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Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures

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ABSTRACT

Mixed-species forest stands are well explored in their favourable ecological, economical, and socio-economical functions and services compared with pure stands, but still poorly understood in their structure and functioning. Canopy structure and tree morphology affect the environmental conditions within the stand, the tree growth, and by this most forest functions and services. Here, I review how canopy structure and crown morphology in mixed stands can differ from pure stands and how this depends on the selection of tree species and interactions between them. The focus is on the macrostructure of canopy and crowns derived from the trees' positions, their convex crown hulls, and their space filling with branches.

In mixed canopies the sum of the crown projection area, but not the ground coverage by crowns, mostly exceeds pure stands due to multiple crown overlaps. The interspecific differences in crown shape and allometric scaling cause a 'selection effect' when complementary species are combined. In interspecific environment furthermore 'true mixing effects' like intraspecific shifts in size, shape, and inner space filling of crowns may occur. The much denser and more plastic canopy space filling in mixed stands may increase light interception, stand density, productivity, and growth resilience to disturbances. I discuss the relevance of interspecific interactions for forest management, model building, and theory development and draw perspectives of further research into stand canopy and crown structure.

Contents

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1. Introduction

Until the middle of the 20th century the strong influence of agronomics on forestry resulted in extensive mono-specific production systems. Since then, forest practice and forest science focused on more complex mixed-species stands (Puettmann et al., 2009). Evidence is growing that mixed-species forest stands can supply many ecological, economical and socio-cultural forests goods and services in a similar or even better way as far-from-nature monocultures (Gamfeldt et al., 2013). Tree species richness may trigger the variety of habitats and species diversity of other forest plants and animals (Gotelli and Colwell, 2001; Noss, 1990; Paillet et al., 2010), improve humus conditions and soil fertility (Binkley, 2003; Rothe and Binkley, 2001), the resilience to disturbances (Griess and Knoke, 2011), and the stand productivity (Morin et al., 2011; Piotto, 2007; Paquette and Messier, 2011). These advantages may be coupled with a depletion of soil water (Schume et al., 2004), loss of wood quality (Knoke and Seifert, 2008), increase of harvesting costs (Hanewinkel, 2001), or other drawbacks of mixed compared with pure stands. Some of the pros and cons may even change spatially (Forrester, 2013) and temporally (Lebourgeois et al., 2013; Río et al., 2014) depending on the prevailing site conditions. While research initially concentrated on comparing growth and yield between mixed and pure stands (Kelty, 1992; Pretzsch et al. 2010, 2013a and b), works by among others Forrester et al. (2006) and Rothe and Binkley (2001) gradually proceeded to analysing and understanding the mechanism behind mixing effects. Especially a better understanding of the species structural and functional traits and the dependency of these traits from the environmental conditions appears indispensable for developing new resource efficient multi-species production systems (Forrester, 2013; Richards et al., 2010).

Research into pure stands provides a wealth of knowledge about the interspecific variation of structural and functional traits (e.g., Augusto et al., 2002; Larcher, 2003; Purves et al., 2007). When cultivating tree species in mixture, complementary structural and functional traits can be useful for improving their resource efficiency and yield. Benefits can result among others from combining light demanding with shade tolerant species (Zöhrer, 1969), shallow with deep rooting species (Schmid and Kazda, 2001, 2002), slim-crowned and height oriented with wide-crowned and more laterally expanding species (Pretzsch and Schütze, 2005, 2009), or nitrogen-fixing with non-nitrogen-fixing species (Forrester et al., 2006).

