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Original article

Forest herb layer response to long-term light deficit along a forest developmental series

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ABSTRACT

Temperate deciduous forest communities are slow-changing systems, with herbaceous understorey communities displaying a delayed response to overstorey canopy and light dynamics. While light availability constrains herbaceous understorey diversity and composition in space and time, its response in the long-term absence of light has seldom been quantified, particularly as it is often confounded by covariation in soil conditions. We studied a developmental high-forest series in two widespread NW-European temperate deciduous forest communities with different dominant canopy tree species: *Stellario-Carpinetum* (Oak-hornbeam canopy) and *Milio-Fagetum* (Beech canopy). All plots had soil conditions which were not significantly different, enabling investigation into the direct effects of the long-term absence of light on the herbaceous understorey, disentangled from the confounding effects of soil variation.

Plant species richness measures declined with canopy cover continuity in the herb layer of the oak-hornbeam stands, whereas richness in the herb layer of the beech stands displayed a unimodal response. Nonetheless, in both plant communities, species richness and closed-forest species richness were negatively affected by the extended absence of light in stands with the longest period of continuous canopy cover. The long-term limitation or decline in quantitative and qualitative light availability as a result of extended periods of canopy cover was shown to be the primary driver behind losses in alpha-diversity, community composition turn-over and individual species dynamics. Heliophilous species were lost from both communities, while closed-forest species also declined, as a direct consequence of the prolonged period without ample light on the forest floor. This study demonstrates how the herb layer is affected by the absence of light on the forest floor mediated by long periods of continuous canopy cover. Despite different temporal responses in herb layer richness and composition between different shade-casting canopy species, the eventual outcome in the prolonged absence of light is independent of dominant canopy species.

1. Introduction

The diversity of the forest herb layer constitutes the largest fraction of the total plant diversity in temperate deciduous forests (Gilliam, 2007). Many studies have therefore been devoted to understanding how the forest herb layer responds to global threats such as climate change (Skov and Svenning, 2004), land use changes (Verheyen et al., 2003), acidification and eutrophication (Baeten et al., 2009a; Verheyen et al., 2012) or invasive species (Hale et al., 2006). Additionally, European forest management has gone through considerable changes (prolongation of harvesting cycles (Baeten et al., 2009a); changing of management systems (Van Calster et al., 2008a); replacement of dominant canopy species (Barbier et al., 2008)), with pronounced effects on the herbaceous forest understorey (Barbier et al., 2008; Van Calster et al., 2008a). One of the most profound changes was the strong shift in light regimes in temperate deciduous forests in Europe. Over the last century, traditional forest management characterised by frequent stand-scale disturbances of the forest canopy (coppice or coppice-with-standards; clearcut every 15–20 year) has been replaced by long-rotational high-forest management with few stand-scale

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canopy disturbances (clearcut every 100–150 years). This has noticeably prolonged the periods in between large canopy disturbances when abundant light reaches the forest floor. Given the extent of these management changes in Europe, an assessment of how species richness, plant communities and closed-forest species respond to long-term light scarcity in such high-forest management systems is necessary (Jules et al., 2008).

Light has often been shown as the primary shaping factor of herbaceous forest communities in time (Baeten et al., 2009a; Jules et al., 2008; Neufeld and Young, 2003; Van Calster et al., 2008a) and space (Emborg et al., 2000; Eycott et al., 2006; Wulf and Naaf, 2009). Many perennial forest plants – including closed-forest herbs which define the herb layer under closed canopy conditions (*sensu* Schmidt et al., 2003) – need recurrent light phases to maintain viable populations in order to assure their long-term survival (Jacquemyn et al., 2008; Valverde and Silvertown, 1998; Van Calster et al., 2008b), notwithstanding their numerous morphological and physiological adaptations to cope with low light levels (Neufeld and Young, 2003). As a result, long periods of light scarcity often still yield adverse effects on the forest herb layer (Baeten et al., 2009a; Jules et al., 2008), even on the well-adapted closed-forest species (Valverde and Silvertown, 1998) despite their average life expectancy of ca. 40 years (non-woody forest perennials in Ehrlen and Lehtilä, 2002). Consequently, we expect that the long-term scarcity of light on the forest floor in high-forest management systems may severely hamper the performance of its plant populations, eventually leading to local plant species extinctions (Barkham and Hance, 1982; Hédl et al., 2010; Schmidt, 2010; Strandberg et al., 2005). However, as both Baeten et al. (2009a) and Van Calster et al. (2008a) point out, the role of light in shaping forest plant communities is often obscured by the significant changes in the soil environment which are intricately linked with forest maturation (Nordén, 1994; Hagen-Thorn et al., 2004; Reich et al., 2005; Hobbie et al., 2006). Therefore, to pinpoint how light constrains herb layer development, the forest understorey light regime must be evaluated in a forest environment where confounding variation in soil conditions is minimal.

