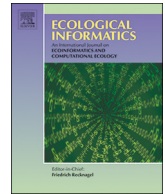




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# Computational analysis of the effects of light gradients and neighbouring species on foliar nitrogen



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## ABSTRACT

Foliar nitrogen is one of the key traits determining the photosynthetic capacity of trees. It is influenced by many environmental factors that are often confounded with the photosynthetic photon flux density (PPFD), which alone strongly modifies the nitrogen content and other foliar traits. We combined field measurements and computational estimates of light transmittance in 3D stands with different combinations of Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*) to decouple the effect of PPFD from other potential effects exerted by the species of neighbouring trees on the leaf nitrogen content per unit leaf area ( $N_{area}$ ) and leaf mass per area (LMA). Independent of the level of PPFD, silver birch had a significantly lower  $N_{area}$  and LMA when Scots pine was abundant in its neighbourhood compared with the presence of conspecific neighbours. In Scots pine,  $N_{area}$  and LMA were only dependent on PPFD and the branching order of shoots. In both species, the relationships between PPFD and  $N_{area}$  or LMA were nonlinear, especially at intermediate levels of PPFD. The levels of PPFD did not show any dependence on the species of the neighbouring trees. The responses of silver birch suggest that the species composition of the surrounding stand can influence foliar nitrogen, independent of the level of PPFD within the canopy.

## 1. Introduction

The mass, area, nitrogen content, age and longevity of leaves are suitable as proxies to describe the photosynthetic capacity of foliage in growth models, because they are simple to measure and show tight coupling with directly measured photosynthetic productivity (Evans, 1989; Niinemets, 2016; Sakschewski et al., 2015). Relationships among the components of photosynthetic capacity have received constant attention, and it is well established that light conditions experienced during the lifetime of foliage influence the traits (Niinemets et al., 2015). On the other hand, it is also known that the coupling of foliar traits with light is not as complete as theoretical models for optimising photosynthesis suggest. For example, the leaf nitrogen content per unit leaf area ( $N_{area}$ ) is almost never distributed optimally in order to maximize carbon gain within the canopy (Hikosaka, 2016; Niinemets et al., 2015). Because plants need to optimise many vital traits in order to ensure their evolutionary continuity (Anten, 2004; Hikosaka, 2016), variation in foliar traits may be linked to trade-offs between photosynthesis and other demands (Kaitaniemi, 2007; Nabeshima et al., 2001; Onoda et al., 2014).

Numerous sources of variation have been reported for foliar traits, but their relative importance in comparison to light gradients is poorly known, because many factors may be confounded with the availability of light. For example, in Scots pine, the levels of foliar nitrogen can vary as a result of the genotype (Reich et al., 1996), herbivory (Ericsson et al., 1985), forest type (Pensa and Sellin, 2002) and needle age (Gielen et al., 2000). Genotypic differences may indicate individual differences in crown structure and self-shading, the removal of foliage by herbivores may alter shading within the crown, the forest type may impose limits on the structure and light transmission capacity of the surrounding vegetation, and needle age may reflect proximity to incoming light. As substitutes to avoid confounding, Hilbert and Messier (1996) proposed artificially constructed trees to control for individual plant differences in light transmission, and Louarn et al. (2015) demonstrated the use of a model to separate the effect of local within-plant light availability from the effect of whole-plant nitrogen status. Tang et al. (2015) provide an example of using 3D tree models to analyse the light interception efficiency of variable crown forms.

Effects of the species mixture on foliar nitrogen have also been reported (Forey et al., 2016; Nickmans et al., 2015; Pollastrini et al.,

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2017), which is in line with the assumption that the potential variety of direct and indirect species interactions with effects on nitrogen increases as a function of tree diversity. Light gradients due to differences in canopy structure may be involved (Bauhus et al., 2004; le Maire et al., 2013), as well as indirect effects through, for instance, soil processes (de Andres et al., 2017; Forey et al., 2016). By combining a model with a large-scale field study, Forrester et al. (2018) concluded that multiple light-related interactions with site-specific variation may be involved in the growth dynamics of mixed stands.

To construct stand models in which foliar nitrogen is one of the driving variables, it would be applicable to identify and quantify the contribution of different confounding factors to nitrogen levels. According to our earlier findings, the identity of neighbouring tree species affected many growth habits in both Scots pine and silver birch, although it remained open whether the effects were a direct consequence of the species or caused by an unknown factor confounded with the species effect (Kaitaniemi and Lintunen, 2010; Lintunen and Kaitaniemi, 2010). The amount of light transmitted in different neighbourhoods remained one of the candidates for confounded factors, because simulations with 3D model trees suggested that the species somewhat differ in their light transmission characteristics (Lintunen et al., 2013). Our assumption is that if the neighbouring species influences  $N_{area}$  and LMA independently of the level of PPFD, the identity of the neighbouring species indicates the contribution of additional factors to the observed differences in growth habits of Scots pine and silver birch with different neighbouring species.

