

Living long by staying small: stem layering as an adaptive life-history trait in shade-tolerant tree seedlings

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Abstract: Suppressed seedling banks are important in replacement dynamics in late-successional forests. However, demographic properties of seedling populations are poorly known, and there has been little attention to traits that might affect fitness in suppressed seedlings. *Acer saccharum* Marsh., a shade-tolerant dominant in eastern North American forests, frequently develops adventitious roots along prostrate portions of stems (“layering”). Measurements of *Acer* seedlings in old-growth forests in Michigan indicate that layered seedlings proportionally reduce structural allocations to older layered stem tissues, retain leaf area/height ratios of younger unlayered seedlings, and tend to survive longer. In tree seedlings, allometric consequences of normal stem growth lead to declining ratios of photosynthetic to nonphotosynthetic biomass, which potentially reduces shade tolerance and limiting age. The layering habit may defer this penalty by changing the allometry of growth. Resulting increases in life expectancy should increase chance of access to increased light and of reaching the canopy. Thus, because flowering is generally restricted to canopy trees, the tendency to layer may increase fitness. Properties of individuals in suppressed seedling banks may be selectively and ecologically important, shaping life histories and population dynamics.

Résumé : Les banques de semis opprimés sont importantes pour la dynamique de remplacement des forêts en fin de succession. Cependant, les propriétés démographiques des populations de semis sont peu connues et peu d’attention a été accordée aux caractéristiques qui pourraient affecter la valeur sélective des semis opprimés. *Acer saccharum* Marsh., une espèce tolérante à l’ombre qui domine les forêts de l’est de l’Amérique du Nord, produit souvent des racines adventives le long des portions procombantes de la tige (marcottage). Des mesures prises sur des semis d’*Acer* dans des forêts anciennes du Michigan montrent que les marcottes maintiennent un rapport entre la surface foliaire et la hauteur semblable à celui de plus jeunes semis non issus de marcotte et tendent à survivre plus longtemps. Les mesures indiquent aussi que les marcottes réduisent proportionnellement leur allocation à la structure des plus vieux tissus de la tige des marcottes. Pour les semis d’arbre, les conséquences allométriques de la croissance normale de la tige mènent à une diminution du rapport entre la biomasse photosynthétique et la biomasse non photosynthétique, ce qui réduit peut-être leur tolérance à l’ombre et limite leur probabilité de survie. Le marcottage peut reporter cette pénalité en modifiant l’allométrie de la croissance. L’augmentation de l’espérance de vie des marcottes qui s’ensuit devrait augmenter leurs chances d’accéder à de meilleures conditions de lumière et d’atteindre la canopée. Puisque la floraison est généralement restreinte aux arbres formant la canopée, la tendance à marcotter peut donc augmenter leur la valeur sélective. Les propriétés des individus dans les banques de semis opprimés peuvent être importantes des points de vue de la sélection naturelle et de l’écologie en modélant le cycle biologique et la dynamique des populations.

[Traduit par la Rédaction]

Introduction

Forest understories typically feature abundant suppressed seedlings of shade-tolerant trees. In these light-limited environments (Finzi and Canham 2000), such “seedling banks” can be important in allowing shade-tolerant species to establish and maintain dominance (Grime 1979; Morin and Laprise 1997; Messier et al. 1999). Well-established seedlings already in place when a canopy gap is created should have an advantage in capturing the light resource thus liberated. Shade tolerance appears to be closely related to a variety of life-history traits involving trade-offs between whole-plant

respiration and potential carbon gain and between resource allocation to photosynthetic and nonphotosynthetic biomass (Chazdon 1986; Walters and Reich 2000).

In particular, persistence of suppressed seedlings may be constrained, in part, by declining ratios of photosynthetic to woody nonphotosynthetic tissue (or leaf area to biomass) imposed by allometric constraints as seedlings grow (Chazdon 1986; Cannell and Dewar 1994; Waring 1987; Givnish 1988; Gerrish 1990; Roberts et al. 1993; Kohyama 1983; Kubota and Hara 1996). This implies a decline in shade tolerance with increasing size and, in persistently light-limited environments, consequent increasing mortality risk (Lusk 2002). Messier et al. (1999) suggest species-specific “maximum sustainable heights” under suppression (see also Messier and Nikinmaa 2000; Antos et al. 2000, 2005). Consistent with this notion, shifts in allocation patterns under suppression may favor light interception over stem growth (Chazdon 1986; Beaudet and Messier 1998;

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King 1997; Klinka et al. 1992). Kobe (1997) suggests that shifts in carbohydrate allocation from growth to storage may enhance survival at low light both by slowing increases in respiratory load and by providing a buffer against stress.

