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Some evidence for an adaptive linkage between leaf phenology and shoot architecture in sapling trees

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Summary

1. We test an expectation regarding the phenology of leafing in sapling trees: that the inclination of the terminal shoot from the vertical in species with a flushing type leaf emergence will be greater than that of species with successive leafing.

2. A large inclination of the terminal shoot will minimize self-shading among leaves that emerge simultaneously; this may be an advantage in maximizing carbon gain. A small inclination leads to more self-shading but allows a sapling to attain a greater height within a shorter period; this may be an advantage in situations where shading by adjacent plants is a greater potential problem than self-shading.

3. We observed that the shoot inclination in Tilia japonica and Quercus crispula, which have a flushing type leaf emergence, was more than 30° in open, sunlit habitat. In contrast, the shoot inclinations of Betula platyphilla var japonica and Alnus hirsuta, which have successive type leaf emergence, were less than 10°. These observations suggest a functional linkage between leaf-emergence pattern and shoot inclination that can be considered adaptive if selection is maximizing carbon gain by the whole shoot over the growing season.

Key-words: Leaf-emergence pattern, self-shading, shoot inclination, tree architecture


Introduction

Broad-leaved trees have certain characteristic patterns of leaf emergence in the spring that prevail in deciduous forests throughout the north temperate zone (Lechowicz 1984). These different patterns of leaf emergence in turn are associated with particular patterns of leaf survival and shoot growth (Kikuzawa 1989). Some species expand their leaves simultaneously as a flush, usually at the onset of the growing season (Kikuzawa 1983, 1989) and in these trees, shoot elongation occurs within a short period after bud-break (e.g. determinate shoot growth; Kozlowski 1971). Other species in the same forests unfold their leaves sequentially over a longer period from spring through summer (Kikuzawa 1983, 1989) and maintain shoot growth over an extended period (indeterminate shoot growth). The former type of leaf and shoot development is termed ‘flushing’ and the latter ‘successive leafing’.

Here we address whether these two extreme leaf-emergence patterns are co-ordinated with shoot angles, although there are many ‘intermediate’ species. Consider the terminal shoot of a sapling with flushing type leaf emergence (Fig. 1a). All the leaves of the shoot unfold at time 0 and are maintained to the end of the growing season (t = T). Compare this to a successive-leafing species (Fig. 1b), where leaves appear one by one at appropriate intervals and all leaves have appeared only at t = T. If there is no self-shading, it is obvious that flushing has an advantage over successive leafing in total seasonal carbon gain because all the leaves on the flushing sapling can utilize the season fully. However, if the light incident upon the leaves (expressed by the size of straight arrow in Fig. 1) decreases largely by self-shading and the photosynthetic capacity of each leaf decreases quickly with aging, then successive leafing will be advantageous over flushing in total amount of photosynthetic gain (expressed by the sum of curved arrows). This advantage occurs because the newly opened leaves can exploit full sunlight and thus can conduct higher photosynthesis in sequence to the benefit of total gains by the shoot over the season. If shoots can avoid self-shading by some morphological traits such as phyllotaxy, leaf shape, or leaf and shoot angles, then flushing will again be advantageous (Fig. 1c). Thus we can expect leaf-emergence patterns to show consistent functional linkages to shoot morphological traits.

Because the effective transparency of a leaf in the canopy can be influenced by the inclination of the leaf itself, we expect that shoot inclinations will be functionally co-ordinated with leaf phenology. This is especially true in more open habitats or large forest gaps where direct beam radiation predominates over
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Fig. 1. Schematic representation of photosynthetic rate influenced by alternative leaf-emergence patterns, the aging of leaves and the degree of self-shading. Straight arrows directed downwards represent the intensity of irradiance and letters to the right of each leaf: the age of the leaf (Y, young; M, medium; O, old). Curved arrows represent the photosynthetic rate which is a function of both the irradiance and the maximum photosynthetic rate determined by the aging of the leaf. (a)_flushing: all the leaves appear at time 0 and are maintained until t = T. Photosynthetic rate of lower leaves at t = T is very small because of weak irradiance and leaf aging. (b) Successive flushing, leaves appear one by one successively from t = 0 to t = T. This pattern can maintain maximum photosynthetic rate of the top leaves throughout the growing season because there always is a new top leaf under successive flushing. (c) Flush with inclined shoots, flushing pattern is the same as (a) but the inclined shoots increase light transmission so that the photosynthetic rate of lower leaves is larger than that of lower leaves with a vertical shoot (a).

