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Consequences of Variation in Tree Architecture and Leaf Traits on Light Capture and Photosynthetic Nitrogen Use Efficiency in Mountain Birch

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Abstract

In the subarctic environment, shortage of nitrogen is common and may have immediate effects on tree survival via lowered photosynthetic capacity in cold periods. Yet, despite the critical role of nitrogen, the subarctic tree mountain birch [*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti] shows remarkable variability in tree architecture and leaf traits, which affect its nitrogen use and its ability to capture light. It is possible that intraspecific variation in these traits exhibits alternative strategies for maintaining efficient nitrogen use, provided it results in equal efficiency despite variation in the underlying traits, but true differences between tree individuals may also exist.

Computer simulations were used to investigate how daily photosynthetic nitrogen use efficiency (DPNUE) and the potential rate of photosynthesis (P_{max}) of whole birch trees depend on tree architecture, the area or number of leaves per shoot, or nitrogen invested per leaf. The simulations showed that mountain birch has the potential to achieve an equal P_{max} or DPNUE by adjusting variation in many traits, but the potential was not realized as a large amount of variation remained when leaf traits measured in the field were used to estimate DPNUE and P_{max} . Trade-offs between P_{max} , DPNUE, and other tree functions such as resistance to herbivores, growth, maintenance, or reproduction are likely causes for variation.

Introduction

The hypothesis that leaves within plant canopies should adjust their light capture and nitrogen allocation in such a way as to maximize net photosynthesis is largely accepted (Hirose and Werger, 1987; Haxeltine and Prentice, 1996; Anten, 2005). Several lines of evidence support this hypothesis, and have shown, for example, that trees can adjust nitrogen content and many structural traits of foliage in response to variation in radiation levels within the canopy (Niinemets et al., 1999; Le Roux et al., 2001; Kitajima et al., 2002; Aranda et al., 2004). On the other hand, there is evidence that nitrogen distribution within the canopy is often more uniform than theoretically predicted, and the observed projection of leaf area within the space can also deviate from what is expected (Anten, 2005). This suggests that trade-offs between various traits contributing to either light capture, photosynthesis, or other essential functions of plant design might prevent the plant from reaching the maximum level of photosynthesis (Anten, 2005).

Ultimately, the presence of trade-offs between multiple traits relates to species coexistence within the same habitat and can explain why many alternative plant designs are equally adapted to their environment (Niklas, 1999; Hubbell, 2005; Marks and Lechowicz, 2006). For example, large interspecific variability in the size and shape of leaves is likely to reflect alternative options for efficient light capture because actual differences in the amount of captured radiation are minor compared with variation in leaf form (Valladares et al., 2002; Falster and Westoby, 2003). While some of the leaf traits may indicate limits set by specific growth conditions and other adaptive demands, such as the intensity of radiation (Evans and Poorter, 2001) or the presence of herbivores (Brown and Lawton, 1991), a wide range of morphological leaf

variety exists even within the same habitat (Valladares et al., 2002).

Besides the form of the leaves themselves, the architecture of the whole plant, its branching structure, and the spatial arrangement of the leaves provide an additional level of plasticity that affects its light-capturing options (Honda and Fisher, 1978; Takenaka, 1994; Kern et al., 2004). Such variability can produce many alternative plant designs of approximately equal fitness when trade-offs between other essential plant functions are taken into account (Marks and Lechowicz, 2006). However, although interspecific variation of plant traits within the same habitat is well recognized, few studies address the large amount of intraspecific variation that can also occur within a uniform habitat (Karlsson, 1991; Leal and Thomas, 2003). Theoretically, it is possible that variation within species, similar to differences between species, results from trade-offs between alternative designs of plant function (Senn et al., 1992; Augner, 1995). On the other hand, one could also assume that selection by the local environment should reduce the variation present within a subpopulation (Slatkin, 1973), as can be seen in the presence of specific ecotypes in many plant species (Westbeek et al., 1999; De Lillis et al., 2004). Such local adaptation is probably related to the presence of strong selective forces, and can occur even in outcrossing tree populations at a fine spatial scale of a few hectares (Sork et al., 1993).

In the mountainous subarctic environment, selective forces should have a strong impact on the nitrogen use of trees, because nitrogen shortage is common and may have immediate effects on tree survival (Weih and Karlsson, 1999a). Low nitrogen levels may lead to a shortage of photosynthates during a short and cold growing season, which probably explains why high-altitude plants usually allocate more nitrogen to leaves and maintain a higher rate

of photosynthesis than their lowland conspecifics (Körner and Diemer, 1987; Weih and Karlsson, 1999b; Westbeek et al., 1999). Yet despite the presumed benefits of high nitrogen in foliage, the subarctic tree mountain birch [*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti], for example, shows remarkable variability in traits affecting its nitrogen use and its ability to capture light for photosynthesis.

In mountain birch, the size and number of leaves in short shoots, which are virtually non-elongating and comprise the majority of light-capturing foliage, vary by up to a factor of four at a fine spatial scale (Senn et al., 1992; Kaitaniemi and Ruohomäki, 2003). The amount of nitrogen invested into individual leaves and lost through leaf senescence varies by a factor of one and a half (Nordell and Karlsson, 1995), and the form of tree crowns ranges from narrow conical to spherical even in trees without any close neighbors (Renton et al., 2005). The causes of variability in these traits are largely unknown. One explanation is that intraspecific variation exhibits alternative strategies for achieving equal efficiency in light capture and nitrogen use. Alternatively, true differences may exist in light capture and nitrogen use between tree individuals provided that some selective forces override the sole priority of these two functions.

In this study, I discriminated between the two explanations by investigating the importance of variation in foliage traits for light capture and nitrogen use efficiency. If the presence of alternative strategies with equal efficiency explains intraspecific variation in mountain birch, both light capture and nitrogen use efficiency should approach a constant value in all trees in spite of variation in the underlying traits. If the differences in light capture or nitrogen use efficiency among individuals are comparable with the amount of variation in the underlying traits, trade-offs with alternative functions are a more likely explanation.

