PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest

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Abstract Saplings of many canopy tree species in winter deciduous forests receive the major portion of their light budget for their growing season prior to canopy closure in the spring. This period of high light may be critical for achieving a positive carbon (C) gain, thus contributing strongly to their growth and survival. This study of saplings of *Aesculus glabra* and *Acer saccharum* in Trelease Woods, Illinois, USA, tested this hypothesis experimentally by placing tents of shade cloth over saplings during their spring period of high light prior to canopy closure in three consecutive years. Leaf senescence began 16 days (year 0) and 60 days (year 1) earlier for shaded *A. glabra* saplings than control saplings. No change in senescence occurred for *A. saccharum.* The annual absolute growth in stem diameter of both species was negligible or negative for shaded saplings, but positive for control saplings. Only 7% of the shaded *A. glabra* saplings were alive after 2 years, while all control saplings survived for 3 years; only 20% of the shaded *A. saccharum* saplings survived for 3 years, while 73% of control saplings were alive after the same period. Early spring leaf out is a critical mechanism that allows the long-term persistence of saplings of these species in this winter deciduous forest. Studies and models of C gain, growth, and survival of saplings in deciduous forests may need to take into account their spring phenology because saplings of many species are actually "sun" individuals in the spring prior to their longer period in the summer shade.

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Introduction

Carbon (C) gain and subsequent growth of understorey plants in forests are greatly constrained by low light availability (Pacala et al. 1994). Numerous experimental studies of understorey plants have demonstrated greatly lower C gain, growth, and survival in shade plants than in sun plants (e.g., Ellsworth et al. 2004). The morphological and physiological adaptations of understorey plants for shade have been well documented (e.g., Abrams and Kubiske 1990; Gross et al. 1996); however, these studies in steady-state light environments assumed that there is no seasonal variation in light availability to understorey plants.

Understorey plants in winter deciduous forests may have earlier leaf out in the spring than canopy trees. This early leaf out results in a period of high light availability and may be an additional mechanism that allows understorey plants to persist in winter deciduous forests (Uemura 1994; Gill et al. 1998). Many herbs (Rothstein and Zak 2001), shrubs (Harrington et al. 1989; Gill et al. 1998), and juveniles of canopy tree species (Augspurger and Bartlett 2003) extend their growing season beyond that of canopy trees by leafing out prior to canopy closure in the spring. In one temperate deciduous forest, bud break by juveniles of canopy tree species occurs, on average, 8 days prior to that of their canopy tree conspecifics (Augspurger and Bartlett 2003). At the extreme end of the spectrum, saplings of *Aesculus glabra* have 24 days at full leaf size prior to complete canopy closure (Augspurger et al. 2005). The light received during early spring can represent 33–98% of the

estimated total irradiance over the growing season for understorey individuals (Augspurger et al. 2005). Other studies have shown that these understorey plants are physiologically primed to maximize their utilization of this enhanced light. Their young leaves have the highest amount of nitrogen and greatest photosynthetic capacity relative to leaves later in the growing season; consequently, they should contribute a substantial amount of the total C gain of the entire growing season (Augspurger et al. 2005). Such studies led to the hypothesis that this enhancement in C gain in the early spring is necessary to create a positive C balance and ultimately increases a sapling's growth and long-term survival. Studies of saplings in a deciduous forest established that light availability predicts their growth (Pacala et al. 1994), which, in turn, predicts their probability of mortality (Kobe et al. 1995; Casperson and Kobe 2001).

The objective of this study was to test this hypothesis by experimentally shading saplings during their normal spring period of high light. The prediction was that these shaded individuals would have lower growth and survival than control individuals. Early observations indicated that experimental shading brought additional negative effects of earlier senescence to one study species, thus reducing its growing season and period of C gain. Consequently, phenological responses were measured as well.

Saplings of the two study species, *Aesculus glabra* Willd. (Ohio buckeye) and *Acer saccharum* Marsh. (sugar maple), differ in their spring phenology. Ohio buckeye completes leaf expansion prior to 50% canopy closure and has fully expanded leaves for 24 days prior to 100% canopy closure. Sugar maple has 24 days with expanding leaves and 7 days with fully expanded leaves in high light prior to 100% canopy closure (Augspurger et al. 2005). The two species also differ in the length of their growing season. From bud break to start of senescence is 125 days in Ohio buckeye and 184 in sugar maple; full leaf expansion to start of senescence is 91 days in Ohio buckeye and 160 days in sugar maple (Augspurger and Bartlett 2003). Therefore, a further prediction is that experimental shading in the spring will have greater and more rapid negative consequences for Ohio buckeye than sugar maple because of the former's shorter growing season and greater portion of the growing season during the period of high light in the spring.

