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Original article

Climate change – Bad news for montane forest herb layer species?

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ABSTRACT

Global warming presents a threat to plant species distributed at montane or alpine altitudes if the topography does not allow upward shifts in distribution ranges. Nevertheless, the species might also benefit from increasing temperatures and secondary effects on dominant species (e.g. bark beetle outbreaks or summer drought affecting the canopy species). As a consequence, disturbance frequency in montane forests might increase and light availability for herb layer species will increase. We addressed these interactions in a common garden experiment in Central Germany at different altitudes, representing cold and moist vs. warm and dry conditions. We investigated three montane species with different life forms, including a herb (*Trientalis europaea*), a grass (*Calamagrostis villosa*) and a dwarf shrub (*Vaccinium myrtillus*) under three shading treatments (3%, 28% and 86% of full sunlight). We hypothesized that montane species are at a disadvantage in the lowland, with the dwarf shrub suffering more than the grass. Furthermore, we hypothesized an antagonistic interaction of increased temperature and increased light conditions. While *T. europaea* and *V. myrtillus* showed only slightly responses to low altitude conditions, *C. villosa* displayed a nearly fifteen fold increase in biomass production, despite higher observed herbivory levels in the lowland. We failed to show an antagonistic effect of increased temperature and increased light availability, as all study species suffered from deep shade conditions and grew best under full light conditions at both sites. In conclusion, both improved temperature and light conditions might be principally beneficial for the investigated boreal species, in particular for the grass species *C. villosa*.

1. Introduction

One important effect of climate change is a shift of species' distribution ranges (Walther, 2003; Hampe, 2011). Mountain species are predicted to move upwards to higher elevations (e.g. Klanderud and Birks, 2003; Skov and Svenning, 2004; Thuiller et al., 2005), unless there is dispersal limitation (Lenoir et al., 2008; Trivedi et al., 2008; Bässler et al., 2010). In particular, species from high altitudes are known to track climatic change faster than species from lowland forests (Bertrand et al., 2011). However, the escape possibilities of species in mid-altitude mountain ranges are limited because of their low maximum elevations and decreasing habitat quality with increasing altitude (e.g. harsh climate) (Pompe et al., 2010). It is still open to debate which type of species will be affected most. One prediction is that rare species, such as *Campanula uniflora*, *Cassiope hypnoides* and *Erigeron humilis* in Norway, will be threatened by climatic change (Sætersdal and Birks, 1997). The investigation of Hollister et al. (2005) on arctic species did not encounter a consistent correlation between trait patterns and species responses (for instance leaf length, plant size or the number of inflorescences) to climate change, neither within growth forms nor within phylogenetic groups. However, equivocal responses of species to increased temperatures have also been described for biomass allocation (Day et al., 2008), with both increased above-ground and below-ground biomass (Arft et al., 1999; Day et al., 2008). Additionally, while some species responded to simulated climate change with increasing height or cover (e.g. dwarf shrubs and graminoids), other species (for instance, *Carex bigelowii* in Alaska) displayed decreasing biomasses (Chapin et al., 1995; Walker et al., 2006). A large variation in vegetation responses was also revealed by transplantation experiments (Bruelheide, 1999). For instance, Bruelheide (2003) translocated a montane meadow from 600 m to 170 m a.s.l., which resulted in the extinction of some, but not all montane species, which in the case of some species such as *Arnica montana* was caused by higher slug herbivory at the low altitude (Bruelheide and Scheidel, 1999). Further species (*Viola palustris* and *Succisa pratensis*) became extinct because of the reduced precipitation at low elevation (Bruelheide, 2003), while other montane species such as the grass

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species *Festuca rubra* increased in cover at low altitude (Bruelheide, 2003). Similarly divergent is the tendency of species to exhibit upward shifts in altitude as response to warming. For instance, Lenoir et al. (2008) noticed an upward shift especially for forbs and grasses, a consequence of their shorter reproductive cycle and higher growth rates compared to woody species.

It is commonly assumed that the decline of boreal species to increased temperatures is the result of a reduced competitive ability compared to species adapted to warmer climates (Callaghan et al., 2004). However, increased temperatures might also have direct effects on the species' life cycle. For instance, a higher fungal attack and consequently reduced germination success has been shown for the dwarf shrub *Vaccinium uliginosum* (Graae et al., 2008). Growth and fitness of plants are also affected by further factors related to increased temperatures, such as higher levels of herbivory as well as lower precipitation and lower wind speed. Wind velocity is an often neglected effect of climate change, but with the upward shift of plant species to higher altitudes, individuals are often exposed to higher wind speeds, resulting in lower canopy height of, for example dwarf shrubs from the Ericaceae (Crabtree and Ellis, 2010).