In cool-temperate forests of eastern North America, several species are capable of maintaining seedling banks, including *Fagus grandifolia* Ehrh., *Tsuga canadensis* (L.) Carrière, and *Acer saccharum* Marsh. among canopy dominants. Species that are present only in subcanopy strata, including *Abies balsamea* (L.) Mill. (a canopy species in other forests, but limited to the subcanopy here), *Ostrya virginiana* (Mill.) K. Koch., and *Acer pensylvanicum* L., are also represented in the seedling bank.

For mature, mesic forests in the study area, estimated intervals between canopy-gap occurrences at a given point range from 50 to 100 years (Seymour et al. 2002; Frelich and Lorimer 1991), which is longer than expected lifespans of continuously suppressed seedlings for most species. Because flowering in most canopy species is restricted to individuals that have reached canopy status, most suppressed seedlings will never reproduce. Any trait prolonging expected survival in the understory would increase the probability of experiencing elevated light levels in a canopy gap and the chance of reaching reproductive maturity, thus conferring increased fitness. By this reasoning, selection should act strongly on demographic and life-history properties influencing survival in suppressed condition. This is consistent with suggestions that survival at low light is more critical in effective shade tolerance than is low-light growth rate (e.g., Pacala et al. 1994; Kobe et al. 1995).

However, there have been few demographic studies of suppressed seedlings, particularly in late-successional forests. For the logic just proposed to apply, suppressed seedlings must have at least the potential for relatively long-term persistence under suppression. Antos et al. (2000, 2005) document suppressed seedlings of several species of western American conifers frequently reaching ages of several decades. However, in some apparent seedling banks, this may not be the case. Szwagrzyk et al. (2001) show that *Fagus sylvatica* L. in Poland rarely survives as long as 4 years without relatively high light availability; Alvarez-Aquino and Williams-Linera (2002) found very high mortality of *Fagus grandifolia* var. *mexicana* (Martinez) Little in the first 2 years after germination. On the other hand, *A. saccharum* can maintain extensive carpets of seedlings that can persist for several decades (Marks and Gardescu 1998), suggesting the potential for selection to act on life-history properties expressed in suppressed seedlings.

Suppressed seedlings of *A. saccharum* freely form adventitious roots along prostrate stem sections buried by leaf-litter (“layering”). Even though this species is an extensively studied canopy dominant, this habit has been documented previously only in successional stands in New Brunswick (Fayle 1964, 1965). Layering is probably initiated when young seedlings are bent to the forest floor by falling debris, leaf litter, or snow (Fayle 1965; unpublished observations) and continues through repeated prostration of flexible new growth in subsequent years. Layering can extend up to 100 cm, and layered sections of stem are sometimes longer than the erect, leaf-bearing portions (personal observation).

Adventitious rooting of buried stems has been observed in several shade-tolerant conifer species, including *Abies balsamea* in northeastern North America (Parent et al. 2000, 2002, 2003), *Picea mariana* (Mill.) BSP in the same forests (DesRochers and Gagnon 1997), *Abies* spp. in Japan (Kohyama 1983), and *Chamaecyparis pisifera* Sieb. & Zucc. in mixed conifer–hardwood forests in Japan (Hayakawa et al. 2004). However, in most of these cases, stems are apparently buried by increasing depth of forest floor rather than through bending of erect stems.

If adventitious roots along younger sections of layered stems in *A. saccharum* contribute substantially to the support of seedling growth, allocation of photosynthate to growth and maintenance of older portions of layered stem could be reduced. Such reductions could result in lower living stem biomass for layered stems compared with unlayered stems of similar age or overall size. Resulting reduction of respiratory load of nonphotosynthetic tissues and higher effective leaf area/plant biomass ratio may allow increased growth rates or accumulation of reserves. If layered portions of stems are partially or completely physiologically abandoned, seedlings may grow older without getting larger and so retain high shade tolerance. Such changes in resource allocation, with similar implied consequences, have been suggested in *Abies balsamea* by missing growth rings and “reverse taper” of layered sections of stems (Parent et al. 2000, 2002, 2003, 2006); this dynamic would complement the shift, noted by Beaudet and Messier (1998), towards higher leaf area/stem length ratios in shade. If genets can increase survivorship under suppression by layering, the capacity (or predisposition) to layer should contribute positively to fitness and be selectively favored.