The study focused on spring phenology because the summer senescence and leaf drop of Ohio buckeye preclude any autumn activity, and sugar maple is well advanced in senescence prior to 50% canopy opening in the autumn (Augspurger et al. 2005). Sugar maple receives an estimated 11% of its light budget during canopy opening in the autumn and its photosynthetic capacity is quite low at this time (Augspurger et al. 2005).

Materials and methods

The study site was Trelease Woods, a 24-ha forest fragment located 3 km northeast of Urbana, Illinois, USA (40°09′N, 88°10′W). The mixed mesophytic deciduous forest has 20 canopy tree species and its canopy height is 20–25 m. The two study species, *Aesculus glabra* (Ohio buckeye) and *Acer saccharum* (sugar maple), predominate among saplings in the understorey.

In late winter 2002, study saplings approximately 2–2.5 m in height were haphazardly selected in the shaded understorey within a 1.25-ha area that was >50 m from any edge and without recently formed light gaps. For each species, 15 individuals each were randomly assigned to experimental and control treatments. Deer damage reduced the Ohio buckeye samples to 13 experimental and 14 control individuals. Mean initial stem diameter (see below) did not differ significantly between treatments for Ohio buckeye (Experimental 1.82 cm; Control = 1.75) (unpaired t test: $t = 0.702$, $df = 25$, $P = 0.490$) or sugar maple (Experimental = 1.31 cm; Control = 1.45) ($t = -1.686$, $df = 28$, $P = 0.103$).

The shade treatment was a single layer of black knitted shade cloth (model KS90; DeWitt Co., Sikeston, MO) designed to transmit 10% of ambient sunlight. An inverted conical "tent", 1.5 m in height, extended to just below all branches of each sapling. It was open at the bottom. A 2.8-m central pole and guy wires to adjacent trees held up the tent and held out its sides to the maximum extent. The tents were set up in mid-March (Ohio buckeye) or early April (sugar maple) of 2002, 2003, and 2004 prior to emergence of any leaves from buds. Tents were removed on May 10 in year 0, when the canopy was 95% closed, and on May 3 in years 1 and 2, when the canopy was approximately two-thirds closed. Prior to tent removal, leaves of saplings of both species had reached full expansion. Control saplings received ambient light.

A quantum sensor (Li-Cor, Lincoln, NE) measured an instantaneous reading of irradiance at each sapling near midday on clear sunny days [approx. weekly from early April 2004 (before bud break of canopy trees) through mid-May 2004 (canopy 95–98% closed)]. The sensor was held horizontally at a fixed point 0.5 m above the bottom of the open tent on a leaf not experiencing sunflecks or self-shading. Readings were also taken in an open field 25 m away from the forest edge at the beginning and end of each approximately 45-min sampling period. Each value was standardized absolute to the mean reading in the open field [(forest/open sky) × 100] because weekly open sky readings varied.

Three plant responses were measured: leaf phenology, sapling growth, and survival. For leaf phenology measured on a single day at weekly intervals from 2002 to 2005, Julian calendar dates of four events were determined: (1) beginning of bud break (bud scales parted, revealing under-

lying leaf tissue); (2) completion of leaf expansion (leaf of full size, flattened, in normal orientation); (3) beginning of senescence (first breakdown of chlorophyll, revealing underlying pigments); (4) completion of leaf drop (leaf abscission complete). Events were defined as follows: for bud break and senescence, more than one-third of the individual's buds or leaves met the criterion, whereas for leaf expansion and leaf drop, more than two-thirds of the leaves met the criterion.

Stem diameter (in mm) of each sapling was measured with a Vernier caliper from 17 to 21 April in each year (2002–2005). Annual radial growth was assumed to be an integrated measure of whole-plant C gain (Kobe et al. 1995). Five consecutive measurements were made from the north side just below the lowest branch at a fixed point marked with a ring of white paint. The height of this branch differed among saplings from approximately 0.5 to 1.5 m. The mean of the five measurements each year was used to calculate the absolute growth in diameter for each sapling that had been alive the previous year.

Survival of each sapling was appraised in the spring and autumn of each year of the study period (2002–2005). A sapling was considered to be dead if it had no bud break or no leaves prior to the normal period of senescence. Each "dead" sapling was revisited in subsequent seasons to determine if any resprouting had occurred.