A combination of measured foliage data and output from computer simulations was used for the analysis of tree traits. In the simulations, the original 3-D architecture of trees was retained, and leaf traits based on either field observations or artificially altered values were used to assess how the light-capturing efficiency and potential photosynthesis per the amount of nitrogen invested depend on some specific properties of mountain birch foliage (individual leaf area, number of leaves per shoot, nitrogen invested in leaves).

Materials and Methods

MEASUREMENT OF TREE ARCHITECTURE

Forty-five mountain birch trees growing at a location 200 m a.s.l. on Puksalskaidi hill, in the vicinity of the Kevo Subarctic Research Station (69°45'N, 27°01'E), were used. The trees were situated in a sparse mixed forest with Scots pine (*Pinus sylvestris* L.). Competition, shading, and other interference between the trees was minimal because the trees were free-standing without any neighbors within a few meters. The experimental trees usually had one main stem 1.5 to 2.5 m high and a small number of young basal sprouts 0.5 to 1 m in height. The trees more closely resembled the monocormic than the polycormic form of mountain birch (Vaarama and Valanne, 1973). One actively growing young sprouting stem, when available, and one old stem were selected for each tree. Of the 45 trees, 24 had a basal stem available. In simulations and data analysis, the young and old stems of the same tree were considered as though they were separate trees. Previous evidence suggests that the individual stems function as largely autonomous units (Kaitaniemi et al., 1997). Based on the

position of the oldest shoots within the tree and on the number of leaf petiole scars in the oldest shoots (Kaitaniemi and Ruohomäki, 2003), the main stems were estimated to be 20 to 50 years old, and the young stems 2 to 5 years old.

Mountain birch trees have two shoot types, short and long. Elongation takes place mainly via the formation of long shoots, which produce successive axillary buds tended with single leaves and separated by 2- to 3-cm-long internodes. The terminal bud of a long shoot often dies in the autumn or transforms into a winter-dormant male catkin. The axillary buds may become new long shoots the following year or may remain short shoots. The short shoots are monopodial, usually bear three leaves and do not elongate more than a couple of millimeters a year. The short shoots contain the majority of leaves, especially in old stems. The apical bud in a short shoot includes primordia for leaves flushing the following year, and in reproductive short shoots, for female catkins as well. Short shoots also retain the capacity to convert into a long shoot. All short-shoot leaves and the basal leaves of new long shoots burst simultaneously in the spring. The new long shoots continue the production of new leaves and buds throughout the summer. Senescence takes place in the autumn, when leaves are shed after resorbing nitrogen and other essential substances for winter storage (Nordell and Karlsson, 1995). Nitrogen is the growth-limiting nutrient (Karlsson and Nordell, 1996) also at the Kevo area (Ruohomäki et al., 1996).

The 3-D architecture of the shoot system was obtained by digitizing in summer 1999. A Polhemus FASTRAK equipped with a stylus and a LONGRANGER transmitter (Polhemus Inc., Colchester, VT, U.S.A.) was used to record the coordinates for the points at the base of each shoot, at the base of branching points, and at the tip of each shoot where the primordial bud for the following year's growth is located. At all levels of the branching hierarchy, from the main stem to the higher order branches, a branch was defined as a structure diverging from the lower order branch and having at least two former (if dead) or current buds capable of producing leaf-bearing shoots. The coordinates were captured with Pol95 software (INRA, Clermont-Ferrand, France) running on a portable computer. A spreadsheet program was used to record the shoot type and age, and the topological connections between shoots. Shoots were classified as dead, short shoots, or long shoots.

The number of leaves per shoot and the mass and area of full-grown individual leaves were determined for samples from different parts of young and old stems (leaf mass was missing for six stems). Results based on the sample were then used to estimate the number, weight, and area of leaves for individual shoots of each stem to be used in light capture simulations (Kaitaniemi and Ruohomäki, 2003).

ESTIMATION OF LIGHT CAPTURE

The 3-D structure of digitized trees was reconstructed in computer simulations to calculate the relative amount of photosynthetic photon flux density (PPFD) captured by each shoot. Both the original leaf traits measured for each tree and the leaf traits that were artificially altered were utilized in the simulations to investigate the light-capturing efficiency and, further, the potential rate of photosynthesis (Fig. 1). The use of original values ensured that combinations of plant traits that were truly present in the tree population were directly considered. The use of the altered values, in turn, enabled separating the effect of individual traits from each other, which helped to assess the specific importance of those traits alone.

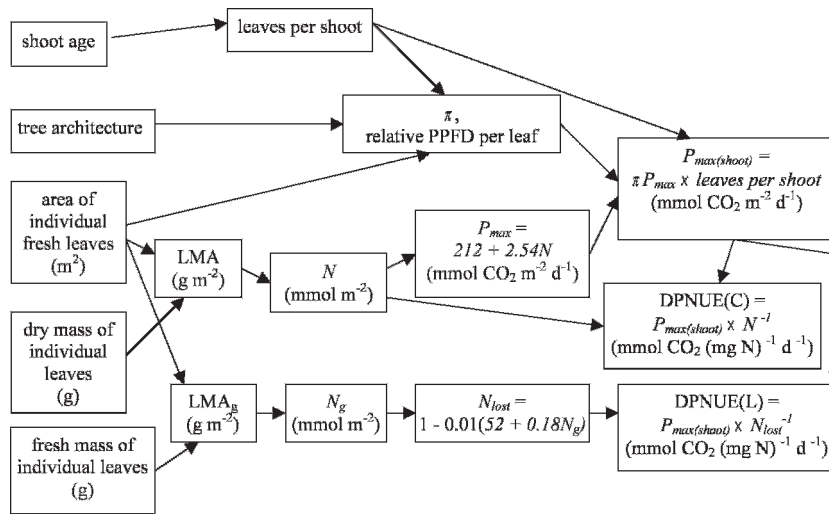


FIGURE 1. A diagram showing the steps for estimating the two values of daily photosynthetic nitrogen use efficiency (DPNUE) and the potential rate of shoot-specific photosynthesis ($P_{max(shoot)}$) examined in the study. The five boxes on the left show the measured values. The intermediate steps were partly based on the literature (see text for details and references).