Here, we analysed the importance of one confounding factor for Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth.) by computationally decoupling the effects of the neighbouring species and photosynthetic photon flux density (PPFD) on  $N_{area}$  and leaf mass per area (LMA). Many studies (Niinemets et al., 2015), including studies with Scots pine and silver birch (Kull and Niinemets, 1993; Palmroth and Hari, 2001), have reported links between  $N_{area}$  and LMA (or its inverse specific leaf area, SLA) and the gradients of light within canopies.

## 2. Materials and methods

### 2.1. Estimation of PPFD

We reconstructed mock-ups of actual field plots, which consisted of structurally detailed 3D trees consisting of internodes (woody parts) and foliage within a core of 5 m radius around and including the study tree, and which had the surrounding forest simulated with a more simplified structure. The 3D construction of the study trees and crown-bordering neighbouring trees was based on the equations in Lintunen et al. (2011, 2012). The model plots were used to estimate the amount of PPFD reaching different crown positions equivalent to the field sampling positions of  $N_{area}$  and LMA. The plots were a subset of the study plots described in Table I of both Kaitaniemi and Lintunen (2010) and Lintunen and Kaitaniemi (2010). Because 3D models were only available for silver birch and Scots pine, we restricted the study to the subset that contained silver birch and Scots pine in different combinations (Fig. 1): Scots pine growing with either Scots pine (31 study trees) or silver birch (23 study trees) as the dominant crown-bordering neighbouring species, or silver birch growing with either Scots pine (15 study trees) or silver birch (20 study trees) as the dominant crown-bordering neighbouring species. Dominant crown-bordering neighbouring trees were defined as those that either touched or were potentially able to touch the study tree crown in the future by growing their current branches straight through an open space within a cylinder of 5-m radius centred at the stem base of the study tree. The study trees were 4 to 35-year-old individuals with a mean height ranging between sites from 2 to 16 m.

We considered PPFD in terms of photosynthetically active radiation (PAR) meaning that the scattering of radiation in the canopy could be

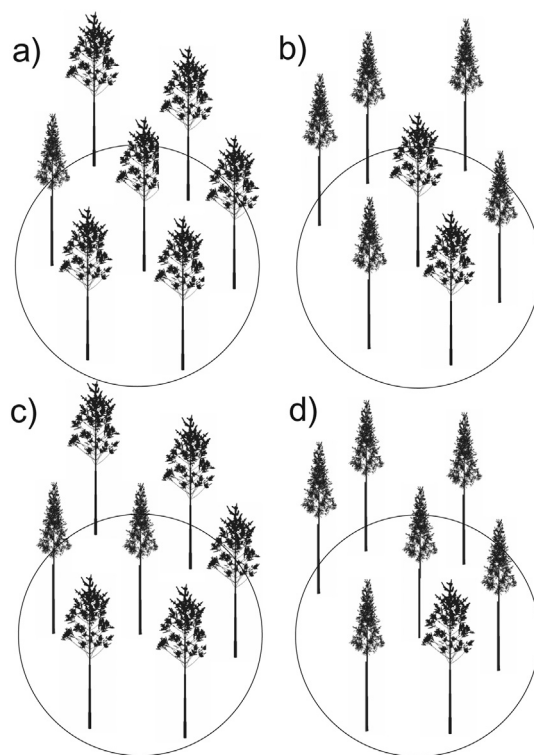


Fig. 1. The four species combinations investigated in the study included either Scots pine or silver birch as the target tree and as the dominant crown-bordering neighbouring species. a) Scots pine with Scots pine, b) Scots pine with silver birch, c) silver birch with Scots pine, and d) silver birch with silver birch. The average basal area of the dominant neighbouring species was around 80% of the total basal area of all neighbouring trees within a circle of 10-m diameter around the target tree (Lintunen and Kaitaniemi 2010).

ignored. PPFD reaching the study trees was estimated with the radiation model described in Lintunen et al. (2013), which included the placement and the detailed 3D structure of the individual target trees and neighbouring trees at the level of internodes and foliage (annual shoot cylinders in Scots pine and of individual leaves in silver birch) (see Appendix A.). A structurally homogeneous ‘edge forest’ extending to infinity was assumed to surround the plot beyond the crown-bordering neighbouring trees. PPFD transmitted through the edge forest was estimated using the species-specific LAI and crown layer depth adopted from the crown-bordering 3D neighbours. Attenuation of radiation in the edge forest was calculated using the Beer–Lambert law (Monsi, 2004).

