

## Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest

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**Summary** In a deciduous forest, differences in leaf phenology between juvenile and adult trees could result in juvenile trees avoiding canopy shade for part of the growing season. By expanding leaves earlier or initiating senescence later than canopy trees, juvenile trees would have some period in high light and therefore greater potential carbon gain. We observed leaf phenology of 376 individuals of 13 canopy tree species weekly over 3 years in a deciduous forest in east central Illinois, USA. Our objectives were: (1) to quantify for each species the extent of differences in leaf phenology between juvenile and conspecific adult trees; and (2) to determine the extent of phenological differences between juvenile *Aesculus glabra* Willd. and *Acer saccharum* Marsh. trees in understory and gap microhabitats. All species displayed phenological differences between life stages. For 10 species, bud break was significantly earlier, by an average of 8 days, for subcanopy individuals than for canopy individuals. In 11 species, completion of leaf expansion was earlier, by an average of 6 days, for subcanopy individuals than for canopy individuals. In contrast, there were no significant differences between life stages for start of senescence in 10 species and completion of leaf drop in nine species. For eight species, leaf longevity was significantly greater for subcanopy individuals than for canopy individuals by an average of 7 days (range = 4–10 days). Leaf phenology of subcanopy individuals of both *Aesculus glabra* and *Acer saccharum* responded to gap conditions. Leaf longevity was 11 days less in the understory than in gaps for *Aesculus glabra*, but 14 days more in the understory than in gaps for *Acer saccharum*. Therefore, leaf phenology differed broadly both between life stages and within the juvenile life stage in this community. A vertical gradient in temperature sums is the proposed mechanism explaining the patterns. Temperature sums accumulated more rapidly in the sheltered understory than in an open elevated area, similar to the canopy. Early leaf expansion by juvenile trees may result in a period of disproportionately higher carbon gain, similar to gains made during summer months from use of sun flecks.

**Keywords:** *Acer saccharum*, *Aesculus glabra*, bud break, canopy tree, leaf drop, leaf expansion, leaf longevity, leaf senescence, sapling, shade, subcanopy tree, sun.

### Introduction

An individual canopy tree encounters great changes in its environment over its lifetime, from understory or gap conditions as a juvenile to canopy conditions as an adult. Plants often display variation in traits, presumably to maximize fitness in a variable environment (Bazzaz 1991). Specifically, in response to a changing light environment, a plant's physiological, morphological and phenological traits may change both during development and in different light environments at the same life stage in order to maximize net carbon gain.

Most previous work has focused on physiological and morphological adaptations of understory plants to shade. Differences in photosynthetic capacity between life stages have been documented for hardwood and coniferous tree species (Bond 2000). Photosynthetic capacity based on leaf mass is higher for saplings than for canopy trees (Thomas and Winner 2002). Shaded seedlings display lower compensation points and light saturation points than either saplings or adults (Koike 1984, Farnsworth and Ellison 1996), indicating a response by seedlings to low irradiances in the forest understory.

Morphological traits also change during development. To increase light interception, younger shaded trees have larger and thinner leaves relative to leaves of canopy individuals. Compared with canopy trees, younger individuals also have different canopy architecture and leaf display to decrease self-shading (Gerrish 1989, Kikuzawa et al. 1996). These changes in physiology and morphology help maximize light interception and increase carbon gain at the various growth stages. In evergreen forests, these adjustments are the only avenues to increase carbon gain.

Understory trees in deciduous forests have a third option for increasing carbon gain: phenological avoidance of canopy shade (Uemura 1994). If understory trees have earlier leaf expansion in spring or later leaf drop in autumn than canopy trees, they partially avoid the period of low light imposed by leaves of canopy trees. Phenological avoidance has been advanced as an important characteristic by which juvenile canopy trees maximize light acquisition, enabling them to persist in shaded forest understories during summer (Gill et al. 1998, Seiwa 1998, 1999a).

The extent and generality of phenological differences be-

tween life stages of temperate deciduous tree species are not well known. Most phenological studies have focused on the canopy stage (Smith 1915, Ahlgren 1957, Maycock 1961, Lechowicz 1984). Studies of canopy tree species in temperate deciduous forests have documented a limited degree of phenological avoidance by juveniles. For *Acer saccharum* Marsh. and *Fagus grandifolia* J. F. Ehrh., leaf expansion was earlier and leaf senescence was later for saplings than for conspecific canopy trees (Gill et al. 1998). For *Acer mono* Maxim., leaf emergence was earlier in younger trees, whereas leaf senescence did not differ among trees of different ages (Seiwa 1999a). For *Ulmus davidiana* Planch. var. *japonica*, leaf emergence was earlier and leaf fall later in seedlings than in adults (Seiwa 1999b). In each of these studies, differences in phenology resulted in greater leaf longevity for juveniles than for adults. However, no community-wide study has been undertaken to examine the generality or variation among tree species in the extent of phenological avoidance of canopy shade by juveniles.

Juveniles of canopy tree species may experience improved light conditions in the understory in two ways: in gaps and by phenological avoidance of canopy shade. The gap environment is more similar to the sun-lit canopy than the shaded understory. Therefore, phenological avoidance by juveniles may be less strong in gaps than in understory conditions.