The leaf traits that were altered in the simulations (number, area, leaf mass per area) were chosen to represent the large variability observed and well-documented in these traits in natural birch populations (Senn et al., 1992; Suomela and Ayres, 1994). The leaf mass per area (LMA) ratio of dry leaves was chosen because of its positive correlation with the total amount of nitrogen invested in foliage (Knops et al., 1997; Bylund and Nordell, 2001), hence indicating traits determining the photosynthetic capacity of leaves (Karlsson, 1991; Lempa et al., 2004; Riipi et al., 2005).

The number of leaves per shoot was included in the simulations because it varies from one to four within a single crown, depending on shoot age, as well as between tree individuals, which may have twofold differences in the number of leaves per shoot even when the shoot age is the same (Kaitaniemi and Ruohomäki, 2003). The area of individual leaves shows up to fourfold differences between trees (Senn et al., 1992; Kaitaniemi and Ruohomäki, 2003) and could be an alternative to the number of leaves per shoot in allocating the amount of photosynthetic tissue per shoot.

A single shoot with all its leaves was considered a separate unit of light capture because it is also the basic unit of growth. Therefore, for all individual short shoots, the contribution of each leaf within a shoot was summed to derive the total value. In long shoots, each leaf subtending a new bud was similarly considered a separate unit of light capture in the calculations. Accordingly, tree-specific averages based on these shoot-specific values were calculated for each tree and then used to compare the different combinations of LMA, individual leaf area, and the number of leaves per shoot.

Both LMA and the area of individual leaves were varied by up to two standard deviations (SD) around the mean of the study population. Different mean values were used for the leaves tending the new buds in long shoots, for one- and two-year-old short shoots and for all short shoots older than two years. The traits of basal long-shoot leaves were determined by the age of their mother shoot. Altogether, five different values were used for each shoot type: -2 SD, -1 SD, 0 SD (mean), $+1$ SD, and $+2$ SD.

Variation in individual leaf area is somewhat dependent on shoot age, with one standard deviation corresponding approximately to one-fourth of the average leaf area (Kaitaniemi and Ruohomäki, 2003). For example, the mean area of individual leaves in old short shoots, which were the most common shoot

type, was 870 mm^2 (SD = 210 mm^2). Compared with the apical parts of the stem, the area of short-shoot leaves in basal parts was 4% larger, but this effect was negligible relative to the effect of shoot age and was not included in the simulations. In LMA, one standard deviation (22 g m^{-2}) was equivalent to 35% of the mean value (63 g m^{-2}).

Both tree architecture and the age of the shoots were held constant for individual trees. In other words, the 3-D position of individual shoots within the crown of each experimental stem was constant in all simulations, and the age of the shoot partly determined the number of leaves in that shoot. The contribution of tree architecture was thus estimated by comparing differences in the light-capturing ability of individual trees, using natural variation in their architecture. The maximum leaf number of old short shoots was varied from two to three or four to represent the variation typical of mountain birch (Kaitaniemi and Ruohomäki, 2003). For new shoots produced by the late leaves of long shoots, the leaf number was always one, as no variation exists. For one-year-old shoots, the leaf number was always two, as very little variation exists, and for two-year-old shoots, it was either constant or varied randomly between two and three to represent within-tree variation. The leaf inclination angle was set to vary randomly between -30° and 30° for each leaf (Kaitaniemi and Ruohomäki, 2003).

The exact 3-D structure of the study trees was reconstructed in the LIGNUM program developed by the Finnish Forest Research Institute, and the amount of PPFD captured by each leaf was estimated as a relative proportion (π) assuming a standard overcast sky (Perttunen et al., 1998), as described in Kaitaniemi and Ruohomäki (2003). The standard overcast sky method was selected since it is computationally simple and known to yield a good estimate of the actual availability of PPFD (Gendron et al., 1998). Moreover, in Finland and other countries with highly variable weather, it is likely to provide simulation results that are much more practical for comparison purposes than methods based on an explicit sunpath, which produce an outcome dependent on the assumed daily weather conditions.

In the simulations, the sky was divided into 36 sectors (16 sectors for the largest tree due to computational restrictions), and the amount of radiation coming from each sector was calculated for each leaf. The proportion of PPFD captured was one for unshaded leaves, and between zero and one for shaded leaves, depending on the amount of self-shading. The relative PPFD

values estimated by LIGNUM are positively correlated with the measured values (Kaitaniemi and Ruohomäki, 2003). The area of green leaves was used in the estimation of light capture.

ESTIMATION OF PHOTOSYNTHETIC EFFICIENCY

The estimation of the potential photosynthetic rate was based on the equation by Karlsson (1991), which gives the potential maximum of daily CO₂ assimilation per unit leaf area in individual leaves (P_{max} , mmol CO₂ m⁻² d⁻¹) as a linear function of leaf nitrogen concentration (N , mmol m⁻²): $P_{max} = 212 + 2.54N$ ($R^2 = 0.68$; Fig. 1). Although the estimation of P_{max} was based on a clearly unconnected Swedish tree population, it was unlikely to cause any systematic bias because of the strong linear relationship between P_{max} and leaf nitrogen, which has also been observed at Kevo where corresponding values of P_{max} have been measured (Lempa et al., 2004; Riipi et al., 2005). Variation in P_{max} between trees was not included in the simulations, because P_{max} of individual leaves varies less than 10% around the regression line (Karlsson 1991), which is minor compared with the effect of leaf nitrogen concentration N .

