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ORIGINAL ARTICLE

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Plasticity in leaf-area density within the crown of *Aucuba japonica* growing under different light levels

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Abstract We assessed leaf-area density (LAD; $m^2 m^{-3}$) within the crown of *Aucuba japonica* (Cornaceae) growing under different light regimes and analyzed the components of crown architecture that most influenced variation in LAD. At a whole-crown level, extension-unit (EU) density (EUs/m^3) had the greatest impact on LAD. The number of leaves per unit EU length and EU length had a wide range of impacts depending on the degree of crowding of foliage on the EU. Leaf size had a lesser impact on LAD. LAD was higher in the uppermost crown and declined towards the base. The non-uniformity of LAD among crown layers was much greater under high irradiance. Individuals under high irradiance achieved greater LAD by increased branching, well-marked EU dimorphism and a larger number of leaves per unit EU length; the reverse was true for the individuals under low irradiance. We identified two distinct modes of growth response to light regime. Under high irradiance, individuals responded by differential growth between the layers of crowns with the lower crown suppressed and growth in the upper crown increased. Conversely, shaded individuals did not respond by differential growth between crown layers.

Key words Crown architecture · Crown organizational levels · Developmental plasticity · Leaf-area density · Light response · Sensitivity analysis

Introduction

Many factors in the forest environment such as edaphic factors, light and temperature affect plant growth (Kikuzawa 1984). Low probable seepage of soil water from the flat experimental site at the foot of mountains, and comparatively fertile soil suggest light, rather than edaphic factors, may be the crucial factor limiting growth in the forest understorey. Of all the environmental factors affecting the growth of plants, light is perhaps the most heterogeneous, spatially and temporally (Pearcy 1999), and the most dominant limiting factor for existence of understory plants (Kikuzawa 1984; Chazdon 1988; Yamamura and Kimura 1992). Therefore, establishment and survival of an individual plant depend on the efficient exploitation of opportunities in the habitat, often by responding to local light availability through modification of vegetative crown development. Plants show phenotypic plasticity in regard to spatially heterogeneous radiation (Rongling and Hinckley 2001; Kull and Tulva 2002), and this plastic growth response is particularly relevant for understory trees and shrubs (Kikuzawa 1984; Takenaka et al. 2001). We can assume that understory plants must be under strong selection pressure to construct crowns that capture light efficiently with the least possible investment of carbon (Takenaka et al. 2001). This might be true for both trees and shrubs in the sense that both growth forms are modular with qualitatively similar component organs or physiological processes (White1979; Wilson 1984; Stoll and Schmid 1998). Despite some significant strategic differences between trees (primarily vertically oriented) and shrubs (horizontally oriented by extensive clonal growth) (Pickett and Kempf 1980), individuals of both growth forms in the forest should respond similarly to light conditions.

Leaf-area density (LAD), which is a surrogate for leaf area and its distribution in the crown, is an important trait characterizing crown architecture. Total area of leaves and the leaves' spatial distribution in the crown are important structural properties for canopy production (Wang and

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Jarvis 1990). For a given crown size, total area of leaves per crown depends on average LAD and distribution of LAD in the crown, while distribution of LAD has a strong influence on radiation regime within the crown (Wang and Jarvis 1990). Development of LAD depends on different macro- (shoot density that depends on branching ratio) and micro-components (shoot length, number of leaves per unit shoot length, leaf size) (Canham 1988; Sterck and Bongers 2001; Kull and Tulva 2002) and their response to local radiation regime. We can expect LAD to be part of any plastic response to ambient light regime.

Any change in LAD can arise in a variety of ways. Branching ratio varies between individuals growing in different habitats (Steingraeber et al. 1979; Pickett and Kempf 1980; Veres and Pickett 1982) even within a single canopy (Borchert and Slade 1981; Steingraeber 1982; Canham 1988; Kull and Tulva 2002). Light affects shoot elongation (Kaitaniemi and Ruohomäki 2003), leaf distribution on stem (Givnish 1984; Carter and Smith 1985; Poorter and Werger 1999) and leaf size (Wardlaw 1952; Allsop 1967; Osada and Takeda 2003). Light availability and thus, light interception by plants play a major role in the development and morphology of trees by influencing these macro- and micro-components (Sterck 1999; Sterck and Bongers 2001) that impact LAD (Canham 1988; Sterck and Bongers 2001; Kull and Tulva 2002), but the relative impact of these different components remains uncertain. The various components of crown architecture are highly organized as an integrated whole and jointly influenced by resource limitation and allometric constraints (Kaitaniemi and Ruohomäki 2003). There may well be some trade-offs among the components in responding to light, but these need not necessarily be uniform within the crown. Different components might neither respond to light condition similarly nor impact LAD equally.

According to optimal foraging theory (Sutherland and Stillman 1988), when a plant encounters a high local resource (e.g. light) availability, branching ratio should increase with corresponding shortening of shoot length to maximize carbon gain. Plants under high irradiance are expected to develop high LAD, i.e. plants exposed to low light conditions should develop a diffuse canopy with low LAD. Similarly it can be assumed that if part of a crown (e.g. upper part) receives more light, then the crown may attain highly localized growth with directed allocation towards the most favorable position (Stoll and Schmid 1998; Kull and Tulva 2002; Kaitaniemi and Ruohomäki 2003) and thus, develop a high LAD through this preferential growth. Contrarily, if the entire crown were exposed to low light conditions then all the parts of the crown would attain similar growth, i.e. growth would be directionally nonpreferential.

