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The dioecious *Populus tremula* displays interactive effects of temperature and ultraviolet-B along a natural gradient

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ABSTRACT

Observed and projected warming has provoked research interest on tree phenology in relation to climate. While both ultraviolet-B (UV-B) radiation and warming has been shown to affect growth and development in plants, the combined effects of the two environmental factors has been little studied. In addition, there is concern for environmental change yielding divergent responses between sexes in dioecious tree species. Here, we present a study of the dioecious *Populus tremula* grown along a natural temperature and UV-B gradient in Central Norway, reducing UV-B using specific screening filters. We tested for effects on growth, timing of terminal bud formation and bud break, carbon and nitrogen content and concentrations of phenolic compounds. Increased elevation had a negative effect on plant growth and promoted bud formation, with effects differing between plant sexes. UV-B attenuation delayed bud formation and enhanced growth of males at the highest elevation, counteracting the effect of low temperature. In addition, elevation and UV-B affected concentrations of different phenolics in stems and leaves. Our data show that interactive effects of warming and other climate factors like UV-B should be considered when predicting climate change effects in woody plants, and add to present evidence of sex-related responses to climate change in dioecious woody plants.

1. Introduction

The boreal forest accounts for a third of Earth's forest area, and is also the biome that exerts the largest biogeochemical influence on average global temperature (Snyder et al., 2004). During the latest decades, substantial warming has been observed at high latitudes (Serreze et al., 2000; Hartman et al., 2013), and observed changes for boreal tree species include increased growth (Jacoby & D'Arrigo 1995; Hember et al., 2012; Kauppi et al., 2014; Schaphoff et al., 2016), latitudinal and elevational range shifts (Kullman 2001; Zhu et al., 2012; Koven 2013; Monleon and Lintz 2015) and advanced spring phenology (Menzel et al., 2006; Bertin, 2008). In relation to phenology, there is evidence suggesting that further warming, which is predicted for the 21st century (IPCC, 2014), yields different responses across tree species (Roberts et al., 2015). It is well known that phenology in temperate and boreal tree species is driven by seasonal fluctuations of temperature and light (Olsen and Lee, 2011), but evidence from the rather few species that have been studied suggests that there is great interspecific variation in how species respond to day-length, temperature and light quality (Hänninen and Tanino, 2011). Furthermore, evidence from

studies involving dioecious tree species show that females and males may respond differently to warming (Tognetti, 2012). Indeed, divergent responsiveness to environmental change between sexes have been shown in *Salix myrsinifolia* (Nybakken et al., 2012; Nybakken and Julkunen-Tiitto, 2013), *Salix arctica* (Dawson and Bliss, 1989) and *Populus cathayana* (Xu et al., 2008, 2010; Zhao et al., 2009, 2012; Jiang et al., 2015; Zhang et al., 2017). If such effects yield different performance between females and males, gender balance may play an important role for population dynamics under environmental change.

In addition to warming, boreal tree species are facing changes in precipitation, freeze/thaw cycles, CO₂ concentration and ultraviolet radiation. Some studies have revealed interactive effects in response to warming and supplemental Ultraviolet B (UV-B) radiation (Nybakken et al., 2012; Randriamanana et al., 2015; Strømme et al., 2015), and UV-B has also been shown to interact with drought (Ren et al., 2007) and soil nutrient availability (Ren et al., 2010; Feng et al., 2014). As climate change is projected to affect the thickness of the ozone column, it will also affect the levels of UV-B radiation received by Earth's surface (McKenzie et al., 2011; Williamson et al., 2014). Even though the successful implementation of the Montreal Protocol reduced the

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depletion of stratospheric ozone, substantial variability of the ozone column thickness is expected due to warming effects on circulation patterns. Indeed, such an effect was observed during the record ozone depletion event over the Arctic in 2011 (Manney et al., 2011), yielding higher than normal levels of UV-B radiation from the North Pole to Southern Scandinavia. Considering available evidence on the physiological responses of species to UV-B radiation, such events are likely to affect ecosystem functioning (see Bornman et al. (2015) for a review). Even so, there are substantial knowledge gaps in relation to interactions between UV-B and other environmental factors undergoing rapid change. Moreover, several studies of UV-B effects on trees have employed supplemental UV-B from lamps either in semi-controlled or in field conditions (Xu et al., 2010; Nybakken et al., 2012; Strømme et al., 2015). To a smaller extent, effects have also been tested under the actual UV-B levels that plants are subjected to in nature (Caldwell et al., 2003), employing UV-B specific attenuation filters (Ballaré et al., 1996, 2001; Huiskes et al., 2001; Singh and Singh, 2014).

Plants are known to respond to UV-B exposure through variations in the synthesis of phenolic compounds, which may in turn affect stress tolerance as well as resistance to herbivory and pathogens (Ballaré et al., 2011). Increased phenolics synthesis under UV-B has been shown for boreal tree species such as *Betula pendula* (Lavola et al., 1997), *S. myrsinifolia* (Tegelberg and Julkunen-Tiitto, 2001) and *Populus tremula* (Lavola et al., 2013; Randriamanana et al., 2015). On the other hand, UV-B has been shown to decrease growth parameters in some woody species (Bassman and Robberecht, 2001; Tegelberg et al., 2003; Ren et al., 2007, 2010; Feng et al., 2014; Terfa et al., 2014), while other reports find no such effect (Tegelberg et al., 2001, 2003; Kotilainen et al., 2009; Morales et al., 2010; Lavola et al., 2013). Even so, growth reduction under UV-B is considered lower for woody plants as compared to herbaceous plants (Caldwell et al., 2003; Li et al., 2010).