Assuming a standard overcast sky, total shading caused by the crown bordering trees and the edge forest was calculated using ray casting from a sample position towards each of 16 sky azimuths divided into 10 inclination classes and the zenith. Shading caused by the needle cylinder of a Scots pine shoot was calculated as in Perttunen et al. (1998) and shading by leaves as in Lintunen et al. (2013); leaf transmittance of silver birch leaves was a constant 0.06, according to Ross (1981). In addition to foliar shading, we checked whether the ray hit any of the internodes (woody parts). When a hit was found, the PPFD coming from the particular sky sector was considered blocked (equal to 0). A brief account of radiation calculations is provided in Appendix A. If the equivalent field-sampling position was located inside the canopy, PPFD was computed for a total of four random positions within a voxel box with 20 cm side lengths around the sampling point, and the average was then used in the analysis. Four positions were used to even out the fine-scale variation of light in the crown.

The model partitioned the total PPFD into components transmitted through the neighbouring trees ( $PPFD_n$ ), that is the surrounding edge

forest was excluded, and with the surrounding forest included ( $PPFD_s$ ). Self-shading by the target tree was included in both  $PPFD_n$  and  $PPFD_s$ .

In the analyses, we transformed the values of  $PPFD_n$  and  $PPFD_s$  to relative  $PPFD$ , which was also estimated in the field on an overcast day, and which has been demonstrated to provide a suitable shortcut method to estimate long-term cumulative  $PPFD$  within forests (Gendron et al., 1998; Yoshimura and Yamashita, 2014). Therefore, the values of  $PPFD$  were only calculated for a single point in time and standardized with respect to the  $PPFD$  of an open overcast sky.

## 2.2. Field sampling

$N_{area}$  and LMA were measured from samples of full-grown foliage collected from two to five randomly oriented sample branches systematically selected from the basal, middle and apical crown parts, as in Lintunen and Kaitaniemi (2010). In order to replicate the topological position in the model, the 3D coordinates of the sampling points were recorded (Lintunen and Kaitaniemi, 2010).

In Scots pine, the samples consisted of full annual shoots, excluding the half-grown current-year shoots. To obtain the needle area and LMA, ten pairs of detached random needles were weighed and measured for width, length and thickness, both fresh and dry. To calculate  $N_{area}$ , the fresh needle area was transformed to the projected area using 2.55 as the ratio of the total to the projected area (Niinemets et al., 2015). The individual dry needle area was used in the calculation of LMA. All the needles of individual shoots were pooled for the analysis of nitrogen with the Kjeldahl method. The branching order of each shoot was recorded using the Gravelius order system.

In silver birch, the leaf samples of lower crown parts mainly originated from non-elongating short shoots, whereas the samples of uppermost crown parts frequently included two fully expanded basal leaves of elongating long shoots. Leaf area was measured digitally from fresh samples, and leaf weight and nitrogen were analysed from dried samples. The thermal sum above 5 °C was recorded for the foliage sampling dates and used as a covariate to control for any seasonal differences in foliar traits (Gielen et al., 2000; Tamm, 1951).

## 2.3. Measurements of $PPFD$

We also measured  $PPFD$  in the field to obtain a more complete evaluation of the radiation model than that presented in Lintunen et al., (2013). Previously, the model suggested that the proportion of transmitted  $PPFD$  increased in dense stands if the proportion of birch substantially increased (Lintunen et al., 2013). Because the largest differences in light transmission were detectable at low sampling heights, we examined the effect of neighbouring species on  $PPFD$  particularly at low measurement heights. These measurements also served as an indirect test to indicate whether the potential effect of neighbouring species on  $PPFD_s$  was fortified by basing the construction of the edge forest on the traits of the crown-bordering neighbours. A non-significant difference in  $PPFD_s$  would indicate that the transmittance of  $PPFD_s$  was not distinctly biased due to the assumed identical composition of the edge forest and the crown-bordering neighbours.

In the field,  $PPFD$  was measured on a uniformly overcast day with calibrated PAR sensors located either adjacent to the foliage sampling points or in other positions under or inside the canopy. Each reading of  $PPFD$  at the measurement point was standardized with respect to a simultaneous  $PPFD$  reading at an open site, and an average of these values was used to obtain the relative  $PPFD$  ( $PPFD_r$ ). The duration of individual measurements varied from one minute to a few hours. The 3D positions of sensors with respect to the neighbouring trees were recorded, and the corresponding sampling positions were used in the model stands to calculate  $PPFD_n$  and  $PPFD_s$ . The measurement height ranged from 0.2 to 5 m. The measured  $PPFD_r$  was also directly compared with  $N_{area}$  and LMA in those foliage sampling positions where  $PPFD_r$  was available.