In this paper, I explore whether layering of stems in *A. saccharum* functions as an adaptive trait in this manner. Specifically, I predict that, if stem-layering is adaptive (i) older, layered portions of stems should show evidence, in the form of reduced growth, of reduced allocation of carbon; (ii) aboveground portions of layered stems should have allometric relationships (ratios of leaf area to plant biomass or photosynthetic to nonphotosynthetic tissues) similar to those for unlayered stems of similar aboveground size; (iii) among seedlings with similar total stem length, those with layered stems should show greater investment in height or diameter growth because of reduced resource allocation to layered stem portion; (iv) layered seedlings should attain greater age, and older suppressed seedlings should be more likely to be layered; and (v) layered seedlings should have the capacity to respond to release. Results reported in the following support, at least in substantial part, all of these conjectures.

Methods

Study site

Research reported here was conducted in old-growth hemlock–hardwood forests at the Huron Mountains in Marquette County, Michigan (46°53'N, 87°54'W), on private lands of the Huron Mountain Club, under the auspices of the Huron Mountain Wildlife Foundation. Two stands were sampled, both >300 years old and dominated by *A. saccharum* with some representation of *Tsuga canadensis*, *Tilia americana*

L., and *Betula alleghaniensis* Britt. (described in Woods 2000). Suppressed *Acer* seedlings were abundant throughout study sites, frequently attaining cover approaching 100%. One sampled stand was on deep sandy loams derived from alluvial deposits, and the other was on gravelly loams derived from shallow glacial till over granitic bedrock. All soils were moderately acidic (pH 5.2–6.2). All analyses were conducted separately for the two stands, but there were no differences in results; results reported here are from pooled samples.

Data collection

In July 2002, we collected all seedlings, including larger roots, with taproot in sixty 1 m × 0.5 m quadrats, placed at uniform distance in the four cardinal directions from centers of permanent monitoring plots in old-growth hemlock–northern hardwood forests (Woods 2000). New germinants of 2002 were not incorporated in analyses reported here, leaving 741 seedlings of *A. saccharum* (“2002 data set”).

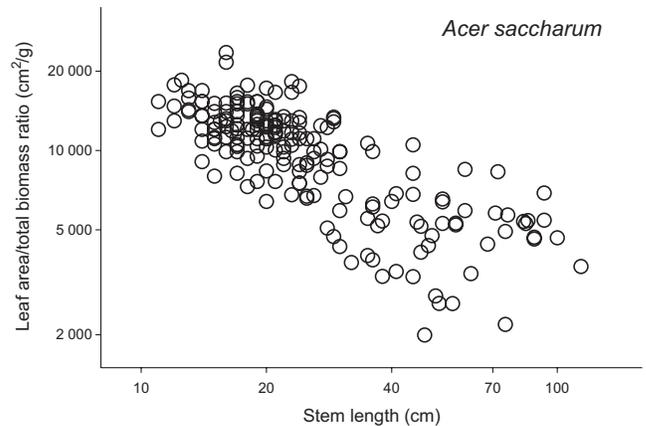
Measurements on each seedling included (i) length of stem axis from original taproot (root–shoot boundary) to terminal bud on longest shoot; (ii) length of layered portion of stem from root–shoot boundary to highest (most distant) adventitious root; (iii) diameter at root–shoot boundary and at highest adventitious root; (iv) air-dried foliage mass (dried to constant mass at room temperature); (v) air-dried mass of woody tissue including large roots; and (vi) estimated age, using terminal bud-scar count where possible and growth-ring count at root–shoot boundary (on stem sections, polished and examined at 50–100× magnification). For 22 stems with unbranched layered portions longer than 20 cm, growth rings were counted at the base of the aerial (unlayered) portion of stem.

Several complications apply in interpretation of some of these measurements. Many shoots had been heavily browsed by deer, affecting stem-length measurements. Age estimates must be treated as minimum age estimates. Terminal bud-scar counts are reliable only to approximately 10 years for *A. saccharum* and only when stems are undamaged. Growth rings in suppressed seedlings are extremely difficult to count, and “missing rings” may be frequent (see results and Parent et al. 2000, 2002). For some very small seedlings, leaf and stem dry masses were too small for accurate measurement with instruments available in the field (<0.05 g). The potential biases introduced by these problems would all tend to counter the trends observed.