Leaf nitrogen concentration was estimated based on simulated or observed LMA, with an assumed nitrogen per leaf dry mass of 2.3%. This proportion of nitrogen is typical of mature foliage in mountain birch (Ayres and MacLean, 1987), with small variation within the tree crown (12% of total variance between and within trees; Suomela and Ayres, 1994).

The average proportion of PPFD captured by the leaves of a shoot was used as a coefficient to estimate the potential shoot-specific photosynthetic rate as $P_{max(shoot)} = \pi P_{max} \times \text{leaf number}$ (Fig. 1). The use of the relative proportion of PPFD captured (π) may overestimate the actual differences in the photosynthetic rate of individual shoots because P_{max} might also be reached with π values of less than one if PPFD is sufficient to achieve photosynthetic saturation. However, even if this is the case, the simulation results based on tree-scale averages will be positively correlated with the field situation since it would be unrealistic to assume that all leaves would experience photosynthetic saturation all of the time.

Two different methods were used to calculate the daily photosynthetic nitrogen use efficiency (DPNUE). The first, DPNUE(L)_{shoot} was calculated for each shoot as $\text{DPNUE(L)}_{shoot} = P_{max(shoot)} / N_{lost}$, where N_{lost} is the amount of nitrogen lost at the abscission of senesced leaves in the autumn (Fig. 1). This was considered to best account for the costs associated with the allocation of nitrogen to foliage since the resorption efficiency of nitrogen (E , %) is linearly related to the nitrogen concentration of green mountain birch leaves (Nordell and Karlsson, 1995). The equation for resorption efficiency was calculated as the average of the equations plotted by Nordell and Karlsson (1995): $E = 52 + 0.18N_g$, where N_g is given in mmol nitrogen per m² of green leaf area. Although the equation is based on a Swedish tree population, it is likely to be applicable at Kevo because no differences in E between sites have been observed (Nordell and Karlsson, 1995). Variation in E between trees is comparable with the amount of variation explained by N_g in the regression line. However, this variation was ignored in the simulations because there are no data to suggest that E would be systematically associated with any other plant trait than that explained by N_g , and thus variation can be considered random with respect to the factors studied.

Similar to the nitrogen content of dry leaves, N_g was estimated on the basis of LMA_g, i.e., the LMA of green leaves.

Because a positive correlation was present between green and dry LMA ($r = 0.37$, $P = 0.005$), LMA_g was assumed to change by one standard deviation when dry LMA changed in the same proportion. Nitrogen per fresh leaf mass was assumed to be a constant 1.5% based on the typical values plotted in Nordell and Karlsson (1995).

The second method for calculating DPNUE was in relation to the total amount of nitrogen allocated to the leaves, which is a more common way of estimating nitrogen use efficiency (Hikosaka 2004), and is denoted as DPNUE(C)_{shoot} (Fig. 1). These values were also calculated for each shoot.

To assess the relationship between the estimated photosynthetic traits and tree growth, the values were correlated with the relative growth rate (RGR) of the experimental trees, which was approximated based on allometric biomass estimates (M) calculated according to Kaitaniemi and Ruohomäki (2003): $RGR = \log(M_t) - \log(M_{t-1})$, where t is the study year and $t - 1$ is the preceding year.

Results

SIMULATIONS WITH OBSERVED TREE TRAITS

$P_{max(shoot)}$ was positively dependent on LMA ($r = 0.49$, $P < 0.0001$; Fig. 2a) in the simulations with the original data, which included the differences between trees in crown architecture and in both leaf number and area (due to missing values of LMA, $N = 62$ in all correlations unless otherwise stated). A more than twofold variation in $P_{max(shoot)}$ around the mean was typical (Fig. 2a). Both LMA ($r = -0.24$, $P = 0.06$) and $P_{max(shoot)}$ ($r = -0.38$, $P = 0.003$) showed a negative correlation with RGR, whereas DPNUE(L)_{shoot} showed no correlation ($r = 0.21$, $P = 0.11$) and DPNUE(C)_{shoot} showed a positive correlation with RGR ($r = 0.62$, $P < 0.0001$; Fig. 2b).

A negative correlation existed between DPNUE(C)_{shoot} and the observed LMA ($r = -0.34$, $P < 0.007$; Fig. 2c), but DPNUE(L)_{shoot} showed no correlation with LMA ($r = -0.11$, $P = 0.38$; Fig. 2c). Both values of DPNUE clearly showed a less than twofold variation around the mean (Fig. 2c).

Based on the negative correlations with the total shoot number of the study trees, the largest stems (which had many shoots) had the lowest RGR ($r = -0.46$, $P < 0.0001$, $N = 69$), the largest leaf area per shoot ($r = 0.32$, $P = 0.01$, $N = 69$), and the smallest DPNUE(C)_{shoot} ($r = -0.61$, $P < 0.0001$, $N = 62$), but DPNUE(L)_{shoot} was not correlated with shoot number ($P > 0.18$). Neither was LMA associated with shoot number ($P > 0.62$).

SIMULATIONS WITH ALTERED TREE TRAITS

In the simulations where LMA, leaf number per shoot, and individual leaf area were varied each in turn, and where tree architecture was held constant, $P_{max(shoot)}$ was dependent on LMA or the area or number of individual leaves within a single shoot (Fig. 3). An increase in LMA by one SD caused an 11 to 16% increase in the average $P_{max(shoot)}$ of all trees (Fig. 3). Adding one more leaf to the shoot augmented the average $P_{max(shoot)}$ by 14 to 30%, with the increase diminishing as the shoot-specific leaf number and leaf area increased (Fig. 3). Increasing individual leaf area by one SD increased the average $P_{max(shoot)}$ by 12 to 44%, with the change becoming smaller toward the high shoot-specific leaf area (Fig. 3).