In this paper, we address the following questions in regard to the effects of local light conditions on crown architecture in an understory shrub: (1) Do all the components of crown architecture respond similarly to shading? (2) Do all components impact LAD equally? (3) Can the net outcome of interactions among the diverse components be considered an example of adaptive plasticity?

Materials and methods

We studied *Aucuba japonica* (Cornaceae), which typically grows under closed evergreen or deciduous forest canopy but is also found in canopy gaps (Yamamura 1986). The genus *Aucuba* is distributed from the Himalayan region through south China and Taiwan to the Japanese archipelago and *A. japonica* is distributed at the easternmost edge (Kanai 1963; Hara 1966) as mentioned by Ohi et al. (2003). *A. japonica* is an evergreen, woody shrub species and is widely distributed from warm temperate to cool temperate forests in Japan. In the adult stage, shoots are produced through syllepsis (Tomlinson 1978). Phyllotaxis is almost always decussate from vegetative appendages to the reproductive ones, including bud scales (Hara 1980). The species is dioecious. The minimum age of flowering is 4 years and flowering is accompanied by branching (Kume and Ino 2000). Self-shading could be severe if *Aucuba* plant deployed more leaves in the canopy (Takenaka et al. 1998). Therefore, it was necessary to investigate how the components of the crown responded to local light conditions to adjust canopy structure in order to increase light acquisition capability (Küppers 1989; Tremmel and Bazzaz 1993).

To evaluate the light response of various components of crown hierarchy in terms of their magnitude of impact on LAD, we selected *Aucuba japonica* plants growing in the Botanical Garden (established in 1923), Faculty of Science, Kyoto University; the garden is situated at 35°02′N and 135°47′E and 60 m above sea level. The site is on the Kitashirakawa alluvial fan with sandy loam soil. It has flat topography and is surrounded by mountains. Annual mean temperature is 16.1°C, ranging from a maximum of 36.0°C in July to a minimum of –5.0°C in January. Mean annual precipitation is 1,539 mm. We selected ten adult male plants of around 20–25 years old (1.5 to about 2.5 m tall); plant age was estimated by counting the number of branching points as branching occurs once a year (Kume and Ino 2000). All the individuals have a primary stem with multi-stem clumps (Ito et al. 1999). Most probably all individuals originated from seedlings [i.e. discrete type (Isobe and Kikuchi 1989)] and a very few other *Aucuba* plants within 2–3 m radius of the sample plants were discrete, and much smaller than sample plants (visual observation).

Stratification of crown and measurement of phytoelements in different layers

The crowns were stratified horizontally, and each stratum we called a layer. The thickness of a layer (50 cm) was selected arbitrarily. To know the distribution of phytoelements within the crown (e.g. leaves and stem length) as well as their quantitative morphological variations, we built a vertical column through the layers of the crown. The dimensions of the column (on horizontal plane) were 60 × 50 cm (arbitrarily selected). Therefore, the three dimensions of a measuring unit in a layer were as follows: 60 × 50 cm×depth of layer (50 cm). Depending on individual crown size, the sampling column was replicated two to four times at different sites within a crown. Within each measuring unit we measured the following phytoelements: (1) number and length of extension units (EU) and their age, (2) number of nodes and internodes per EU, and (3) number of leaves per EU. In cases of trespassing of an EU across units within the column or outside the unit, we sampled the EU only if about 80% of its length (visual observation) was inside the unit – otherwise we excluded the EU from sampling. Because of this inclusion and exclusion, we assumed insignificant variation in results. We carried out these measurements in July after full elongation of the current EU.

We defined an EU as 1-year elongation growth of the axillary bud axis enveloped by the bud scales of the terminal reproductive bud or terminal axis of terminal vegetative bud (Hara 1980; Kume and Ino 2000) or sprouting from a dormant bud on stems. If there were two axillary axes growing from one terminal reproductive bud, then the number of EUs for the plant was taken as three by including the supporting axis. This definition of an EU was applied to current-year or older EUs which had produced leaves (including EUs more than 1 year old in basipetal direction).

Branching ratio was defined as the ratio of current EUs to year-old EUs. This was applied to determine branching ratio both within a crown (among different layers) and between crowns.

We also measured the laminar length and width of sample leaves to estimate individual leaf size (area) as $Y = 0.682 \times X$ ($r = 0.999$) where X = lamina length×width. This relationship was established between leaf area (measured by scanning) and laminar dimensions (lamina length × width) using freshly sampled leaves ($n = 81$). Lamina length was measured as the distance between the point of attachment to petiole and the tip of the lamina. Lamina width was measured as the distance between the laminar margins at the widest point.

Measuring light

We measured instantaneous light for each layer along the vertical column of the crown (from top to bottom). For a particular layer we put two sensors, one above and the other beneath the layer and measured light simultaneously. Light transmittance was defined as the ratio of photon flux density (PFD) beneath a particular layer to the PFD above that layer.

