Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient

David I. Forrester [a,*], Axel T. Albrecht [b]

[a] *Faculty of Environment and Natural Resources, Freiburg University, Tennenbacherstr. 4, 79108 Freiburg, Germany*
[b] *Forest Research Institute of Baden-Württemberg, Wonnhaldestr. 4, 79100 Freiburg, Germany*

ABSTRACT

There is great interest in how species interactions change along spatial gradients in resource availability and climatic conditions. Many studies have shown that facilitation or complementary effects increase as growing conditions become harsher, however, several studies in forests have recently shown the opposite trend. Increasing complementary effects with improving growing conditions may result when species interactions influence light absorption or use. This hypothesis was tested in mixed-species forests of *Abies alba* Mill. and *Picea abies* (L.) Karst. in south-western Germany where complementary effects on growth increased as climatic conditions improved. The absorption of photosynthetically active radiation (APAR) by individual trees was predicted using a detailed light model. Light-use efficiency (LUE) of individual trees was estimated as basal area growth per unit APAR. APAR and LUE were modelled as functions of crown size, climatic variables and the species composition and density of the neighbourhood of individual trees. For a given tree size, APAR (for both species) and LUE (of *A. alba* trees) were greater for trees in mixed-species neighbourhoods than monospecific neighbourhoods and this complementary effect increased as climatic conditions improved and on sites with faster growing trees. Increases in APAR for *A. alba* probably resulted because shading from *P. abies* trees was less intense than that from other *A. alba* trees on the more productive site. The species composition of individual tree neighbourhoods did not influence relationships between stem diameter and crown diameter or height to the crown base, for either species. However, the height of each species, for a given stem diameter, increased as the proportion of a given tree's neighbourhood basal area that was composed of the same species increased. This change in crown architecture could also have contributed to the complementarity effects in these stands. Increasing complementary effects with improving growing conditions is consistent with the stress-gradient hypothesis if competition for light is considered to be the stressor. This study shows that such a spatial pattern in species interactions could be associated with increasing differences in APAR or LUE between mixtures and monocultures as climatic conditions become more favourable.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Many studies have shown that mixed-species forests and plantations can have higher biomass productivity than monocultures, given the correct conditions (Assmann, 1970; Binkley, 1992; Kelty, 1992; Forrester et al., 2006; Forrester, 2014). The complementary interactions driving this response are often described in terms of facilitation and competitive reduction. Facilitation occurs where at least one species has a positive influence on the growth or survival of another. Competitive reduction occurs where intense intra-specific competition in monocultures is replaced by a less

intense inter-specific competition in mixtures (Vandermeer, 1989). Many studies have shown that the interactions between a given pair of species are not static, but change spatially within and between stands, and temporally as stands develop and climatic conditions change (Brooker, 2006; Forrester, 2014). These dynamics are often described using the stress-gradient hypothesis, which suggests that facilitative interactions become more important as growing conditions become harsher (Bertness and Callaway, 1994; He et al., 2013). However, several studies in forests have shown that complementary effects for a given species combination can also increase as resource availability increases or climatic conditions improve (Pretzsch et al., 2010; Coates et al., 2013; Forrester et al., 2013b). At first glance this appears to contradict the stress-gradient hypothesis. However, increasing complementarity with increasing productivity could occur if

* Corresponding author. Tel.: +49 7612038628.
 E-mail addresses: david.forrester@waldbau.uni-freiburg.de (D.I. Forrester), axel.albrecht@Forst.bwl.de (A.T. Albrecht).

interactions influence the absorption of photosynthetically active radiation (APAR) or light-use efficiency (LUE; growth per unit APAR) (Forrester, 2014). That is, as productivity and stand leaf area increases, so does competition for light, so any interaction that improves APAR or LUE could become increasingly useful. Interactions that influence light are probably present in most mixtures, even if they are not the most important interactions.

Increased individual tree APAR could occur in mixtures due to inter-specific differences in crown heights and crown architectures. Several studies have found intra-specific changes in crown architecture in response to thinning, spacing treatments or mixing species (Bauhus et al., 2004; Ryan et al., 2004; Forrester et al., 2012a; Bayer et al., 2013; Dieler and Pretzsch, 2013; Metz et al., 2013). Causes of increased LUE (calculated as aboveground growth per APAR) could be increases in the availability of other resources that enable higher rates of photosynthesis for a given APAR or shifts in biomass partitioning from belowground to aboveground as a result of increasing belowground resource availability (Binkley et al., 2004; Litton et al., 2007; Poorter et al., 2012).

