood treatments in either species. Mean leaf C_i/C_a was significantly higher in the light-limited U stands than in the shelterwoods, but did not differ between species within overstory treatments.

Leaf mass per leaf area increased seasonally with leaf maturation, and was higher in the U stands relative to the M and L stands, and lower in red oak seedlings relative to sugar maple seedlings (Figure 1). Increased LMA in seedlings in shelterwoods was positively correlated with P_n ($r = 0.91^{***}$) in both

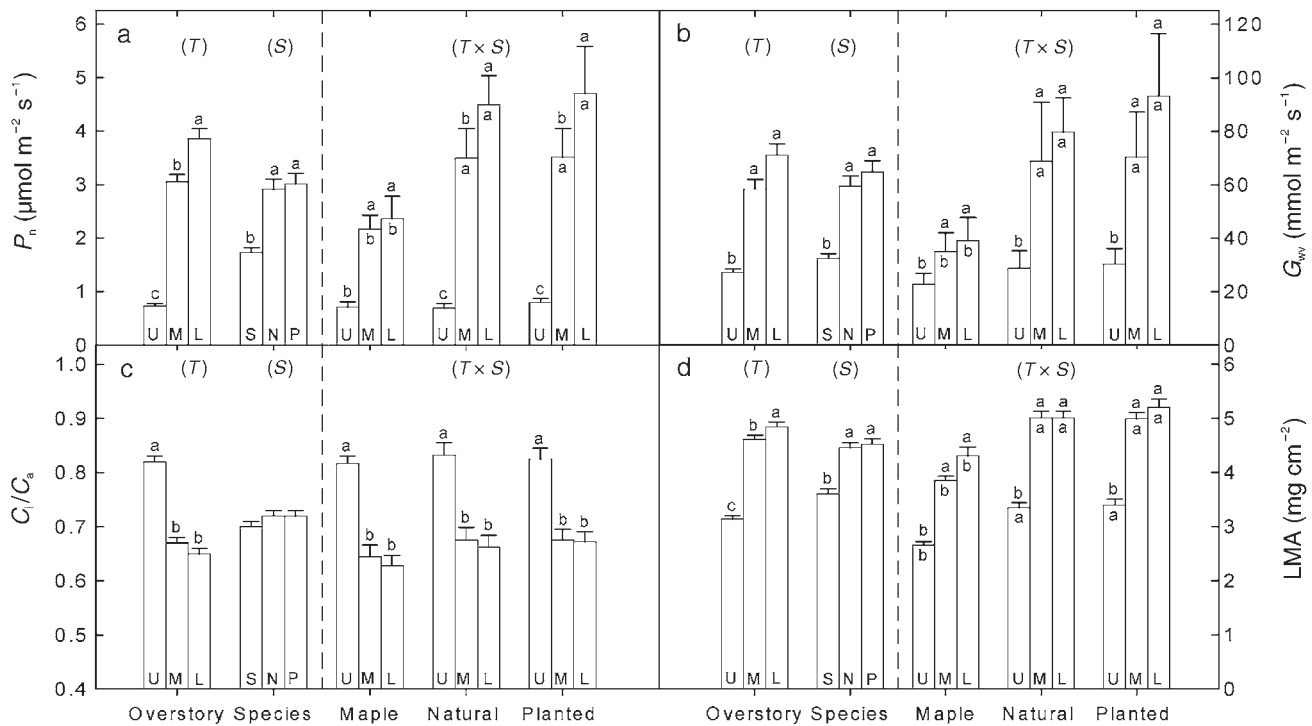


Figure 1. Overstory treatment (T), species (S) and $T \times S$ interaction effects on seasonal mean (a) net photosynthesis (P_n), (b) leaf conductance to water vapor (G_{wy}), (c) ratio of intercellular to ambient CO_2 (C_i/C_a) and (d) leaf mass per unit area (LMA) in sugar maple (S), natural red oak (N) and planted red oak (P) seedlings growing in uncut stands (U) and in moderate (M) and light (L) shelterwoods. Mean values for overstory treatment and species comparisons having the same letter or without letters above bars do not differ significantly ($P < 0.05$). For $T \times S$ interactions, letters above the error bars refer to treatment comparisons within a given species, and letters within the histogram bars refer to species comparisons within a given overstory treatment.

species owing to the strong influence of PPF ($r = 0.85^{***}$) on LMA. Compared with red oak seedlings, the lower LMA of shade-tolerant sugar maple seedlings in the U stands enhances light harvest per unit investment in leaf biomass in heavy shade (Givnish 1988, Ellsworth and Reich 1992a). Although LMA can influence area-based measures of P_n independently of microclimatic factors (Jurik 1986b, Reich et al. 1991, Ellsworth and Reich 1992a), LMA had little effect on overstory treatment differences in leaf area-based gas exchange rates in our study (data not shown). These results indicate that observed treatment differences in leaf gas exchange were more strongly associated with microclimatic and physiological factors than with leaf ontogeny and LMA.