To characterize crown light regime, we also measured instantaneous light on individual plants (five to ten locations randomly, depending on crown size) using LI-COR sensors (LI-190SA) between 10:30 a.m. and 2:00 p.m. Japan standard time. Relative photon flux density (RPFD) was estimated in relation to simultaneous PFD in the open. All the above measurements were carried out on an overcast day around the middle of August.

Grouping of sample plants

To compare morphological variations at different levels of crown organization under different light conditions, we grouped individuals into two insolation regimes. Insolation of individual plants ranged from 0.95–8.5% RPFD. Out of ten sample plants, two subgroups of three individuals were selected. For one group (group I) insolation ranged from about 0.95–1.4% RPFD and these plants were treated as deeply shaded. The RPFD in a second group (group II) ranged from 2.5–8.5% RPFD and these plants were treated as only lightly shaded. Plants with intermediate insolation were excluded from grouping to make the contrasting categories reasonably discrete.

Determining leaf-crowding index, stem weight and specific stem length

To determine crowding of foliage on EU, we defined a leaf-crowding index as the ratio of the distance of the lowermost leaf from the base of the EU to EU length. Higher values indicated closer packing of leaves near the tip of the EU. The maximum value was one for EUs having only one node (or pair); this could be taken as the result of severe crowding. As a tree grows taller, current EU lengths become gradually shorter (Bonser and Aarssen 1994; Osada et al. 2002) and leaves are produced along shorter internodes that increase mutual shading among leaves (Osada et al. 2002). Shortening of EU length causes reduction in sites for leaf deployment (Aarssen 1995). As a result, the proportion of EUs with only one cohort (or pair) of leaves increases in the canopy (Osada et al. 2002) indicating a threshold limit of EU length for the display of a certain number of leaf pairs. Below that limit, to avoid crowding, the EU should reduce the number of leaf pairs.

For determination of stem weight, collected samples (current EUs) were oven-dried at 80°C to constant weight. Specific stem length was estimated as the length of stem acquired per unit biomass (cm g^{-1}).

Determination of leaf-area density

The LAD per unit crown space ($cm^2\ m^{-3}$) was determined as follows: LAD ($m^2\ m^{-3}$) $= D \times L \times N \times S$ where D is mean shoot density (no. of shoots m^{-3}), L is mean shoot length (cm $shoot^{-1}$), N is mean number of nodes per unit shoot length (no. cm^{-1}), and S is mean leaf size (cm^2). Number of nodes was used as a synonym for half the number of leaves.

Sensitivity analyses

We defined sensitivity as the ratio of mean values of a component; for example, EU density under different light conditions, i.e. $\text{sensitivity} = \dfrac{\text{mean at brighter site}}{\text{mean at darker site}}$ where the ratio index 1 indicates no response. The ratio index we considered as an indicator of the relative impact of a particular level on LAD. To evaluate relative impact, we took all the levels into account since changes at various levels of organization of the crown occur simultaneously, keeping balance with each other.

Statistical analyses

For statistical analyses, one-way ANOVA, Mann-Whitney *U*-test, and for obtaining graphs, SPSS and Excel were used. Results are expressed as mean ± SE wherever shown.

Results

All the sample shrubs showed a similar pattern of displaying EUs mostly in the top layer (Fig. 1a). Mean EU length followed a declining pattern from the top to the bottom layer (5.20 ± 0.11 cm at top and 1.90 ± 0.14 cm at bottom, respectively). This decline in EU length between two consecutive layers was insignificant (Mann-Whitney *U*-test; $P > 0.05$) for individuals entirely exposed to low irradiance (Fig. 1b) while such a decline was significant (Mann-Whitney *U*-test; $P < 0.001$) for the individuals under high irradiance (Fig. 1c). Mean EU density was highest in the surface layer (386 ± 25.5 EUs m^{-3}, $n = 10$) of the crown and lowest in the bottom layer (86 ± 27.11 EUs m^{-3}) (Fig. 2a). Mean number of nodes per unit EU length increased significantly towards the bottom of the canopy (0.57 ± 0.01 and 1.97 ± 0.11 at top and at bottom, respectively) (Fig. 2b). Individual leaf area was significantly larger in the upper layer (32.52 ± 0.4 cm^2 at top and 26.42 ± 0.55 cm^2 at bottom) (Fig. 2c).

At the individual plant level, average EU density was higher (one-way ANOVA; $P < 0.05$) under high irradiance (Fig. 3a) and thus, the average EU density was higher fo group II than group I (198 ± 11.28 and 288 ± 25.26 EUs m crown space for groups I and II, respectively). Mea[illegible] EU length varied among the individuals (Fig. 3b) and was significantly different (Mann-Whitney *U*-test; $P < 0.001$ between the groups: it was longer under low irradianc (4.96 ± 0.15 cm for group I and 3.73 ± 0.11 cm for group II) Also, the mean number of leaves per unit EU length wa greater under high irradiance (Fig. 3c) and the differenc was significant (Mann-Whitney *U*-test; $P < 0.001$) betwee the groups of plants (0.58 ± 0.02 for group I an 1.01 ± 0.02 no. of leaves cm^{-1} for group II, respectively) Mean leaf size (cm^2) did not follow any specific patter (Fig. 3d) although there were significant differences (Mann Whitney *U*-test; $P = 0.003$) between the groups (28.30 ± 0.6 and 31.81 ± 0.52 cm^2 for groups I and II, respectively).

