Plastic response of crown architecture to crowding in understorey trees of two co-dominating conifers

Running title: *Crown architecture of two conifer saplings*

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ABSTRACT

Crown architecture and growth rate of trunk height, trunk diameter and lateral branches of understorey trees (5-10 m tall) were compared between two co-dominating conifers, *Abies sachalinensis* and *Picea glehnii*, in relation to the index of local crowding intensity, *W*, represented as a function of density, distance and basal area of taller neighbours. For the two conifers, the growth of trunk height and diameter was decreased and crowns became flat with *W*, keeping crown projection area. Self-pruning of lower branches was more intense in *Abies* than in *Picea* in crowded conditions, while both the conifers showed similar crown forms in less crowded conditions. These suggest that the growth in lateral branches exceeded that in height in crowded conditions, especially in *Abies*. Tree age of both conifers increased with *W*, resulting from the low growth rate in crowded conditions. The age of the longest and lowest branch of *Picea*, up to 150 years, was positively correlated with the tree age ranging from 70 to 250 years, whereas that of *Abies* was constant at around 30 years irrespective of tree age varying from 40 to 140 years. It agrees with the result that aged *Abies* had more flat-shaped crowns than in aged *Picea* in crowded conditions. These results suggest that each conifer adapted to crowding in different ways: high elongation of branches with high turnover rate for *Abies* and *vice versa* for *Picea*.

Key words: *Abies*, crown form, neighbourhood interference, *Picea,* plasticity.

INTRODUCTION

We observe a wide variety of crown forms between two extremes with alternative strategies: one is multilayer and the other is monolayer. The multilayered and monolayered species are thought to assimilate more efficiently than the other under full-lit and shaded conditions, respectively (Horn, 1971). The former adapts to early successional stages but is then replaced by the latter with the progression of succession. Thus, the optimal tree form depends largely on the stage of succession. This suggests the importance of crown architecture and assimilate partitioning among dimensions or organs of trees in relation to carbon gain (Küppers, 1985, 1989).

Saplings of co-occurring species in rain forests show a wide variety in the architecture and allometry (Kohyama, 1987, 1991; King, 1990). Such variety reflects alternative choices between height growth for future gain and investment for survival at present height. Species with wider crown and thicker trunk increase assimilative capacity and the probability of survival under canopy, while those with narrower crown and thinner trunk can grow faster in gaps due to lower biomass increment required per unit height growth. Kohyama and Hotta (1990) suggested that the latter species cannot regenerate until a gap is created in canopy because these species tended to show a bimodal size distribution, while a reverse J-shaped size distribution indicates a continuous regenerating population (Whittaker, 1974; Hett and Loucks, 1976). All tree species, including emergent trees, should regenerate from a seed stage and must pass through the understorey to the canopy. Clearly, crown forms of tree species affect their demographic functions and regeneration properties.

Many studies have examined the characteristics of crown form by allometric relationships among dimensions. This method is useful and convenient to gain an insight into quantitative characteristics of architecture at the level of the species. Architecture of tree form is determined mainly by the product of growth in each dimension. Self-pruning of branches is another significant factor determining tree form. The growth rate is evidently affected by light environments. Moreover, the growth of each dimension can differently respond to environments from others within an individual tree. It is generally observed in shade-tolerant species that the elongation of branches is not so decreased as height growth in suppressed conditions (Kohyama, 1980; Canham, 1988). Plasticity in growth rate among dimensions increases the variety in architecture within a species. Therefore, studies on the architecture of crown forms should take account of the heterogeneity in local environments. There are a few studies on the response of growth rate and assimilate partitioning to local light environments (King, 1991, 1994). There is, however, no study that addresses the response of a whole architecture to environments.

Immediate neighbours rather than average density have been appreciated to affect the survival and the growth of a target plant (Watkinson, Lonsdale and Firbank, 1983; Mithen, Harper and Weiner, 1984; Weiner, 1984; Penridge and Walker, 1986; Goldberg, 1987; Jones and Harper, 1987a, b). It is worth introducing an index of neighbourhood interference to describe the local environment of examined trees. This study aims to (1) compare the change in growth rates of trunk height, trunk diameter and the change in self-pruning of lower branches with local crowding between two co-dominating conifers, and to (2) demonstrate the plasticity in crown architecture resulting from growth in each dimension and self-pruning, applying an index of the neighbourhood interference.