Seedling water relations

Shelterwood overstory treatments significantly increased seasonal mean Ψ_{pd} (Figure 2a), suggesting that reductions in overstory density increased soil water availability relative to that in U stands, by either increasing throughfall precipitation or reducing stand leaf area and transpirational water loss, or both (Dunlap and Helms 1983, Crunkilton et al. 1992, Kloppe et al. 1993, Aussenac 2000, Coomes and Grubb 2000). An increase in soil water availability in shelterwoods would improve seedling water balance when previously shaded seedlings are adjusting root–shoot balance to acclimate to the environment created by partial overstory removal (Naidu and

DeLucia 1997). This effect will likely be short-lived because significant regrowth of understory vegetation in more open stands can result in seedling water deficits as a result of higher VPDs and increased overstory and seedling water use (Reich and Hinckley 1980, Ellsworth and Reich 1992b). Leaf Ψ_{md} did not differ among overstory treatments (Figure 2b), suggesting that the increase in soil water availability following partial harvesting was large enough to offset diurnal seedling water deficits that could result from higher VPDs in the shelterwoods, particularly on water-limited sites (Dalton and Messina 1995).

There was a significant overstory treatment effect on Ψ_{pd} of sugar maple seedlings, with lower values observed in the U stands than in the L stands. Despite this apparent improvement in seedling water status caused by overstory reduction, leaf Ψ_{pd} and Ψ_{md} were lower in sugar maple than in red oak where species differences occurred. This difference between species may be related in part to deeper rooting and other drought-tolerance adaptations that enable red oak to better avoid leaf water stress than sugar maple in more exposed habitats and during periodic droughts (Abrams 1990, Pallardy and Rhoads 1993).

Microclimatic and seedling water status influences on gas exchange

Seasonal variation in overstory treatment response of leaf gas exchange of red oak and sugar maple seedlings was strongly

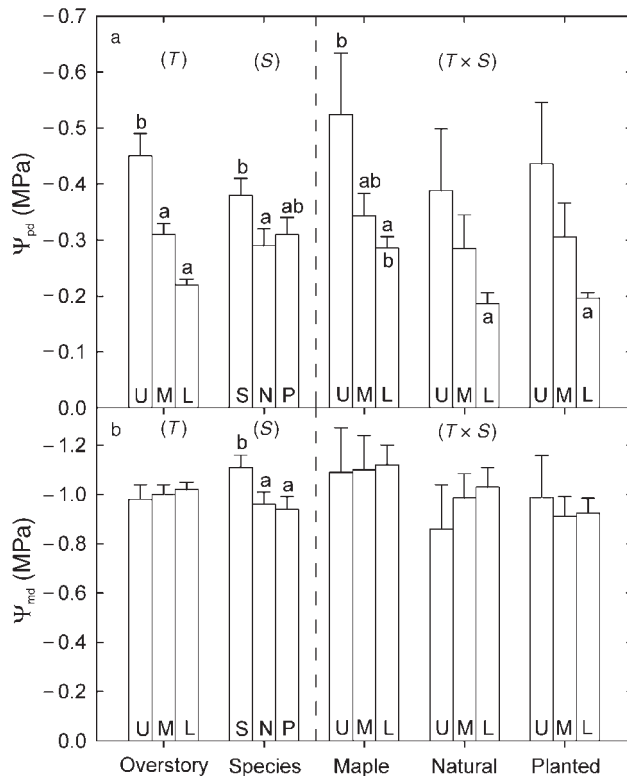


Figure 2. Overstory treatment (T), species (S) and $T \times S$ interaction effects on seasonal mean (a) predawn (Ψ_{pd}) and (b) midday (Ψ_{md}) water potentials for sugar maple (S), natural red oak (N) and planted red oak (P) seedlings growing in uncut stands (U) and in moderate (M) and light (L) shelterwoods. Mean values for overstory treatment and species comparisons having the same letter or without letters above error bars do not differ significantly ($P < 0.05$). For $T \times S$ interactions, letters above error bars refer to treatment comparisons within a given species, and letters within histogram bars refer to species comparisons within a given overstory treatment.