Mean branching ratio was larger for the individual under high irradiance than under low irradiance (Fig. 4a Under high irradiance, there was greater within-crown variation in branching (Fig. 4b), and branching ratio decline sharply towards the bottom layer, and there was a significant difference between the top and the bottom laye ($P < 0.001$, one-way ANOVA). In contrast, under low irradiance, variation in branching ratio was not remarkable an there was an insignificant difference ($P > 0.05$, one-wa ANOVA) between the top and the bottom layer (Fig. 4b The ratio was significantly larger ($P < 0.05$, Mann-Whitne *U*-test) for group II than group I. Light transmission insid the crown was inversely related to LAD (Fig. 4c). As consequence, light became scarce inside the crown especially for the bottom layer.

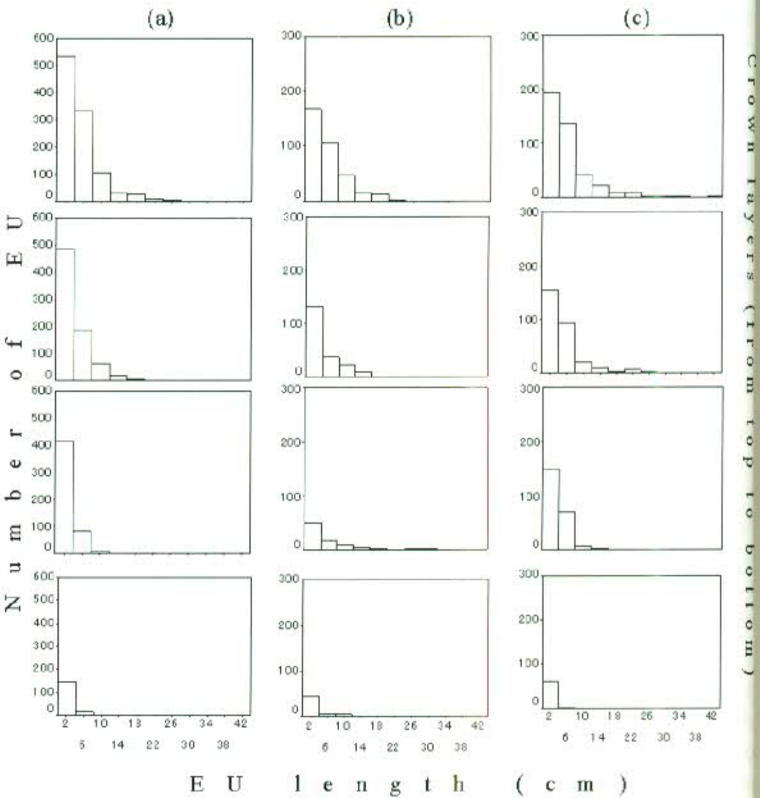


Fig. 1. **a–c** Frequency distribution of extension unit (EU) lengths (intracrown and intercrown variation). **a** Overall distribution pattern of EU lengths (pooled layer by layer from all ten individuals). **b** EU-length distribution pattern under low irradiance (data pooled layer by layer from individuals in group I. **c** EU-length distribution pattern under high irradiance (data pooled layer by layer from individuals under group II)

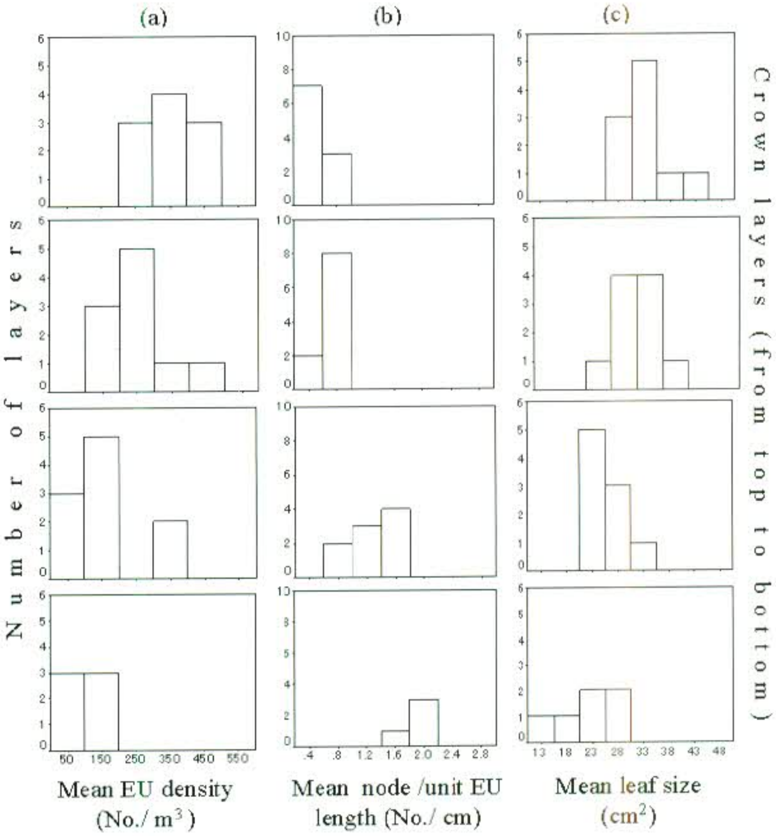


Fig. 2. a–c Within-crown frequency distribution of EU density, nodes per unit EU length and leaf size. **a** Mean EU density. **b** Mean number of nodes per unit EU length [inc[illegible]sed significantly ($P < 0.01$) towards the bottom (Mann-Whitney *U*-test)]. **c** Mean leaf size. Data pooled layer by layer from all the ten individuals. Values indicate means at different layers. A crown was stratified horizontally and each stratum was termed a layer