## 2.4. Data analysis

We first evaluated model behaviour by testing the equality of slopes between modelled  $PPFD_s$  and measured  $PPFD_r$  for both neighbouring species using the full set of measurements. Then, we used generalized linear models to statistically decouple the effects of  $PPFD$  and neighbouring species on  $N_{area}$  and LMA for both Scots pine and silver birch. The models included as explanatory factors an estimate of  $PPFD$ , the neighbouring species, and also the thermal sum of the sampling date, because there was a weak linear negative association between  $N_{area}$  and the thermal sum and a weak linear positive association between LMA and the thermal sum in both Scots pine and silver birch. For Scots pine, the branching order of foliage sampling positions was also considered as a factor, because it influences many crown traits in Scots pine (Lintunen et al., 2011).

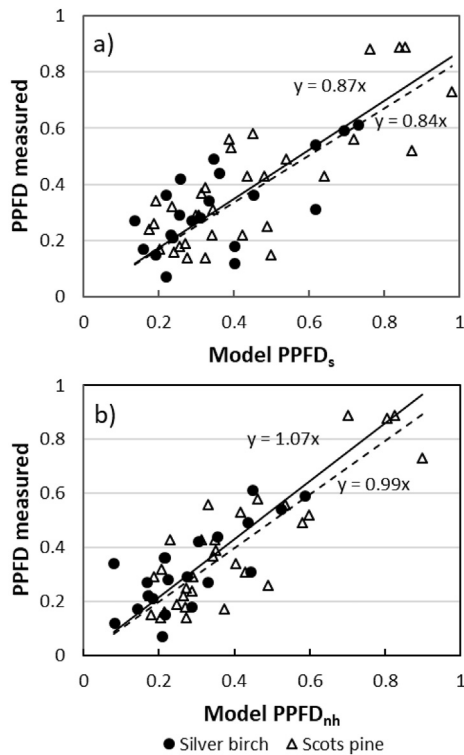
In the first step, we included both the neighbouring trees and the surrounding edge forest in the calculations using  $PPFD_s$  as an estimate of  $PPFD$ . However, because there was a risk of bias due to the assumed identical species distribution of the edge forest and the neighbourhood, we verified the result in the second step by considering only light transmitted through the neighbouring trees ( $PPFD_n$ ) to estimate  $PPFD$  for foliage sampling points. Because shading exerted by the edge forest was excluded from  $PPFD_n$ , we used the relative height of the sampling point ( $h_r$ , measurement height/tree height) as a replacement that was independent of model assumptions.  $h_r$  was considered to estimate proximity to the firmament visible through the gap formed by the trees of the edge forest. Due to observed nonlinearity, the combination of  $PPFD_n$  and  $h_r$  ( $PPFD_{nh}$ ) was calculated as  $PPFD_{nh} = -0.11 + 0.85Q_i + 0.61h_r$ , where the parameterisation giving the best fit with the measured values of  $PPFD_r$  was  $Q_i = 0.073 e^{2.14 PPFD_n}$  for Scots pine and  $Q_i = 0.04 e^{2.64 PPFD_n}$  for silver birch.

Significance tests of factors included in the statistical models were conducted using generalized estimating equations. An individual tree nested within a sampling site was considered as a repeated subject because of multiple samples taken from the same tree individual. Before final analyses, it was checked that none of the covariates had significant interactions with the explanatory factors. The residuals of the models were found to be normally distributed. In addition, we used correlative analyses to check the presumed positive relationship of  $PPFD$  with both  $N_{area}$  and LMA.

## 3. Results

$PPFD_s$  estimated with the model had a positive linear relationship with measured  $PPFD_r$  throughout the whole measurement range (Fig. 2a; for both species combined the slope was 0.86 with  $R^2 = 0.62$  and  $RMSE = 0.15$ ). A slightly stronger positive relationship was detected when  $PPFD_{nh}$  as the combination of  $PPFD_n$  and  $h_r$  was used to estimate the measured  $PPFD_r$  (Fig. 2b; for both species combined the slope was 1.01 with  $R^2 = 0.70$  and  $RMSE = 0.10$ ). The values of individual slopes for different neighbouring species (Fig. 2ab) were not significantly different from each other (for  $PPFD_r t_{49} = 0.40$  and  $P = .69$ ; for  $PPFD_{nh} t_{49} = 0.90$  and  $P = .37$ ). Neither was the effect of neighbouring species on the measured  $PPFD_r$  significant ( $\chi_1^2 = 1.33$ ,  $P = .25$ , 95% confidence range of measured  $PPFD_r$  for silver birch neighbours was 0.21–0.33 and for Scots pine 0.27–0.37). In both Scots pine ( $N = 310$  sampling points with  $PPFD_s$  and  $N = 16$  to 53 with  $PPFD_r$ ) and silver birch ( $N = 200$  sampling points with  $PPFD_s$  and  $N = 8$  with  $PPFD_r$ ), both  $N_{area}$  and LMA had a slight positive correlation with  $PPFD_s$  and  $PPFD_{nh}$  ( $r > 0.36$ ,  $P < .001$ ), as well as the measured  $PPFD_r$  ( $r > 0.31$ ,  $P < .1$ ).