The effect of tree architecture is indicated by the amount of variation in $P_{max(shoot)}$ around any single point of the mean curve, i.e., when the other traits are constant. Its contribution was highest

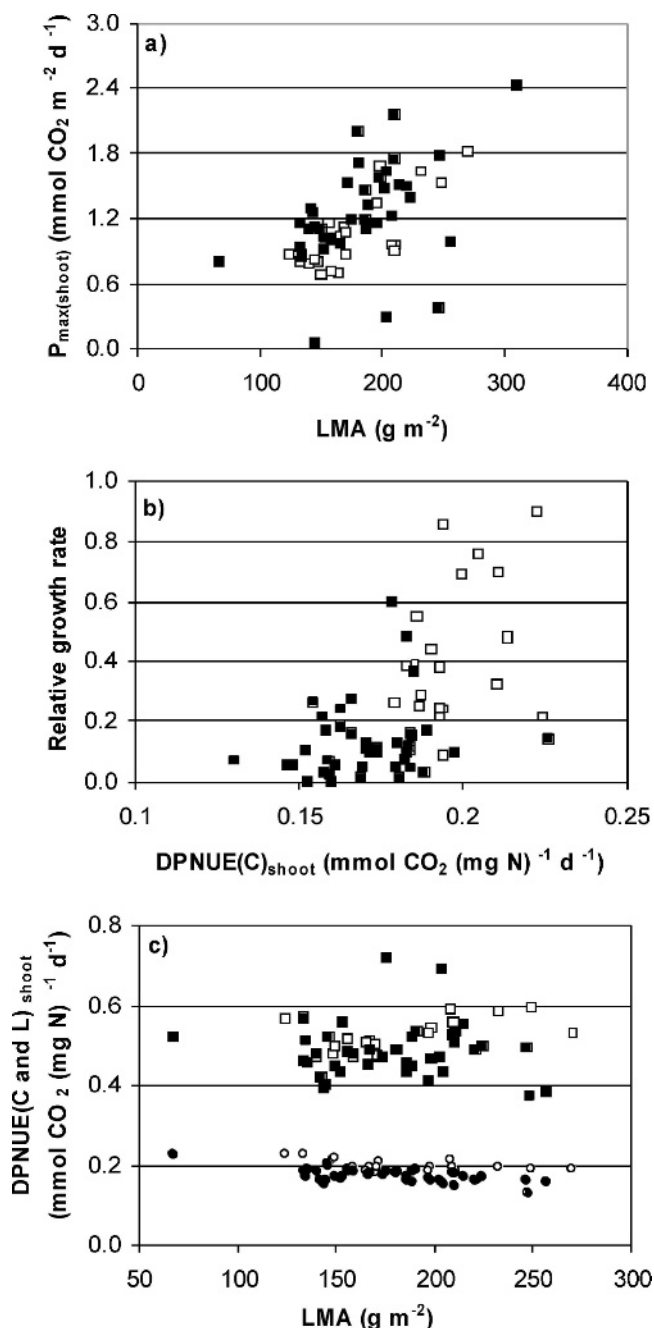


FIGURE 2. Values estimated for mountain birch trees using the leaf traits observed in the field. Young (white squares) and old (black squares) stems are shown separately. Graph (a) shows the dependence of the potential photosynthesis ($P_{max(shoot)}$) on leaf mass per area ratio (LMA), (b) shows the relationship between relative growth rate and daily photosynthetic nitrogen use efficiency based on the nitrogen invested in leaves (DPNU(C)_{shoot}), and (c) gives both DPNU(C)_{shoot} (bottom) and daily photosynthetic nitrogen use efficiency based on the nitrogen lost through leaf senescence (DPNU(L)_{shoot}, top) as function of LMA.

when the leaf area per shoot was the highest, but generally there was less than a twofold variation (Fig. 3).

The variation in age structure of shoots among individual trees or stems resulted in diverse proportions of shoots with a different number of leaves, producing variation in the average leaf area per shoot and resulting in overlapping values of $P_{max(shoot)}$ for tree groups belonging to adjacent leaf size classes

(Fig. 3). The amount of variation in the average leaf area within leaf size classes easily exceeded the contribution of one leaf to $P_{max(shoot)}$ (Fig. 3).

The mean values of both DPNU(L)_{shoot} and DPNU(C)_{shoot} decreased by 5 to 8% with the increase of individual leaf area within shoots by one SD (Fig. 4). Increasing the leaf number per shoot by one caused a 2 to 7% decrease in both DPNU values, with the decrease being the smallest toward the large shoot-specific leaf area (Fig. 4). In groups with different leaf numbers, the slopes indicating the relationship between leaf area per shoot and DPNU appeared equal, and the potential slight differences (not tested) were unlikely to have any biological importance compared with the amount of variability between individual tree stems (Fig. 4).

An increase in LMA by one SD had opposite effects on DPNU(L)_{shoot} and DPNU(C)_{shoot}. DPNU(L)_{shoot} increased 5 to 13%, with the increase being the highest toward high LMA (Figs. 4a–4c). In DPNU(C)_{shoot} there was a 2 to 5% decrease, the smallest decrease being toward high LMA (Figs. 4d–4f).

The effect of crown architecture on DPNU(C) and DPNU(L) was again indicated by variation around the mean curves and was generally less than 1.5-fold with all values of LMA and leaf area per shoot (Fig. 4). Similar to $P_{max(shoot)}$, variation in the average leaf area per shoot resulted in overlapping values of DPNU for tree groups belonging to adjacent leaf size classes when the average leaf area per shoot increased (Fig. 4).