diffuse radiation, where shoot angle influences the degree of self-shading within the canopy. Consider the effects of orientation of the terminal shoot on a sapling in particular. Large shoot angles from the vertical will tend to provide sufficient light to all leaves while leaves on shoots at small angles will intercept much irradiance. We should expect terminal shoot angles (angle from the vertical) of species with flushing-type phenology to be large to minimize self-shading of the leaf cohort. Conversely, successive-leafling species can grow upwards more directly as it is only their uppermost leaf at any time that depends on being in full sunlight. This paper reports on a test of these expectations.

Although the solar azimuth is inclined from the vertical in the northern hemisphere in the temperature zone, we used the vertical as the reference of shoot inclination (i.e. the angle between shoots and the vertical was used as shoot inclination). This is reasonable when we consider saplings that grow with other saplings competing for light. When saplings of similar age grow together, the canopy layer of the saplings is parallel to the ground. In this case, the shortest way to access light above the canopy is to grow vertically, even if the light comes from an angle. Thus we can consider the vertical shoot as a basic strategy for saplings growing in a competitive environment when we do not take self-shading into consideration. The mechanical stability achieved by growing vertically is another reason to make this strategy the basic frame of spatial reference.

Materials and methods

We studied four species that are common in the deciduous broad-leaved forest communities of Hokkaido, northern Japan: Quercus crispula Blume (Q. mongolica Fisch var. grosseserrata Rehd et Wils, here abbreviated Qc) and Tilia japonica Simonskai (Tj) are flushing species in which most of the current year's leaves appear within 10 days after bud-break (Kikuzawa 1983). Alnus hirsuta Teule. (Ah) and Betula platypilthla var japonica Hari (Bp) have successive-type leaf emergence (Kikuzawa 1983). Both these successive-leafling species have an extended period of leaf emergence, usually about 100 days from bud-break to the emergence of the last leaf. We studied 27 saplings of Qc: 19 3-year-olds and eight 5–10-year olds), 19 of Ah (nine 5–10 year olds and 10 15 year olds), 21 of Ah (3 year olds) and 26 of Bp (5–10-year olds). The 3-year-old saplings of Qc had been planted in the nursery of the Hokkaido Forest Research Institute (HFRI; altitude = 35 m), 15-year-old saplings of Tj planted on a mountain slope in the HFRI Experimental Forest (c. 8 km away from HFRI, altitude = 220 m), and the 5–10-year-old saplings of all four species were growing naturally in the HFRI Experimental Forest. All the saplings were open grown and there was little evidence of crowding by neighbouring individuals. Saplings in the nursery were planted at 1-m intervals and their heights were 40–50 cm. The Tj saplings in the Experimental Forest were planted at 1.5 m intervals and their heights were 1–2 m. Naturally grown saplings were 1–2 m in height and grew in open sites along trails or in artificial openings. Saplings of different ages of Qc and Tj are combined because the objective of this study is to illustrate species-specific relationships between phenology and shoot inclination.

We measured the lengths of vertical and horizontal projections from the terminal leader shoot of each sapling once a month from June to October in 1992. These projections formed the sides of a right triangle with the terminal shoot as its hypotenuse and the intersection of the two projections forming the right angle; the angle between the vertical side and the hypotenuse
was calculated and is equal to the angle by which the terminal shoot deviates from the vertical. The length of the shoot was measured and the number of leaves attached to the terminal shoot was counted at each sampling time.

On 18 to 22 June, the irradiance at each leaf was measured using an illuminance meter (TOPCON, Toshiba Co.) set parallel to the ground at each leaf's position. Weather conditions were sunny with only a few intermittent clouds and measurements were taken between 1100 and 1500 solar time. Care was taken to avoid shading by the sampler's body. Irradiance was converted to values relative to that of the top leaf of the shoot (RFPD, relative photon flux density %).

Results

The terminal shoots of Tj reached full extension by June (cf. Fig. 2). The shoot of Qc also attained nearly full length by June but in June and July some shoots showed secondary flushes of growth. Shoots of successive-leafling species elongated until September (Bp) and October (Ah). A small decrease in mean shoot length of Bp was observed from September to October owing to die-back of several shoots. The mean shoot lengths of the two successive-leafling species (Ah and Bp) were far greater than those of the two flushing species (Qc and Tj).