STUDY SITE

The study site (43˚21'N, 143˚9'E, 1,000 m a.s.l.) was located on the east-northeast slope of Mount Onsen in the east of Taisetsu Mountains in Hokkaido, Japan. At 540 m above sea level, two kilometers distant from the study area, the mean monthly temperatures in July and January 1993 were 13.3 and -13.9˚C, respectively, and annual precipitation is 1,591 mm from Nukabira weather station. In 1991, a 150-by-150 m plot was established and subdivided into 225 contiguous 10-by-10 m stands. These stands were classified into three forest floor types, soil (SL), rock-soil (RS) and rock-moss (RM). The soil depth on mother rocks decreased and moss cover increased in the order of SL, RS and RM type stands (Takahashi, 1994). The dwarf bamboo *Sasa senanensis* Rehder covered the forest floor at SL type stands. This study was carried out exclusively at SL type stands to avoid the effect of edaphic heterogeneity. SL type stands were covered by a dense old-growth forest up to 30 m in top canopy height, dominated by two conifers, *Abies sachalinensis* Masters and *Picea glehnii* Masters. In this forest, *Abies sachalinensis* was more abundant in stem number, while *Picea glehnii* was dominant in basal area. Subordinate trees were all hardwoods: *Betula ermanii* Cham., *Sorbus commixta* Hedland, *Acer ukurunduense* Trantv. et Meyer and *Acanthopanax sciadophylloides* Fr. et Savat. Total basal area of trees larger than 10 cm in trunk diameter was 38.8 m^2 ha^{-1}, and the basal area percentage of each component species was as follows: *Abies sachalinensis* 35.6%, *Picea glehnii* 44.2%, *Betula ermanii* 13.8% and others 6.4%. Further details of the forest structure are described in Takahashi (1994).

METHODS

MEASUREMENT OF CROWN ARCHITECTURE

To examine effects of the local crowding on the crown architecture of understorey trees, 5-10 m tall trees were surveyed in this study. Trees of this size were entirely under the forest canopy except in canopy gaps, and their trunk diameters were large enough to allow for taking core samples. All *Abies* (44 trees) and *Picea* (38 trees) of this size within subquadrates of 0.39 ha and 0.47 ha, respectively, were examined in 1991 to 1992. Crown forms of conifers can be approximated by elliptic cones. Therefore, crown architecture can be described by three dimensions, i.e., the top height of trunk, the height of the lowest branch (i.e. almost the longest one), and the horizontal width of crown. The trunk diameter (at breast height) is another important component reflecting the capacity of physical support and the total foliage mass, as examined in the pipe model theory (Shinozaki *et al*., 1964a, b; Robichaud and Methven, 1992). These four dimensions were examined along the gradient of local environments expressed by the crowding index *W* (*see* next section).

The depth of crown (top height minus the height at the base of lowest living branch) and the widths of crown in two perpendicular directions (including that of the maximum width) were measured. The whole canopy shape of examined trees was evaluated by two indices, the crown depth ratio (CDR) and the crown width ratio (CWR). CDR was defined as the ratio of crown depth to the top height, and CWR as the ratio of the mean crown width to the top height. The last 10-year increment of trunk height was measured by counting the number of annual bud scars from the top of the trunk in 1992. The growth in trunk diameter at breast height of target trees between 1991 to 1994 was obtained by repeated diameter measurements. The elongation of lateral branches was not measured, because it was difficult for the size of sampled trees (5-10 m tall) with non-destructive methods. A relationship between tree age and the age of the lowest (and oldest) branch gives an insight into the process of self-pruning. Tree age was determined from increment cores sampled from the trunk at 30 cm above the ground level. The age of the lowest branch was measured by counting the number of annual bud scars on trunk and branch, or cores sampled at the base of the branch.