Discussion

SIMULATIONS WITH OBSERVED TREE TRAITS

The study was designed to examine whether intraspecific variation in a set of foliage traits of mountain birch results from alternative strategies for achieving equal efficiency in light capture ($P_{max(shoot)}$) and nitrogen use (DPNU). Another possibility was that there is substantial variation among tree individuals also in light capture and nitrogen use due to potential trade-offs with other essential tree traits. Simulations with the tree traits observed in the field suggested that variation in foliage traits was unlikely to represent alternative strategies for maximizing $P_{max(shoot)}$ because a large amount of variation persisted in $P_{max(shoot)}$ when the intraspecific differences in the crown architecture and leaf traits were taken into account. DPNU (both C and L), in turn, had a magnitude of variation that was small compared with the magnitude of variation in its constituents, and almost equal DPNU could be achieved with different combinations of leaf traits and crown architecture originating from the tree population studied.

The seemingly small amount of variation in DPNU(C), however, was correlated with large differences in RGR, which indicates either a high sensitivity of RGR to changes in DPNU(C) or the contribution of yet-unidentified factors to RGR. This positive correlation, together with the observed lack of positive correlation between $P_{max(shoot)}$ and growth rate, is similar to that reported in interspecific comparisons of nitrogen use (Poorter et al., 1990) and suggests that a comparable relationship can be detected also within a single species.

DPNU(L), in turn, had no significant relationship with RGR despite its role as an indicator of nitrogen loss at leaf senescence. It is possible that the potential costs associated with lost nitrogen become realized in some other tree trait than RGR, which has a direct connection with DPNU(C) via the amount of photosynthates captured during the growth season.

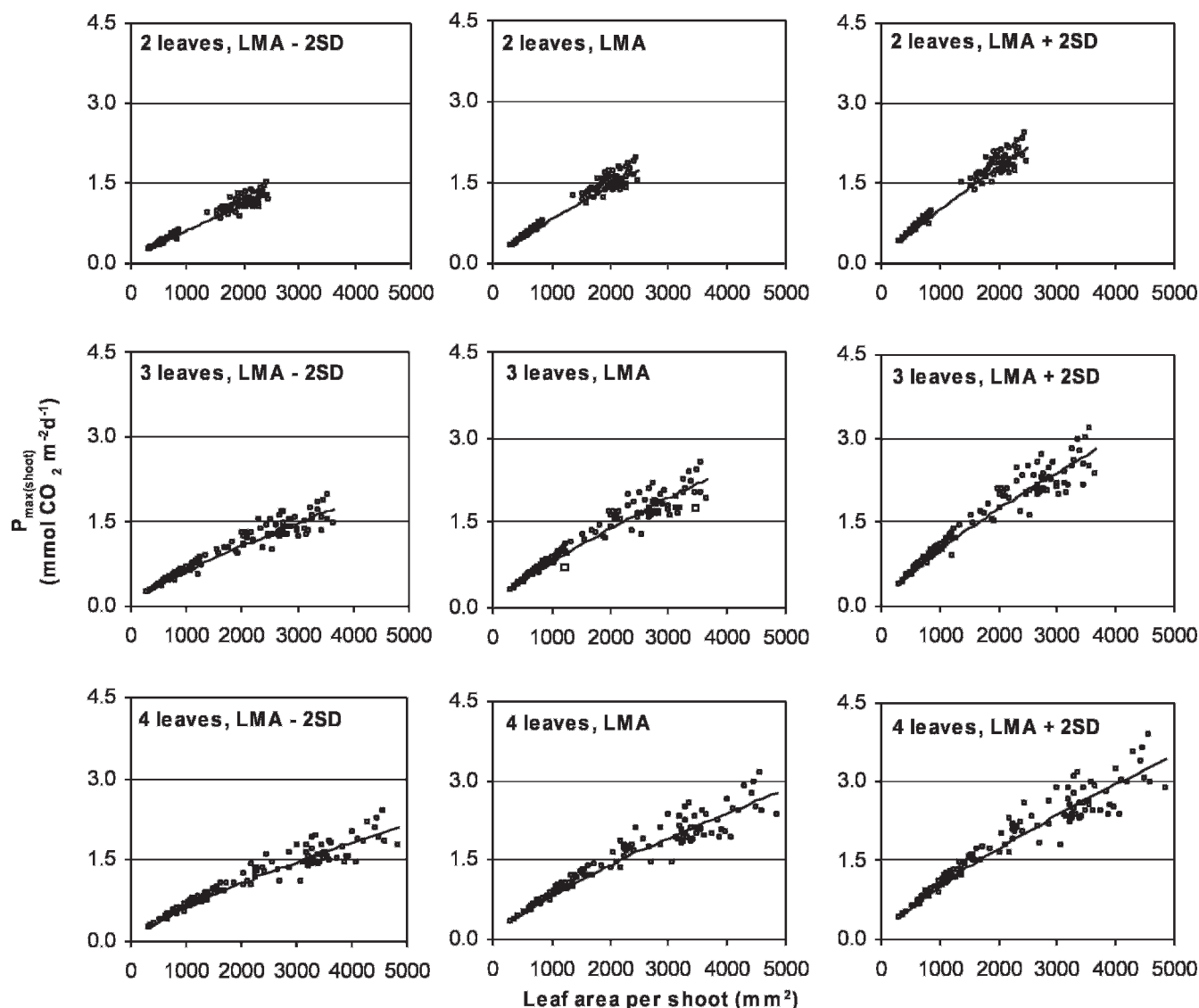


FIGURE 3. The relationship between the estimated maximum rate of shoot-specific photosynthesis ($P_{max(shoot)}$) and individual leaf area in mountain birch shoots with variable leaf number and leaf mass per area ratio (LMA). LMA was varied by up to ± 2 standard deviations (SD), and the same value was used for each shoot within the tree. Each subfigure shows the average values of shoots in individual tree stems calculated with two extreme leaf areas per shoot (-2 SD toward the left and $+2$ SD toward the right) and combined as a single series. The nonlinear regression lines show the average values for whole data.