We randomly subsampled one-fifth of the seedlings from the 2002 data set for measurement of (i) leaf area (leaves were scanned, and area was calculated using SigmaScan Pro version 5.0; Systat Software, Inc., San Jose, California); (ii) oven-dried foliage mass (dried at ca. 90 °C to constant mass); and (iii) oven-dried mass of woody tissue separated into roots, layered stem and adventitious roots, and above-ground tissues.

In 2004, we collected an additional sample of all seedlings rooted in twelve 1 m² quadrats placed at regular intervals along a line transect through the same stand ($n = 238$ seedlings). For these seedlings, we measured stem and layer lengths and diameters, as for the 2002 data set, along with extension growth of dominant (longest) axis for the previous two growing seasons, as identified from terminal bud scars.

Fig. 1. Changes in the ratio of leaf area to total biomass with seedling size (indicated by stem length) for unlayered seedlings (seedlings lacking adventitious stem roots). Log–log transformation produces a linear relationship (slope = -8.4 , $r^2 = 0.59$, and $n = 197$). The figure includes only seedlings with leaf biomass >0.1 g.



About 2% of sample stems were so severely browsed that no stem had two seasonal increments intact; these were discarded.

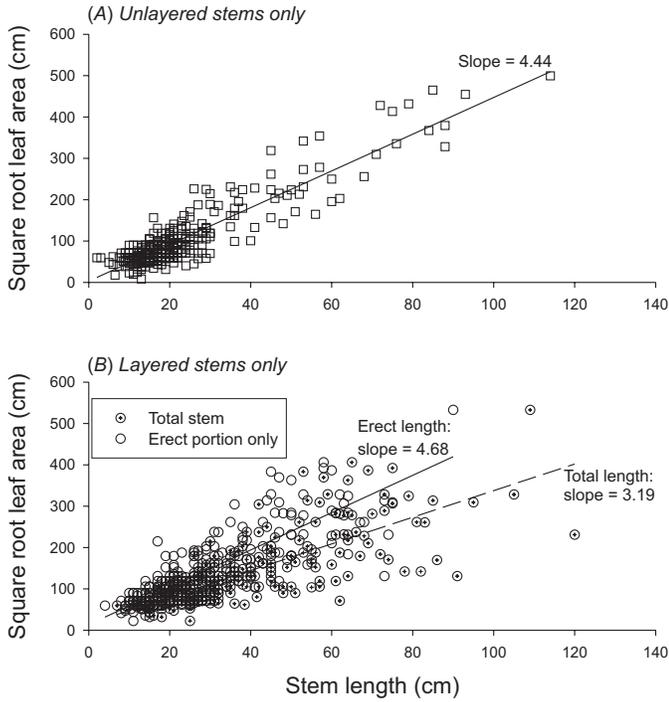
Results

Allometric relationships

As predicted by general allocation theory, the ratio of leaf area to total biomass for unlayered stems decreased with size of stem as measured by basal diameter or stem length (Fig. 1). The observed distribution for unlayered stems suggests that this ratio may become debilitatingly small as stems approach 100 cm length. For unlayered stems, leaf area (square-root transformed) was well predicted as a linear function of stem length (Fig. 2). Slopes were indistinguishable when unlayered stems were compared with the aerial (unlayered) portion of layered stems. However, when total stem length was considered, longer layered stems (which also had greater mean lengths of buried stem, Table 1) supported smaller leaf area than unlayered stems of similar total stem length.

Aerial stem lengths rarely exceeded approximately 75 cm; longer stems tended to have increasing proportions of the stem prostrate and layered (Table 1). For aerial stems, “apparent” basal diameter was well predicted as a linear function of stem length, and relationships were similar for unlayered stems and aerial portions of stems with significant layering (ANCOVA for diameter aerial section in millimetres, aerial length in centimetres as covariate, group (layered >15 cm, unlayered) as categorical variable, with length × group interaction: only length effect significant, $p < 0.01$. Pooled regression aerial diameter on aerial length: slope = 0.11, and $r^2 = 0.68$). However, the “true” basal diameter at the root–shoot boundary of layered stems increased at a lower rate with total stem length (ANCOVA, similar design: length and interaction effects significant $p < 0.01$; group effect $p = 0.06$. Regression slope for unlayered stems was 0.13 and the regression slope for stems with >15 cm layered length was 0.03). These results indicate proportionally slower diameter growth and lower allocation