Mathematical models predict that maximum carbon gain is achieved by altering leaf phenology to match favorable light conditions (Iwasa and Cohen 1989, Kikuzawa 1991, Sakai 1992). Empirical studies that compare leaf phenology for individual trees of different life stages and for juveniles in gap and understory conditions are needed to test the theory. Determining phenological differences between life stages is also important for modeling forest dynamics and forest carbon budgets, defining the light environment of so-called shade-tolerant species, and predicting tree responses to global climate change.

We conducted a comparative community-level study of temperate deciduous tree species to investigate three questions. (1) What differences in leaf phenology exist between juveniles and conspecific adult trees? (2) Is phenological avoidance of canopy shade by juveniles greater in spring or autumn? (3) What differences in leaf phenology exist between juveniles in understory and gap conditions? Comparisons are based on the assumption that observations made for sets of trees at different life stages reflect changes during the lifetime of one individual tree.

One mechanism that could create differences in spring phenology between life stages of these species is a vertical gradient in temperature. Spring phenology of most temperate deciduous tree species is linked to a requirement for winter chilling followed by an accumulation of thermal degree days above some threshold (Hänninen 1990, Hunter and Lechowicz 1992, Heide 1993, Myking and Heide 1995, Chuine and Cour 1999). If radiation cooling at night is greater in the canopy, then thermal degree hours will be greater, and spring phenology earlier, in the understory than in the canopy. Therefore, spring temperatures were measured in the forest understory and in an open elevated site similar to the canopy.

## 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 upland deciduous forest is an old-growth remnant of a large presettlement forest known as The Big Grove (Pelz and Rolfe 1977). The University of Illinois has managed the forest without human disturbance since 1917. The forest has 20 canopy tree species and its canopy height is 20–25 m. The site has no slope.

In early spring 1993, before bud break, 376 individuals of 13 common canopy species were tagged within five 50 × 300 m quadrants located in the interior of the north half of the forest, at least 50 m from an edge. For most species, 12–15 individuals of each of two life stages were observed: subcanopy (> 2 m to < 10 m) and canopy. We also observed 12 saplings (< 0.5 m) for four of the 13 species observed: *Acer saccharum* (sugar maple), *Gymnocladus dioica* (L.) K. Koch (Kentucky coffee tree), *Aesculus glabra* Willd. (Ohio buckeye) and *Carya cordiformis* (Wangenh.) K. Koch (bitternut hickory). The remaining nine species were: *Carya ovata* (Mill.) K. Koch (shagbark hickory, including shellbark hickory var. *pubescens* Sarg.), *Fraxinus americana* L. (white ash), *Fraxinus quadrangulata* Michx. (blue ash), *Quercus macrocarpa* Michx. (bur oak), *Quercus rubra* L. (red oak), *Ulmus rubra* Muhlenb. (slippery elm), *Ulmus americana* L. (American elm), *Tilia americana* L. (basswood) and *Celtis occidentalis* L. (hackberry). Nomenclature follows Mohlenbrock (1986). All species exhibited a flush type of leaf emergence (Kikuzawa 1983) in which all leaves emerged in a short period in the spring and no new leaves appeared in the summer.

Phenology was also compared between subcanopy individuals of *Aesculus glabra* and *Acer saccharum* growing in understory and gap-like conditions (western edge of forest fragment). Ten individuals of each species were observed from 1999 to 2001 in each microhabitat.

Julian calendar dates of four phenological events were determined: (1) beginning of bud break (bud scales parted, revealing underlying 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); and (4) completion of leaf drop (leaf abscission complete). From these event variables, durations of three phenological phases were calculated: (1) expansion duration (beginning of bud break to completion of leaf expansion); (2) senescence duration (beginning of senescence to completion of leaf drop); and (3) leaf longevity (completion of leaf expansion to beginning of senescence). Event refers to a single Julian date, whereas duration refers to the number of days between two events.

From mid-March to early December during 1993–1995, observations with binoculars were made on a single day at weekly intervals. The observational unit was the entire crown of each individual. Phenological events were often asynchronous over the entire crown. Likewise, entire crowns of canopy trees were not always visible. Therefore, events were defined as follows: for initiation events (bud break and senescence),

more than one-third of the individual's buds, or leaves, met the criterion, whereas for completion events (leaf expansion and leaf drop), more than two-thirds of the leaves met the criterion.

Temperatures were recorded at 30-min intervals from January to June 2001 at 1 m above ground level in the understory and 1 m above a 7-m high barn roof located adjacent to Trelease Woods. Although not as high as the 20–25 m canopy, the site was fully exposed, similar to the top of a canopy tree. For calculations of cumulative degree hours, the threshold temperature was 0 °C and the starting date was January 1.

