Ecological Informatics 48 (2018) 171–177

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

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

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ARTICLE INFO

Keywords:
3D stand model
Leaf nitrogen
Light gradient
Species interactions
Stand composition

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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https://doi.org/10.1016/j.ecoinf.2018.09.009
Received 2 November 2017; Received in revised form 5 September 2018; Accepted 6 September 2018

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 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).

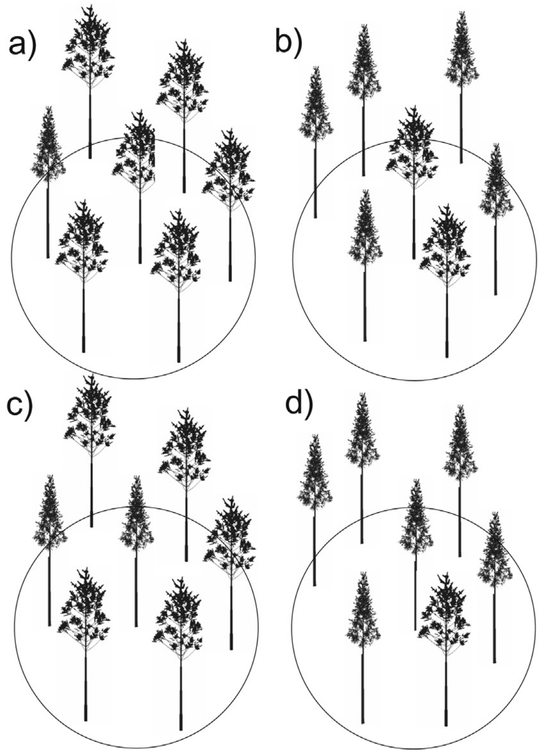

Fig. 1. The four species combinations investigated in the study included either Scots pine or silver birch as the target tree and as the dominant crown-bordering neighbouring species. a) Scots pine with Scots pine, b) Scots pine with silver birch, c) silver birch with Scots pine, and d) silver birch 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).

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