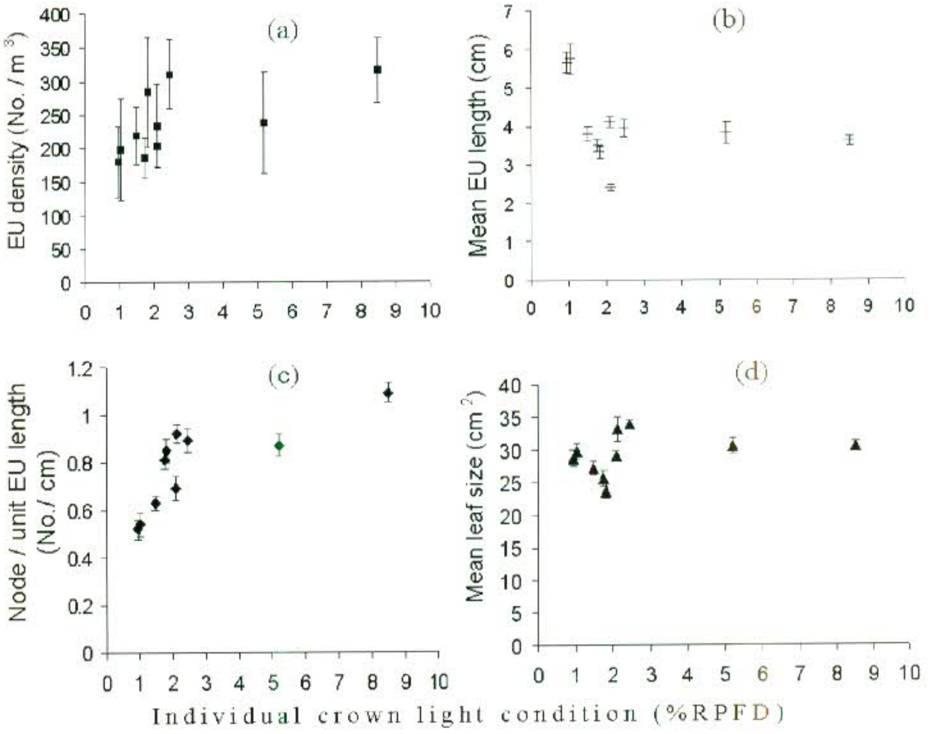


Fig. 3. a–d Difference in EU characteristics among the crowns. **a** Mean EU density. **b** Mean EU length. **c** Mean number of nodes per unit EU length. **d** Mean leaf size. *Vertical bar* indicates standard error. *X-axis* shows crown light condition of the individual plants

Mean stem weight (g) was significantly larger in the surface (Mann-Whitney *U*-test; $P < 0.001$) than in the bottom layer of a crown (Fig. 5a) whereas specific stem length (cm g^{-1}) was significantly longer in the darker lower layer (Mann-Whitney *U*-test; $P < 0.001$) than in the brighter surface layer (Fig. 5b). All the individuals showed a similar pattern. Mean stem weight was larger for the individuals under high irradiance (Fig. 5c) and also the mean for group

Fig. 4. **a–c** Branching and light transmission through the crown. **a** Mean branching ratio at the individual level. **b** Relationship between coefficient of variation (*CV*) of mean branching ratio within a crown and relative photon flux density (RPFD) at individual level. **c** The relationship between leaf-area density at different layers of the crowns and light transmittance through the respective layers. I_0 Irradiance above a given layer, I irradiance beneath that layer. Data pooled for the sample plants. *Note:* In some cases the lowermost layer contained almost no leaves and was slightly brighter compared to the next higher layer. This may be due to diffused light that caused $I/I_0 > 1$