ESTIMATION OF LOCAL CROWDING

To describe the local crowding around each target understorey tree, this study employs the Weiner's (1984) measure of neighbourhood interference (hereafter crowding index W):

$$W = \sum_{i=1}^{n} \left(s_i d_i^{-2} \right),$$

where n is the total number of neighbours, d_i is the distance (m) from the target tree to the i-th neighbour and s_i is the size of the i-th neighbour. In this study, the size of neighbour (s_i) is represented by its basal area (cm^2), because individual basal area is roughly proportional to the individual leaf mass (Shinozaki *et al.*, 1964a, b). The neighbour was defined as any tree (including hardwood tree) taller than the target understorey tree and within 8 m from the target tree; this is beyond the mean distance (6.3 m) of crown spread for overstorey trees taller than 10 m.

Weiner defined a neighbour as any tree within a given distance regardless of the size of the target tree. In contrast, this study calculates the crowding index only for taller neighbours, because the primary interest of this study is to express the effect of shading on understorey saplings in a forest with developed crown stratification. The present one-sided crowding index was very similar to Weiner's two-sided crowding index for the examined height range of understorey trees (5-10 m tall) in this forest after log-transformation (R = 0.997). Gaudet and Keddy (1988) showed dealing with herb species that the shading effect is proportional to the above ground biomass irrespective of species. It is, however, expected that the shading effect per unit basal area of deciduous hardwoods is smaller than that of evergreen conifers. The percentage of basal area occupied by hardwoods was relatively small (20.2%), and the crowding index for pooled species was not so different from that only for conifers after log-transformation ($R = 0.802$). For simplicity, the shading effect was assumed to be equal among component species.

All statistical analyses were carried out with SYSTAT 5. Data for CDR and CWR were arcsine-transformed before statistical analysis due to proportion data (Sokal and Rohlf, 1981).

RESULTS

The growth in top height was depressed by local crowding in both *Abies sachalinensis* and *Picea glehnii* (Fig. 1a). Although the rate of height growth of *Abies* was higher in less crowded conditions than that of *Picea*, the height increment was similar between the two conifers in more crowded conditions. *Abies* was thus more susceptible to crowding, because of higher decline of growth rate with crowding W (ANOVA, $F_{1,73} = 4.82$, $P < 0.05$). The growth in trunk diameter of the two conifers decreased significantly with crowding W (Fig. 1b). *Abies* showed higher growth rate in diameter than *Picea* in any crowded conditions (ANCOVA, $F_{1,79} = 5.31$, $P < 0.05$). The regression of the relationship between absolute growth rate in height (AHGR, cm year-1) and that in trunk diameter (ADGR, cm year-1) was AHGR = 73.3 ADGR + 8.8 ($R = 0.82$, $P < 0.001$) for *Abies* and AHGR = 35.5 ADGR + 11.1 ($R = 0.44$, $P < 0.05$) for *Picea*. A difference in the regression between two conifers was found in the slope (ANOVA, $F_{1,72} = 8.61$, $P < 0.01$). Thus, it is expected that *Abies* grows more in trunk height than in trunk diameter in less crowded conditions as compared with *Picea*. The trunk shape was determined by the relationship of growth rates between trunk height and diameter. Consequently, *Picea* had a thicker trunk per trunk height than *Abies* (ANCOVA, $F_{1,78} = 7.206$, $P < 0.01$, data not shown).