Fig. 2. Changes in leaf area (square-root transformed) with stem length. Slopes for unlayered stems (A) and aerial portions of layered stems (B) are not different (ANCOVA for square-root leaf area with stem length as covariate, group (unlayered or layered) as categorical variable, and length \times group interaction: no effects significant). Slope is lower for layered stems when regression is on total stem length (B) (ANCOVA, $p = 0.04$ for group effect and $p < 0.001$ for interaction). Unlayered stems: slope = 4.44, $r^2 = 0.83$, and $n = 45$. Layered stems, aerial portion: slope = 4.68, $r^2 = 0.72$, and $n = 256$. Layered stems, total length: slope = 3.19, $r^2 = 0.59$, and $n = 256$.



to wood production in lower portions of layered stems. Layered sections of stems frequently had reverse taper, with larger diameter at the younger base of the aerial portion of the shoot than at the older root–shoot boundary. This pattern became more pronounced with greater layered length; for stems with layer length >15 cm, mean difference between the basal (root–shoot) diameter and diameter at base of aerial shoot was negative; in some cases, the original taproot was lacking, having decayed, leaving the seedling entirely dependent on adventitious roots.

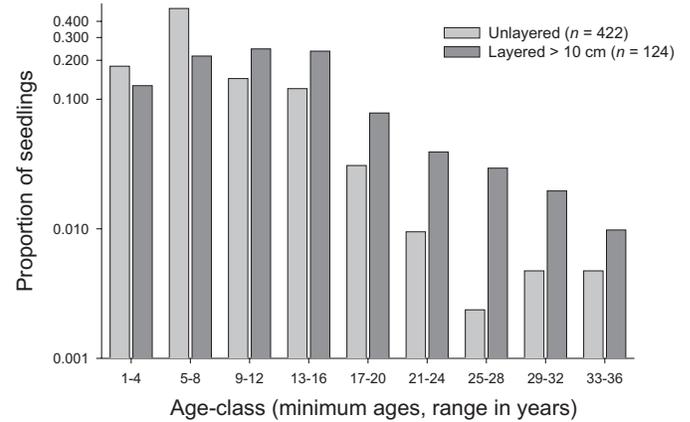
Age, growth, and survival

Growth rings can be missing or unrecognizable in suppressed *Acer* seedlings. Only 39 stems could be aged reliably from terminal bud scars; scars are clear for only 10–12 years, and a large proportion of stems had been damaged and lacked a continuous main axis. However, among these stems, bud-scar counts were always higher than ring counts for the 21 cases where the two age estimates differed (most differences were 1 or 2 years). For 44 stems with layered length >15 cm, rings were counted both at the root–shoot boundary and just above the highest adventitious root. Even though the oldest portion of the stem is necessarily at the root–shoot boundary or “true base,” apparent age at the base aerial stem was >2 years older than that at the true base for 11 stems (maximum difference = 8 years). Counts differed by <2 years for 14 stems. Only 19 had ring counts

Table 1. Layering in maple seedlings, summary statistics (2002 and 2004 data pooled; $n = 973$).

Total stem length (cm)	No. of stems	Proportion layered	Mean layer length (cm)
<20	388	0.14	4.2
20–30	246	0.41	6.1
30–40	99	0.66	9.4
40–50	63	0.79	11.1
50–60	56	0.80	14.6
60–70	55	0.84	18.9
70–80	28	0.71	23.2
80–90	19	0.79	24.9
90–100	11	0.91	20.9
>100	18	0.94	33.5

Fig. 3. Age distributions for seedlings with >10 cm layered stem and unlayered seedlings. Layered seedlings were significantly older (Kolmogorov–Smirnov test, $p < 0.001$). Proportions of layered stems are higher for older age-classes. Age estimates are conservative, particularly for layered stems.



at the true base more than two greater than counts at base of aerial stem (maximum difference = 9 years). Basal ring counts averaged 18 (range 14–33).

