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High-elevation plants have reduced plasticity in flowering time in response to warming compared to low-elevation congeners

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Abstract

Global warming has caused shifts in the flowering time of many plant species. In alpine regions the temperature rise has been especially pronounced and together with decreasing winter precipitation has led to earlier snowmelt. The close association between time of snowmelt and plant growth at high elevations makes climate change for alpine plants particularly threatening. Here we transplanted eleven congeneric pairs of high- and low-elevation herbaceous species to common gardens differing c. 800 m in elevation, and c. 4 °C in mean growing season temperature to test whether reproductive phenologies of high- and low-elevation plants differ in their respective responses to temperature. Results indicate that high-elevation plants were less plastic in response to transplantation than their low-elevation congeners as the onsets of phenophases on average shifted 7 days less than in low-elevation plants. Plasticity of phenophase durations was overall weaker than that of phenophase onsets, and slightly stronger in high-elevation species compared to low-elevation congeners. We suggest that weaker plasticity in the onsets of early stages of reproductive phenology of high-elevation plants is related to spring frost, which constitutes a strong selective agent against early loss of winter hardiness. Some of the plastic responses of both low- and high-elevation species might potentially be adaptive under predicted climate change. However, the observed plasticity can be largely explained as a passive response to temperature and not as the result of natural selection in heterogeneous environments. The strong temperature-sensitivity of low-elevation species might promote their upward range expansion, but only to a certain threshold after which it becomes limited by the short growing season.

Keywords: Phenology; Canalization; Alpine plants; Warming; Flowering

Introduction

Most biological processes are influenced by abiotic events and follow seasonal cycles (Forrest & Miller-Rushing, 2010). A striking example is plant reproduction in seasonally variable climates. The phenology of plant reproductive events critically affects pollination, seed ripening and dispersal, and therefore the overall success of a species (Rathcke & Lacey 1985; Schemske et al. 1978).

Pollinator limitation and freezing damage early in the season, and the risk of seed ripening failure due to early snowfall in the late season constitute the specific challenges for the timing of flowering in arctic-alpine plants (Hülber, Winkler, & Grabherr 2010; Inouye, Morales, & Dodge 2002).

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In recent decades, global warming has caused shifts in the flowering time of many species (Cleland, Chuine, Menzel, Mooney, & Schwartz 2007; Fitter & Fitter 2002; Pauli et al. 2012; Sherry et al. 2007). In alpine regions of Europe, the temperature rise in the last decades has been higher than the global average (Auer et al. 2007; Hansen et al. 2006), and was accompanied by decreasing snowfall in winter, causing earlier snowmelt and prolonged growing seasons (IPCC 2014). The close association between time of snowmelt and plant growth at high elevation makes climate change for alpine plants particularly challenging (Odland & Munkejord 2008).

An important plant response to environmental change is phenotypic plasticity in key functional traits (Nicotra et al. 2010). Phenotypic plasticity is the capacity of an organism to produce a range of phenotypes across multiple environments (Bradshaw 1965; Hoffmann & Sgro 2011). The sensitivity of phenological events to external conditions is an exemplary case of phenotypic plasticity and has received considerable attention as a potential way to mitigate rapid climate change (Matesanz, Gianoli, & Valladares 2010; Nicotra et al. 2010; Pluess, Frei, Kettle, Hahn, & Ghazoul 2011; Richter et al. 2011; Scheepens & Stöcklin 2013). Shifting flowering phenology due to earlier springtime is broadly documented (Cleland et al. 2007; Peñuelas, Filella, & Comas 2002; Walther et al. 2002). In Europe, plant phenology has advanced by 1.5 days per decade since 1976, and climate warming has caused an advance in flowering and fruiting in almost 80% of the observed species (Menzel et al. 2006).