The ratio of crown depth to top height (CDR) for *Abies* was decreased more steeply than that for *Picea* with local crowding (ANOVA, $F_{1,78} = 4.94$, $P < 0.05$; Fig. 2a), although the two conifers had similar crown depth in less crowded conditions. *Abies* suffered severer self-pruning in crowded conditions than *Picea*. There was no significant difference in the crown projection area per top height of trunk between the two conifers (ANCOVA, $P > 0.05$, data not shown). The ratio of crown width to top height (CWR) for *Picea* was positively correlated with W ($P < 0.05$; Fig. 2b), while that for *Abies* was neither positively nor negatively correlated. A significant correlation between CWR and W in *Picea* was, however, found when one point at the highest W was deleted ($R = 0.164$, $P > 0.05$). Thus, crown width was less affected by local crowding. In crowded conditions, the two conifers develope a flat-shaped crown without expanding the crown projection area, which is due to the self-pruning of lower branches resulting in the small CDR. This tendency was more conspicurous in *Abies* than in *Picea*. There was no significant difference between the two conifers in mean CWR leaving the W-dependence out of consideration (*Abies* 0.394, *Picea* 0.398, ANOVA, $P > 0.05$). Crown depth and width reflect integrated lengths grown in the same period, since the base of the longest branch is at the bottom of the cone-shaped crown. Self-pruning of *Abies* was severer in crowded conditions (Fig. 2a). Nonetheless, similar crown width ratio between the two conifers (Fig. 2b) suggests that branch elongation of *Abies* was not so decreased as was growth in trunk height relative to *Picea*. High trunk diameter growth of *Abies* should be related to the branch elongation for mechanical crown support. Moreover, the crown projection area per trunk basal area of *Abies* was higher than that of *Picea* (ANCOVA, $F_{1,80} = 9.66$, $P < 0.01$; Fig. 3). These suggest that branch elongation per trunk diameter increment is higher in *Abies* than in *Picea*.

No significant correlation was detected at 0.05 level of probability between trunk height and tree age ($R = 0.146$ for *Abies*, $R = 0.249$ for *Picea*) and between trunk height and crowding index W ($R = 0.124$ for *Abies*, $R = 0.068$ for *Picea*). The age of understorey trees of the two conifers, however, increased with the crowding index W (Fig. 4). These suggest that trees in locally crowded conditions could hardly enter into and come out of the examined height class of 5-10 m. The age of the lowest branch of *Picea* was in proportion to tree age, while *Abies* had an upper age of the lowest branch around 30 years for aged individuals (Fig. 5). The two conifers showed different ways to maintain the branch system with aging in crowded conditions. *Picea* conserves old branches, while *Abies* replaces old branches with new ones with high turnover rate. The relationship between tree age and branch age was in accordance with the W-CDR relationship in Fig. 2a. The age structure of branches within a tree is primarily a consequence of growth and self-pruning, which is in turn determined by environments. There was no significant difference in the frequency distribution of crowding index W between the two conifers sampled as target trees (Kolmogorov-Smirnov test, $P > 0.05$, data not shown). This suggests that the two conifers adapt to crowding in different ways.

DISCUSSION

Both *Abies sachalinensis* and *Picea glehnii* showed plastic responses in growth rate among dimensions and in crown architecture. *Abies* grows more in trunk height in less crowded conditions, but does more in trunk diameter and branches in crowded conditions as compared to *Picea*. Hara, Kimura and Kikuzawa (1991) reported that suppressed trees of *Abies mariessii* Mast. and *A. veitchii* Lindl. grew more in trunk diameter than in trunk height, while those of the early successional species *Betula ermanii* showed the reversed manner. They discussed that the growth in diameter of suppressed *Abies* spp. should be related to crown development, because trunk diameter is roughly proportional to the leaf mass of individual trees (Shinozaki *et al*., 1964a, b). Thus, the high plasticity in growth rate among dimensions enables *Abies sachalinensis* both to gain height efficiently in less crowded conditions, i.e., lower biomass increment required per unit height growth, and to invest for crown development in crowded conditions. As a result, *Abies* showed high plasticity in crown forms, i.e., crowns became more flat-shaped with a constant crown projected area.

A flat-shaped crown has long been appreciated as an adaptive form to crowding or shading (Horn, 1971; Küppers, 1989). Saplings suffer shading not only from neighbouring trees, but also from their own leaves. The gross photosynthesis per unit leaf area within a crown is greatest in the top of the crown, and decreases with depth (Kurachi, Hagiwara and Hozumi, 1986). Expanding horizontal systems resulting in a flat crown is an adaptive choice to avoid self-shading within the same individual crown (Kohyama, 1980, 1987). Thus, the flat-shaped *Abies* enhances to canopy carbon gain efficiently. This crown shape of *Abies* was, however, formed on fair waste, i.e., recruitment of upper branches and self-pruning of lower branches at high rates. On the contrary, *Picea* conserves branches present thus resulting a low turnover rate, which compensates for low growth rate of branches in crowded conditions. The reason there was an upper age of the longest branch for *Abies* could not be adequately clarified in this study, probably due to mechanical constraints (Chazdon, 1986).