Differences between life stages in initiation or completion of phenological events and duration of phenological phases were tested separately for each of the 13 species. Life stages consisted of sapling (if available), subcanopy and canopy trees. These comparisons used a repeated-measures analysis of variance (rmANOVA) with year as the within-subject variable and life stage as the between-subject variable. When the assumption of compound symmetry for rmANOVA was not met, the probabilities were adjusted using the Huynh-Feldt statistic (Stevens 2002). Subsequent univariate *F*-tests were used to determine in which year(s) a difference between life stage(s) occurred. Mean values for the 3 years are presented

throughout, but the number of years with significant differences between life stages is provided in figures.

In the understory versus gap comparisons, statistical analyses for each event and duration were performed separately for *Aesculus glabra* and *Acer saccharum* to compare subcanopy individuals in the two microhabitats. These comparisons used rmANOVA with year as the within-subject variable and microhabitat as the between-subject variable.

## Results

### Subcanopy versus canopy individuals

All species displayed phenological differences between life stages but differed in the extent to which they displayed differences in initiation or completion of phenological events and in duration of phases (Figures 1 and 2, Table 1). For the spring events, bud break was significantly earlier for subcanopy individuals than for canopy individuals in 10 species by an average of 8 days. In 11 species, completion of leaf expansion was earlier for subcanopy individuals than for canopy individuals by an average of 6 days. Expansion duration of subcanopy indi-

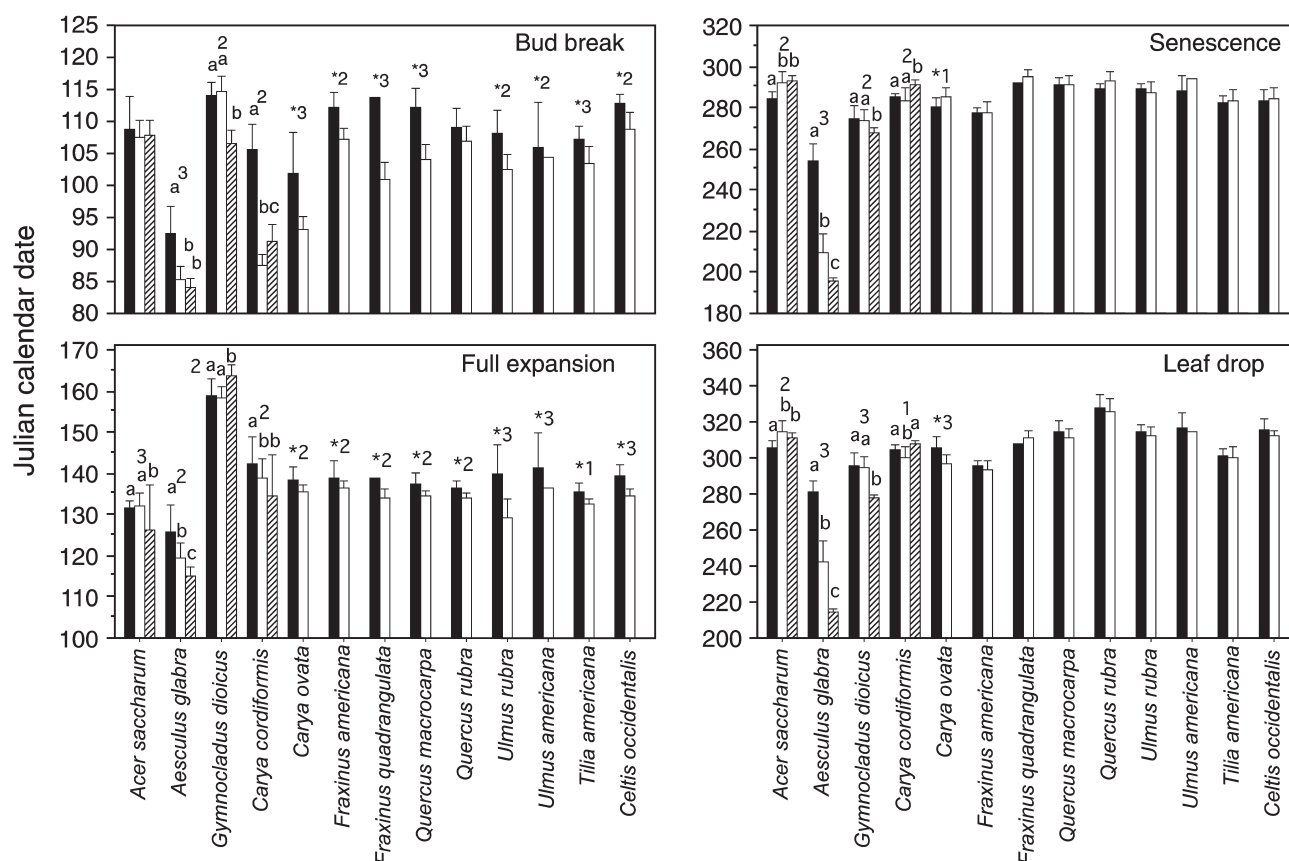


Figure 1. Comparisons among canopy (solid bars), subcanopy (open bars) and sapling individuals (hatched bars) of 13 tree species based on the Julian calendar date of initiation or completion of four phenological events. Means + 1 SD are shown for 3 years combined. Note different vertical scales among panels. Different lowercase letters above bars for a given species indicate significant differences ( $P < 0.05$ ) in species for which three life stages were studied; asterisks indicate differences for which two life stages were studied. Numbers above bars indicate the number of years in which there were significant differences between stages.