Photoperiod and temperature are the key abiotic variables co-determining the timing of reproduction in most herbaceous plants (Dunne, Harte, & Taylor 2003; Price & Waser 1998; Rathcke & Lacey 1985). While photoperiod strongly influences plant phenology in most temperate climates, alpine plants have been found to be less sensitive to this factor (Hülber et al. 2010; Menzel et al. 2006). In a study of Keller and Körner (2003), an experimental one-hour shortening of the photoperiod, which equals a one-month advancement of phenology, had only little effect on flowering time in a large set of alpine species. In contrast, temperature and time of snowmelt have been shown to strongly affect alpine plants' flowering phenology (Hülber et al. 2006; Inouye et al. 2002; Inouye 2008; Jonas, Rixen, Sturm, & Stoeckli 2008), and therefore, alpine plants might be particularly good at tracking climate change (Cleland et al. 2012).

Plants that track climate change have been shown to be at a fitness advantage both at low (Cleland et al. 2012; Quinn & Wetherington 2002; Springate & Kover 2014) and high elevations (Anderson, Inouye, McKinney, Colautti, & Mitchell-Olds 2012). However, a number of studies suggest that at high elevations, more plastic species run an increased risk of freezing damage when they flower early in response to warm temperatures (Rixen, Dawes, Wipf, & Hagedorn 2012; Wheeler et al. 2014; Wipf, Stoeckli, & Bebi 2009). This is in part due to an increased susceptibility to freezing damage, because winter hardiness is lost earlier, but also because under earlier snowmelt plants are more exposed to frost events (i.e. lack of the protective snow cover). Ice formation in flowering stems of alpine plants can cause the loss of all fruits (Ladinig, Hacker, Neuner, & Wagner 2013) and is therefore expected to exert strong selection on frost avoidance traits. Preventing early flowering is perhaps the most effective frost avoidance strategy, and alpine plants might therefore have evolved limits as to how early they can start flowering (i.e. reduced phenotypic plasticity in reproductive timing).

In addition to shifts in flowering time, there is also an upward migration of species occurring on Europe's mountains as a response to climate warming (Pauli et al. 2012). On mountain summits, high-elevation species cannot migrate further upwards, and therefore a scenario of stationary high-elevation species and low-elevation species invading high-elevation habitats might be a typical one in the near future (Wipf, Stöckli, Herz, & Rixen 2013). If low-elevation species migrate only slowly in comparison to the rate of warming, frost might not be a relevant selective agent. However, it is more likely that frost events causing plant damage remain frequent or even increase despite warming temperatures, firstly because early snowmelt reduces protection by snow cover in spring (Inouye et al. 2002; Inouye 2008), and secondly because the speed of migration currently appears to track warming nearly in real-time (Wipf et al. 2013). Low-elevation species invading high-elevation habitats are therefore expected to be under selection for early frost avoidance.

Here, we transplanted congeneric pairs of low- and high-elevation herbaceous species to two common gardens differing c. 800 m in elevation, and c. 4 °C in the growing season temperature. We tested the following three hypotheses: (1) The onset and the duration of reproductive phenophases is affected by transplantation to different elevations simulating changing temperatures. (2) Low- and high-elevation species show an overall difference in their mean reproductive phenological timing across both gardens. (3) Plasticity in reproductive phenology as a response to transplantation differs between low- and high-elevation species. Based on early season frost emerging as a key selective agent for reproductive timing at high elevations, we additionally posit that plasticity is adaptive (evolved by means of selection rather than rooted in developmental instability) when: (i) Low-elevation plants postpone their reproduction and shorten phenophases when transplanted to the higher elevation so as to avoid freezing damage early in the season and seed ripening failure late in the season. (ii) When transplanted to a lower elevation, high-elevation plants do not advance reproduction much, because they remain stationary at high elevation where frost events are frequent and exert strong selection; and high-elevation plants extend phenophases when transplanted to the lower elevation to utilize the longer growing season for increased reproductive output (this latter prediction is based on climatic considerations; additional factors such as herbivory for example might select against extended phenophases; but see Pilson 2000).