Differences between treatments in phenological dates were analyzed with unpaired t tests. Repeated measures ANOVA tested for differences in annual absolute growth. For Ohio buckeye only, the analysis included growth only through year 2 because of substantial early mortality and diminished sample size. Differences between treatments in survival after 3 years were determined by chi-square analysis.

Results

Light

The experimental treatment reduced light transmission to 7–8% of full sunlight during the period prior to two-third canopy closure; light transmission slowly diminished to 3% at two-third closure and <1% at 95% closure (Fig. 1). The tents were removed at 95% closure in year 1, but, more conservatively, at two-third closure in years 2 and 3. Control individuals received 83% of full sunlight prior to any canopy leaf out, then 29% at two-third closure and <1% at 95% closure (Fig. 1). Overall, the experimental individuals during their period with tents received about 10% of the light available to control individuals. Both experimental and control individuals received <1% of full sunlight throughout the period of full canopy closure from June to mid-October (data not shown).
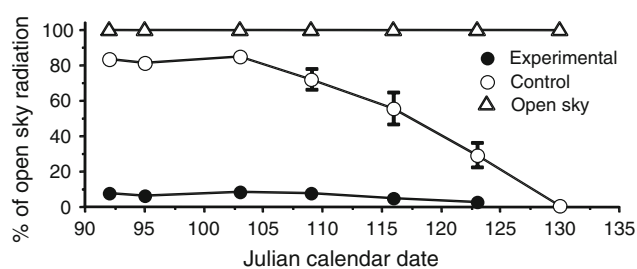

Fig. 1 Percentage of radiation in the open sky transmitted to experimental versus control treatments during spring phenological activity of saplings and canopy trees. Values represent mean ± 1 SE. The experimental shade treatment was imposed prior to date 92 and removed around date 123 of each year

Phenology

Spring phenology for Ohio buckeye did not differ between treatments (Table 1). However, the start of senescence was earlier (by 16 days in year 0 and 60 days in year 1) in the experimental group than in the control saplings (Table 1); leaf drop was also earlier (by 23 days in year 0 and 52 days in year 1). Thus, the growing season was markedly shorter for the experimental samplings than for the control saplings.

In sugar maple, bud break and full expansion of leaves were slightly earlier in the experimental than control treatment, but only in year 1 (Table 1). Leaf drop was later in the experimental saplings than in control saplings, but only in year 2; all other phenological events were equivalent between treatments.

Growth

The annual absolute growth of stem diameter for Ohio buckeye saplings differed significantly between treatments (repeated measures ANOVA, $df = 1$, $F = 19.877$, $P < 0.0003$) (Fig. 2a). The significant time × treatment interaction ($df = 1$, $F = 9.461$, $P < 0.007$) arose because experimental individuals had negative growth, which increased in year 2, while control individuals had positive growth in all 3 years. Likewise, the absolute growth of sugar maple saplings differed significantly between treatments ($df = 1$, $F = 8.057$, $P < 0.0025$) (Fig. 2b). Experimental individuals largely had negative growth, while control individuals had positive growth, although the time × treatment interaction was not significant for sugar maple ($df = 2$, $F = 1.109$, NS).

Survival

For Ohio buckeye, the number of surviving saplings after 3 years differed significantly between treatments ($\chi^2 = 9.882$, $df = 1$, $P < 0.005$) (Fig. 3a). The number of

Table 1 Comparison of Julian calendar date of phenological events in experimental versus control treatments over 3 year

Phenological event	Year	Treatment	Ohio buckeye Mean ± SE	Sugar maple Mean ± SE
Senescence	0	Experimental	165.9 ± 64*	301.4 ± 0.6
		Control	181.5 ± 2.6	300.6 ± 1.0
Leaf drop	0	Experimental	189.2 ± 2.7**	317.2 ±0.8*
		Control	212.4 ± 5.1	319.3 ±0.9
Bud break	1	Experimental	80.5 ± 1.6	98.0 ±0**
		Control	78.0 ± 0.7	100.3 ± 0.9
Expansion	1	Experimental	107.3 ± 1.5	119.8 ±1.8
		Control	105.5 ± 0.5	126.0 ± 1.0
Senescence	1	Experimental	125.2 ± 4.0***	297.0 ± 0
		Control	185.3 ± 4.9	294.0 ± .9
Leaf drop	1	Experimental	167.2 ± 9.6***	314.0 ± 1.0
		Control	218.9 ± 3.9	312.7 ± 1.3
Bud break	2	Experimental	–	103.0 ± 0
		Control	88.0 ± 0.7	103.0 ± 0
Expansion	2	Experimental	–	117.0 ± 0
		Control	109.0 ± 0.7	118.8 ± 0.9
Senescence	2	Experimental	–	295.0 ± 0
		Control	203.2 ± 3.0	292.5 ± 1.1
Leaf drop	2	Experimental	–	306.7 ± 2.3***
		Control	235.4 ± 6.5	292.5 ± 1.1
Bud break	3	Experimental	–	102.0 ± 0
		Control	93.5 ± 0.8	102.0 ± 0
Expansion	3	Experimental	–	116.0 ± 0
		Control	107.5 ± 0.8	117.4 ± 0.9

* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$

No data are available for Ohio buckeye in years 2 and 3 because only 1 (year 2) or no (year 3) saplings survived

survivors in the experimental treatment declined sharply over the 3-year study period, while all individuals survived in the control treatment. Only one experimental individual survived to the spring of year 2. In the spring of year 3, four experimental individuals declared "dead" in prior years resprouted from the base of the trunk, but these continued to have no leaves on the initial higher branches covered by the shade treatment.

Likewise for sugar maple, the number of survivors after 3 years differed significantly between treatments ($\chi^2 = 8.572$, $df = 1$, $P < 0.005$) (Fig. 3b). After 3 years, there were three survivors in the experimental and 11 survivors in the control treatments. No resprouting occurred in sugar maple. The two species differed in the season of mortality. All mortality for Ohio buckeye occurred during the winter, while it occurred in both the growing season and the winter for sugar maple (Fig. 3).

Discussion

This study supports the hypothesis that having early spring leaf out is critical to the growth and survival of saplings of *Aesculus glabra* and *Acer saccharum* in this winter deciduous forest. Depriving saplings of their normal spring light period prior to canopy closure had major negative cascading effects. First, Ohio buckeye saplings accelerated senescence, thus reducing their already short growing season. Second, both species had lower—and often negative—growth that led to a high probability of mortality. These very strong effects were found in spite of moderate sample sizes. As predicted, Ohio buckeye, with its shorter growing season, had a more rapid and more pronounced response than sugar maple. The study underscores the tightness of the C budget for saplings growing under canopy trees and indicates that the substantial C gain in early spring is critical for the persistence of these species in this deciduous forest. Sunflecks in the summer months (Chazdon 1988) do not appear to add adequate light.

Field studies (Harrington et al. 1989; Gill et al. 1998; Augspurger et al. 2005) and simulation models for the understorey (Jolly et al. 2004) and for *Acer saccharum* saplings (Walters and Reich 1999) confirm the importance of spring light for short-term C gain of saplings at the leaf level. To understand the overall significance of a plant trait, short-term gains of a plant's organs must be scaled to the
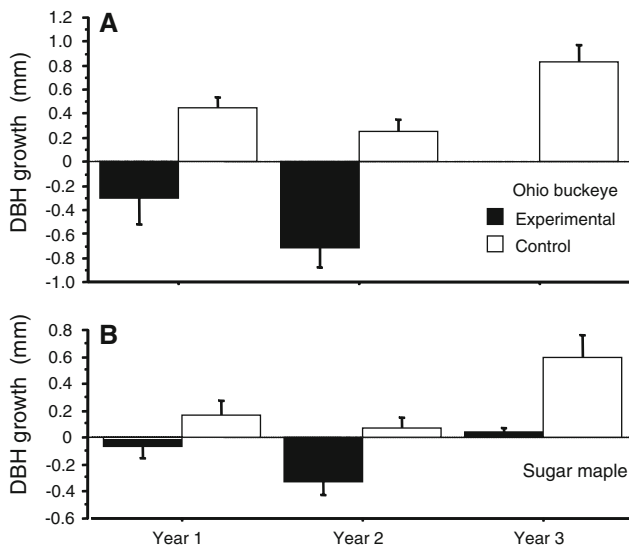
Fig. 2 Comparison of absolute growth of stem diameter in experimental versus control treatments over 3 years for Ohio buckeye (**a**) and sugar maple (**b**). Values represent mean (±1 SE). Only saplings alive in each prior year are included
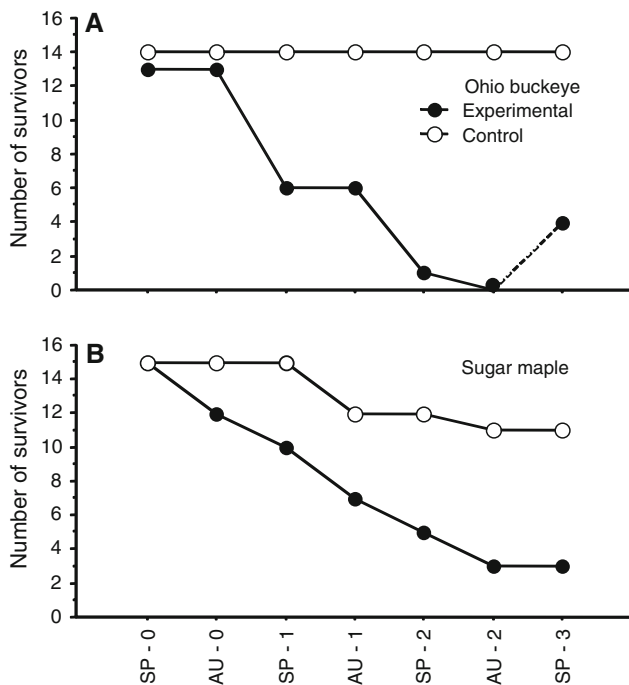