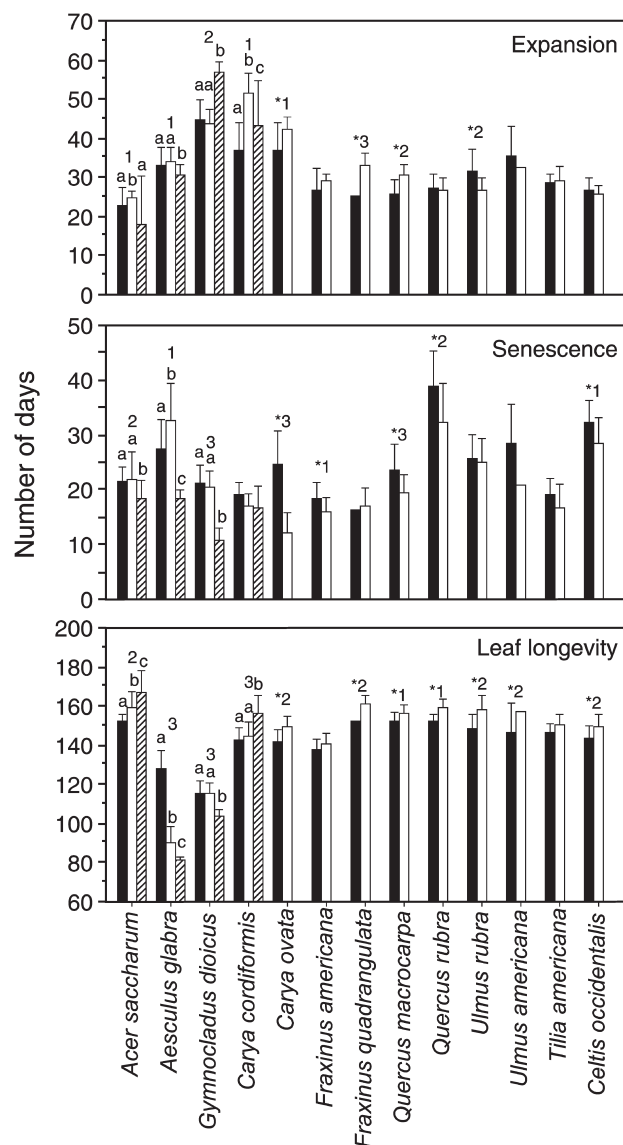


Figure 2. Comparisons among canopy (solid bars), subcanopy (open bars) and sapling individuals (hatched bars) for each of the 13 species during three phenological phases. Note different vertical scales between panels. Different lowercase letters above bars for a given species indicate significant differences ( $P < 0.05$ ) in species for which three life stages were studied; asterisks indicate differences for which two life stages were studied. Numbers above bars indicate the number of years in which there were significant differences between stages.

viduals significantly exceeded that of canopy individuals in five species by an average of 5 days, whereas expansion duration was similar in canopy and subcanopy individuals of seven species. In contrast, for the autumn events, no significant differences between life stages were observed for senescence in 10 species and for leaf drop in nine species. Senescence duration of canopy individuals significantly exceeded that of subcanopy individuals in five species by an average of 6 days, whereas senescence duration did not differ in seven species.

Leaf longevity did not differ between life stages in four species, and was less for subcanopy individuals than for canopy

individuals in one species; however, in eight species, leaf longevity was significantly greater, by an average of 7 days (range = 4–10 days), for subcanopy individuals than for canopy individuals (Figure 2, Table 1). For these eight species, subcanopy individuals achieved greater leaf longevity by having earlier leaf expansion (six species), later senescence (one species), or both (one species), relative to canopy individuals (Table 2). Only in *Aesculus glabra* was leaf longevity less, by a mean of 38 days, for subcanopy individuals than for canopy individuals, largely because of much earlier leaf senescence in subcanopy individuals (Figure 2, Table 2).

#### Comparisons of sapling, subcanopy and canopy individuals

Analyses restricted to the four species with saplings revealed fewer consistent patterns in leaf phenology between life stages. In general, for the four events, saplings tended to differ more from canopy individuals than from subcanopy individuals (Figure 1, Table 1). Saplings tended to have shorter leaf expansion and senescence durations than subcanopy individuals. In two species, leaf longevity was less for saplings than for canopy and subcanopy trees, but was less for canopy and subcanopy trees than for saplings in two other species (Figure 2, Table 1).