associated with environmental and physiological factors. Understory light had the largest influence on gas exchange of both species, with seasonal treatment plot mean values ($n = 12$) of P_n and G_{wv} being positively correlated ($r \geq 0.81^{**}$) and C_i/C_a being negatively correlated ($r \geq -0.80^{**}$) with PPF. The differential species response of leaf gas exchange to increased irradiance after overstory reduction was primarily associated with stomatal response to atmospheric humidity as modified by seedling water status. Under light-saturating conditions, leaf gas exchange was influenced most by VPD, with significant inverse relationships exhibited with P_n ($r \geq -0.47^{***}$) and G_{wv} ($r \geq -0.56^{***}$). However, because of the higher gas exchange rates of red oak, light-saturated P_n and G_{wv} were 40 to 100% higher in red oak than in sugar maple at a given VPD. Leaf C_i/C_a was inversely correlated with VPD in sugar maple ($r = -0.37^{**}$) and planted red oak ($r = -0.36^*$). Leaf water status had a greater influence on light-saturated leaf gas exchange of sugar maple than of red oak. Both Ψ_{pd} and Ψ_{md} were positively correlated with P_n ($r = 0.38^{**}$) and G_{wv} ($r = 0.28^*$), and Ψ_{pd} was inversely correlated with C_i/C_a ($r = -0.33^*$) in sugar maple. Leaf Ψ_{pd} of natural red oak was

positively correlated with P_n ($r = 0.43^{**}$) and negatively correlated with C_i/C_a ($r = -0.35^*$), whereas no relationships were apparent for planted red oak seedlings.

Limited photosynthetic acclimation in sugar maple to increasing PPF because of high VPD and low Ψ in the M versus L shelterwoods is similar to that observed in canopy gaps versus clearings (Ellsworth and Reich 1992a, 1992b). In our study, gas exchange showed less response to leaf Ψ than to VPD in red oak than in sugar maple, consistent with results of several studies conducted with potted or field-grown seedlings (Reich and Hinckley 1989, Ni and Pallardy 1991, Ellsworth and Reich 1992b, Loewenstein and Pallardy 1998). The limited ability of sugar maple to acclimate photosynthetically to increased understory light availability is typical of late-successional shade-tolerant species (Bazzaz and Carlson 1982, Ellsworth and Reich 1992a, Bazzaz and Wayne 1994), and may reflect adaptations in this drought-sensitive species that conserve water in more open habitats (Bahari et al. 1985, Martin et al. 1987, Ellsworth and Reich 1992b, Pallardy and Rhoads 1993). By comparison, the relatively high P_n and G_{wv} maintained in red oak growing in shelterwoods was likely associated with its high drought tolerance (Abrams 1990, Dey and Parker 1996).

Seedling water-use efficiency

In both species, leaf $\delta^{13}C$ (and WUE) was lower in the shaded, more humid U stands than in shelterwoods (Figure 3), likely because of the positive relationships of PPF ($r = 0.71^{**}$) and VPD ($r = 0.76^{**}$) with leaf $\delta^{13}C$ observed in our study and elsewhere (Sharifi and Rundel 1993, Berry et al. 1997). Within each shelterwood treatment, leaf $\delta^{13}C$ was lower in natural red oak than in planted red oak and sugar maple; however, in the U stands, leaf $\delta^{13}C$ was ranked as: natural red oak < planted red

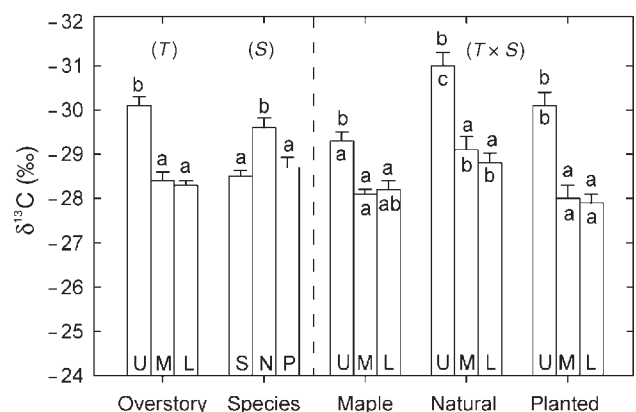


Figure 3. Overstory treatment (T), species (S), and $T \times S$ interaction effects on leaf carbon isotope ratio ($\delta^{13}C$) for sugar maple (S), natural red oak (N) and planted red oak (P) seedlings growing in uncut stands (U) and in moderate (M) and light (L) shelterwoods. Mean values for overstory treatment and species comparisons having the same letter or without letters above error bars do not differ significantly ($P < 0.05$). For $T \times S$ interactions, letters above error bars refer to treatment comparisons within a given species, and letters within histogram bars refer to species comparisons within a given overstory treatment.