In silver birch, the neighbouring species ( $\chi_1^2 = 5.85$ ,  $P = .02$ ) and  $PPFD_s$  ( $\chi_1^2 = 14.4$ ,  $P = .0001$ ) both had a significant effect on  $N_{area}$ , which was generally higher with silver birch neighbours and increased along with  $PPFD_s$  (Fig. 3a). The effect of species on LMA was marginally significant ( $\chi_1^2 = 2.75$ ,  $P < .1$ ), and followed a largely similar pattern



**Fig. 2.** The measured relative PPFD predicted with two alternative models. Prediction with  $PPFD_s$  in the upper figure was based on the assumption that the species composition of the whole stand was similar to the crown-bordering neighbourhood of the measurement point. Prediction with  $PPFD_{nh}$  included light transmittance only by the crown-bordering neighbours, and the effect of the remaining stand was considered using the relative height of the measurement point as an additional factor. Different symbols indicate the prominent crown-bordering species. The slope for silver birch is shown with a solid line and that for Scots pine with a dashed line.

in relation to  $PPFD_s$  as  $N_{area}$  (Fig. 3ab). The effect of  $PPFD_s$  on LMA was significant ( $\chi_1^2 = 16.7, P < .001$ ). The thermal sum somewhat influenced both  $N_{area}$  ( $\chi_1^2 = 3.14, P < .1$ ) and LMA ( $\chi_1^2 = 9.10, P = .003$ ).

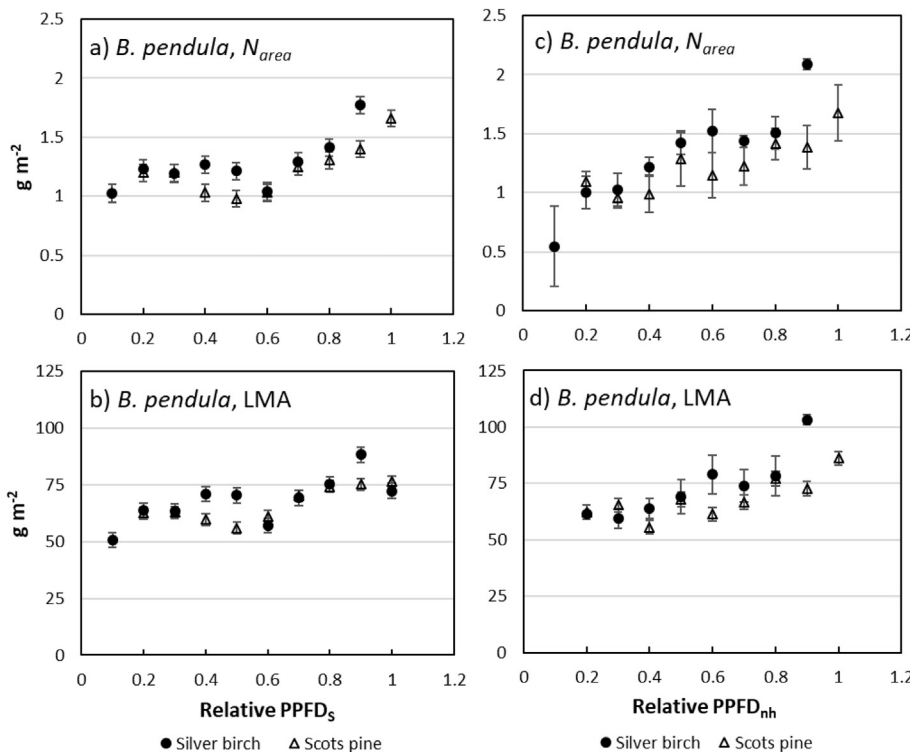
The results followed similar trends when  $PPFD_{nh}$  was used instead of  $PPFD_s$ .  $N_{area}$  was significantly increased with silver birch neighbours ( $\chi_1^2 = 9.22, P = .002$ ) and along with  $PPFD_{nh}$  ( $\chi_1^2 = 16.1, P < .0001$ ) (Fig. 3c), and LMA followed a similar pattern affected by silver birch ( $\chi_1^2 = 5.4, P = .02$ ) and  $PPFD_{nh}$  ( $\chi_1^2 = 17.14, P < .001$ ) (Fig. 3d). Again, the thermal sum influenced both  $N_{area}$  ( $\chi_1^2 = 10.56, P = .001$ ) and LMA ( $\chi_1^2 = 3.63, P = .06$ ).