Further analyses in this paper will distinguish between 'selection effects' and 'true mixing effects'. Suppose species with complementary traits are mixed but each species sticks to its behaviour which is known from pure stands, the mixed stand provides hardly any surprises. In this case the performance of the mixed stand is equal to the weighted mean of the growth of the neighbouring pure stands. As this kind of mixing effect results from nothing more than selecting the species, it is called selection effect or 'additive effect' (Forrester, 2013; Kelty, 1992). A 'true mixing effect' in contrast means that the interspecific environment triggers species traits which go beyond their behaviour known from pure stands (Forrester, 2013). Compared with the restriction in pure stands, interspecific neighbourhood may trigger abilities of crown expansion and interlocking which the species acquired by their mutual co-evolution in the past, but which are rather irrelevant, undesired by forestry, or even unknown as long as the species grow in pure stands. However, when crowns and roots are let off the leash in mixed stands they may develop a behaviour not known from pure stands but highly relevant for understanding, modelling and predicting mixed stand dynamics. A synonymous term for the true mixing effect is 'multiplicative effect' (Kelty, 1992; Rothe, 1997, pp. 4, 150).

Because of their size, firm position, and longevity, tree crowns both reflect and determine many ecosystem characteristics, functions, and services (Franklin and Spies, 1991; Ishii et al., 2004; Ozanne et al., 2003). On the one hand the crown size indicates leaf area and reflects the light interception and growing conditions of individual trees within the stand (Assmann, 1970, pp. 111–122; Binkley et al., 2013). Thus crown and canopy structures reflect the individual trees' light interception (Sterba and Amateis, 1998; Webster and Lorimer, 2003). On the other hand crown morphology and the resulting canopy structure determines among others the within-stand environmental conditions, the stand productivity, stand stability and resilience, habitat structure, and even the aesthetic value of a stand.

By forming the local environmental conditions within the stand (e.g., interception of light and precipitation) the structure of the canopy and crowns is crucial for the feedback between structure → environment → growth which drives population dynamics (Fig. 1). By selecting two species with differing morphological traits the canopy structure is varied compared with pure stands. The modified structural pattern of the canopy can form interspecific environmental conditions which trigger 'true mixing effects' which go beyond the species' behaviour in pure stands. A result of the slow but continual feedback between structure, environment, and tree growth (bold arrows in Fig. 1) can be the morphological acclimation of the coexisting trees to their interspecific environment. This reflects that the crown morphology and resulting canopy structure which are in the focus of this review are both pivotal drivers and result of stand dynamics.

This review of canopy space filling and tree crown morphology in mixed stands is based on literature, own data of classical tree crown measurement on long-term experimental plots, and advanced measurements by terrestrial laser scanning (TLidar). The focus is on the macro-structure of canopy and crowns accessible by measuring the position (tree coordinates) and convex crown hull (tree height, height to the crown base, 8 crown radii) of individual trees in pure and mixed stands. Based on the degree of crown engagement and the degree of ground cover by crowns I first show how the canopy structure of mixed stands can differ from pure stands. Canopy space filling in mixed stands is determined by both the interspecific differences (selection effects) and the intraspecific variability of tree crown morphology (true mixing effects). Therefore the review continues with the interspecific differences in crown size and morphology. Subsequently the focus is on the intraspecific morphological shift which trees show when growing in mixed instead of pure stands. These emergent properties were hardly analysed so far and are essential for understanding, modelling, and developing efficient mixed species production systems. In the discussion I stress the relevance of knowledge of canopy structure and crown morphology for forest management

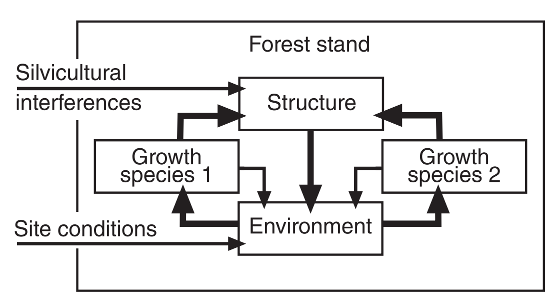

Fig. 1. Feedback loop between stand structure, environmental conditions, and tree growth in a two-species stand. The outer feedback loops structure → environment → growth → structure (bold arrows) are slow, the inner loops environment → growth → environment work faster. Further explanation given in the text.

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