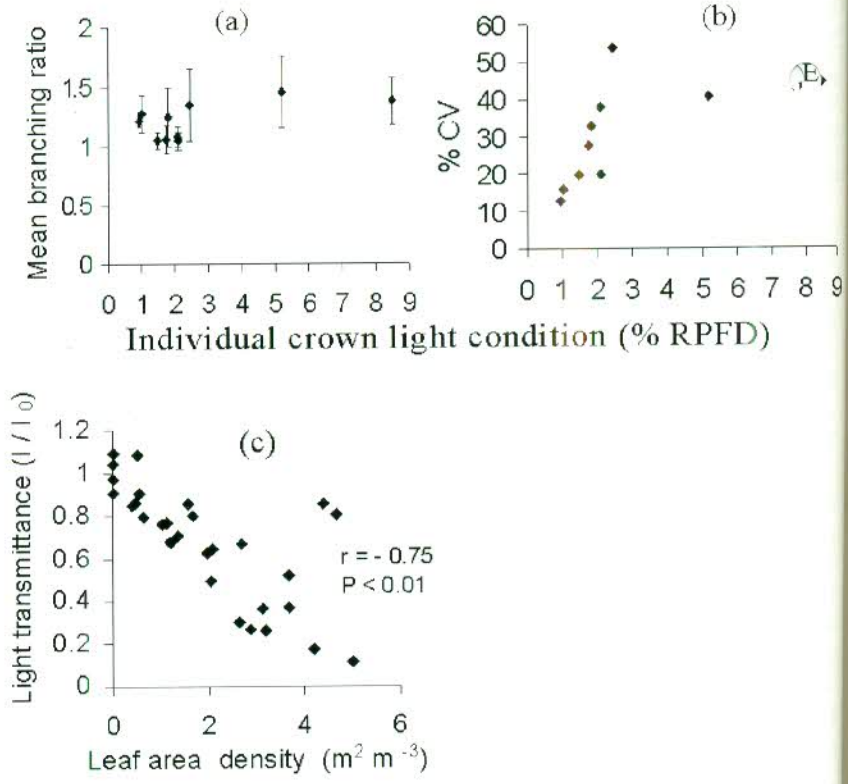
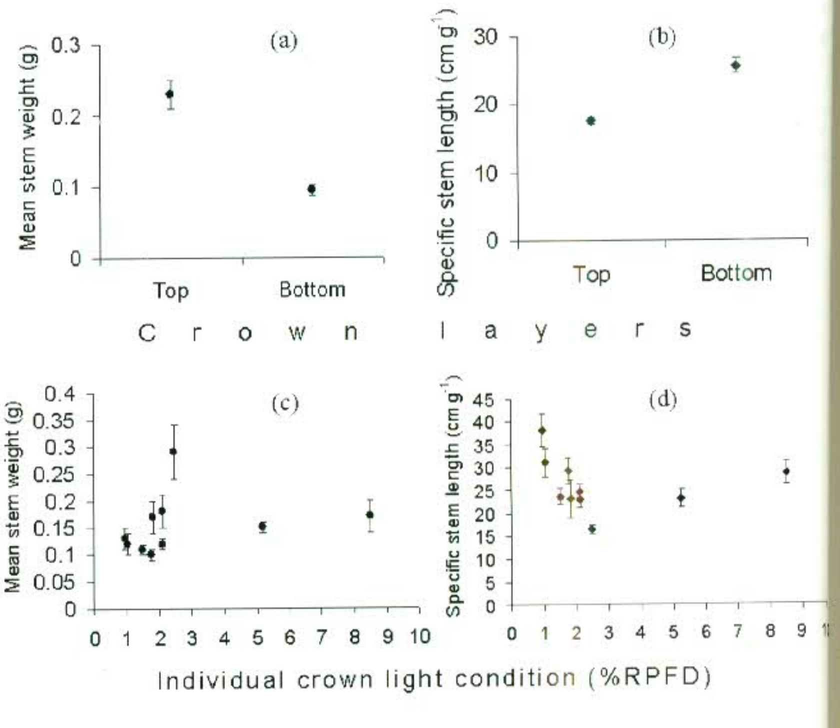


Fig. 5. **a–d** Biomass allocation and stem elongation growth. **a** Mean stem weight. **b** Mean specific stem length between the top and the bottom layer of the crown (data pooled for all the individuals). **c** Mean stem weight. **d** Mean specific stem length of different individuals. *X-axis* shows crown light (mean % RPFD) condition of the individual plants



II was significantly larger (Mann-Whitney *U*-test; $P < 0.001$) than group I (0.19 ± 0.03 and 0.11 ± 0.01 g for groups II and I, respectively). Mean specific stem length was greater under low irradiance (Fig. 5d) and the mean for group I was significantly larger (Mann-Whitney *U*-test; $P < 0.001$) than group II (30.5 ± 1.37 and 22.66 ± 0.86 cm g^{-1} for groups I an II, respectively).

Leaf-crowding index varied among the individua depending on light conditions (Fig. 6), and the index di fered significantly (Mann-Whitney *U*-test; $P < 0.00$

between the plant groups (0.85 ± 0.01 for group I and 0.62 ± 0.03 for group II).

Sensitivity of organizational levels in the crown

The magnitude of contribution of a particular component to LAD is perhaps related to the ability to respond to environmental factors, e.g. light. Within a single crown, EU density was the most important contributing factor to LAD. Depending on light condition, the number of leaves per unit EU length could vary and had the second largest impact on LAD. EU length had the next largest impact on LAD and individual leaf size contributed least to variation in LAD (Fig. 7a). When compared between the groups of plants, the number of leaves per unit EU length appeared to have the largest impact on LAD followed by EU density. EU length had a wider impact (ranging from positive to negative) on LAD compared to leaf size (Fig. 7b). So, as a whole-crown trait, EU density impacted LAD to the greatest extent (positively). The number of leaves per unit EU length also had a wider impact on LAD. The magnitude of impact ranged from negative (within crown) to positive (between crowns). Similarly, EU length also had large and reversible impacts depending on light condition. Individual leaf size had lesser but unidirectional positive impacts.