At the level of an individual leaf, acclimation to shade have been explained in terms of leaf longevity and specific leaf area: plants grown under suppressed conditions generally have thinner leaves (Young and Smith, 1980; Ellsworth and Reich, 1993) and leaves with longer lifespan (Shukla and Ramakrishnan, 1984; Kikuzawa, 1988). The leaf longevity of *Abies* *sachalinensis* is about 10 years and that of *Picea glehnii* is 13 years (Fujimoto and Shimada, 1991). The ratio of current-year leaf mass to total leaf mass for *Abies sachalinensis* is 9.4-25.9 % (average 16.7), and that for *Picea glehnii* is 4.1-19.0 % (9.7) (Shidei, 1960). This study shows that the same is true for branches that are main components of crown architecture beside leaves, i.e., higher turnover rate of branches was coupled with that of leaves for *Abies* and *vice versa* for *Picea*. The turnover rate of leaves is not independent of that of branches, since new leaves recruit with shoot growth. Thus, one can recognize two different growth fashions between the two conifers: *Abies* can be regarded as an "optimistic" growth type and *Picea* as a "pessimistic" growth type (*sensu* Kohyama, 1987). *Abies* grows to maximize height growth in less crowded conditions and to enhance crown development with short-lived branches in crowded conditions at the expense of construction cost of new branches. In contrast, *Picea* reduces growth rates in all dimensions with conserving the branches present in crowded conditions.

A choice between high growth rate of branches with high turnover rate (optimistic type) and low growth rate of branches with low turnover rate (pessimistic type) may be related to the intrinsic tree longevity. *Abies* is a considerably shorter-lived species than *Picea*. Longevity of *Abies sachalinensis* is ca. 100-200 years, while that of *Picea glehnii* is 400-500 years (Suzuki *et al*., 1987). Average tree ages of canopy trees taller than 10 m in this study site were 94.7 years for *Abies sachalinensis* and 260.5 years for *Picea glehnii* (Hiura, Sano and Konno, 1992). Average tree ages of the target trees of 5-10 m tall were 81.7 years (± 25.1) and 127.3 years (± 42.9) for *Abies* and *Picea*, respectively. This age of understorey trees for *Abies* is closer to the tree age of trees in the forest canopy than that for *Picea*. Thus, it is more significant for *Abies* to grow in height than to lose present branches even in crowded conditions because of its short longevity. On the other hand, long-lived *Picea* affords to wait with little growth until a canopy gap is created and avoids the exceeding construction cost. Local variation and unpredictability of gap turnover within a forest are concluded to enable these two contrasting growth/architecture strategies to co-occur.

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FIGURE LEGENDS

FIG. 1. Growth rates (cm year^{-1}) in trunk height (a) and diameter (b) in relation to crowding index *W* for the two conifers. The correlation coefficients are -0.745 ($P < 0.001$) and -0.684 ($P < 0.001$) for height growth rate of *Abies sachalinensis* (○) and *Picea glehnii* (●), respectively, and -0.691 ($P < 0.001$) and -0.500 ($P = 0.001$) for trunk diameter growth rate of *Abies sachalinensis* and *Picea glehnii*, respectively.

FIG. 2. Crown depth ratio (a) and crown width ratio (b) in relation to crowding index *W* for the two conifers. The correlation coefficients are -0.571 ($P < 0.001$) and -0.396 ($P < 0.05$) for crown depth ratio of *Abies sachalinensis* (○) and *Picea glehnii* (●), respectively, and -0.107 (not significant) and 0.369 ($P < 0.05$) for crown width ratio of *Abies sachalinensis* and *Picea glehnii*, respectively.