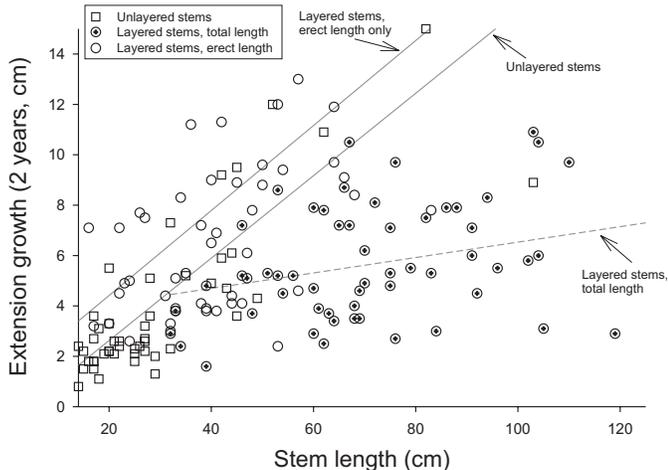
Apparent age distributions for layered stems (layer length >10 cm) were biased toward older age-classes as compared with unlayered stems (Fig. 3); in fact, because of systematic and increasing underestimation of age for layered stems, the difference in age distributions was probably greater than indicated. Only 2% of unlayered stems exceeded 20 years estimated age, whereas 12% of stems with >10 cm layering were >20 years old.

Extension growth rate (2004 data) increased with either diameter or length for both layered and unlayered stems (Fig. 4). Considering total length including layered portion, layered stems showed lower growth rates, especially for greater stem lengths. However, when only aerial portions of layered stems were considered, layered stems grew faster than unlayered stems of similar aerial length, even though slopes of growth–stem length relationships were the same.

Discussion

Findings for *A. saccharum* support the notion that adventitious rooting of buried stems allows seedlings to shift resource

Fig. 4. Changes in extension growth with stem length for layered and unlayered stems. Growth rates for layered stems of a given aerial length were greater than growth rates for unlayered stems of equivalent length, but slopes of relationship were similar (ANCOVA of growth rate, stem length as covariate, layered or unlayered as category: $p = 0.03$ for main effect of class (intercept) and $p = 0.45$ for interaction (slope)). Extension growth increases more slowly with full length of layered stems (slopes for unlayered stems and layer stem \times total length differ: ANCOVA, $p = 0.03$ for interaction).



allocation so as to maintain advantageous ratios of photosynthetic to nonphotosynthetic tissues. This should reduce the deleterious consequences of increasing size in light-limited environments, allowing longer persistence of individual shade-suppressed seedlings. If so, it is appropriate to regard the capacity or tendency to layer as an adaptive life-history trait. By allowing stems to remain “physiologically small” layering should increase expected longevity, the chance of a stem’s experiencing release and, consequently, fitness. Each of the initial predictions is substantially borne out.

Seedlings appear to reduce growth allocation to layered portions of stems

Reverse taper in layered portions of stems, frequent missing rings in layered segments, and proportionally slower diameter growth in older portions of layered stems indicate reduced growth allocation to and biomass in older layered stem sections. In a few extensively layered seedlings that were more intensively examined, maximum numbers of rings always occurred closer to the base of the aerial shoot (apparent base) than to the root–shoot boundary. Parent et al. (2000) report as many as 20 missing rings in comparable analyses of *Abies balsamea*. These results are consistent with layered stems imposing reduced respiratory load on the plant as compared with fully erect stems of comparable total length. Older sections of extensively layered stems sometimes appeared to be relatively brittle and, in some instances, decayed; this suggests that, in some cases, portions of layered stems can be completely abandoned.

Upright portions of layered stems are morphologically similar to unlayered stems of similar apparent length

In keeping with general allocation theory and the expectation of decreasing shade tolerance with size, ratios of pho-

tosynthetic to nonphotosynthetic biomass decreased with increasing basal diameter or stem length for unlayered stems (Fig. 1). However, in layered *Acer* seedlings, aerial portions of stems maintain ratios comparable with unlayered seedlings of the same apparent aerial length (Fig. 2). If nonphotosynthetic tissues in part or all of the layered stem receive reduced allocation of resources (relative to aerial stem tissues), this suggests that layered seedlings should be more shade tolerant than unlayered seedlings of comparable total shoot length.

