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Mechanical abrasion, and not competition for light, is the dominant canopy interaction in a temperate mixed forest

Peter Hajek [a], Dominik Seidel [b], Christoph Leuschner [a,*]

[a] Plant Ecology and Ecosystems Research, Albrecht von Haller Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany
[b] Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, 97331 Corvallis, OR, USA

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ABSTRACT

Competition for canopy space is a key process in forest dynamics, but the underlying mechanisms are not well understood in old-growth forests.

We combined laser-based canopy structural analysis and length-increment measurements of canopy branches for studying lateral and vertical crown expansion in four temperate broad-leaved tree species (*Fagus sylvatica*, *Fraxinus excelsior*, *Carpinus betulus*, *Tilia cordata*) in an old-growth temperate mixed forest. Using a 30 m-tall mobile canopy lift for accessing the canopy contact zone between different pairs of species, we were able to analyse the growth dynamics of more than 230 branches in their dependence on local light availability and neighbour species identity. The minimum distance between neighbouring crowns (crown shyness) was also determined for different species pairs.

Contrary to expectation, lateral branch increment in the contact zone was not dependent on light availability for three species; a positive relationship existed only for *Fraxinus*. More than 50 percent of the lateral branches of *Fagus*, *Carpinus* and *Tilia* were broken due to mechanical abrasion at least once within the last six years prior to our measurements (2006–2011). Only the thicker more robust branches of *Fraxinus* showed minor damages. Mechanical interaction in allospecific neighbourhood was highly asymmetric for the species combinations *Fraxinus–Tilia*, *Fraxinus–Carpinus*, *Fagus–Tilia*, and partly asymmetric in the pair *Fraxinus–Fagus* (lower damage in the respective first species). Crown shyness was highest in the *Fagus–Fraxinus* neighbourhood (average minimum distance: 1.0 m), intermediate in *Carpinus–Fagus* pairs (0.6 m), and low in *Fagus–Fagus* (0.2 m) and *Fagus–Tilia* pairs (0 m; direct contact).

We conclude that the dynamics of lateral canopy expansion in this mixed forest are mainly determined by mechanical interactions and not by competition for light. Interactions were in many cases asymmetric and depended on the species. This has important implications for forest dynamics modelling and forest management in mixed stands.

1. Introduction

Competition for canopy space is a key process shaping plant community dynamics (Purves et al., 2007). Since access to light is achieved through canopy space occupation, plant strategies to explore canopy volume are decisive for plant productivity, competitive success and eventually persistence in the community (Valladares and Niinemets, 2008). Competition for canopy space can be largely asymmetric when the neighbours differ in size or vitality, and/or the competing plants pursue different strategies to explore canopy volume through branch growth and leaf area placement, as may be the case in interspecific competition. Due to their importance for yield in agricultural and forestry systems, the mechanisms leading to competitive superiority for canopy space have been addressed in both modelling exercises and empirical studies (Shugart, 1984; Paquette and Messier, 2011). Most explanations relate to two mechanisms, (i) the efficiency of light interception and shade generation by the foliage (Niinemets, 2010), and (ii) the resource costs of canopy space exploration through branch and leaf production (Muth and Bazzaz, 2003; Reiter et al., 2005). According to the light-related theory, superiority is related to larger leaf areas per canopy volume or ground area and/or higher specific absorption of the foliage resulting in reduced light availability for competitors (Niinemets et al., 1998). An alternative, but not mutually exclusive, explanation of superior canopy space occupation is offered by the resource-based approach which

* Corresponding author at: Plant Ecology, University of Göttingen, Albrecht von Haller Institute for Plant Sciences, Untere Karspüle 2, 37073 Göttingen, Germany. Tel.: +49 (0)551 39 5718; fax: +49 (0)551 39 5701.
E-mail address: cleusch@gwdg.de (C. Leuschner).

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postulates that species with lower investment and maintenance costs in terms of carbon and nutrients spent for branches and foliage per canopy volume should gain superiority in aboveground competition (Givnish, 1988).

Yet, canopy interactions may not only be controlled by the efficiency of light capture and the resource economy of space exploration. There is increasing evidence that mechanical interactions may represent another important mechanism of canopy space competition besides resource competition. It has long been observed that mechanical abrasion of twigs and foliage due to wind-induced tree sways may represent a major structuring force in the crown development of trees (Putz et al., 1984; Rudnicki et al., 2004; Meng et al., 2006). By restricting the lateral growth of canopies, mechanical abrasion could shape the three-dimensional structure of trees in closed stands and influence the outcome of interspecific competition in mixed stands. Franco (1986) proposed three pathways of how crown expansion could proceed in forests, (1) by avoidance of neighbours through decelerated lateral growth which may lead to 'crown shyness', (2) superior lateral canopy expansion of one species which may suppress the lateral growth of others, or (3) lateral growth until mechanical abrasion occurs which also may result in crown shyness.