SIMULATIONS WITH ALTERED TREE TRAITS

Simulations with a range of altered leaf traits showed that mountain birch has the potential to achieve an equivalent level of $P_{max(shoot)}$ or $DPNUE(C \text{ or } L)$ by simply varying the combination of four traits: leaf area, leaf number, LMA, and tree architecture. Leaf number, leaf area, and LMA almost additively increased $P_{max(shoot)}$. No maximum was achieved with the values used even though the relative change in $P_{max(shoot)}$ slowed toward the high leaf area per shoot. This probably indicated the increased effect of self-shading, as probably did also the more prominent effect of tree architecture as leaf area per shoot increased.

$DPNUE(L)$ and $DPNUE(C)$ both reached their maxima when the leaf area per shoot was the smallest, and linearly decreased as the leaf area per shoot increased, independent of whether the increase was caused by adding more leaves or by increasing individual leaf area. Both were also nonlinearly associated with LMA. The slight decrease in $DPNUE(C)_{shoot}$ with increasing LMA was also observed in the field and has been

documented in other species as well (Hikosaka, 2004). The increase in $DPNUE(L)$ with high LMA, in turn, was caused by the dependence of nitrogen resorption efficiency on the nitrogen concentration of leaves when LMA was high, as nitrogen resorption was simultaneously enhanced (Nordell and Karlsson, 1995). Similar to $P_{max(shoot)}$, $DPNUE(C)$ and $DPNUE(L)$ both showed more variation as the leaf area per shoot increased.

TRADE-OFFS BETWEEN MULTIPLE TRAITS?

It seemed unlikely that mountain birch uses different combinations of leaf traits and tree architecture to maintain equal efficiency in light capture and nitrogen use. A large amount of variation remained in $P_{max(shoot)}$, and $DPNUE$ (both C and L) also was far from a constant value in the simulations with the field data, together with the large variation observed in RGR. Trade-offs between the studied foliage traits and tree traits not covered in the simulations are a probable explanation for the variation

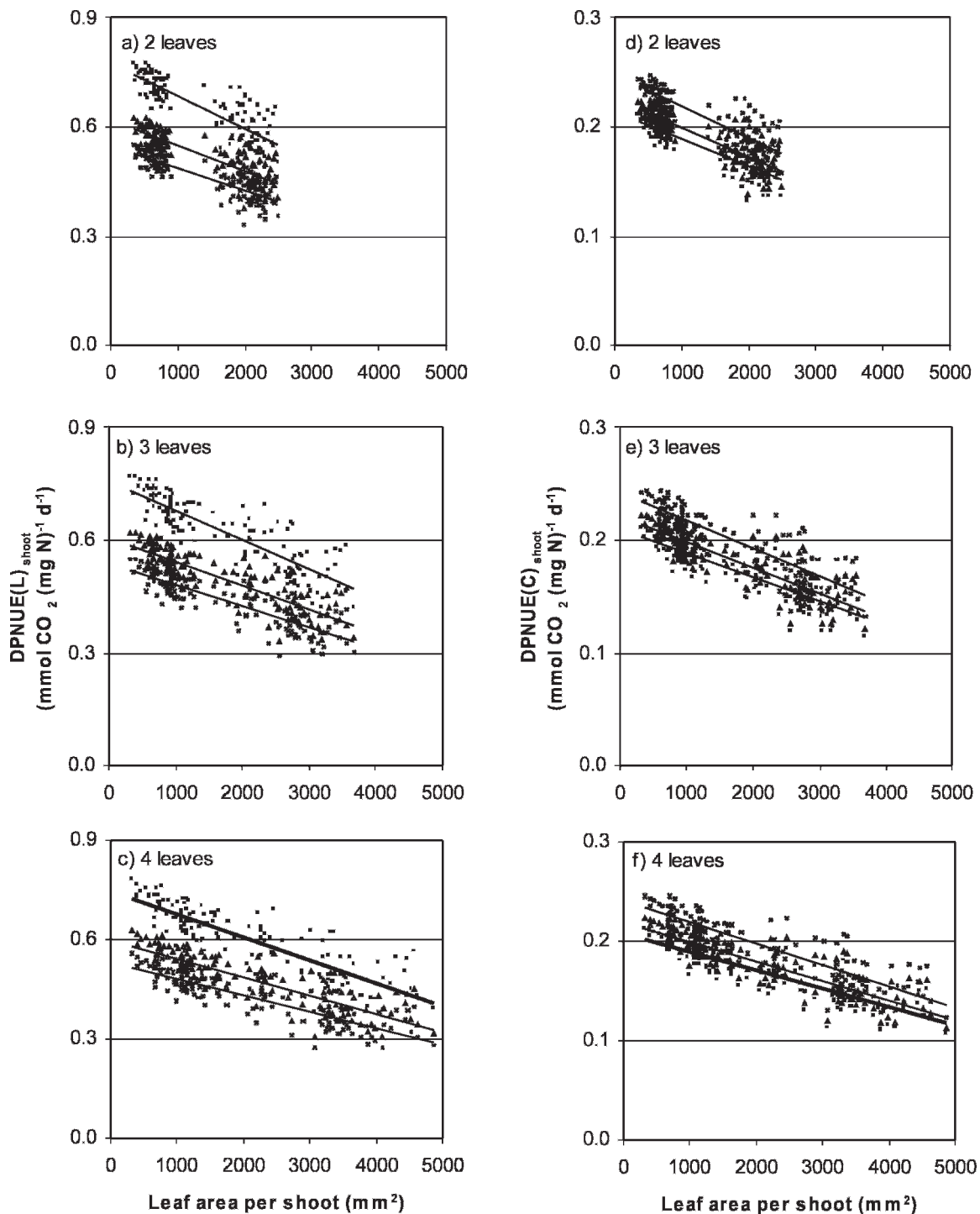


FIGURE 4. Relationships between $DPNUE(L)_{shoot}$ (a to c), $DPNUE(C)_{shoot}$ (d to f), and the total area and number of leaves per shoot in individual tree stems. Each of the three lines based on three different groups of dots represents the values for different LMA ratios. Stems having leaves with LMA + 2 SD are shown as squares, the mean LMA as triangles, and LMA - 2 SD as crosses. Each subfigure shows two extreme values of the leaf area per shoot (-2 SD toward the left and +2 SD toward the right) combined as a single continuous series. The linear regression lines show the average values for whole data. See Figures 2 and 3 for more information.