In Scots pine,  $PPFD_s$  ( $\chi_1^2 = 8.24, P = .004$ , Fig. 4a) and the branching order ( $\chi_1^2 = 18.01, P = .001$ , Fig. 5a) were the only factors that significantly influenced  $N_{area}$ , and the effect of thermal sum was marginal ( $\chi_1^2 = 3.22, P < .1$ ). The effect of species was negligible ( $\chi_1^2 = 0.03, P = .86$ ). LMA was similarly significantly affected by  $PPFD_s$  ( $\chi_1^2 = 7.56, P = .006$ , Fig. 4b) and the branching order ( $\chi_1^2 = 29.66, P < .001$ , Fig. 5b), whereas the effect of neighbouring species was absent ( $\chi_1^2 = 0.17, P = .68$ ). The effect of the thermal sum was significant ( $\chi_1^2 = 3.95, P = .05$ ).

When  $PPFD_{nh}$  instead of  $PPFD_s$  was used for Scots pine,  $N_{area}$  was again affected by  $PPFD_{nh}$  ( $\chi_1^2 = 18.36, P < .001$ ) and branching order ( $\chi_1^2 = 17.73, P = .001$ ), and marginally by the thermal sum ( $\chi_1^2 = 3.4, P < .1$ ). The effect of neighbouring species was not significant ( $\chi_1^2 = 1.18, P = .28$ ). The relationships were largely similar to those with  $PPFD_s$  (Figs. 4c and 5c). Similarly, LMA was also affected by  $PPFD_{nh}$  ( $\chi_1^2 = 22.34, P < .001$ ) and branching order ( $\chi_1^2 = 27.27, P < .001$ ), and marginally by the thermal sum ( $\chi_1^2 = 3.67, P < .1$ ) (Figs. 4d and 5d). The effect of neighbouring species remained non-significant ( $\chi_1^2 = 1.07, P = .3$ ).

#### 4. Discussion

PPFD and other light characteristics may influence plant development in subtle ways (Niinemets et al., 1998; Niinemets and Valladares, 2004). Hence, light is a factor frequently considered in competition studies in which competition indices (Stadt et al., 2007), model-



**Fig. 3.** The effect of relative PPFD on  $N_{area}$  and LMA in the foliage of silver birch with different species as the prominent crown-bordering neighbour (circles = silver birch, triangles = Scots pine). The results are depicted using estimated marginal means (with 95% confidence limits, if available) calculated with values rounded to classes and adjusted for other effects in the model. The left side (a and b) shows the effect of  $PPFD_s$  and the right side (c and d) the effect of  $PPFD_{nh}$  (see Fig. 2).