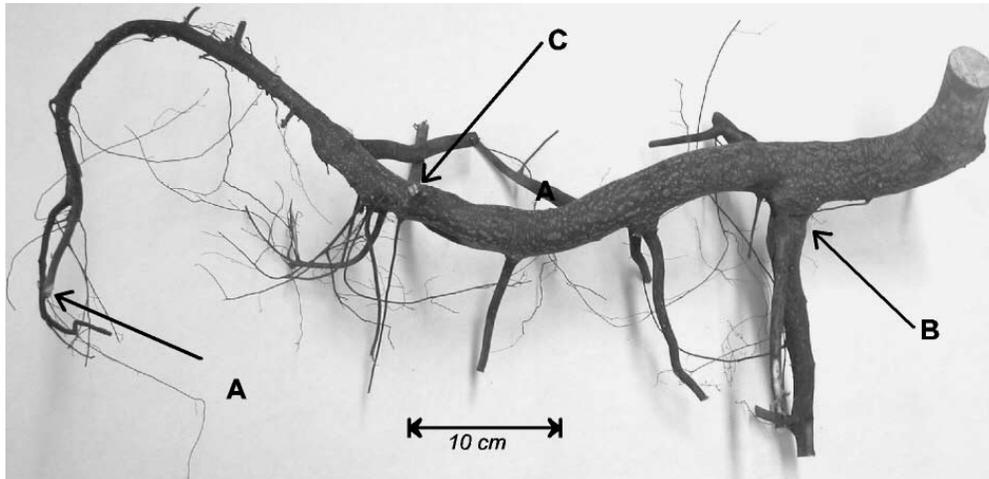
Layering allows seedlings to maintain higher extension growth rates

All classes of *Acer* seedlings showed increasing growth rate with stem length (Fig. 4). If only aerial stem length is considered, growth increased with size at similar rates for unlayered and layered stems. Further, layered stems tended to grow faster than unlayered stems of comparable apparent length by a nearly constant 1.2 cm/year. However, when comparing full shoot length (including layered sections), layered stems >30 cm long grew more slowly than unlayered stems, and the difference increased with size. The similar relationships between aerial length and extension growth for the two classes may further suggest that aboveground structure is the primary determinant of growth and layered portions of stems are of less consequence. However, consistently greater extension growth for layered stems compared with unlayered stems of similar aerial height also suggests that layered portions of stems retain some influence and are not fully abandoned. Layered stems may have more extensive root systems and so are more effective in obtaining water or mineral nutrients. Layered portions of stems may also act as reservoirs for storage of carbohydrates so that layered seedlings are more tolerant of stressful periods (see Kobe 1997). In any case, greater extension growth of layered seedlings is likely to play an important role in the highly competitive light environment of dense seedling carpets and may enhance survival (Walters and Reich 2000).

Layered seedlings are likely to survive to greater age

The apparent differences in age distributions of layered and unlayered seedlings (Fig. 3) are consistent with longer survival for layered seedlings. Observed differences in age distributions could be due to higher survival rates for layered seedlings or to an increased likelihood of layering with age. However, the latter explanation would require that older, larger stems be bent prostrate to initiate layering. This may happen occasionally, but all stems observed developing new layering were small, suggesting that shoots with more than 2 or 3 years growth become too stout to be pressed easily to the ground by leaf litter or snow. If layering is primarily initiated when seedlings are young, greater survival rates of layered stems is the more likely explanation of different age distributions. Systematic underestimation of *Acer* seedling ages does not change this implication; in fact, the underestimates are likely to be greater for layered seedlings, where older sections of stem have ceased growing or have even been lost. True age distributions would likely show even greater divergence. It is not possible to establish maximum ages for layered seedlings from current data, but unlayered seedlings older than ca. 20 years appear to be rel-

Fig. 5. Released saplings in gaps show evidence of layering as seedlings and of abandonment of the layered stem. In this specimen, the base of the aerial stem (3.1 cm diameter) is about 85 cm along the stem from the oldest portion of layered stem (A). (The original seedling tap-root has been lost.) Adventitious roots near the aerial stem base have become dominant (B), and older portions of layered stem have remained small. One additional aerial branch (C), approximately 25 cm tall, arose about halfway along the layered section; before excavation, it appeared to be a separate seedling.



atively rare. Marks and Gardescu (1998) document *A. saccharum* aerial stems persisting >30 years; however, with >80% mortality over 23 years for seedlings present at the beginning of their study; they do not address layering of stems. Hett (1971) shows a maximum age of about 65 years but very low proportions of seedlings more than 10–20 years old. It appears safe to say that very few unlayered stems survive more than 20–30 years under suppression.