FIG. 3. Allometric relationship between crown projection area (m^2) and trunk basal area (cm^2) for the two conifers. The correlation coefficients are 0.726 ($P < 0.001$) and 0.716 ($P < 0.001$) for *Abies sachalinensis* (○) and *Picea glehnii* (●), respectively.

FIG. 4. Relationship between tree age and crowding index *W*. The correlation coefficients are 0.407 ($P < 0.01$) and 0.565 ($P < 0.001$) for *Abies sachalinensis* (○) and *Picea glehnii* (●), respectively.

FIG. 5. Relationship between ages of the tree and of the lowest branch. The correlation coefficients are 0.156 (NS) and 0.783 ($P < 0.001$) for *Abies sachalinensis* (○) and *Picea glehnii* (●), respectively.

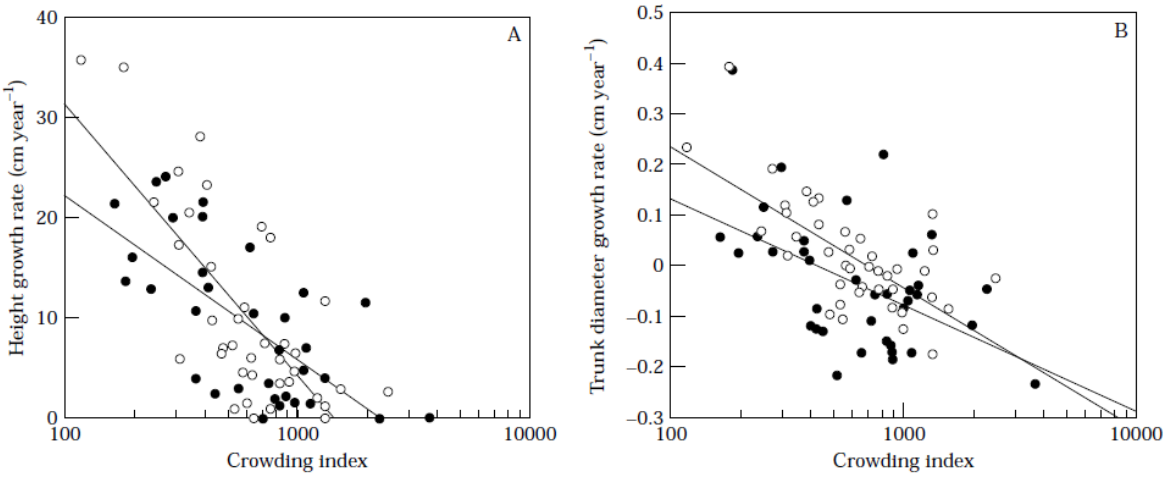
A
Height growth rate (cm year^{-1})
40
30
20
10
0
100
1000
10000
Crowding index
B
Trunk diameter growth rate (cm year^{-1})
0.5
0.4
0.3
0.2
0.1
0
−0.1
−0.2
−0.3
100
1000
10000
Crowding index

Fig. 1

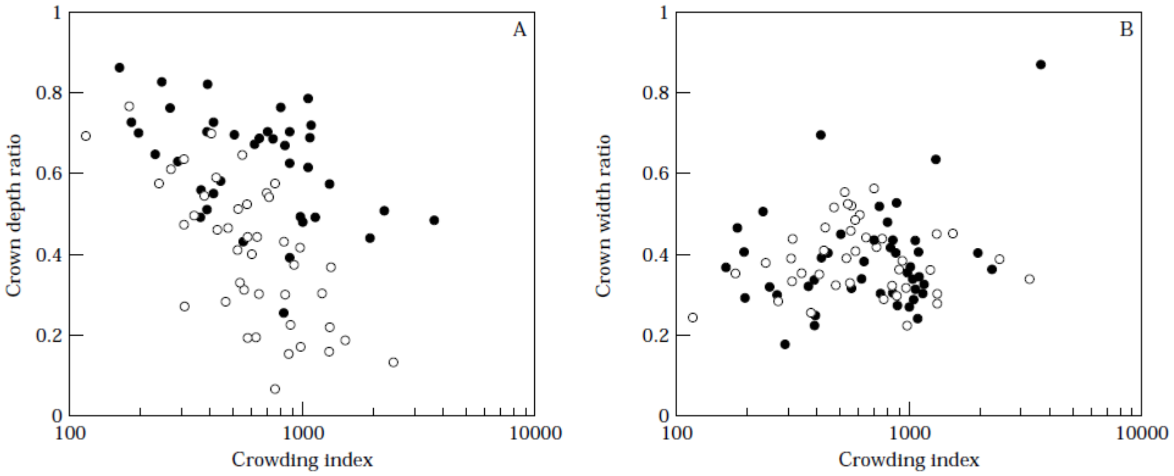
A
B
Crown depth ratio
Crown width ratio
Crowding index
Crowding index
0
0.2
0.4
0.6
0.8
1
100
1000
10000