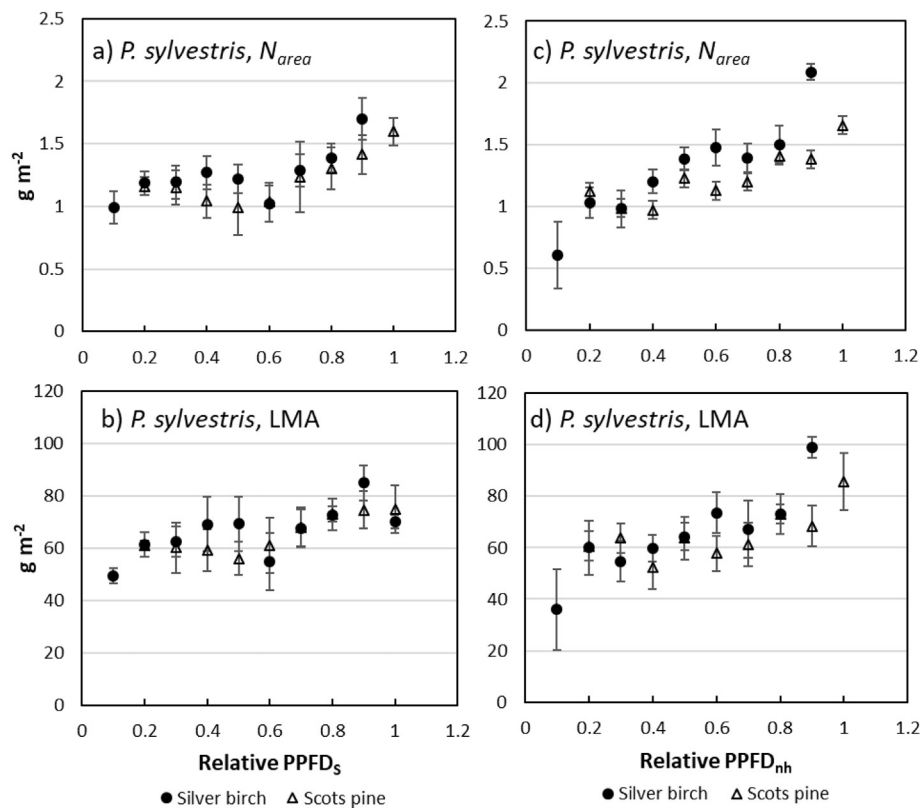


Fig. 4. The effect of relative PPFD on  $N_{area}$  and LMA in the foliage of Scots pine with different species as the prominent crown-bordering neighbour (circles = silver birch, triangles = Scots pine). The results are depicted using estimated marginal means (with 95% confidence limits, if available) calculated with values rounded to classes and adjusted for other effects in the model. The left side (a and b) shows the effect of  $PPFD_s$  and the right side (c and d) the effect of  $PPFD_{nh}$  (see Fig. 2).

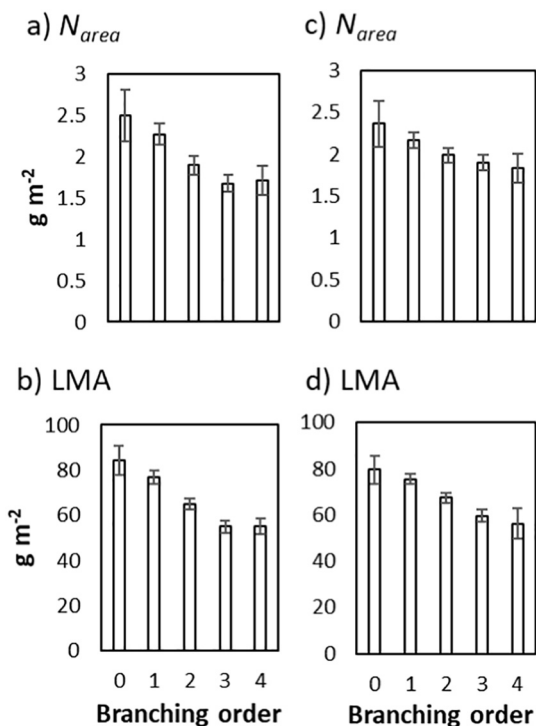


Fig. 5.  $N_{area}$  and LMA for different branching orders in Scots pine (0 = main trunk). Estimated marginal means and 95% confidence intervals are presented for models using either  $PPFD_s$  (a and b) or  $PPFD_{nh}$  (c and d).

estimated light levels (Percy et al., 2005), tree density treatments (Barbeito et al., 2014) and local measurements of light (Canham et al., 1994) serve as estimates of PPFD. However, it is laborious to separate PPFD from other confounding factors, especially in field competition

experiments with trees. Our study demonstrated how a 3D stand model can be used to decouple the amount of shading from other potential effects that neighbouring trees may have had on target trees in a field experiment.

Compared with conspecific neighbours, silver birch had a consistently lower  $N_{area}$  and lower LMA when Scots pine was abundant in its crown-bordering neighbourhood. Shading was estimated from PPFD received by the target tree foliage, which produced a predictable pattern where  $N_{area}$  and LMA increased with light, as also repeatedly observed in other studies (Ellsworth and Reich, 1993; Hollinger, 1996; Osada et al., 2014). However, in silver birch,  $N_{area}$  and LMA were also influenced by the identity of the neighbouring species beyond the effects of PPFD alone, because the levels of PPFD did not show any dependence on species identity. We assume that the observed PPFD was not affected by the neighbouring species because the density of field stands was lower and the species distribution of the surrounding stand more uniform than in the previous study in which a species effect was detected (Lintunen et al., 2013).

Soil-mediated factors are an obvious candidate for the neighbourhood effect observed at the whole plant level. The higher decomposition rate of birch foliage compared to pine foliage (Mikola, 1960) and the higher rate of microbial activity and nitrogen mineralization in soils with birch litter (Smolander and Kitunen, 2002) may contribute to the local availability of nitrogen, and gradually also influence other soil features (Hansson et al., 2011). In early summer, the quantity of light, and hence also PPFD, is higher with silver birch neighbours because the leaves are still emerging. Potential neighbourhood differences also exist in the quality of light (Aasamaa and Aphalo, 2016), i.e. in the radiation intensity of different wavelengths, which can alter plant allocation (Tegelberg et al., 2004). Both silver birch and Scots pine have shown photosynthetic responses that may reflect the dependence of light quality on the tree species composition of stands (Pollastrini et al., 2014). Overall, the processes may be complicated because somewhat contrasting foliar traits for silver birch were detected in a related study in which older trees, a less controlled spatial arrangement of

neighbouring species, and more restricted sampling positions for foliage were utilized (Pollastrini et al., 2017).

