



Light-driven host-symbiont interactions under hosts' range shifts caused by global warming: A review



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ABSTRACT

The spectrum of light has received little attention as an ecological factor and in this review we highlight the importance of a changing light environment in plant range shifts under conditions of global warming. Although distinct clinal responses to light quality have not been earlier reported, some studies have shown that northern ecotypes are more sensitive to changes in light quality. The northern light environment may significantly modify competition between plant species and within photoperiodic ecotypes, if predicted rapid range shifts of forest trees are realized. Southern photoperiodic ecotypes of forest trees migrating northward will encounter both changed light quality and a different photoperiod. Our special focus is on carbon economy and biomass partitioning between the autotrophic hosts and heterotrophic ectomycorrhizal fungal (EMF) symbionts, reciprocally dependent on each other. This applies also to the level of fungal community structure, which is assumed to be determined in part by host carbon economy. We hypothesize, that (1) Carbon allocation to roots and EMF in different host species and locally adapted photoperiodic ecotypes will respond differentially to northern light climate, especially to photoperiod and proportionally higher diffuse blue light; (2) Since carbon flux belowground may start later in northward-shifted southern populations in the autumn, also mycelial growth and reproduction in the EMF associated with southern populations could occur later. This may also lead to changes in fungal community composition; (3) EMF phenology and community composition may show different responses to changing light climate when associated with host trees of fixed or free growth pattern; and (4) Responses of EMF symbionts associated with locally adapted host populations vary, possibly leading to changes in EMF communities. We also discuss potential experimental approaches mimicking range shift conditions in terms of light quality due to global warming and compare reaction norms in key traits between southern and northern populations and species. Further, we exemplify how data obtained from experimental studies may be used for modelling of host plant and symbiont growth, which may in turn affect species competitive ability and distribution.

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1. Introduction

Global climate change has provoked serious discussion about near-future impacts on ecosystem services and biodiversity (e.g. Hautier et al., 2014; Martin et al., 2014). This is of special importance in boreal and arctic ecosystems because of the predicted rapid changes in these areas (ACIA, 2005). Increased attention directed toward northern areas encompasses problems associated with invasion ecology and range shifts of species and their populations (Saikkonen et al., 2012; Taulavuori, 2013; Leiblein-Wild and Tackenberg, 2014). Light environment, and

especially differences in the spectrum of light, as an ecological factor, however, has received little attention in this respect.

Here we address certain key questions related to global warming and consequent interactions of dominant forest trees species, their populations adapted to local light environment (i.e. ecotypes), and their ectomycorrhizal fungal (EMF) symbionts under host range shifts towards the northern light environment, where blue light is enriched (Taulavuori et al., 2010). The special focus is on carbon economy and biomass partitioning between an autotrophic host and heterotrophic fungal symbionts, but this applies also to the level of fungal community structure, which is assumed to be determined in part by host carbon economy. The host tree–fungal symbiont pair interaction is of specific interest, as EMF symbionts consume a substantial proportion of the net carbon fixed by the host, but may also significantly aid host adaptation to a

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changing environment due to their distinctly shorter life span and high diversity compared to their host trees.

2. Light environment and growth patterns of boreal forest trees

2.1. Importance of light

Light is probably the most important resource plants compete for (e.g. [Schwinning and Weiner, 1998](#)). Light intensity (irradiance) determines photosynthetic potential until the level of saturation, and thereby net primary production. Light quality (spectral composition) affects plant phenotype through many photomorphogenic processes, and acts as a signal for metabolic regulation ([Cashmore, 2006](#)). Light duration (daylength, photoperiod) is responsible for adjusting biological clock for phenological events ([Thomas and Vince-Prue, 1997](#)). Changes in any of these characteristics of a plant's light environment can cue phenological transitions, such as flowering and seed germination, and determine biomass partitioning between foliage, roots and supporting tissues, as well as the allocation of photosynthates to symbiotic partners. Impacts of future climate change on vegetation have attracted considerable interest during past years. Increases in plant growth due to global warming and elevated CO₂ are well-documented ([Bazzaz, 1990](#)). Such impacts on EMF symbionts of trees and shrubs have also been reviewed ([Pickles et al., 2012](#); [Morgado et al., 2015](#)). In contrast, the light environment has been largely neglected in this context. It is therefore crucial to investigate how forest trees respond to changes in light climate when migrating to the north along with climate warming.

2.2. Northern light environment

The light environment at northern high latitudes is markedly different from the mid latitudes and likely to affect plant competitive performance during the growing season. Day length begins to extend from the winter solstice at a rate that increases until the vernal equinox, being 12 h on the 20th March, and reaching 24 h (i.e. polar day) at a diminishing rate by the summer solstice around the 21st June at the Arctic Circle (66.56°N) and northwards, and lasting for two months at 70°N ([Nielsen, 1985](#); [Taulavuori et al., 2010](#)). In addition to the missing darkness during the growing season, the light environment in the north is characterized by lower light intensity (irradiance) compared to mid or low latitudes. For example, vegetation around the Arctic Circle in Scandinavia receives only about 55% of the irradiance of that in the Alps (47°N) ([Körner, 2003](#)). Moreover, light quality is different since the polar summer nights are enriched with a relatively high proportion of diffuse blue because of the light scattering due to the low angle of solar radiation ([Taulavuori et al., 2010](#)).