Layered seedlings are capable of responding to release

Data from seedling measurements reported above do not directly address the capacity of layered seedlings to respond to release and reach the canopy. However, other observations at the Huron Mountain study site clearly indicate that they can. Groups of released *Acer* saplings up to 10 cm diameter can be found in association with patchy disturbances several decades old. Excavation of 10 haphazardly selected individuals from one such area showed eight to have derived from extensively layered seedlings, and horizontal stem sections are often identifiable without complete excavation. In excavated saplings, sections of buried stem up to 1 m in length showed extreme reverse taper, and the oldest portions of buried stem were often decayed, whereas adventitious roots near the base of the aerial stem had become dominant (Fig. 5). Fayle (1964, 1965) noted similar phenomena in *A. saccharum* in New Brunswick.

These results strongly support the possibility that stem layering can play an important role in promoting longer survival and more vigorous growth of suppressed seedlings of *A. saccharum* and so become an important factor in the chance of a particular individual experiencing release. Results are consistent with the implications of general allocation theory: apparently larger seedlings—those with larger aerial structure—appear to suffer from proportionally larger respiratory load. This may support suggestions of Kobe (1997). Comparisons among species have been cast in terms of more shade-tolerant species minimizing respiratory losses through reduced growth in nonphotosynthetic tissues, as sug-

gested for *A. saccharum* here, by Beaudet and Messier (1998) for several temperate tree species, and by Chazdon (1986) for tropical understory palms, whereas shade-intolerant species maximize whole-plant photosynthetic capacity (Walters and Reich 2000).

Stem layering appears to be one distinct mechanism for managing these trade-offs by allowing physiologically effective size to be at least partially decoupled from seedling age through reduced allocation to older stem sections. Similarly, Parent et al. (2006) suggest that rooting of buried stems in *Abies balsamea* may increase seedling persistence in shade. Layered *Acer* seedlings may be seen as behaving, in effect, like rhizomatous herbs or shrubs. Some *Acer* seedlings with long buried stem sections had multiple aerial shoots, sometimes separated by over 50 cm of buried connecting stem, but current data do not allow assessing whether these shoots have become physiologically independent.

This mechanism amounts to a case of the gearing-down strategy for coping with resource shortage in Grubb's (1998) classification. Beaudet and Messier (1998) noted that carbon gain dynamics in *A. saccharum*, as compared with *F. grandifolia* and *B. alleghaniensis*, seemed inconsistent with the relative shade tolerance and dominance of these species; perhaps the ability to remain physiologically small for long periods contributes to the dominance of *Acer* in the seedling bank and to consequent persistence in the canopy. The layering habit, although thus far documented only in Michigan and New Brunswick, may be common in populations of suppressed *A. saccharum* seedlings in late-successional forests in other areas (personal observations).

Studies of seedling demography and growth form in other shade-tolerant species are few, so it is difficult to assess the generality of related phenomena. As noted, stem layering has been observed in several coniferous species but, apparently, has not been documented for other shade-tolerant angiosperm seedlings, although larger *Fagus* seedlings and saplings can produce root sprouts. Of the few demographic studies of suppressed seedling banks, most have described

relatively low long-term survival of aerial stems (*F. sylvatica*, Szwagrzyk et al. 2001; *A. saccharum*, Marks and Gardescu 1998; *Carpinus* spp., Shibata and Nakashizuka 1995). However, Antos et al. (2000) found substantial proportions of suppressed seedlings of *Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt. in subalpine forests to be over 50 years old; they did not note stem layering.

Other studies have shown changes in growth pattern and allocation under low light so as to slow increase in ratios of nonphotosynthetic to photosynthetic tissues. Several shade-tolerant conifers appear to shift allocation to production of branches and foliage rather than stem extension (Klinka et al. 1992; Parent and Messier 1995; King 1997; Kubota and Hara 1996; Beaudet and Messier 1998); understory palms change leaf morphology (Chazdon 1986). Plasticity in growth response to light may play a further role in facilitation of stem-layering habit. Etiolated growth of leaders in low light may predispose young seedlings to being prostrated by leaf litter, falling debris, or snow; more robust extension growth in response to higher light would make this unlikely and make for more effective competition for light in a canopy gap. Damage to seedlings by falling debris is well documented for tropical forests (e.g., Aide 1987, Clark and Clark 1991, Scariot 2000) but not for temperate forests; layering of prostrated stems may be an opportunistic, adaptive response to some types of debris-fall.

The stem-layering habit may be more common than has been documented, because it appears to foster longer survival under suppression. Because successful fillers of small canopy gaps frequently originate from seedling banks, longer survival in the seedling bank should have high selective value.

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