The unmanaged forest reserve and managed forest stands in *Hasbruch* forest (northern Germany) provided a rare opportunity to assess the impact of the long-term scarcity of light in two herbaceous forest understorey communities [*Milio-Fagetum* (beech canopy) and *Stellario-Carpinetum* (oak-hornbeam canopy)], unbiased by the lack of significant differences in dominant soil characteristics between the studied plots (Plue et al., 2010). In this study, we define the herbaceous forest understorey as the suite of all vascular species that are 0.5 m or less in height, i.e. combining herbaceous species and the seedlings and saplings of woody species (Gilliam, 2007). By studying a high-forest developmental series with differing shade-casting canopies, we can assess the impact of a long-term light deficit on the herbaceous understorey community. Specifically, we addressed the following questions: 1) Does the long-term light deficit during forest development drive a decline in plant species richness, the species richness of different species groups and the abundance of closed-forest herb species?; 2) does the herb layer consequently change significantly and predictably in response to a long-term light deficit? and finally; 3) does the herb layer changes depend on different light transmittance in dominant canopy species?

2. Materials and methods

2.1. Study site

The *Hasbruch* forest (53° 04′ 11″N – 8° 29′ 08″E, northern Germany) is a 640 ha semi-natural forest with a temperate suboceanic climate (mean annual temperature of 8.4 °C; yearly average precipitation of 745 mm). The soilscape is heterogeneous with soils ranging from sandy–clay loam to loamy sand soil texture. Several semi-natural woodland types are represented in *Hasbruch* forest (Peppler-Lisbach and Peters, 1999; Pott and Hüppe, 1991). Beech-dominated stands are characterised by plant community types following a decreasing soil acidity gradient. Oak-hornbeam stands are divided between the *Stellario-Carpinetum lonicerotosum* Dierschke 1986 (acid, dry soil) and the *S.-C. stachyetosum* Dierschke 1986 (base rich, moist soil).

The entire forest was designated as a nature conservation area in 1952 (Pott and Hüppe, 1991). Historically, the entire forest served as a wood pasture (Pott and Hüppe, 1991). Nowadays, the silvicultural regime in the managed forest stands aims at sustaining typical oak-hornbeam forests against the natural development towards beech forest. Oak-hornbeam stands are thinned every five years to remove beech in favour of hornbeam and to promote crown development in the oak trees (Fig. 1). When oak-hornbeam stands reach the age of 120 years, management focus is relayed to prevent hornbeam trees entering the oak-dominated canopy (every 7–8 years). Beech stands are thinned every five years, increasing to 10 years as stands reach 100 years (Fig. 1). Two centrally located forest stands (*Heue* and *Gruppenbührer seite*, ca. 15 ha) were designated as *Naturwald* in 1889, with another 25 ha added in 1988. When abandoned, forest stands in the *Naturwald* developed spontaneously in the absence of forest management. At present, a dense mixed uneven-aged stand has developed in-between and under the veteran oak (*Quercus robur*) and hornbeam (*Carpinus betulus*) trees of the 40 ha forest reserve. The beech (*Fagus sylvatica*) dominated regeneration, aged between 40 and 100 years, forms a subordinate canopy to the veteran tree layer.

2.2. Data collection

2.2.1. Plot selection

Our main goal was to identify the long-term effects of the absence of light on the herbaceous forest understorey which followed the shift in forest management during the 20th century. We use two, four-stage developmental forest series with different shade-casting canopies (Fig. 1), where all stands had experienced a continuous period with significant overshading by the forest canopy, without full removal of tree canopy cover. Each forest developmental series contained forest stands that were subject to 40, 80, 120 years or >120 years of continuous canopy cover (later referred to as canopy cover continuity). The managed high-forest stands (40, 80 and 120 yrs) originated from wood pasture but have been managed as described in Section 2.1. The treatment times thus reflect the time of continuous canopy cover since the last full removal of the canopy. The treatment times of the managed high-forest stands (40, 80 and 120 yrs) were selected as they 1) were abundantly available within each forest plant community [oak-hornbeam stands (*Stellario-Carpinetum*) and beech stands (*Milio-Fagetum*)] and 2) were proportionally divided over the forest developmental stages. The fourth stage of the forest developmental series (>120 yrs) consists of unmanaged uneven-aged stands situated in the 40 ha forest reserve. These stands originate directly from former wood pasture, and prior to the abandonment of forest management 121 years ago experienced more open canopy conditions than today. They are still ranked last in the developmental series, as these stands have always known a significant and continuous degree of canopy overshading, but the overshading intensity increased over the last 121 years.

Twelve 10 m × 10 m plots per canopy-age category combination (96 plots in total) were visited in the field after being randomly selected per canopy-age category combination in ArcView 3.3