



Disentangling juvenile growth strategies of three shade-tolerant temperate forest tree species responding to a light gradient



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ABSTRACT

Light availability in forests is a strong driver for forest development and diversity. Tree species develop differently under varying levels of light. Understanding the reasons for the individual growth strategies of tree species is crucial to understand dynamics of forest communities. This study aims at further disentangling aboveground biomass allocation patterns and growth variables for saplings of the tree species sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.), and European ash (*Fraxinus excelsior* L.). Plants were destructively sampled along a light gradient. European beech allocated more biomass to its branches and less to its stem, in comparison to the other two species. The relative growth rate (RGR) and leaf mass area (LMA) of all species increased towards an asymptote along the increasing light gradient, whereas the leaf area ratio (LAR) decreased. The rate of increase and decrease differed among the tree species. Net assimilation rate (NAR) and absolute growth rate (AGR) both also increased with light availability, but the distinction among the species was not as clear. This study showed varying reactions of all three species to light and allowed a quantitative distinction among the species regarding their shade tolerance (ash < maple < beech), whereas the individual reaction was not always the typical reaction associated with shade tolerance.

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1. Introduction

The varying abilities of plant species to acclimate to and grow under specific site conditions determine their survival and success in colonizing an ecosystem. Site conditions are characterized by a certain supply of abiotic factors (e.g. water, nutrients, light, and temperature). Plant species have adapted to various combinations of abiotic factors, as resources for their growth. Favorable resource combinations result in maximal growth rates for the plants, because these factors influence the distribution of assimilate products among the plant organs (Kadereit, 2014). However, resources are limited and due to common demands for limited resources of associated species, plants growing in communities are then forced to compete intra- or interspecifically, leading to detriments or propagation in survival, growth and general performance (Begon et al., 2006).

Competitive interactions and understory development are strongly driven by the vertical and horizontal forest canopy structure, as indicator for the past forest development. This structure

strongly affects ecosystem stability and resulting ecosystem services (Beckschäfer et al., 2013; Fahey et al., 2010; Tews et al., 2004). The structure mainly affects light availability which is considered to be one of the most heterogeneous and dynamic aboveground factors affecting the understory structure (Percy, 1999; Smith, 1982) and tree regeneration development. This makes competition for light one of the driving abiotic factors of forest development.

The net competitive ability of a species is a result of its effect on and response to limited resources. A strong negative effect on resource availability and a high tolerance as response to low resource levels increase the species' net competitive ability (Goldberg, 1990). In other words, the ability of a plant to survive, grow and regenerate successfully is strongly related to its ability to tolerate abiotic stress through resource limitation and to produce and allocate its biomass, aside from its ability to tolerate biotic disturbances (Kadereit, 2014).

Consequently, the competitive ability of a species is substantially influenced by its ability to occupy and exploit space and resources. This ability manifests itself by distributing assimilate products among the respective plant organs at a given point in time, measured as biomass present in these organs. This is directly

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associated with 'biomass allocation' as specific form of resource allocation. The species' ability to control the allocation determines its survival and growth vigor.

Natural selection has led to genotypes with different suites of traits that allow species to develop various patterns of biomass allocation, as result of their plasticity, to react to varying levels of resource availability. These patterns are interpreted and referred to as '**growth strategy**' to indicate the functionality of traits in an ecological context. Analyzing growth strategies helps explain a plant's performance in an ecological and evolutionary context (Lambers et al., 1998). Some general patterns of biomass allocation strategies have been described, theorized and partly confirmed in scientific literature (e.g. Grime, 1977; Hilbert, 1990; Perrin, 1992; Thornley, 1998; Tilman, 1990), which are described in the following. Widely accepted are the 'functional equilibrium hypothesis' (Brouwer, 1962, 1983) or 'balanced growth hypothesis' (Davidson, 1969; Garnier, 1991; Hunt, 1975). It states that there is a close relationship between biomass allocated to the roots (belowground) and to the shoots (aboveground) under constant conditions (e.g. Pearsall, 1927) and that biomass is preferentially allocated in the direction of the limiting resource (e.g. Brenchley, 1916; Shirley, 1929) under changing environmental conditions. The 'allometric allocation hypothesis' (Müller et al., 2000), explains differences in biomass allocation simply through the underlying allometric principle (Shipley and Meziane, 2002).

These theories focus on general allocation patterns towards belowground and aboveground plant compartments. However, less is known about the effect of limited resources on the allocation between the different aboveground plant compartments, e.g. the photosynthetic compartments (leaves) and/or the non-photosynthetic compartments (branches, stems) (Zeng, 2003). Deeper insights into the interrelationships of these compartments is required (Kadereit, 2014; Poorter et al., 2012), not only in terms of how allocation patterns change with ontogeny (e.g. Bond, 2000), but also elucidating species-specific responses to varying resource availability.