Interspecific comparisons illustrated wide variation in phenological patterns in the community (Figures 1 and 2, Table 1). In *Acer saccharum*, life stages showed little difference in bud break and leaf expansion, but senescence and leaf drop occurred earlier in canopy trees. Consequently, saplings and subcanopy trees of *A. saccharum* had significantly greater leaf longevity than canopy trees. In *Carya cordiformis*, canopy trees, despite their later bud break, accelerated development so their expansion duration was shorter than other ontogenetic stages. Among life stages of *Gymnocladus dioica*, saplings had the earliest bud break but prolonged expansion duration and thus the latest leaf expansion. These saplings also had the earliest senescence and shorter senescence duration, and thus shorter leaf longevity than other stages. *Aesculus glabra* had the greatest differences among life stages. Its saplings and subcanopy trees completed leaf expansion earlier than canopy trees by means of 11 and 6 days, respectively. However, leaf senescence in saplings and subcanopy trees in midsummer was a mean of 58 and 44 days earlier, respectively, than in canopy trees. Thus, despite earlier bud break and leaf expansion, the extremely early senescence caused leaf longevity of *Aesculus glabra* saplings and subcanopy trees to be a mean of 47 and 38 days less, respectively, than leaf longevity of canopy trees.

#### Annual variation

In some species, rmANOVA indicated a significant life stage  $\times$  year interaction, indicating that differences between life stages varied among years. For those species with significant differences between stages, Figures 1 and 2 indicate the number of years for which the difference was significant. For the four events as well as the three phases, significant differences occurred on average in 2 out of 3 years.



Table 1. Summary of statistical analyses for each species to determine differences between life stages in calendar date of each phenological event and duration of each phase. Shown are the total number of species with a significant difference ( $P < 0.05$ ) between stages and the direction of the difference as indicated by <, > and = (no significant difference between stages (see Figures 1 and 2)). In parentheses are grand means of the number of days difference between stages. The top three rows refer to comparisons between subcanopy and canopy stages for all 13 species. The remaining rows refer to comparisons among three stages for *Acer saccharum*, *Aesculus glabra*, *Gymnocladus dioica* and *Carya cordiformis*.

Comparison	Bud break begun	Leaf expansion complete	Senescence begun	Leaf drop complete	Expansion duration	Senescence duration	Leaf longevity
Subcanopy < canopy	10 (8)	11 (6)	1 (41)	3 (22)	1 (5)	5 (6)	1 (35)
Subcanopy > canopy	0	0	2 (6)	1 (8)	5 (5)	1 (6)	8 (7)
Subcanopy = canopy	3 (0)	2 (0)	10 (0)	9 (0)	7 (0)	7 (0)	4 (0)
Sapling < canopy	3 (10)	3 (8)	2 (32)	2 (41)	1 (3)	3 (10)	2 (28)
Sapling > canopy	0	1 (5)	2 (8)	2 (2)	2 (10)	0	2 (12)
Sapling = canopy	1 (0)	0	0	0	1 (0)	1 (0)	0
Sapling < subcanopy	1 (8)	2 (4)	2 (10)	3 (16)	3 (4)	3 (8)	2 (10)
Sapling > subcanopy	1 (4)	1 (6)	1 (8)	1 (8)	1 (15)	0	2 (8)
Sapling = subcanopy	2 (0)	1 (0)	1 (0)	0	0	1 (0)	0

#### Gap versus understory comparisons of subcanopy individuals

For *Acer saccharum*, dates of bud break and leaf expansion were significantly earlier for subcanopy individuals in the understory than in gaps (Figure 3). In contrast, senescence was significantly earlier in gaps than in the understory. Dates of leaf drop did not differ significantly between microhabitats. For the first three events, the dates differed significantly among years. For leaf expansion and senescence, there was a significant year  $\times$  microhabitat interaction, indicating that the differences between microhabitats were greater in some years than in others. Year 1, which included a summer drought, showed the greatest difference between microhabitats; leaf senescence was much earlier for individuals in gaps than for individuals in the understory in that year (Figure 3).

For *Acer saccharum*, expansion duration and senescence duration were significantly greater in gaps than in the understory by 3 and 9 days, respectively (Figure 3). In contrast, leaf longevity was significantly greater, by an average of 14 days, in the understory than in gaps. The differences were significantly greater in some years than in others for all three phases, and there were significant microhabitat  $\times$  year interactions for all three phases.

For *Aesculus glabra*, dates of all four events were significantly earlier for subcanopy individuals in the understory than in gaps, markedly so for senescence and leaf drop (Figure 3). Dates differed significantly among years for all four events. For bud break and leaf expansion, there was a significant year  $\times$  microhabitat interaction, indicating that differences between microhabitats were greater in some years than in others. Year 2, in which bud break was earliest, showed the greatest differences between habitats, with both spring events occurring much earlier in the understory than in gaps (Figure 3).

For *Aesculus glabra*, expansion duration did not differ for subcanopy individuals in the two microhabitats (Figure 3). However, senescence duration was significantly greater, by an average of 16 days, in gaps than in the understory. Leaf longevity was significantly greater in gaps by an average of

11 days (Figure 3). These differences were consistent in all three years.

Cumulative degree hours were greater in the understory than in the open area above the barn roof throughout winter and spring 2001 (Figure 4).