The marked effect of neighbouring species on leaf traits in silver birch suggests that it may be similarly rewarding to consider the species composition of stands when examining the photosynthetic traits of other tree species. In silver birch, many features of crown construction and allometric scaling have been found responsive to the neighbourhood (Kaitaniemi and Lintunen, 2008; Lintunen and Kaitaniemi, 2010). Forrester et al. (2018) also detected structural responses in species mixtures and concluded them to be important for light capture. In our models, these effects were largely built-in through the use of competition indices and other input parameters for crown construction (Lintunen et al., 2011). We also found a tendency for transient growth to be lower with Scots pine neighbours (Lintunen and Kaitaniemi, 2010), although no neighbourhood effects on long-term growth were detected (Kaitaniemi and Lintunen, 2010). Thus, the dynamically changing and potentially weather-dependent features of nitrogen allocation may also contribute to growth responses (Portsmouth and Niinemets, 2006; Sellin et al., 2013).

In both silver birch and Scots pine, the relationships between PPFD and  $N_{area}$  or LMA were nonlinear, especially at intermediate levels of PPFD. Part of this obviously indicated sensitivity to rounding when forming discrete classes for the values of PPFD, as well as potential sensitivity to the method for estimating PPFD without considering direct light. However, it seems unlikely that this was purely an artefact because similar nonlinearity was detected in both target species and with both neighbouring species. Fotis and Curtis (2017) also observed nonlinear relationships between PPFD and LMA and reported canopy complexity to be associated with the variable proportion of sun- and shade-acclimated leaf phenotypes at different canopy heights. In general, the relationships between PPFD,  $N_{area}$  and LMA exhibit considerable variation within a crown (Leal and Thomas, 2003; Niinemets, 1997), and may involve azimuthal or other positional effects beyond the effect of relative PPFD alone (Han et al., 2003; Iio et al., 2005). The probability of light gaps at boreal latitudes can also be sensitive to small variations in height within the mid-crown, where intermediate levels of PPFD are likely to occur (Ni et al., 1997). We consider it possible that the observed nonlinearity indicates limitations to the applicability of diffuse relative PPFD, and hypothesize that it may indicate foliar acclimation related to sun elevation and the amount of direct PPFD at boreal latitudes (Kuuluvainen and Pukkala, 1989; Ni et al., 1997).

In Scots pine,  $N_{area}$  and LMA were not significantly affected by the neighbouring species. However, our previous studies provided some evidence that Scots pine growth was augmented by silver birch neighbours (Kaitaniemi and Lintunen, 2010), as also reported in other studies with some limitations regarding growth conditions (Lappi-Seppälä, 1930; Mielikäinen, 1980; Valkonen and Ruuska, 2003; Shanin et al., 2014). Mixtures with other broadleaved species may also augment Scots pine growth (Pretzsch et al., 2015). In our experiment, soil-mediated effects were probably responsible for enhanced growth with silver birch neighbours, because PPFD was not influenced by the neighbouring species. In dense mixed stands, light may also contribute, because the proportion of transmitted PPFD was found to increase as the proportion of birch increased within the stand (Lintunen et al., 2013).

The finding that  $N_{area}$  and LMA in Scots pine were dependent on the branching order seems not to have been previously reported. However, in an otherwise more detailed analysis, except that PPFD was not directly estimated, we found the specific leaf area to primarily depend on shoot length (Lintunen et al., 2011). Because shoot length in Scots pine is largely determined by the branching order, we consider the alternatives as interchangeable explanations that indicate the favourability of growth positions in terms of the branching hierarchy and associated hydraulic architecture (Nikinmaa et al., 2003).

The growth dynamics of mixed stands remain a focus of research, because modern management practices favour species diversity.

Compared with monocultures, the complexity of study questions in mixtures rapidly increases as a function of the number of species interactions. Our results, including those reported in Lintunen et al. (2013), show how a model can help to eliminate factors that potentially have considerable importance. We can conclude that the allocation of nitrogen to silver birch foliage is partly governed by other mechanisms than the levels of PPFD. A future puzzle is to determine how these transient tree properties translate into long-term stand dynamics in conditions with more variability in the spatial arrangement of trees.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2018.09.009>.

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