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Interactive effects of supplemental UV-B and temperature in European aspen seedlings: Implications for growth, leaf traits, phenolic defense and associated organisms

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ABSTRACT

Past studies reveal opposite effects of elevated UV-B and temperature on plant growth and concentrations of UV-B absorbing compounds, yet few studies have dealt with the combined and interactive effects of these two climate change factors on woody dioecious plants. We investigated the interactive effects of UV-B and temperature treatments on growth, leaf traits and phenolic concentrations in *Populus tremula* L. (European aspen) seedlings. We also considered the consequences of these effects on their associated organisms: herbivorous insects, rust pathogens, the presence of endophytic fungi and whether or not the responses differ between genders and genotypes. Supplemental temperature and UV-B were modulated to +2 °C and +30.77% above ambient conditions, respectively. Warming increased growth, photosynthesis and foliar nitrogen concentration but reduced leaf thickness and phenolic concentrations. On the other hand, supplemental UV-B increased total phenolic glycosides, mainly flavonols and phenolic acids, and partially counteracted the positive effects of warming on growth. Fast growing genotypes were less susceptible to the growth-reducing effect of combined UVB + T, less infected with rust disease and less prone to insect damage probably due to their higher salicylate and lower nitrogen concentrations. Under ambient temperature, the males of European aspen were taller and had bigger leaves than the females, while under elevated temperature, females grew bigger and, under UV-B, had more tremulacin than males. The multiple interactive effects of UV-B and temperature on growth, leaf traits and phenolic compounds, highlight the importance of multifactor experiments as a realistic predictor of plant responses to climate change.

1. Introduction

Plant physiology is in continuous interplay with ever fluctuating biotic and climatic factors. By the year 2100, most climate scenarios predict a likely increase of global mean surface temperature by at least 1.5 °C relative to its level in 1850–1900 (IPCC, 2013). Besides, despite the decreasing trend regarding ozone-depleting substances and in the future UV-B (280–315 nm), the recovery rate of the ozone is uncertain, mainly as a result of the strong interactions between ozone depletion and climate change (McKenzie et al., 2011). In addition, springtime destruction of stratospheric ozone over the Arctic might lead to significantly elevated UV irradiances in the northern mid- and high-latitudes (United Nations Environment Program, 2012). In general, past studies have reported that elevated UV-B radiation incurs a slight decrease in plant height growth (3–10%), total leaf area (6–13%), aboveground biomass (15–16%), while the concentrations of UV-B absorbing compounds are often enhanced (Searles et al., 2001; Newsham and Robinson, 2009). On the other hand, warming rather has a positive effect on plant growth but reduces the concentrations of phenolic compounds (e.g. Zvereva and Kozlov, 2006; Lavola et al., 2013). Thus, UV-B and temperature might affect plant growth and phenolic concentrations in opposite directions.

Climatic changes are expected to have important consequences for the structure and regulation of forest ecosystems. One major component of natural ecosystems is the interaction that plants have with herbivorous insects. Studies involving woody plant–insect interactions under UV-B are few and do not appear to be in agreement. In *Nothofagus antarctica*, UV-B reduced herbivory (Rousseaux et al., 2004). However, in *Betula pubescens*, UV-B had no

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marked effects on the performance of autumnal moths, nor on the phenolic compounds of the plant hosts (Anttila et al., 2010). Dark-leaved willows exposed to enhanced UV-B hosted more insect herbivores per leaf area, yet did not experience more herbivore damage than did their non-treated counterparts (Veteli et al., 2003). In a study with *Populus trichocarpa*, UV-B increased feeding preferences of specialist herbivores, through an increase in leaf salicylates (Warren et al., 2002). The effect of warming, on the other hand, points towards an improvement of the performance of plant generalist herbivores and a decrease in the preference of specialist herbivores due to reduced leaf salicylates (Zvereva and Kozlov, 2006; Kosonen et al., 2012).

Another component of the forest ecosystem is the trophic interaction involving plants and fungi. *Melampsora* sp. (rust) fungi are biotrophic parasites common to poplars and willows. Rust infection might induce premature defoliation and increased susceptibility to other diseases and pests (Feau et al., 2007). The resistance of *Populus* spp. to different races of rusts was previously reported to be temperature-sensitive, as rust disease severity and rust aggressiveness were lower at higher than at lower temperatures (Chandrashekar and Heather, 1981a,b). In contrast to pathogenic rust fungi, fungal endophytes are microorganisms that live inside plants for all, or at least a significant part of their life cycle, without causing any immediately visible negative effects (Saikkonen et al., 1998). Endophytes are ubiquitously present in plants and the relationships they maintain with their host plants vary along a symbiotic continuum that ranges from parasitism through commensalism to mutualism (Saikkonen et al., 1998; Aly et al., 2011). When associating with grasses, fungal endophytes are able to produce alkaloids that are toxic to herbivores and thus increase plant fitness in the presence of herbivores; this concept is known as defensive mutualism (Saikkonen et al., 1998, 2010; Aly et al., 2011). In woody plants, there is some evidence indicating that there might be relationships between endophytic fungi, condensed tannin concentration and herbivore damage. In the bark of *Populus fremontii* × *Populus angustifolia* hybrids, fungal endophyte infection was negatively correlated with condensed tannin concentrations (Bailey et al., 2005), while in some European aspen clones, the presence of endophytic fungi was negatively associated with herbivore damage (Albrectsen et al., 2010). Further studies are needed to investigate whether there are any functional associations between woody plants and endophytes.