Table 2. Summary for each species of whether dates of leaf expansion and senescence differ significantly between subcanopy and canopy trees (see Figure 1). Patterns 1–3 result in greater leaf longevity for subcanopy trees; Pattern 4 results in no difference between stages; and Pattern 5 results in greater leaf longevity for canopy trees. Also given is the number of days by which leaf longevity is greater (+) or less (–) for subcanopy trees than for canopy trees (see Figure 2). Symbols: \* =  $P < 0.05$ ; \*\* =  $P < 0.001$ ; \*\*\* =  $P < 0.0001$ ; and ns = not significant.

Pattern and species	No. days
1. Completion of leaf expansion earlier for subcanopy than canopy	
<i>Celtis occidentalis</i>	+5 *
<i>Quercus macrocarpa</i>	+4 *
<i>Quercus rubra</i>	+7 **
<i>Ulmus americana</i>	+10 **
<i>Ulmus rubra</i>	+9 ***
<i>Fraxinus quadrangulata</i>	+9 **
<i>Fraxinus americana</i>	+3 ns
<i>Tilia americana</i>	+4 ns
<i>Carya cordiformis</i>	+2 ns
2. Start of senescence later for subcanopy than canopy	
<i>Acer saccharum</i>	+7 *
3. Patterns 1 + 2	
<i>Carya ovata</i>	+7 **
4. Both expansion and senescence equal for subcanopy and canopy	
<i>Gymnocladus dioica</i>	–1 ns
5. Both expansion and senescence earlier for subcanopy than canopy	
<i>Aesculus glabra</i>	–38 ***

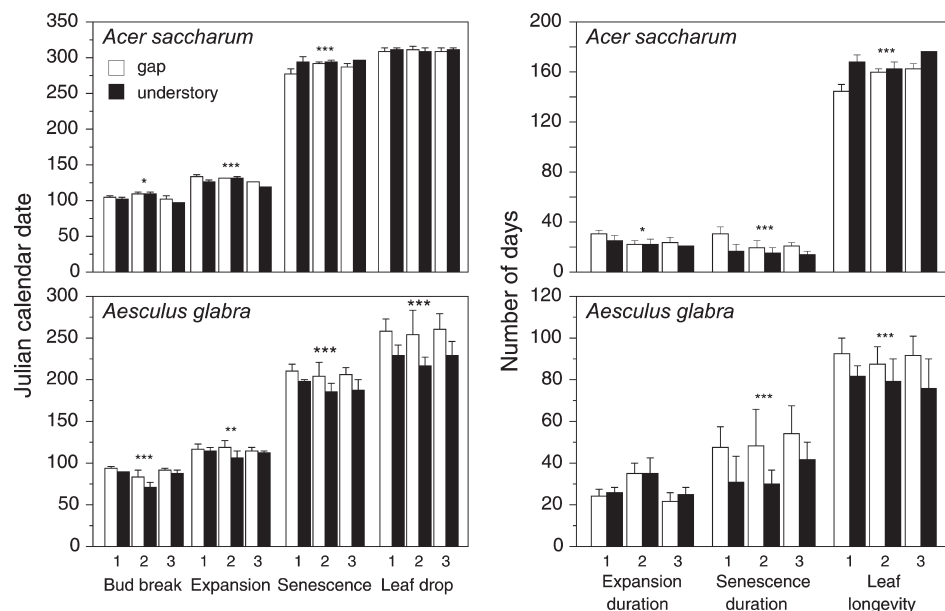


Figure 3. Comparisons between subcanopy individuals of *Acer saccharum* and *Aesculus glabra* in the understory versus gap microhabitats for four phenological events and three phases in each of 3 years. Means + 1 SD are shown. Stars indicate significant differences between microhabitats. Symbols: \* =  $P < 0.05$ ; \*\* =  $P < 0.001$ ; and \*\*\* =  $P < 0.0001$ .

## Discussion

In this community-wide comparative study, all species displayed differences between life stages in some aspect of their leaf phenology. Species varied in which phenological event differed and whether spring or autumnal phenology differed more. Differences were most evident in spring phenology when subcanopy trees of almost all species displayed some avoidance of canopy shade. Subcanopy trees underwent spring events a mean of 1 week earlier than conspecific canopy trees. In contrast, autumnal phenology differed between life stages

in only a few species. Only *Acer saccharum* and *Carya ovata* had subcanopy trees with autumnal phenology that was later than that of canopy trees, and the lag was about 1 week.

Almost all species had slight differences between life stages in duration of phenological phases. Most importantly, leaf longevity was greater, by a mean of 7 days, for subcanopy trees than for canopy trees in eight species. Greater leaf longevity in subcanopy trees was accrued most commonly through earlier leaf expansion, not later senescence, than canopy trees.

When comparisons included the smaller saplings, the patterns were less conclusive. In general, leaf phenology of saplings tended to be more similar to that of subcanopy trees than that of canopy trees. Leaf longevity of saplings relative to canopy trees varied among species, being less in two species and greater in two other species. Similarly, Seiwa (1999a, 1999b) found that seedlings of two temperate deciduous species had greater leaf longevity than conspecific adults.