Fig. 2

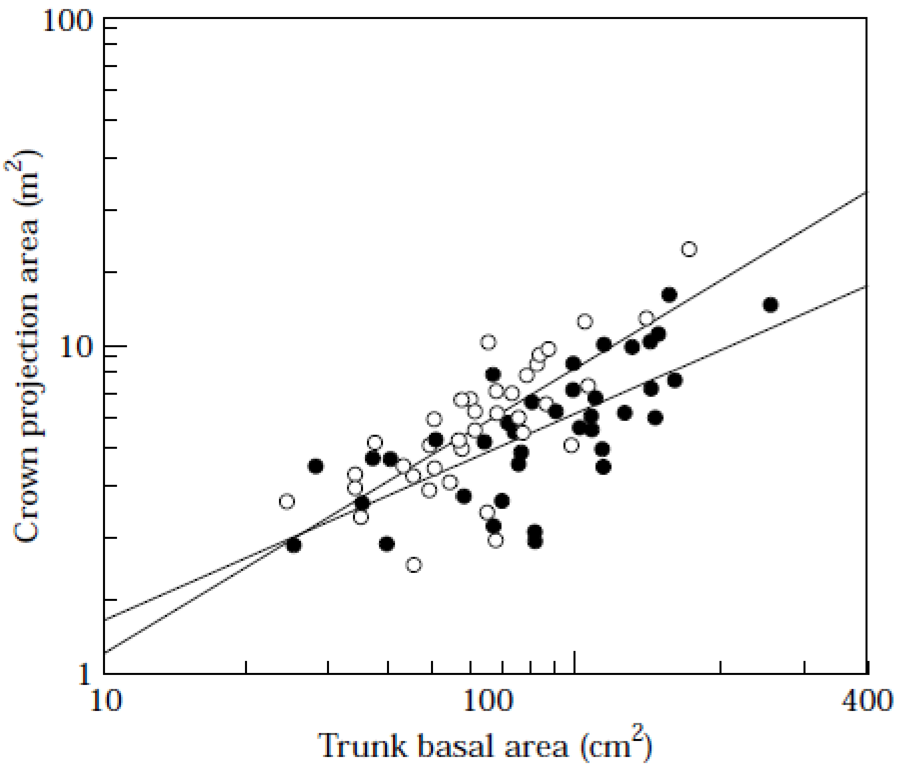
100
10
1
Crown projection area (m^2)
10
100
400
Trunk basal area (cm^2)