UV-B may affect tree growth through environmental signalling pathways, and such effects have gained increased attention following the characterisation of a UV-B specific photoreceptor, known as UV-B resistance locus 8 (UVR8), in *Arabidopsis thaliana* (Jenkins, 2009). There is considerable evidence showing that UV-B is a signal that regulates plant growth and morphology through action on metabolism of hormones such as auxin and gibberellin (Rozema et al., 1997; Jansen, 2002; Rizzini et al., 2011; Jansen and Bornman, 2012; Hayes et al., 2014; Roro et al., 2017). UV-B was also shown to be involved in photoperiodic sensing in *A. thaliana* (Fehér et al., 2011). UV-B can thus act as an environmental cue in relation to phenology in plants. For a range of boreal tree species, light quality has been shown to be involved in phenological transitions (Olsen and Lee, 2011), namely far red (FR) (Junttila and Kaurin, 1985; Olsen et al., 1997a; Clapham et al., 1998; Tsegay et al., 2005; Møllmann et al., 2006) and blue light (Opseth et al., 2016). Thus, possible UV-B effects on boreal tree species should be investigated using an integrated approach that considers phenological transitions, phenolic synthesis and growth.

Moreover, effects of UV-B radiation on boreal trees should be tested in combination with warming. A survey of previous literature suggests that warming may both delay and accelerate phenological events in autumn, namely growth cessation and bud formation (Hänninen and Tanino, 2011). Day-length was early recognised to govern autumnal growth cessation and bud formation in trees (Wareing, 1956; Nitsch, 1957; Weiser, 1970). It has also been shown that temperature also affect these processes (Kalcits et al., 2009; Tanino et al., 2010; Hänninen and Tanino, 2011; Rohde et al., 2011a; Strømme et al., 2015, 2017). As such, warming may interact with day-length (Ruttink et al., 2007; Sogaard et al., 2008; Tanino et al., 2010; Olsen et al., 2014), yielding a different phenological response to the day-length signal.

The dioecious Eurasian aspen (*Populus tremula*) has a wide distribution across the Eurasian continent, and is host to numerous species of birds, mammals, invertebrates, lichens and fungi. Due to its ease of propagation and wide environmental tolerance, it is widely used in plant physiological research. In a recent field study on Eurasian aspen

grown in a modulated temperature and UV-B enhancement system, we found interacting effects of temperature and UV-B radiation on autumnal bud formation and bud break (Strømme et al., 2015). Autumn warming delayed bud formation, while enhanced UV-B levels in the same period had an opposite effect. Furthermore, we found that male plants were more responsive to both treatments, which also yielded advanced bud break the following spring.

The aim of this study was to simulate dual-factor climate change for female and male plants of the dioecious Eurasian aspen by employing a natural temperature and UV-B gradient. For this purpose, we established three experimental locations at different elevations in a valley slope in Central Norway. With increasing elevation, we obtained decreasing temperature and increasing UV-B radiation. We conducted two field experiments at the same locations over two consecutive years, and during the second year we employed attenuation filters mounted over plots to obtain reduced UV-B levels on subsets of new plant materials. Using the same clones as in Strømme et al. (2015) in order to account for possible responses related to genotypes, we hypothesised that 1) higher temperature at low elevation would lead to a more pronounced growth of plants, while also yielding a longer growing season due to delayed bud formation in autumn as well as earlier bud break in spring. We further hypothesised that 2) delayed bud formation for plants at low elevation would be accompanied by higher leaf nitrogen content due to delayed relocation from leaf to stem. Based on Strømme et al. (2015), we also hypothesised that 3) attenuating UV-B radiation would delay autumnal bud formation, and that elevated temperature and UV-B would yield stronger responses in males. Based on available literature, we hypothesised that 4) UV-B attenuation would yield reduced synthesis of polyphenols in leaves, particularly flavonoids and thereby higher growth rates due to reduced allocation to defence.

2. Materials and methods

2.1. Plant material

Plants used in the field experiments originated from six female and six male aspens located in Southern and Eastern Finland (62°54'–60°43' N, 24°27'–29°41' E). For a thorough description of sampling locations and micropropagation of individuals see Strømme et al. (2015). Plants were potted on 4 June 2013 and on 10 June 2014 using 70% non-fertilised peat and 30% vermiculite. Prior to planting in the field, plants were kept in growth chambers under $237 \pm 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 400–700 nm and a red: far-red (R:FR) ratio of 1.6 ± 0.1 provided by 400W Philips MASTER HPI-T Plus metal halide lamps (Royal Philips, Amsterdam, Holland) and incandescent light bulbs (60 W, Osram, Munich, Germany). Photosynthetic active radiation (PAR) was measured using a LI-250 Light Meter with an attached Quantum Sensor (LICOR, Lincoln, Nebraska, USA), while R:FR ratio was measured using a Sky 100 radiometer with an attached 660/730 nm sensor (Skye Instruments, Llandrindod Wells, UK). The first days after potting, the plants were kept under a semi-translucent plastic sheet, which was gradually removed. This provided a gradual climatic shift in terms of irradiance, temperature and relative air humidity (RH). In the growth chambers, temperature and RH were 20 °C and 75%, respectively, and progressively lowered to 16 °C and 65% over seven days in 2013 and four days in 2014 to allow acclimation to lower temperature and RH. Plants were planted in the outdoor experimental locations on 4 July in 2013 and on 24 June in 2014. Later planting in 2013 was due to cooler spring/early summer conditions this year as compared to 2014.

2.2. Experimental set up

We established experiments at three different elevations in Fåvang, Central Norway (61°27' N, 10°11' E) along the eastern side of the Gudbrandsdalen valley. Each location was a pasture selected with the aim of having three sites at different elevations along a natural gradient

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