None of the forest studies that found increasing complementarity with increasing resource availability or improving climatic conditions actually measured or predicted light absorption (Pretzsch et al., 2010; Coates et al., 2013; Forrester et al., 2013b), however some suggested that differences in APAR, LUE or shade tolerance might have contributed to the effect (Forrester et al., 2013b). Studies at single sites have shown that mixtures that were more productive than monocultures also absorbed more light and were more light-use efficient (Binkley et al., 1992; Forrester et al., 2012b) and a recent review showed that LUE generally increases (but does not decline) as growth increases in forests or plantations (Binkley, 2012). However, those single-site studies measured total stand APAR and measurements of individual tree light-use efficiency are generally restricted to monocultures (Binkley, 2012), with only a few studies in mixtures (Charbonnier et al., 2013; le Maire et al., 2013), each of which focused on single sites. By using stand-level measures it is not possible to separate the total APAR by each species, or to examine whether trees of all sizes responded in the same way. Also, single sites cannot be used to examine the spatial dynamics of these complementary effects. The objective of this study was to model individual tree APAR and LUE in mixed-species *Abies alba* and *Picea abies* forests where complementary effects were found to increase as site quality or climatic conditions became more favourable (Forrester et al., 2013b). We hypothesised that the complementary effect on growth increased because the differences in APAR and LUE between trees in mixtures vs. monocultures also increased as site quality or climatic conditions improved.

2. Methods

2.1. Site characteristics and experimental design

Tree growth, APAR and LUE were examined at six sites in Baden-Württemberg, Germany (Table 1). These were in the Black Forest (Schwarzwald; sites: 221–223, 225), the Swabian-Franconian Forest (Schwäbisch-Fränkischer Wald; site 224), and the southwestern Swabian Alp (Südwest-Alb; site 220). The climate is temperate to cool-temperate and the annual precipitation ranges from about 900 to 1900 mm, with winter maxima at the high precipitation sites and summer maxima at the low precipitation sites. Additional site and stand information is provided in Table 1 and more detail can be found in Forrester et al. (2013b).

The plots were about 50 m × 50 m to 60 m × 60 m and were established between 1979 and 1981, when there had been no harvesting for the previous ten years and the trees were aged between

85 and 125 years. The stands were dominated by *A. alba* and *P. abies* but there were also some *Pinus sylvestris* and *Fagus sylvatica* trees present. *P. silvestris* was only present as scattered individuals while *F. sylvatica* comprised more substantial proportions in the standing volume at the beginning of the experiment (220: 0–9%, 222: 12–26%, 223: 14–26%, 225: 0–6%). At each site, four harvesting regimes were applied including a control as well as short, medium and long regeneration periods. This resulted in a wide range of growing conditions at the individual-tree level including a range of densities as well as trees that experienced anything from only intra-specific competition to only inter-specific competition (Forrester et al., 2013b).

2.2. Data collection

The diameters (at 1.3 m) of all trees were measured at approximately 5-year intervals between 1979 and 2007 and the stem positions of all overstory trees were mapped. Climatic data, including monthly sunshine hours, precipitation and mean daily maximum and minimum temperatures, were obtained from the German Weather Bureau (Deutscher Wetterdienst; DWD). Solar radiation data are not available for these sites so monthly solar radiation was calculated from the mean of two forms of the Angstrom formula, one that uses sunshine hours (Allen et al., 1998) and another that uses the difference between minimum and maximum temperatures (Kolebaje and Mustapha, 2012). On average the latter were 25% greater than the former.

2.3. Light model, parameterisation and predictions

The measurement or prediction of APAR by an individual tree crown within a forest canopy is difficult and requires three dimensional modelling or very intensive field measurements. The canopies in this study were about 30 m tall so APAR was predicted using the Maestra model (Grace et al., 1987; Wang and Jarvis, 1990; Medlyn, 2004). This three dimensional tree-level model predicts APAR by individual trees based on their crown architecture (crown dimensions, leaf area and leaf angle distributions, etc.) while also considering shading from neighbouring trees by representing the canopy as an array of tree crowns (shaped as spheres, cones, ellipses, half-ellipses) whose positions are defined by *x* and *y* coordinates. The slope and aspect of a site is also taken into account in the *x* and *y* directions. Each crown is divided into horizontal layers and each layer is divided into several segments, and for each, the leaf-area density (LAD; leaf area per crown volume, $m^2 \ m^{-3}$), leaf angle distributions and leaf optical properties are used to model APAR. The penetration of radiation through the canopy is modelled using the radiative transfer model of Norman and Welles (1983). Transmission of diffuse radiation is modelled using the method of Norman (1979) and the beam fractions of radiation are calculated according to the hourly zenith and azimuth angles of the sun.

The data used to parameterise Maestra were obtained from field measurements and the literature. Vertical LAD distributions of *P. abies* (Ibrom et al., 2006; Gspaltl et al., 2013) and *A. alba* (Cescatti and Zorer, 2003) are very similar with a peak close to the middle of the crowns. Distributions were not available for *F. sylvatica*, however, the distributions for several other deciduous broadleaved species also peaked close to the middle of the crown (Nelson et al., 2014) and so for all species in this study the 3-parameter beta distribution by Gspaltl et al. (2013) was used (*a* = 3.53, *b* = 0.58, *c* = 0.78). The "a" parameter was adjusted from 1.09 in Gspaltl et al. because the Maestra model requires that the integral of the beta distribution is equal to one. Allometric leaf area equations for trees of this size are rare, but are available for these species in Bugmann (1994) and Burger (1949, 1951, 1952, 1953).