Attention to the mechanisms of competitive interactions in mixed forest canopies has rapidly increased in the last decade since foresters increasingly plant mixed stands instead of monocultures in the temperate zone and also in some tropical and boreal regions (Knoke et al., 2008; Bauhus and Schmerbeck, 2010). Species-rich forests and their functioning are a key topic of recent functional biodiversity research (Lang et al., 2011; Ratcliffe et al., 2015). Even though research was carried out considering resource allocation such as light or soil resource availability (Ng, 1977; Coomes and Grubb, 2000; DeClerck et al., 2006) our understanding of competition processes in the canopy of mature mixed forests is very limited. Main obstacles of scientific progress are the inaccessibility and complex structure of tree crowns and the long timespans involved in canopy interactions. Modelling approaches have generated insight to canopy interactions in virtual mixed forests with trees of idealized crown shape, but they can hardly mirror processes in the contact zone of real mixed forest canopies, where crown shape greatly deviates from the idealized form (Seidel et al., 2011).

In our study we combined laser-based three-dimensional canopy structure analysis with branch growth measurements in the canopy contact zone of different tree species in order to analyse the size of the inter-crown space and the dynamics of canopy space exploration under natural conditions in an old-growth mixed forest. Canopy access was achieved with a mobile 30 m-canopy lift that allowed comparing the contact zone in various combinations of four common broad-leaved tree species (genera *Fagus*, *Fraxinus*, *Carpinus*, *Tilia*) and to contrast the contact zone of conspecific and allospecific neighbourhood constellations. In the interspecific contact zones, we searched for asymmetry in lateral crown space exploration among the competitors and attempted to relate the degree of 'crown shyness' (i.e. the distance between two adjacent tree crowns) to the identity of the involved species. We put a special emphasis on the separation of light vs. possible abrasion effects on the growth dynamics of terminal branches in the contact zone.

With the overall goal to study the mechanisms of canopy interaction in mixed forests, we tested the hypotheses that (i) the branches in the contact zone grow significantly less than those in the upper sun canopy without neighbour contact, and (ii) the growth reduction is mainly caused by mechanical interaction and not by light deficiency. We further hypothesized that (iii) the growth reduction in interspecific contact zones is typically asymmetric between the species, and (iv) species differences in lateral crown space exploration are related to different branch morphological properties of the species.

2. Materials and methods

2.1. Study site and tree species

The study was carried out in an old-growth species-rich, temperate broad-leaved forest in Hainich National Park, Thuringia (Central Germany, 51°05′29″N, 10°31′23″E) close to the village of Weberstedt. The study area is located at an elevation of 350 m a.s.l. and characterized by a sub-oceanic, cool-temperate climate with a distinct continental influence (mean annual temperature: 7.7 °C, mean annual precipitation: 590 mm; 1973–2004, Weberstedt station, data provided by Deutscher Wetterdienst). Mono-specific beech stands (*Hordelymo–Fagetum* and *Galio–Fagetum* communities) and mixed oak-hornbeam forests (*Stellario–Carpinetum* community) co-occur in the national park. Moderately fertile base-rich Luvisols developed from loess over Triassic limestone are the most widespread soil type (Mölder et al., 2008).

The five most abundant tree species in the forest, Fagus sylvatica L. (European beech), Fraxinus excelsior L. (European ash), Carpinus betulus L. (European hornbeam), Tilia cordata Mill. (small-leaved lime) and Acer pseudoplatanus L. (sycamore maple), form mixed patches with variable tree species composition and diversity. The investigated mixed stand is located in a forest that has been managed extensively by selection cutting during the past decades until all forest operations ceased with the declaration of the national park in 1997. The site is covered by forest since several centuries and thus represents ancient woodland with respect to stand continuity. For the study of neighbourhood interactions, we selected groups of trees with up to seven individuals forming different neighbourhood constellations (cluster) between the four chosen tree species (*F. sylvatica*, *F. excelsior*, *C. betulus* and *T. cordata*). Tree clusters varied from patches dominated by *Fagus* to mixed patches with neighbourhoods built by all four species. With tree heights of 19 to 29 m, all trees reached into the upper canopy layer and the diameters at breast height (DBH) ranged between 12.3 and 66.8 cm. Due to only minimal impact by forest management, the canopy structure in the selected patches developed under naturally occurring competitive processes for at least 40 years. The average stand age of the canopy trees varies between 90 and 120 years (Schmidt et al., 2009).

2.2. Plot selection and terrestrial laser scanning (TLS) of canopy structure

We selected 63 pairs of trees in which one tree was always *Fagus* and the other one either *Fagus* ($n = 20$), *Fraxinus* (17), *Carpinus* (22) or *Tilia* (4). These 63 pairs were part of 19 clusters of trees with variable species composition (see above). All 19 clusters were analyzed in leaf-less condition in March 2009 for canopy structure with a terrestrial laser scanner (Z + F Imager 5006; Zoller und Fröhlich GmbH, Wangen i.A., Germany). The instrument was placed at different positions within the tree clusters (up to 12 positions) to capture the three-dimensional structure of the trees as completely as possible from several scanning positions. The focus was put on the contact zones of the canopies of the selected tree pairs. Operating in an angular step-width of 0.036 degrees in both horizontal and vertical direction and with a field of view of 310 (vertical) by 360 (horizontal) degrees, the Imager 5006 captured up to 43 million measurement points per scan. Each measurement point can be considered a laser beam that was reflected by an object in the vicinity of the scanner and detected by the receiver