The phenological differences between life stages in this temperate forest paralleled those of the same species or genera in other temperate forests. *Acer saccharum* in Illinois (this study) and New Hampshire, USA (Gill et al. 1998) are similar, with greater leaf longevity in saplings than in adults, primarily because of their later senescence and leaf drop. Likewise, *Ulmus* spp. in Illinois (this study) and a congeneric species in Japan (Seiwa 1999b) are similar, with earlier leaf emergence and greater leaf longevity in saplings than in adults. Juveniles of *Aesculus glabra* in Illinois (this study) and adults of *Aesculus sylvatica* Bartr. (Georgia buckeye), an understory tree in oak-hickory forests, display the same early senescence (dePamphilis and Neufeld 1989). They are similar to herbaceous spring ephemerals, limiting their carbon gain to a few months in spring and early summer (dePamphilis and Neufeld 1989). These similarities among congeners may be explained by their shared evolutionary or phylogenetic history. Four pairs of congeners were included in this study of 13 species.

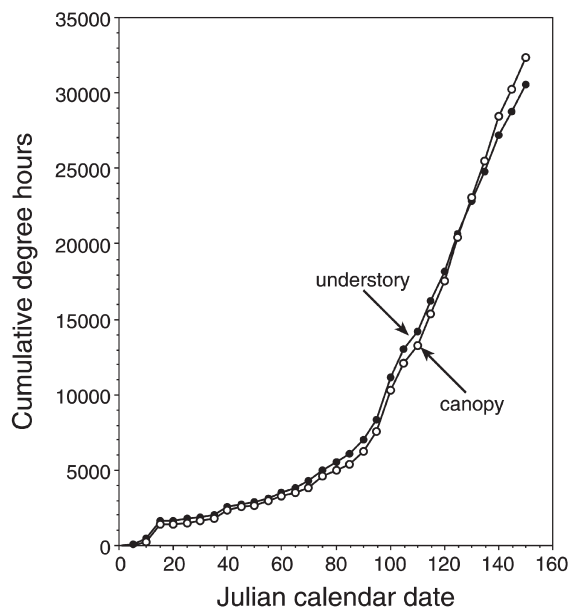


Figure 4. Cumulative degree hours from January to May 2001 in the understory and in the canopy above a barn roof adjacent to the study forest.

Each congeneric pair generally had the same pattern of differences between life stages and congeners in other locations display the same qualitative patterns. In contrast, Lei and Lechowicz (1990) found that *Acer saccharum* juveniles are more similar to conspecific adults in their leaf physiology and morphology than to congeneric understory species.

The extent of phenological avoidance of canopy shade by juveniles in our study was relatively limited. Likewise, four species of understory treelets and shrubs display a limited amount of spring phenological avoidance in the same study forest (C. Augspurger, unpublished data). In comparison, phenological differences between understory herb species and canopy tree species in this study forest are much greater (C. Augspurger, unpublished data). Almost all herb species display at least some phenological avoidance of canopy shade, markedly so in some species.

Subcanopy individuals also demonstrated phenological plasticity in response to their microhabitat. As predicted, the phenology of subcanopy trees in gap conditions was more similar to that of canopy trees than that of understory subcanopy trees, particularly for *Aesculus glabra*. *Acer saccharum* and *Aesculus glabra* were dissimilar in both microhabitat responses and differences between life stages. Their phenological responses to microhabitat differed for senescence, leaf drop, expansion duration and leaf longevity, but were similar for bud break, leaf expansion and senescence duration. In contrast, congeneric species may be more similar. Juveniles of six species of *Quercus* had earlier bud break and leaf appearance under canopy than in sunny clearcuts (McGee 1986). Likewise, comparisons of juveniles of two congeners, *Acer mono* in Japan (Seiwa 1999a) and *Acer saccharum* (this study), revealed similarities, i.e., longer expansion duration, earlier leaf drop and shorter leaf longevity in gaps than in the understory; they differed only in leaf expansion.

Whether earlier bud break and leaf expansion by subcanopy trees is adaptive depends on the relative costs and benefits (Lockhardt 1983). Advantages of early spring events for juveniles include increased light availability and carbon gain (Gill et al. 1998) and decreased damage by herbivores and pathogens (Seiwa 1998). A disadvantage is a greater risk of frost damage to leaves (Cannell and Smith 1986, Sakai and Larcher 1987, Hänninen 1991, Kramer 1994). Although the leafless canopy trees may partially protect understory individuals from radiation cooling and frost (see below), the lower temperatures of early spring may also limit photosynthetic activity. However, studies of subcanopy trees of *Aesculus glabra* and *Acer saccharum* in this forest indicate that their net photosynthesis peaks during leaf expansion in spring and declines steadily thereafter (C. Augspurger, unpublished data).

Although few, relative to the length of the growing season, the extra days in the high light of spring for juveniles in the understory may contribute a large proportion of their carbon gain. Previous studies of deciduous tree species have demonstrated that juveniles gain a substantial amount of annual carbon (Gill et al. 1998) and growth (Jones and Sharitz 1989, Seiwa 1998) prior to leaf emergence of canopy species. Harrington et al. (1989) found that early leaf emergence was more

important than late senescence for carbon gain in four shrubs in a deciduous forest. However, low temperatures in both early spring and late fall limited photosynthetic rates. Adults of *Juniperus virginiana* L., an understory evergreen tree in a deciduous forest, had highest photosynthetic rates in spring, and high autumnal photosynthetic rates as well (Lassoie et al. 1983). This evergreen species adjusts only its physiology, not its phenology.