Fig. 3 Comparison of number of survivors in experimental versus control treatments over 3 years for Ohio buckeye (**a**) and sugar maple (**b**). *SP* Spring, *AU* autumn. *Numbers* refer to years since the initiation of the experiment (year 0). The Ohio buckeye increase at SP 3 is due to resprouting from the base of the stem; all parts above the base continued to have no leaves

whole-plant level (Givnish 1986). This study extends earlier studies by demonstrating the long-term consequences of diminished spring light on the sapling's growth and survival. Similar advantages of early emerging cohorts of *Acer* seedlings have been shown (Jones et al. 1997; Seiwa 1998).

The mortality in this study may have been due directly to a negative whole-plant C balance or indirectly to their increased vulnerability to drought, wind, or winter desiccation or to a lack of sufficient carbohydrate reserves for new growth in the spring (Kobe 1997; Canham et al. 1999). Sugar maple seedlings and saplings accumulate large carbohydrate reserves in their roots (Canham et al. 1999; Gaucher et al. 2005). Species with a greater concentration of total nonstructural carbohydrates in roots have greater survival under low light (Kobe 1997; Canham et al. 1999).

Even though saplings are not in perpetual shade during a growing season, many experimental studies have compared growth and survival of juveniles in two steady-state light environments, shaded understorey versus light gaps. By imposing shade at a constant level for the entire growing season, these studies underestimate the potential of "shade" individuals. Similarly, field studies that predict sapling mortality based on light availability only during the period of a closed canopy (Kobe et al. 1995) may lead to inaccurate estimates.

Re-formulation of the meaning of shade tolerance of species may be warranted so that the role of the early spring leaf out for saplings is taken into account. Foresters state that Ohio buckeye is shade tolerant (Baker 1949) because it is found in the heavy shade of beech–maple forests (Burns and Honkala 1990). However, the phenology of Ohio buckeye reflects its intolerance of shade. It has the earliest bud break and the earliest senescence among temperate deciduous forest species (Augspurger and Bartlett 2003). Its natural senescence begins as early as late July when its photosynthetic capacity is quite low (Augspurger et al. 2005). Experimental shading evidently placed Ohio buckeye at a negative C balance much earlier, resulting in its even earlier senescence. Overall, Ohio buckeye (*A. glabra*) as well as Georgia buckeye (*A. sylvatica*) are both vernal species (dePamphilis and Neufeld 1989) and not tolerant of shade.

A similar re-evaluation of shade tolerance is necessary for sugar maple, which is considered to be very shade tolerant (Baker 1949; Burns and Honkala 1990) or shade tolerant (Kobe et al. 1995). This study qualifies those designations by adding the caveat that sugar maple saplings survive in shade in the long-term only because of their substantial C gain in the early spring. In the future, designations of shade tolerance should explicitly incorporate the mechanism by which saplings of a species persist in the understorey. It appears that many so-called shade-tolerant species exploit spring light.

The results of this study demonstrate that the early spring leaf out of saplings has consequences for the fitness components of growth and survival. Selection may act directly on this ontogenetic stage, favoring individuals with earlier bud break. An alternative scenario is that a cue requirement of accumulated thermal degree units is identi-

cal for all life stages, but that saplings meet the requirement earlier due to the warmer night temperatures in the understorey (Augspurger 2004). It is nevertheless possible that this cue, which is used by all stages, may be set primarily by selection acting on the sapling stage, given how critical the early leaf out is for the survival of this young stage. Consistent with this alternative scenario, Poorter (2007) found that leaf traits are adapted to the light environment of the juvenile—and not the adult stage—of tropical moist forest trees.