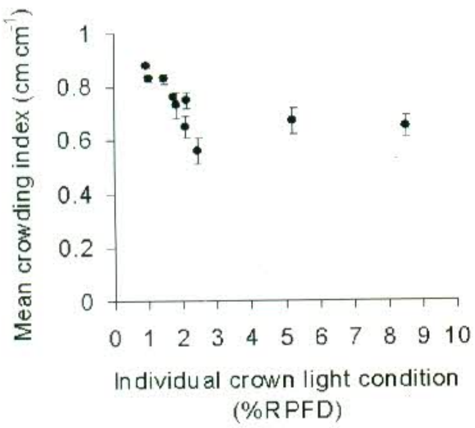
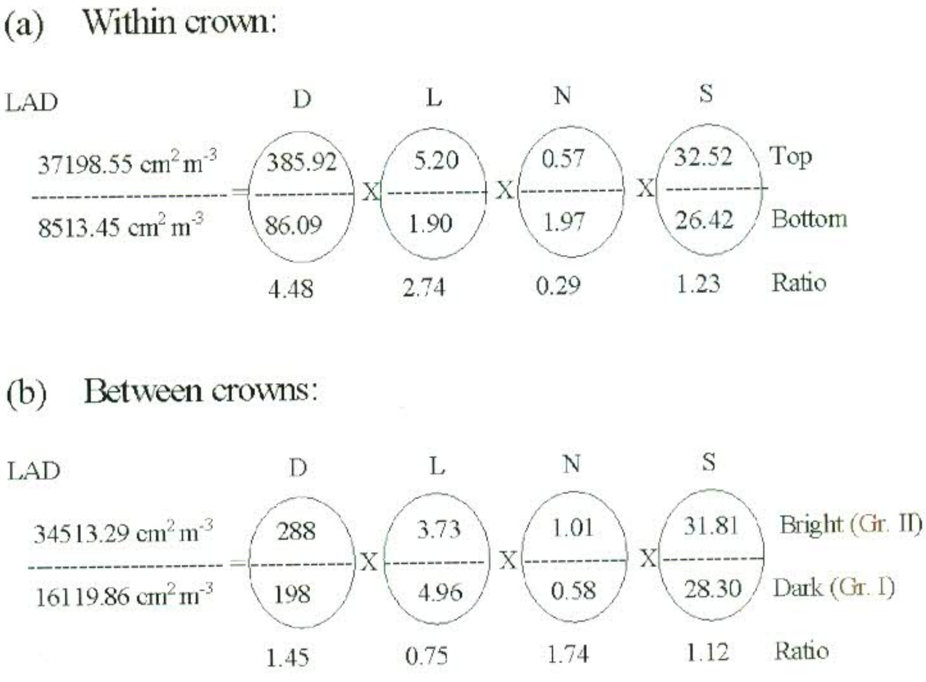


Fig. 6. Foliage distribution on EU. Leaf-crowding index at individual plant level. Leaf crowding was significantly higher for group I than for group II

Discussion

Differential response of the crown components depends on the irradiance levels to which an individual plant is exposed (Sterck and Bongers 2001; Kull and Tulva 2002). With decreasing canopy light, branching ratio, i.e. EU density at individual levels, decreased (Kull and Tulva 2002) with corresponding increase in mean EU length, while the reverse was true for the individuals under high irradiance. Thus, total EU growth was determined by the EU density to EU length interaction. In a "within-crown" context, these components failed to respond along the light gradient similarly. Individuals under high irradiance showed well-marked differential growth (e.g. branching ratio, EU length) between the layers of the crown possibly due to correlative growth inhibition in the shaded lower canopy (Stoll and Schmid 1998), and the lower part of the canopy was degraded. But the individuals that were entirely exposed to low irradiance did not respond by markedly differential growth but rather tolerated shade and unfavorable conditions without significant differential growth between the layers (branching ratio, EU length) (Stoll and Schmid 1998; Takenaka 2000),

Fig. 7. **a**, **b** Sensitivity analysis of various levels of crown organization. The between-level ratio was determined from the magnitude of impact or sensitivity. **a** The order of magnitude of impact within crown was *D* > *N* > *L* > *S*. Means were obtained from data pooled for all the individuals. **b** The order of magnitude of impact between crowns was *N* > *D* > *L* > *S*. Means were obtained from data pooled from all the layers of individuals in the group. *D* Mean EU density (no. of shoots m^{-3}), *L* mean EU length (cm EU^{-1}), *N* mean number of nodes per unit EU length (no. cm^{-1}), and *S* mean leaf size (cm^2)



and growth in the lower canopy was not degraded. Thus, at the individual plant level, when averaged over brighter surface layer and darker lower layers of a crown, mean EU length became shorter for individuals under high irradiance than the individuals that were entirely exposed to low irradiance. Shade-induced leaf crowding (Givnish 1984) on shorter EUs (especially in the darker lower layer) significantly increased the number of leaves per unit of EU length under high irradiance. In contrast, higher crowding of leaves at the tip of longer EUs due to shade effect decreased the number of leaves per unit EU length for the plants that were entirely exposed to low irradiance (Figs. 3c, 7b). This difference arose mainly due to the differential response to light exposure of individual crowns regarding EU elongation. Differences in EU length cause variation in support structure that might affect potential sites for leaf deployment (Aarssen 1995) through reduction in number of leaves per EU or individual leaf size or both. Accordingly, longer EUs in the surface layer provided greater structural support for leaves and allocated much space (Poorter and Werger 1999; Sterck and Bongers 2001) for individual leaves to grow larger, while the reverse was true for shorter EUs in the lower layer. Light resource availability also has to play a significant role in making leaf size different (Wardlaw 1952; Allsop 1967; Osada and Takeda 2003). Close packing of leaves on EUs due to shade might also invoke adjustments between leaf size and the number of leaves. Leaf size might also vary due to changes in specific leaf area (cm^2 g^{-1}) as per irradiance level (Smith 1990). Variations in response levels of the components to light would lead to different impacts on the development of LAD.