In forest ecosystems, a change in environmental conditions often involves a change in the disturbance regime (Littell et al., 2010). Kathke and Bruelheide (2010) showed that the number of new gaps increased in the last 60 years in the Harz Mountains in Germany, brought about both by an increase in bark beetle outbreaks and extreme weather events (e.g. gales, heavy rainfalls, summer drought). Jönsson et al. (2011) predicted a higher future frequency of bark beetle calamities and consequently a higher risk of disturbance in spruce forests in Europe. Therefore, it may be expected that the magnitude of gap creation will further increase in montane forest ecosystems. With gap creation, environmental conditions, especially light availability for species, change fundamentally. In most cases, forest herb layer species benefit from higher light availability in newly created gaps (Mihók et al., 2005; Kirchner et al., 2011). In contrast, some species are also at a disadvantage at high light availability. For instance, Rünk and Zobel (2007) described a higher mortality of seedlings of three *Dryopteris* species from mesic woodlands in Estonia under full sunlight. Such detrimental effects of increased light conditions are usually explained by reduced levels of air humidity and soil moisture (Arunachalam and Arunachalam, 2000; Rünk and Zobel, 2007). However, little is known about how different plant species will respond to increased gap creation, and nothing is known about how the responses to direct effects of climate change (as for instance, more extreme weather events, less precipitation, higher temperatures) interact with gap dynamics.

The ability to make use of improved growing conditions is reflected in the species phenotypic plasticity, defined as the ability of one genotype to produce different phenotypes according to the environmental conditions (Sultan, 2000). However, the degree of plasticity strongly depends on the species' life form. Because of higher growth rates, forb and grass species are expected to exhibit a higher phenotypic plasticity than woody species (Genney et al., 2002; Rich et al., 2008). Thus, the responses of plant species to increasing temperatures seem to be diverse and idiosyncratic (Chapin et al., 1995; Hollister et al., 2005). Therefore, the effects of global change and ensuing changes in environmental conditions may be more detrimental for woody species than for herbaceous species. Additionally, phenotypic plasticity does not only vary between species but also within species (Albert et al., 2010), rendering high-altitude populations less plastic than their lowland counterparts. For example, for *Fagus sylvatica* Jump et al. (2006) detected an allele which had a different frequency at different altitudinal levels, thus offering the potential of short-term adaptation to climate change. We studied these possible effects of global warming in interaction with gap dynamics in a common garden experiment by transplanting typical montane forest herb layer species with different life forms to high and low altitudinal environmental conditions.

The aim of this study was to gain insight into the possible responses of montane forest herb layer species to climatic change. In particular, we tested the following hypotheses: 1. Montane species have a disadvantage at lower altitude. 2. There is an interaction of life form with the responses to changing environmental conditions caused by climate change. More specifically, we predicted that grass species and herb species will be less negatively affected by increasing temperatures compared to dwarf shrub species, which are assumed to have less phenotypic plasticity. 3. There is an antagonistic interaction of increased temperature and increased light conditions, mainly brought about by a reduced relative humidity at higher temperatures.

2. Material and methods

2.1. Study area

Our study took place in Central Germany in the Botanical Garden at Mt. Brocken (1142 m a.s.l.) in the Harz National Park, Saxony Anhalt as well as in the Botanical Garden of the Martin Luther University in Halle Wittenberg (93 m a.s.l.), see Photo S1. These two sites differed with respect to mean annual temperature of 3.1 °C and 9.1 °C at Mt. Brocken and in Halle, respectively (long term weather records, Deutscher Wetterdienst). For the future climate of Central Europe, Schär et al. (2004) predicted a higher risk of drought events and heat waves. Therefore, we established one of our experimental sites in a region of Germany with very low annual precipitation of about 450 mm in Halle, in contrast to Mt. Brocken with very high annual precipitation of 1727 mm.

2.2. Plant material

The goal of our study was to investigate the influence of simulated climate change by transplanting montane forest herb layer species from a high-altitude site to a low-altitude site. Therefore, we excavated five clones with 24 ramets each of each of the three target plant species (the herb species *Trientalis europaea* L., the grass species *Calamagrostis villosa* (CHAIX) J.F. GMEL. and the dwarf shrub *Vaccinium myrtillus* L.) at an altitude of 900 m a.s.l. at Mt. Brocken, in the Harz National Park, Central Germany. These three species were the most common herb layer species in our study area (for a species list see Kirchner et al., 2011). Plants of *T. europaea* and *C. villosa* were sampled in July 2008 and planted in pots, using the greenhouse of the Botanical Garden of the Martin Luther University in Halle. In every pot, we planted one individual of *T. europaea* or three shoots of a *C. villosa* tussock, using soil collected close to Mt. Brocken outside the core zone of the Harz National Park (close to the locality Elend, 51°44′01″N, 10°41′03″E). The plants were raised at 17 °C in the greenhouse for three months. In October 2008, the plots were prepared at both sites. On Mt. Brocken, on the ground of the Mountain Garden, the sward of subalpine grassland vegetation was removed. To provide the same soil conditions in the lowlands, soil from Mt. Brocken (from a location next to the experimental site on Mt. Brocken) was transported to Halle and used to prepare a bed with a soil depth of 40 cm. Soil type for both study fields was secondary Podzol. In both sites we planted *T. europaea* as well as *C. villosa* for hibernation. As the cultivation of *V. myrtillus* failed, we sampled cuttings in April 2009 and planted them directly in the experimental plots.