In response to light availability (Smith, 1982; Zervoudakis et al., 2012), plants have adapted physiologically, anatomically, and morphologically to varying levels of light (e.g. Czczuga, 1987; Matyssek et al., 2010; Muraoka et al., 2002; Zhang et al., 2003). These adaptations are primarily species-specific and result in differences in terms of biomass increment and allocation along light gradients (e.g. Ammer, 2003; Coates and Burton, 1999; Drever and Lertzman, 2001; Lüpke, 2004; Schall et al., 2012).

A lot of work on species' responses to resource availability, and the hypotheses and theories derived, has been conducted with seedlings (e.g. Walters and Reich, 1996, 1999), partly resulting in controversial findings, possibly as a result of differing starting conditions in terms of seed size (Poorter and Rose, 2005). Less is known about later stages of ontogeny, which is why this study focused on saplings of similar age. The species considered in this study were sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.), and European ash (*Fraxinus excelsior* L.). All three species are of silvicultural relevance in Germany and all three species are considered to be at least partially shade-tolerant. *F. sylvatica* is most shade-tolerant, the other two species (*A. pseudoplatanus*, *F. excelsior*) are commonly classified as half-shade-tolerant (Ellenberg and Leuschner, 2010). As young plants, the shade-tolerance of *A. pseudoplatanus* and *F. excelsior* is also considered to be high but it seems as if their demand for light increases with ontogeny (Roloff et al., 2002).

In this study we analyze the underlying aboveground growth strategies of the three forest species along a light gradient, by investigating allocation patterns and applying a functional growth analysis, based on established parameters (compare Ammer et al., 2004; Lambers et al., 1998). The objective of this study was to

quantitatively describe the individual plant strategies and identify threshold values of light availability for strategical advantages of the individual growth strategies, respectively.

Specifically the following hypotheses were tested:

1.1. Hypotheses

H1. Biomass allocation patterns will vary among the three tree species. Due to the higher shade tolerance of *F. sylvatica*, the effect of the light gradient on the allocation among the aboveground plant compartments (stem mass fraction (SMF), branch mass fraction (BMF), leaf mass fraction (LMF)) will be more pronounced for the other two species (*A. pseudoplatanus*, *F. excelsior*).

H2. Total biomass accumulation (absolute growth rate (AGR)) will increase with increasing light availability for all species, as a result of the increasing net assimilation rate (NAR), because the efficiency of the leaf unit area, expressed as photosynthetic efficiency, should increase with light availability. *F. sylvatica* will be more efficient under low light conditions, but the other two species will surpass *F. sylvatica* with increasing light availability (the slope increases from *F. sylvatica* over *A. pseudoplatanus* to *F. excelsior*).

H3. Mean leaf area (MLA) and leaf mass area (LMA) will increase with light availability, whereas species demanding more light (*A. pseudoplatanus*, *F. excelsior*) are expected to have a higher plasticity in their leaf organs to increasing light availability than the more shade tolerant species *F. sylvatica*.

H4. Leaf area ratio (LAR) will behave reciprocally to NAR and will decrease with increasing light availability, since the efficiency to deploy photosynthetic resources should increase with light availability. Due to the higher shade tolerance of *F. sylvatica*, LAR will be higher for this species under low light levels, but lower under high light levels, compared to the other two species.

H5. As indicator for competitiveness and productivity, in dependence of species and light availability, the relative growth rate (RGR) will reach its maximum at lower light levels for *F. sylvatica* than for *A. pseudoplatanus* and *F. excelsior*, because *F. sylvatica* is better adapted to shaded conditions.

H6. Leaf nitrogen per unit area (NUA) will be related to light exposure. The nitrogen content per g leaf mass (NLM) is mainly a function of nitrogen availability and will not be affected by light availability. Finally, nitrogen use efficiency (NUE), i.e. biomass production per unit N will increase with increasing light availability, due to the decrease of resource limitation.

2. Methods

2.1. Study site

The study was conducted in a forest in Lower Saxony, Germany. The forest is a community forest belonging to the forest district Münden, near Göttingen (10° 02' 11" E, 51° 34' 46" N). The forest stand is a mixed deciduous forest and the overstory is comprised of European beech (*F. sylvatica*), sycamore maple (*A. pseudoplatanus*), Norway maple (*Acer platanoides*), sessile oak (*Quercus petraea*), and hornbeam (*Carpinus betulus*). The overstory has an age of 120–130 years.

The study site is located at 150–200 m above sea level. The temperate climate of the study area lies in the transition zone between

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