The angles of terminal shoot inclination were small in the two successive-leafling species (Ah and Bp), usually around 10° throughout the season. In contrast, the shoot inclinations of the two flushing species were large (Fig. 3). The mean shoot angle of Tj in June was c. 70°, but it decreased to 40° in July. Mean shoot angles of Qc were c. 30–40° (Fig. 3). A two-way (species and month) analysis of variance revealed that the effect of species and month, and their interaction were highly significant (P<0.0001). Because the interaction was significant, one-way (species-month) multiple comparison by Scheffe's method was carried out, which confirmed the difference between two types of foliar phenology and the changing shoot angle in Tj (Fig. 3).

The RFPD of each leaf tended to decrease towards lower leaves on a shoot in the two successive-leafling species (Ah and Bp) (Fig. 4). For example in Ah, the RFPD of the fifth leaf from the top was about 78% and that of the eighth leaf was 56%. While no consistent decreasing trend in RFPD on leaves along the shoot was found in the two flushing species, the RFPDs of lower leaves were low in Qc; self-shading does occur in this species despite its high shoot angle. In Tj, which showed the largest shoot angle, there was no decrease in RFPD on leaves along the shoot (Fig. 4); each leaf of Tj receives approximately full irradiance, at least at midday under clear skies. To evaluate the different relationship between RFPD and leaf order, an empirical expression RFPD = k(LO \cdot 1) was applied, where LO and k denote leaf order from the top and a model parameter to be estimated by the data, respectively. The estimated values for k were −0.90, −1.16, −0.39 and −0.00 for Ah, Bp, Qc and Tj, respectively. These values differed from each other significantly (P<0.05). The successive-leafling species had more negative k than the flushing species, indicating that RFPD decreased more rapidly with leaf order for the successive-leafling species than for the flushing species.

Discussion

Our observations support the idea of a functional and perhaps adaptive co-ordination between terminal shoot inclination and foliar phenology. We found that trees with a flushing leaf phenology have a larger shoot inclination that acts to reduce the self-shading of leaves along a shoot. The inclined shoots of flushing species counter a potential disadvantage of flushing, greater shading of lower leaves by upper leaves throughout the growing season, but is not the only compensatory trait available to flushing species. Other methods to avoid self-shading may be spiral phylotaxy, long-perioted narrow leaves (Takanaka 1994), large angles of secondary lobe divergence and deeply indented simuses (Steingräber 1982) and high leaf angle (Monsi & Saeki 1953; Hutchison et al. 1986). Additionally, there are some physiological ways to tolerate self-shading. These include efficient photosynthesis under low-light conditions with leaves that reach saturation at low irradiance (Koike 1987; Kozlowski, Kramer & Pallardy 1991) or having leaves whose decrease in photosynthetic capacity with time is small (Koike 1990). These physiological
Fig. 3. Seasonal trends in mean shoot angles (±SE) for the terminal leader shoots of open-grown saplings of four deciduous broad-leaved tree species in Hokkaido. Means with the same letter (a-f) do not differ significantly (P < 0.05) from each other by Scheffe's multiple comparison. Abbreviations as in Fig. 2.

Fig. 4. Mean relative photon flux density (RPFD; ±SE) on each leaf from the top of the terminal leader shoot of open-grown saplings of four deciduous broad-leaved tree species in Hokkaido. Measurements were carried out from 18 to 22 June 1992 under clear skies and between 1100 and 1500 solar time. Lines in diagrams are fitted to the expression RPFD = 100 - k (LO - i)^2, where LO and k denote leaf order from the shoot apex and a model parameter, respectively. See text for details.
adjustments may be more important in *Quercus crispula*, which unlike *Tilia japonica*, did show some self-shading despite its inclined terminal shoot. The nearly vertical terminal shoot of successive-leafing trees, which leads to greater self-shading of leaves in the shoot, forces related physiological adjustments. Because each successive leaf can utilize full sunlight during only a brief period between its emergence and that of the next leaf on the growing shoot, a rapid decrease in leaf photosynthetic capacity with time (Koike 1990) and a high photosynthetic rate in high irradiance (Koike 1987; Koziolowski et al. 1991) are characteristic of successive-leafing species. With this combination of traits, trees of successive leaf emergence can attain greater height growth under conditions of full sunlight, which may be advantageous in the early successional habitats where species with successive-leafing phenology predominate (Kikuzawa 1983).