oak < sugar maple. Seedling water status had less effect on WUE, with leaf Ψ_{pd} being positively correlated with leaf $\delta^{13}C$ ($r = 0.70^{**}$) in sugar maple and natural red oak seedlings, but not in planted red oak seedlings. Leaf $\delta^{13}C$ was not related to Ψ_{md} .

Water-use efficiency is a measure of a plant's ability to balance CO_2 fixation with water loss, and can be viewed as one determinant of drought tolerance. Leaf $\delta^{13}C$ was higher beneath shelterwoods because increased light and VPD in the understory increased the stomatal limitation of P_n . Higher WUE of hardwood species in more open field environments has been reported previously (Harrington et al. 1989, Ellsworth and Reich 1992b, Kloeppel et al. 1993). The positive correlation of leaf $\delta^{13}C$ with Ψ_{pd} exhibited by sugar maple and natural red oak is consistent with the greater relative sensitivity of G_{wv} than of P_n to mild drought and increased WUE previously observed in these species (Ni and Pallardy 1991, Ellsworth and Reich 1992b, Kleiner et al. 1992).

Leaf $\delta^{13}C$ was higher in sugar maple than in natural and planted red oak in the U stands. The isotopic signature of foliar tissue in U stands may largely reflect the influence of relatively brief sunflecks (Percy and Pfitsch 1991, Berry et al. 1997) that may provide 40 to 70% of total growing season PPF and thus account for a large proportion of seasonal carbon gain in northern hardwood stands (Weber et al. 1985, Chazdon 1988, Canham et al. 1990). Higher leaf $\delta^{13}C$ of sugar maple suggests a slower response of G_{wv} than of P_n to short-lived sun–shade transitions associated with sunflecks, resulting in increased WUE (Weber et al. 1985). The capacity of sugar maple to maintain a high WUE in low light and in response to sunflecks may help this drought-sensitive species avoid water stress when growing in the understory of undisturbed forests where competition for soil water may be intense (Davies and Kozlowski 1975, Chazdon 1988, Coomes and Grubb 2000).

Natural versus planted red oak seedlings

Compared with naturally established seedlings of similar size, recently planted tree seedlings must quickly acclimate to site conditions to avoid a prolonged period of low physiological activity or stress (Burdett 1990, Struve 1990, Bernier 1993, Munson and Bernier 1993). The largely similar leaf gas exchange rates and water relations of natural and planted red oak seedlings suggest no adverse physiological effects of transplanting. In contrast, leaf $\delta^{13}C$ was significantly higher in planted red oak seedlings than in natural red oak seedlings in each overstory treatment, indicating a stomatal limitation to gas exchange in planted seedlings, perhaps because of impaired water uptake capacity (Waring and Silvester 1994, Panek 1996); however, small statistical differences in leaf $\delta^{13}C$ ($> 1\text{‰}$) should be interpreted with caution (O'Leary 1993). Underplanting in U stands and moderation of the understory environment by shelterwood canopies may have enhanced the rate of acclimation by planted seedlings.

Conclusions

Increases in irradiance and perhaps soil water availability

in shelterwoods were associated with increased leaf gas exchange in red oak and sugar maple seedlings, but the relative improvement in photosynthetic capacity was larger in red oak. Lower photosynthetic response of sugar maple under the higher-light environment of the shelterwoods was related in part to stomatal limitations that minimize leaf water stress. Red oak was better able to take advantage of higher light in shelterwoods because of its comparatively well developed drought tolerance. Steady-state leaf photosynthetic rates measured in our study are only one component of whole-plant carbon balance. Other factors include plant allometry, crown architecture, leaf display and relative growth rate. Therefore, the improved leaf gas exchange of red oak noted here may not be directly related to regeneration potential. Nevertheless, increased seedling carbon gain in response to higher irradiances and improved soil water availability beneath shelterwoods, in combination with understory treatments to reduce the abundance of sugar maple and delay the regrowth of competing vegetation, should provide some initial advantage to this species.

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