Species differ in the extent of their early spring leaf out (Augspurger and Bartlett 2003) and likely in their dependence on spring light for C gain and persistence. Consequently, growth and survival will differ among species, thus affecting their absolute abundance, the order of species replacement during succession, and the overall productivity of the understorey (Jolly et al. 2004). Studies and models undertaken to study light regimes, C gain, growth, and survival of "shade" individuals, as well as the productivity of the understorey, may need to be expanded to include the seasonal variation in light. In reality, understorey individuals of many tree species are actually "sun" individuals in the spring prior to moving into the summer shade.

References

Abrams MD, Kubiske ME (1990) Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin USA: influence of light regime and shade-tolerance rank. For Ecol Manage 31:245–254

Augspurger CK (2004) Developmental vs environmental control of early leaf phenology in juvenile Ohio buckeye (*Aesculus glabra*). Can J Bot 82:31–35

Augspurger CK, Bartlett EA (2003) Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. Tree Physiol 23:517–526

Augspurger CK, Cheeseman JM, Salk CF (2005) Light gains and physiological capacity of understorey woody plants during phenological avoidance of canopy shade. Funct Ecol 19:537–546

Baker FS (1949) A revised shade tolerance table. J For 47:179–181

Burns RM, Honkala BH (1990) Silvics of North America. Hardwoods, vol 2. USDA Handbook 654. U.S. Department of Agriculture, Washington D.C.

Canham CD, Kobe RK, Latty EF, Chazdon RL (1999) Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121:1–11

Casperson JP, Kobe RK (2001) Interspecific variation in sapling mortality in relation to growth and soil moisture. Oikos 92:160–168

Chazdon RL (1988) Sunflecks and their importance to forest understory plants. Adv Ecol Res 18:1–63

Ellsworth JW, Harrington RA, Fownes JH (2004) Survival, growth and gas exchange of *Celastrus orbiculatus* seedlings in sun and shade. Am Mid Nat 151:233–240

Gaucher C, Gougeon S, Mauffette U, Messier C (2005) Seasonal variation in biomass and carbohydrate partitioning of understorey sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) seedlings. Tree Physiol 25:93–100

Gill DS, Amthor JS, Bormann FH (1998) Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. Tree Physiol 18:281–289

Givnish TJ (ed) (1986) On the economy of plant form and function. Cambridge University Press, New York

Gross K, Homlicher A, Weinreich A, Wagner E (1996) Effect of shade on stomatal conductance, net photosynthesis, photochemical efficiency and growth of oak seedlings. Ann Sci For 53:279–290

Harrington RA, Brown BJ, Reich PB (1989) Ecophysiology of exotic and native shrubs in Southern Wisconsin 1 Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia 80:356–367

Jolly WM, Nemani R, Running SW (2004) Enhancement of understory productivity by asynchronous phenology with overstory competitors in a temperate deciduous forest. Tree Physiol 24:1069–1071

Jones RH, Allen BP, Sharitz RR (1997) Why do early-emerging tree seedlings have survival advantage? A test using *Acer rubrum* (Aceraceae). Am J Bot 84:1714–1718

Kobe RK (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos 80:226–233

Kobe RK, Pacala SW, Silander JA Jr, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. Ecol Appl 5:517–532

Pacala SW, Canham CD, Silander JA Jr, Kobe RK (1994) Sapling growth as a function of resources in a north temperate forest. Can J For Res 24:2172–2183

dePamphilis CW, Neufeld HS (1989) Phenology and ecophysiology of *Aesculus sylvatica*, a vernal understorey tree. Can J Bot 67:2161–2167

Poorter L (2007) Are species adapted to their regeneration niche, adult niche, or both? Am Nat 169:433–442

Rothstein DE, Zak DR (2001) Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. Funct Ecol 15:722–731

Seiwa K (1998) Advantages of early germination for growth and survival of seedlings of *Acer mono* under different overstory phenologies in deciduous broad-leaved forests. J Ecol 86:219–228

Uemura S (1994) Patterns of leaf phenology in forest understory. Can J Bot 72:409–414

Walters MB, Reich PB (1999) Low-light carbon balance and shade tolerance in the seedlings of woody plants: Do winter deciduous and broad-leaved evergreen species differ? New Phytol 143:143–154