Fig. 3

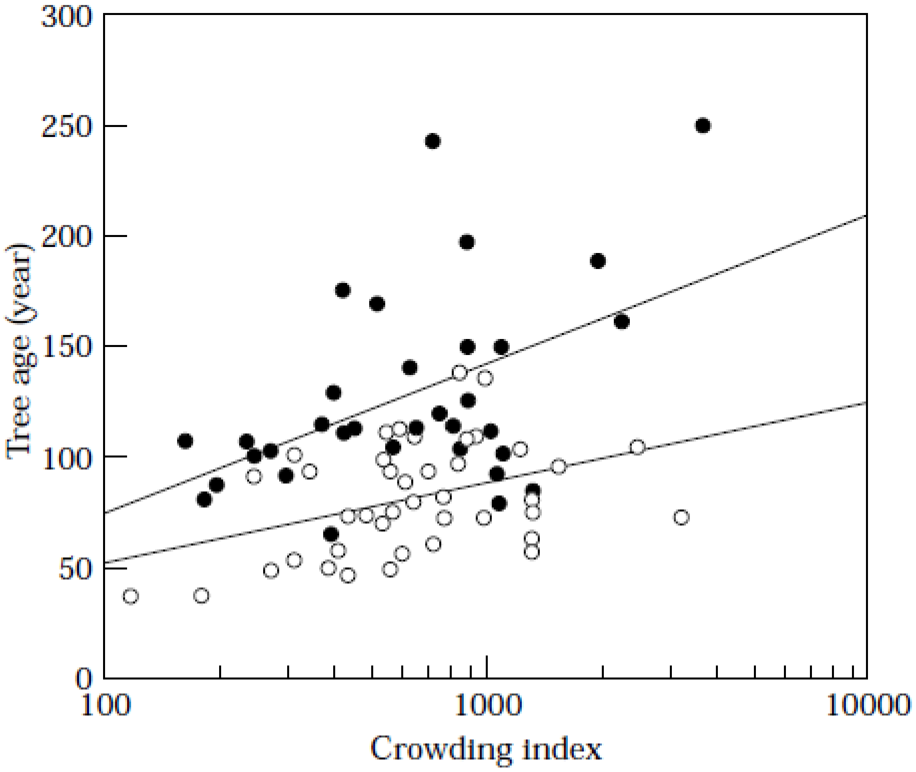
Tree age (year)
300
250
200
150
100
50
0
100
1000
10000
Crowding index

Fig. 4

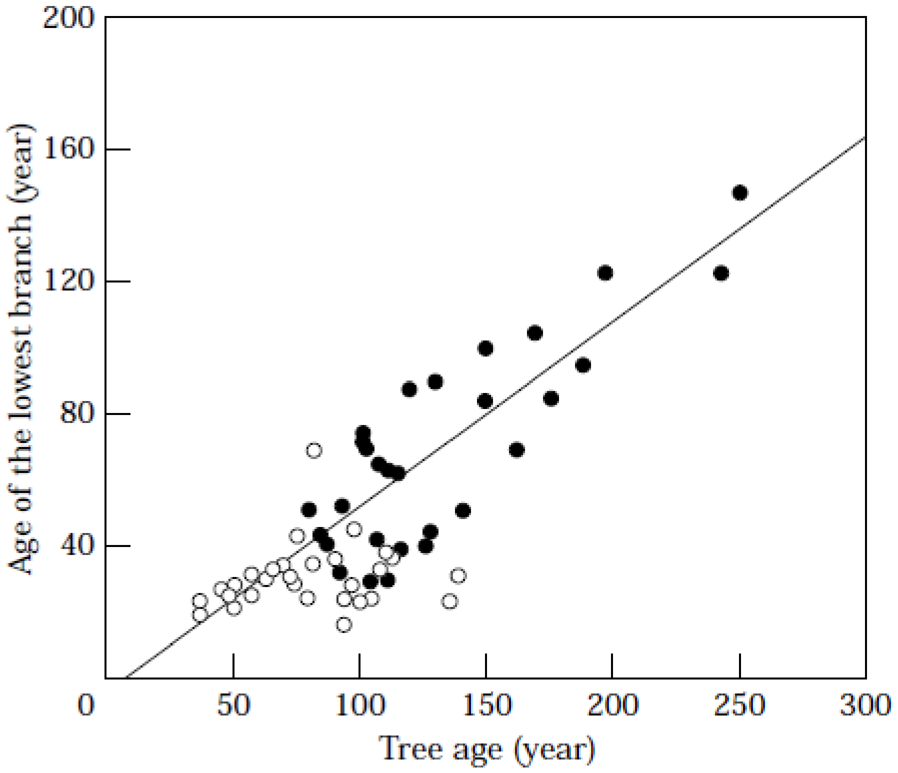
200
160
120
80
40
0
50
100
150
200
250
300
Age of the lowest branch (year)
Tree age (year)

Fig. 5