because a large number of characteristics can contribute to overall plant performance (Anten, 2005). A large number of potential trade-offs inevitably suggests the possibility of multiple alternative designs of equal fitness (Marks and Lechowicz, 2006). The potentially large range of different biotic and abiotic factors experienced by tree individuals through time has also been suggested to contribute to variation between trees (Leal and Thomas, 2003).

An obvious trade-off relates to the high growth rate of young birch stems, or young plants in general, as it requires a choice between the allocation of nitrogen to either short-shoot foliage or wood formation. The young stems, which had the lowest leaf number and the smallest leaves per shoot (Kaitaniemi and Ruohomäki, 2003), and hence the lowest total amount of nitrogen invested in short-shoot leaves, were the ones that had the fastest growth rate due to a high investment in long-shoot production.

More than half of all shoots in young stems can be new long shoots (Kaitaniemi and Ruohomäki, 2003), which have almost as high nitrogen concentration in their woody parts as leaves have (Partanen et al., 2001). It is, therefore, plausible to assume a trade-off can exist between nitrogen invested in long-shoot growth and in short shoots. Whether this is a true trade-off in terms of costs for mountain birch remains unknown since it was not possible to quantify the potential costs of these allocation alternatives. In many tree species a low growth rate might pose a risk in terms of poor competition for light within dense forest stands (Walters and Reich, 1996), but a high growth rate might also include risks due to lower mechanical support (King et al., 2006).

Part of the differences in the investment into long-shoot growth or short-shoot leaves may also indicate the local availability of nitrogen for individual trees, because a high availability of nitrogen in mountain birch typically becomes directly translated into increased growth instead of increased nitrogen investment in foliage (Weih and Karlsson, 1999a). In accordance with this allocation pattern, there was no correlation between LMA and growth rate.

The simulations also suggested a number of other potential trade-offs, including those between the traits studied, which can all contribute to the high variability in the foliage traits of mountain birch. They probably indicate potential benefits of alternative ways of allocating resources for different tree functions. A cost associated with the low nitrogen level of leaves with low LMA may be that a high proportion of captured photosynthates ($P_{max(shoot)}$) are required for maintenance purposes, with a consequent reduction in other tree functions. This can explain why high nitrogen content is typical of leaves of trees originating from the coldest high-altitude environments where temperature limits nutrient acquisition and photosynthesis (Körner and Diemer, 1987; Weih and Karlsson, 1999b; De Lillis et al., 2004).

A potential cost linked with high LMA, in turn, may be the slight decrease in $DPNUE(C)_{shoot}$ and the associated reduction in RGR, which was also observed in the field. A potential cost is also associated with producing less than the maximum leaf area per shoot because this, similar to low LMA, prevents $P_{max(shoot)}$ from reaching its peak value. The costs of reducing $P_{max(shoot)}$ may become realized during successive cold summers when nitrogen availability is low (Karlsson and Nordell, 1996) and mortality rates are higher (Tenow et al., 2004). $P_{max(shoot)}$ may also contribute to the reproductive success of old trees because old trees with high $P_{max(shoot)}$ seem to capture and store resources that are used for long shoot growth in young trees (Kaitaniemi and Ruohomäki, 2003).

LMA, as assumed in this study, may not always be directly proportional to the nitrogen concentration of leaves because the proportion of nitrogen may increase after a defoliation event to enhance compensatory photosynthesis (Hoogesteger and Karlsson, 1992). This suggests potential for flexibility in nitrogen usage, which is a prerequisite for the high intraspecific variation observed in the LMA ratio and nitrogen concentration of leaves (Suomela and Ayres, 1994). The combinations of foliage traits used in this study covered the potential consequences of this variation, but it is noteworthy that sometimes LMA may be associated with structural traits other than the total nitrogen amount of leaves (Hikosaka, 2004). Leaf thickness, for example, is one component of LMA (Hikosaka, 2004) and may have specific importance for mountain birch due to its role in resistance against herbivores (Riipi et al. 2005) because mountain birch stands experience frequent insect outbreaks (Ruohomäki et al., 2001).

Undoubtedly, variation also exists in leaf traits not altered in the simulations, such as nitrogen concentration and nitrogen

resorption, but their effects were partially estimated by varying the total amount of nitrogen in foliage. Irradiation-related variation in nitrogen allocation within the tree crown is typical for many species, but within the mountain birch crown nitrogen content per leaf is rather constant (Suomela and Ayres, 1994) and does not seem to vary in any systematic way according to shoot position (Bylund and Nordell, 2001), which probably relates to the high availability of light within sparse stands.

Yet another source of variation in mountain birch is its introgressive hybridization with *B. nana* (Kallio et al., 1983) and the consequent genetic component involved in the determination of foliage traits and crown architecture (Weih and Karlsson, 1999b; Haviola et al., 2006). This poses a challenging question as to whether or not the genetic component is an ultimate cause or a consequence of variation because it can simultaneously enhance the production of multiple adaptive solutions for the extremities of subarctic environment, as well as prevent the trees from obtaining the best possible solutions for specific growth conditions. This question suggests the need for studies where the allocation strategies of trees are investigated along with long-term monitoring of environmental variables and simultaneous quantification of genetic variability.

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