The density of leaf-bearing EUs impacted LAD to the greatest extent due to its multiplicative nature (since EU density equals the number of parent axes within some crown space × the branching rate) (Wilson 1984). Well-marked EU dimorphism within a crown under high irradiance also contributed to development of a higher LAD (Kull and Tulva 2002) because of the leaf display-oriented nature of shorter shoots (Yagi and Kikuzawa 1999). Individual crowns acquired space by producing fewer longer EUs (Kull and Tulva 2002), and a greater number of shorter EUs maintained the acquired space (Wilson 1984). Owing to EU dimorphism, for a given leaf area to display, plants require a smaller amount of stem tissue (Whitney 1976) and thus, slight increases in stem length would cause significant increases in LAD (Canham 1988). Lack of dimorphism lowered LAD under low irradiance; such low LAD might be beneficial in reducing self-shading (Takenaka et al. 1998), because a low degree of self-shading under shady environments would have a large impact on net photosynthesis near the compensation-point light level (Givnish 1984). Depending on exposure to light, EU density and EU length complemented each other in determining EU growth while the number of leaves per unit EU length determined variation in LAD (Fig. 7b). The wide range of impacts of the number of leaves per unit EU length and EU length on LAD (Fig. 7a, b) was due to differential response of individual crowns (within versus between crowns as explained earlier) with regard to EU elongation growth and distribution of leaves on EU. Under high irradiance, larger numbers of leaves per unit EU length could not, however, increase LAD by a notable extent but compensated for the overall reductive effect of lower EU density and shorter EU length in the lower layer. The effect of increased number of leaves per unit EU length was a trade-off for smaller leaf size. Unidirectional positive impact of individual leaf size on LAD seemed due to its greater plasticity (Dale 1986) in response to light exposure as explained earlier. Thus, differential impact of the components on LAD appeared to occur within whole-plant integration (Dostál 1967; Stoll and Schmid 1998).

Because of the nature of response of the components of crown structure to local light condition, LAD was highest in the surface layer. Longer-living leaves in the surface layer (Osada and Takeda 2003) also contributed to LAD to some extent. The greater LAD in the upper canopy affected light transmission in the lower layer (Smith et al. 1991) causing earlier leaf shedding (Harper 1989). Self-pruning in the lower layer paved the way for resource retranslocation to brighter surface layers (Harper 1989; Schimd and Bazzaz 1994; Osada and Takeda 2003) in order to allocate greater resources to maximize light capture where more light was available (Goulet et al. 2000; Novoplansky 2003). Thus, growth was highly directed towards the top (Kull and Tulva 2002) where the top layer achieved greater growth by means of a higher branching ratio, longer mean EU length and larger leaf size; the reverse was true for the darker lower layer. Therefore, growth was highly localized (Kull and Tulva 2002; Kaitaniemi and Ruohomäki 2003) under high irradiance. Contrarily, the lower layer achieved less growth by lower EU density and shorter mean EU length. This difference in growth between the layers could be explained by correlative growth inhibition, and the differential growth of EUs between the layers of a crown reflected their foraging behavior in the context of a local environment (Takenaka 2000) within the crown. Thus, when a crown was partially shaded it responded by EU elongation at the brighter site (top) and shortened at the darker site (bottom), which was controlled by the whole-plant integrity (Dostál 1967; Stoll and Schmid 1998). Light response of *Aucuba japonica* provided support for the foraging theory (Kull and Tulva 2002), and foraging behavior was realized through biomass allocation and EU extension growth per unit biomass (Stoll and Schmid 1998) and polarized construction of LAD as well.

Conclusion

Development of LAD and its distribution (within and between crowns) was impacted to different degrees by crown components according to their variable response to local light within the whole plant. The magnitude of impact of the components followed a descending order of hierarchy. The number of leaves per unit EU length had a larger and wider impact (ranging from positive to negative) followed by EU length. Individual leaf size had a lesser impact on LAD but changes at this micro-level accrued to the whole-crown level. Thus, the impact of macro-level of the crown organization on LAD was larger, but the scope of that impact was rooted in the micro-level.

While analyzing LAD, two modes of plastic response were identified. Under high irradiance, individuals responded opportunistically to their local environment by mobilizing resources towards favorable parts of the crown and minimizing investment in parts that were shaded or unsuitable for growth. Asymmetric distribution of resources might be linked to EU dimorphism, which played a significant role in acquiring and maintaining space and development of high LAD. In the case of entire exposure to low irradiance, development of high LAD in the crown was prohibited to reduce self-shading. Individual crowns did not respond by well-marked differential growth, but rather attained persistent growth and waited for favorable conditions, which is an essential trait for survival (Canham 1985, 1988) and establishment and for maintaining the potential to exploit future opportunities (Novoplansky 2003).

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