In this paper, we considered only the two extreme types of leaf emergence: successive leafing and flushing. However, there are many 'intermediate' types of leaf emergence. In some species such as *Magnolia obovata* and *Kalopanax pictus*, many leaves appear as a flush but additional leaves unfold successively. These intermediate species are predicted to have some traits to avoid self-shading. For example, *M. obovata* unfolds five to eight leaves as a flush on a shoot with very short internodes and well-dispersed phyllotaxy. Internodes of successive leafing occurring later in the season are relatively long (K. Kikuzawa, personal observation). This correspondence of leaf-emergence pattern and shoot elongation in *M. obovata* may help to avoid self-shading.

Our observations also are consistent with earlier discussions of crown architecture and foliar phenology. Early successional tree species that are adapted to high light conditions usually have a shorter leaf life span than later successional species (Kikuzawa 1978, 1982, 1983, 1991; Chabot & Hicks 1982) and show successive leaf emergence (Kikuzawa 1982, 1983) together with indeterminate shoot growth (Maruyama 1978; Boojh & Ramakrishnan 1982; Shakla & Ramakrishnan 1986). The architecture of early successional tree species usually involves more vertically elongated and multilayered canopies (Horn 1971; Boojh & Ramakrishnan, 1982; Shakla & Ramakrishnan 1986). On the other hand, late successional species usually have a lower rate of leaf turnover (Kikuzawa 1988), flush type leaf-emergence (Kikuzawa 1983) and determinate shoot growth (Maruyama 1978; Boojh & Ramakrishnan 1982). The architecture of late successional tree species usually involves horizontally extended monolayers of shoots (Horn 1971; Shakla & Ramakrishnan 1986). Because small differences in shoot angles and length can affect crown form (Honda 1971; Fisher 1986), we suspect that patterns set in the terminal shoot will be carried into axillary shoots to achieve consistent crown form.

In general the angles of the lower shoots should become larger if the terminal shoot inclination is large. Sakai (1990) measured shoot angles on the leader branches of several maple species and found that larger shoot inclinations were associated with multilayered crown architecture and smaller inclinations with multilayered crown. We might then expect successive-leafing trees to develop a more columnar crown, while flushing trees should have a more umbrella-shaped crown. These two types correspond to the multilayer and monolayer canopies of Horn (1971) and have a major influence on light interception in forest trees (Kuuluvainen & Pukkala 1989).

There are also some apparent exceptions to our results. For example, *Sorbus commixta* has vertically oriented terminal shoots even though it expands leaves almost simultaneously. This may be related to its compound leaf form as casual observation of many other simple-leaved species appear consistent with our results. Other Alders (Alnus japonica, *A. maximowiczii*), Birches (*Betula maximowiciana*), Willows (*Salix* spp.) and *Ceratiphyllum japonicum* have erect shoots and successive leafing while Maples (*Acer* spp) and Cherries (*Prunus* spp) have inclined shoots and flushing type leaf emergence (K. Kikuzawa, personal observation). Perhaps a leaflet should be considered functionally as a single leaf and the midrib of a leaf as a shoot in the case of compound leaves (Givnish 1978). Certainly in either simple- or compound-leaved species, the effects of leaf angle, phyllotaxy, bifurcation ratio and shoot lengths will all influence the degree of self-shading in tree crowns (Niklas 1992). These additional factors almost certainly are involved in determining the relatively simple functional co-ordination observed between terminal shoot inclination and leaf emergence pattern. More extensive comparative studies are necessary to test the generality of our results and to refine the model linking tree architecture and tree phenology.

While the linkage between terminal shoot angle and foliar phenology can be understood from the viewpoint of maximizing carbon gains, this does not ensure that the adaptive value or evolutionary origins of linkage is tied simply to carbon gain. For example, the observed shoot inclinations may result instead from ontogenetic and mechanical constraints. Flushing trees attain their full shoot elongation within a short period after bud-break and the complement of fully expanded leaves will be a mechanical load on the young, immature shoot (Bozzuto & Wilson 1988). Thus, the shoot of flushing species may simply be inclined by the load. The larger inclination of *Tj* in June compared to drastically decreased inclination in July when the wood of the current-year twig gains strength supports this interpretation. Whatever the balance of adaptation and constraint, it is clear that the linkage between terminal shoot inclination and foliar phenology does show functional coordination with leaf array and leaf physiology related to carbon gains over the season.
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