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

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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 (Narea) 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.,...
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 $N_{\text{area}}$ and LMA. The plots were a subset of the study plots described in Table 1 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 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<sub>n</sub>). Self-shading by the target tree was included in both PPFD<sub>d</sub> and PPFD<sub>n</sub>. In the analyses, we transformed the values of PPFD<sub>d</sub> and PPFD, 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

\( N_{\text{area}} \) 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 \( N_{\text{area}} \) the fresh needle area was transformed to the projected area using 2.55 as the ratio of the total to the projected area (Ninemets 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., 2006; 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 was fortuitous by basing the construction of the edge forest on the traits of the crown-bordering neighbours. A non-significant difference in PPFD would indicate that the transmittance of PPFD 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). 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<sub>d</sub> and PPFD. The measurement height ranged from 0.2 to 5 m. The measured PPFD was also directly compared with \( N_{\text{area}} \) and LMA in those foliage sampling positions where PPFD, was available.

2.4. Data analysis

We first evaluated model behaviour by testing the equality of slopes between modelled PPFD and measured PPFD, 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 \( N_{\text{area}} \) 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 \( N_{\text{area}} \) 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, 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<sub>d</sub>), to estimate PPFD for foliage sampling points. Because shading exerted by the edge forest was excluded from PPFD<sub>d</sub>, we used the relative height of the sampling point (h<sub>r</sub>, measurement height/tree height) as a replacement that was independent of model assumptions. h<sub>r</sub> 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<sub>d</sub> and h<sub>r</sub> (PPFD<sub>d0</sub>) was calculated as PPFD<sub>d0</sub> = -0.11 + 0.85Q<sub>0</sub> + 0.61h<sub>r</sub>, where the parameterisation giving the best fit with the measured values of PPFD was \( Q_0 = 0.073 \pm 0.14 \text{PPFD} \), for Scots pine and \( Q_0 = 0.04 \pm 0.04 \text{PPFD} \), 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 \( N_{\text{area}} \) and LMA.

3. Results

PPFD<sub>d</sub> estimated with the model had a positive linear relationship with measured PPFD 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<sub>d0</sub> as the combination of PPFD<sub>d</sub> and h<sub>r</sub> was used to estimate the measured PPFD, (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<sub>d0</sub> = 0.40 and P = .69; for PPFD<sub>d0</sub> = 0.90 and P = .37). Neither was the effect of neighbouring species on the measured PPFD significant (\( \chi^2 = 1.33 \), P = .25, 95% confidence range of measured PPFD, 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, and N = 16 to 53 with PPFD<sub>d</sub>) and silver birch (N = 200 sampling points with PPFD, and N = 8 with PPFD<sub>d</sub>), both \( N_{\text{area}} \) and LMA had a slight positive correlation with PPFD<sub>d</sub> and PPFD<sub>d0</sub> (r > 0.36, P < .001), as well as the measured PPFD, (r > 0.31, P < .1).

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

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

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

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

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

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-
estimated light levels (Pearcy 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 $N_{\text{area}}$ 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 $N_{\text{area}}$ 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, $N_{\text{area}}$ 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

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**Fig. 4.** The effect of relative PPFD on $N_{\text{area}}$ 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, and the right side (c and d) the effect of PPFD$_{\text{nh}}$ (see Fig. 2).

**Fig. 5.** $N_{\text{area}}$ 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$_{\text{s}}$ (a and b) or PPFD$_{\text{nh}}$ (c and d).
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 neighbour- hood (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 $N_{\text{max}}$ 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, $N_{\text{max}}$ 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; Iío 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, $N_{\text{max}}$ 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 neigh- bours (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 $N_{\text{max}}$ 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 di- rectly 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.

References