European aspen (*Populus tremula)* is a sexually dimorphic species with a male-biased sex ratio of 2:1. Many studies have reported sex-related differences in size, resource allocation, adaptation to biotic and abiotic factors (Cornelissen and Stiling, 2005; Xu et al., 2008, 2010; Zhang et al., 2010; Randriamanana et al., 2014, 2015). Female plants are expected to grow less but invest more in sexual reproduction and chemical defense than do males (Ågren et al., 1999; Delph, 1999). In addition, there are some indications that males are more susceptible to herbivore damage but more tolerant to rust infection than are females (Cornelissen and Stiling, 2005; Zhang et al., 2010). Gender responses to UV-B and warming are rather variable. On the basis of their height growth, male plantlets were also more responsive to warming than were females in dark-leaved willows (*Salix myrsinifolia)* (Nybakken et al., 2012). However, in well-watered *Populus cathayana* plants, the positive effect of warming on growth was greater in females than in males (Xu et al., 2008). Likewise, males of *P. cathayana* were more tolerant while reproductive male plants of dark-leaved willows were less tolerant to UV-B than females (Xu et al., 2010; Randriamanana et al., 2015). Thus, additional studies are needed in order to elucidate gender responses to UV-B and temperature.

Many climate change studies have been single-factor experiments. However, in nature, different climatic change factors are expected to change simultaneously. Therefore, studies manipulating multiple climate change factors in combination, including the study of interactions among organisms, are needed in order to advance our understanding of the effects of climate change on natural ecosystems. Our experimental field was set up in order to investigate the separate and combined effects of two climate change factors, UV-B and temperature, on European aspen. We used a modulated system, which is known to be more realistic than indoor studies due to the use of natural solar spectrum lighting as background light, amongst other environmental parameters. The objectives of the present study were to test the following questions: (1) whether the effects of elevated UV-B and temperature on the growth, leaf traits and the phenolic defense of European aspen seedlings will add up or cancel out, (2) whether this will this affect insect herbivory, rust fungi and fungal endophytes, and (3) how these responses differ between genders and genotypes. We hypothesized that (i) warming would promote growth but decrease phenolic concentrations, while UV-B would have the opposite effect on growth and a compound-specific effect on phenolic concentrations; (ii) warming might decrease rust infection and herbivore damage, but promote leaf colonization by endophytic fungi, although the combined effect of UV-B and temperature might have only minor effects on these three variables; and (iii) in terms of growth, males might be more tolerant to UV-B and could benefit more from the positive impact of warming than females.

2. Materials and methods

2.1. Plant materials and experimental set up

The seedlings used in the field experiment originated from adult European aspen trees that were selected from different locations in eastern and southern Finland (Randriamanana et al., 2014). The seedlings were micropropagated from the axillary buds of six female and six male clones and acclimated in the greenhouse under the same photoperiod and similar soil, temperature and air relative humidity conditions as in Randriamanana et al. (2014). On 7th June 2012, potted seedlings were transported to the field site.

The experimental field was set up in 2012, in the Botanical Garden in Joensuu, Finland (Fig. A1). At the beginning of the experiment, a 10 cm layer of mineral soil (Puutarhan musta multa 45l, Biolan Oy, Kauttua, Finland) was added to each plot (experimental unit). A total of 12,160 seedlings of different genotypes and genders were planted directly in the ground on 11th June 2012, and randomly distributed to each treatment plot. Each treatment plot was then divided into five subplots, in which individuals of different genotypes were placed randomly. The plots were randomly assigned to the following treatments and treatment combinations: control (C), supplemental UV-A radiation (UV-A), supplemental UV-B radiation (UV-B), and elevated temperature (T), UV-A+T, UV-B+T. There were six replicate plots per treatment and treatment combinations and the combined 36 plots were randomly distributed in the field site. Each plot initially contained 30 male and 30 female seedlings (six male and six female genotypes per subplot with five individual seedlings per gender).

2.2. UV-B and temperature treatments

Temperature and UV-B in treated plots were modulated to achieve a mean increase of +2 °C and +30.77% (based on energy irradiance), respectively, with ambient conditions as references. The 30.77% increase in UV-B corresponds to a 20% decrease in stratospheric ozone (30th June), as calculated by the TUV model (Koepke et al., 1998), and based on the predicted average ozone column in spring 2012 in Jokioinen, Finland (60.8°N, 23.5°E, Finnish