We did not investigate proximate reasons for the observed differences. Both genetic controls (Billington and Pelham 1991, El-Kassaby and Park 1993, Li and Adams 1993) and environmental influences (Murray et al. 1989, Beuker 1994, Kramer 1995, Partanen 1998, Chuine et al. 2000) affect phenology, but their interaction at different life stages and in different microhabitats is largely unknown. A direct test of the role of genetic versus environmental control requires that juveniles be placed experimentally in the canopy environment and compared with understory juveniles.

Several of our results point to the importance of temperature differences in explaining the results. First, the patterns were consistent, on average, in only two of three study years. Annual variation in temperature may interact with intrinsic mechanisms, causing the differences between life stages to vary among years. Second, juveniles growing in different microhabitats had different responses, indicating an environmentally induced response. Similarly, McGee (1976) found that bud break of *Quercus* saplings was earlier for plants transplanted to shade than for plants left in the sun. Third, a thermal gradient exists in the forest. Thermal degree hours in spring accumulated at a greater rate in the understory than on the barn roof. The barn site was too low to fully mimic the canopy. The temperature gradient would likely be even greater from understory to canopy. More detailed micrometeorological studies of forests confirm that night temperatures are lower at canopy height than at ground level (Lee 1978, Eliás et al. 1989, Larcher 1995). This temperature gradient appears to be the phenological cue, and hence phenology occurred sooner for juveniles than for adult trees. Therefore, the phenological differences appear to be a consequence of a temperature cue that differs among years, between gap and understory microhabitats, and between understory and canopy locations. The limited differences observed between life stages may simply reflect the relatively small differences in temperature along the vertical gradient in this forest.

Wood anatomy may be one alternative, intrinsic mechanism creating phenological differences between life stages. Ring-porous species must repair xylem vessels in spring, and generally have later leaf emergence than diffuse-porous species (Lechowicz 1984, Wang et al. 1992). Extending this argument, the extent of and time to complete hydraulic repair may be less for short subcanopy trees than for tall canopy trees. However, an analysis of wood anatomy of the current study species yielded no pattern. Early leaf expansion of subcanopy trees occurred in both ring-porous and diffuse-porous species.

Phenological differences may also result from the relative ability of juveniles versus adults to synchronize phenology among modules (branches). Subcanopy trees with fewer

branches may synchronize their phenology more readily than canopy trees. Crowns of canopy trees of many species are asynchronous in their phenology, advancing either from top to bottom or vice versa (C. Augspurger, unpublished observations). This asynchrony does not occur as extensively in subcanopy trees. Alternatively, observation of canopy phenology is less precise than observation of understory phenology and this may contribute, in part, to the observed differences.

In contrast to spring phenology, the general lack of differences in autumnal phenology among life stages may be associated with little to no difference in cues between the understory and canopy environments. Differences in autumnal phenology between life stages would be less if these species respond more to photoperiod alone or to photoperiod and temperature in the fall than in the spring, because subcanopy and canopy trees would experience such cues more equally. However, autumn events of subcanopy trees showed much phenological plasticity in the gap versus understory observations. Models involving cues to explain senescence are not as well developed as for spring events (Halverson et al. 1986, Hänninen et al. 1990).

From an adaptive viewpoint, earlier leaf expansion would increase light availability and potential carbon gain more than later leaf senescence because of lower solar elevation, shorter day length and lower temperatures in autumn, relative to the time of spring canopy closure. Also, seasonal changes in physiology must be considered. For example, older leaves have lower photosynthetic capacity than young leaves (Gill et al. 1998, Bond 2000). Furthermore, for juveniles to benefit from late senescence, they would have to delay senescence until after canopy leaf drop because senescing leaves of canopy trees still cast shade.

This community-wide study demonstrates that phenological avoidance facilitates greater light acquisition and the potential for greater net carbon gain for juveniles of most species. However, these comparisons between juveniles and conspecific adults did not directly evaluate the full extent of light gained by juveniles by phenological avoidance because juveniles are frequently in the shade of a non-conspecific adult. Thus, conspecific comparisons do not fully elucidate the amount of light gained by phenological avoidance. Such an evaluation requires a comparison for subcanopy trees with canopy closure achieved by the community as a whole, based on the relative phenology and canopy cover of each tree species. A community-wide preliminary analysis demonstrated that juveniles of most species had longer periods of high light in the spring than the limited amount demonstrated in the current study of life stage differences (C. Augspurger, unpublished data).

Additional studies are needed in this forest to quantify the full extent of gain in light acquisition, to determine experimentally whether growth and survival of juveniles are enhanced by spring phenological avoidance, and to determine whether the differences between life stages are controlled by genetics or the environment. In addition, attention should be given to the amount of carbon gain achieved by phenological avoidance of canopy shade in the spring and by sunflecks during canopy shade in summer months.

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