2.3. Day length impacts on phenology of trees

Day length is the most accurate and consistent environmental cue in northernmost environments, providing a fixed calendar for plant seasonality, which is especially important for plant preparation for winter (e.g. [Taulavuori et al., 1997](#); [E. Taulavuori et al., 2010](#); [Saikkonen et al., 2012](#); [Taulavuori, 2013](#)). Weather conditions (temperature, precipitation) are too unpredictable to provide reliable signals for autumn preparation, and can therefore only fine-tune plant seasonality (e.g. [Taulavuori et al., 1997](#); [Taulavuori, 2006](#); [Rohde et al., 2011](#)). Hence, many phenological events are coordinated by day length.

Pattern of shoot elongation characterizes tree species. Trees with a *free growth pattern* have shoots that elongate producing new internodes throughout the growing season until a critical

photoperiod. The final length of the shoot is determined by prevailing weather conditions. In trees with a *fixed (predetermined) growth pattern*, the weather conditions of the previous growing season determine the number of internodes in the bud. Elongation of internodes in these species is controlled by temperature of the next growing season (e.g. [Kramer and Kozłowski, 1979](#); [Junttila, 2007](#)). The elongation in fixed growth pattern plants occurs during a relatively short period in the beginning of the growing season elongation is then followed by needle and diameter growth, apical bud set and subsequent frost hardening processes. Shortening days induce winter hardening of trees irrespective of growth pattern (e.g. [Sakai and Larcher, 1987](#); [Taulavuori et al., 1997](#)). In addition, temperature signals may contribute to the timing of photoperiod growth cessation ([Rohde et al., 2011](#)). It is also proposed that the signal function of annual change in photoperiod is replaced by changes in light quality in the high Arctic (78°N), where midnight sun continues until leaf shedding, and thus cannot provide a signal for growth cessation ([Nielsen, 1985](#)). [Nielsen \(1985\)](#) proposed that a reduction in the ratio of red to far-red light (R:FR) may provide an alternative signal, analogous to an increase in blue to red light ratio ([Taulavuori et al., 2010](#)), in the context of reduced elongation of many species growing in the light of subarctic polar summer ([Taulavuori et al., 2005](#); [Sarala et al., 2007, 2011](#)).

2.4. Adaptations to local light environment under range shifts

Responses to photoperiod may vary to such an extent, that populations within a tree species could form so-called photoperiodic ecotypes, which are genetically differentiated ([Oleksyn et al., 1998](#); [Junttila, 2007](#)). This is typical for northern species (e.g. *Betula* spp.), which exhibit clinal adaptation over latitudes, indicating that the critical day length for growth cessation increases with increasing latitude of a population ([Junttila, 2007](#); and references therein). Interestingly, adaptation to local photoperiodic conditions seems to differ also within tree species, e.g. certain woody species in the Rosaceae family do not show such clinal variation ([Heide and Prestrud, 2005](#)).

Although distinct clinal responses to light quality has not been reported yet, some studies have shown that northern ecotypes are more sensitive to changes in light quality (e.g. [Mølmann et al., 2006](#); [Sarala et al., 2011](#)). Northern light environment may thus significantly modify the competition between plant species and photoperiodic ecotypes, if predicted rapid range shifts of forest trees are realized ([Taulavuori et al., 2013](#)). In a century, estimated shift distances are in the range of 300–800 km ([McKenney et al., 2007](#)), and species ranges may shift northward as much as 1000 km ([ACIA, 2005](#)). In Finland, for example, a shift of this magnitude approaches the full latitudinal range of the boreal forest in this region and is similar to a transition from southern provenances to the most northern provenances, i.e. close to the Arctic Sea which prevents further shifts towards the north.

Shift predictions vary among forest tree species due to different populations and genotypes, which may possess contrasting adaptation to local climate ([Savolainen et al., 2007](#); [Kremer et al., 2012](#); see [Fig. 1](#)). When considering northward range shifts of plant populations, temperature is the most efficient ecological filter against the shifts. In practice, under a rapidly warming climate, temperature will shift first and vegetation is expected to follow. Thus, populations shifting northwards will experience no change in temperature, while they experience a significantly different light environment ([Taulavuori et al., 2010, 2013](#)). This is most pronounced in boreal forest trees with a long generation age. Different ecotypes will therefore exhibit characteristic responses to the existing new light environment. While temperature signals may contribute to the timing of photoperiod growth cessation

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