



Research article

Quantitative genetic differentiation and phenotypic plasticity of European beech in a heterogeneous landscape: Indications for past climate adaptation



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ABSTRACT

Tree growth and species distributions are expected to be altered by climate change. European beech (*Fagus sylvatica*), one of the major tree species in Central Europe, is considered to be particularly threatened by the expected changes in local water regimes. Basic knowledge on the species' genetic variation, environmental adaptation, and phenotypic plasticity is required to assess its potential for climate change adaptation, but sufficient information is lacking. Here, we describe a seedling common garden study at two field sites incorporating 77 natural populations of European beech from an environmentally heterogeneous mountain region in the center of its distribution. We aimed to identify patterns of genetic variation and phenotypic plasticity in growth and phenology, and to associate these with seed source environments. Population differentiation was greater for phenology than for growth ($Q_{st} = 0.18\text{--}0.32$ vs. $0.00\text{--}0.16$), but within-population genetic variation was large for all seedling traits. The phenotype–environment associations indicated adaptive divergence in phenology and growth with respect to temperature and water availability, but not to soil characteristics, latitude, longitude, or topography of the seed source locations. Phenotypic plasticity was detected in growth and leaf duration, the magnitude of which differed among populations with different seed source temperatures. We conclude that seedling phenology is key to temperature and drought adaptation in European beech. Changes in local temperature and water regimes might result in local phenological maladaptation of European beech populations, although within-population genetic variation, gene flow, and phenotypic plasticity might mitigate the negative effects of climate change.

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1. Introduction

Climate change is affecting the growing conditions of European forests (Lindner et al., 2010). The combination of increasing temperatures and more variable precipitation will likely lead to longer and more severe droughts that may push trees at marginal sites beyond their physiological limits. In fact, drought has been implicated, for example, in the recent dieback of Scots pine (*Pinus sylvestris* L.) in the Swiss Rhone valley (Bigler et al., 2006; Rigling et al., 2013), and in the reduced growth of European beech (*Fagus sylvatica* L.) in Switzerland during the exceptionally dry year of 2003 (Leuzinger et al., 2005).

“What potential have existing (meta)populations to be self-sustaining?” This question raised by Oliver et al. (2012) is key to improving our ecological and evolutionary understanding of species sensitivity to climate change, and guiding adaptive management strategies. To address these needs, it is important to examine the amount of genetic variation and the magnitude of climate adaptation that influence a population's potential for evolutionary adaptation (Mátyás, 1996). Also, the amount of phenotypic plasticity that may buffer populations against fast environmental changes should be considered (Nicotra et al., 2010).

Genecological research seeks to understand within-population genetic variation and population differentiation in potentially adaptive phenotypic traits, such as growth and phenology (e.g., St. Clair and Howe, 2007; St. Clair et al., 2005). Strong phenotype–environment associations can be used to identify environmental factors that may have driven population differentiation, and thus are indicators of past and future microevolutionary processes (Alberto et al., 2013; Mátyás, 1996). For example, populations that

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appear to be adapted to higher temperatures and increased drought – conditions that will likely become more frequent on currently mesic sites – represent a source of pre-adapted alleles (Pluess et al., 2016). These beneficial alleles could spread via gene flow and, thereby, enhance climate change adaptation elsewhere (Kremer et al., 2012).

Phenotypic plasticity (PP), the ability of individuals to change their phenotype in response to the environment, is one way plants may cope with climate change. PP allows individuals to adjust their growth and physiology seasonally, developmentally, or to new environments, potentially buffering them against rapid environmental changes (Nicotra et al., 2010). In contrast, when PP is low, the long-term processes of migration or in situ evolutionary adaptation may be required (Aitken et al., 2008; Anderson et al., 2012). PP is considered adaptive when it increases fitness, but in many cases, it simply represents a non-adaptive response to physical processes or resource limitations (van Kleunen and Fischer, 2005). The extent of PP can be assessed from the magnitude of genotype by environment ($G \times E$) interactions (Nicotra et al., 2010). Thereby, the presence of $G \times E$ interactions indicates that genotypes (or populations) differ in their phenotypes relative to each other when grown in different environments.

We studied the genecology and phenotypic plasticity in European beech seedlings (referred to as “beech”). Beech is a deciduous, wind-pollinated, and highly outcrossing tree species. It represents the most abundant broadleaved forest tree in Central Europe, presumably due to its wide tolerance of site conditions (shade, soils) and its high competitiveness (Bolte et al., 2007; Ellenberg, 2009; Heiri et al., 2009; Peters, 1997; Pretzsch, 2014). Still, the distribution of beech is limited by low temperatures, drought, and waterlogged soils (Ellenberg, 2009; Gessler et al., 2007). Consequently, beech occurs primarily on moist sites under oceanic and temperate climates that have mild winters and humid summers (Bolte et al., 2007). Drought, in particular, negatively affects the species' growth and competitive ability. Therefore, drought is an important limiting factor for beech populations in the face of climate change (Gessler et al., 2007; Zimmermann et al., 2015). In the long term, the distribution of beech is expected to shift toward higher elevations and latitudes, and may even diminish overall (Hanewinkel et al., 2013; Meier et al., 2011; Zimmermann et al., 2006).

Several studies have shown that beech exhibits population variation in phenotypic traits, e.g., leaf phenology, leaf anatomy, growth, and sensitivity to drought (reviewed by Bussotti et al., 2015). In most cases, this variation tracks environmental gradients, suggesting divergent natural selection based on population-scale differences in temperature (e.g., Vitasse et al., 2009, 2013) and water availability (e.g., Peuke et al., 2002; Pluess and Weber, 2012). Furthermore, several studies characterized plastic responses for traits such as radial growth (Eilmann et al., 2014), leaf anatomy (Stojnic et al., 2015), and seedling bud phenology (Vitasse et al., 2013).

However, genecological studies rarely addressed variation in beech at high spatial resolution using many populations from environmentally heterogeneous and genetically well-connected regions (Pluess et al., 2016). Additionally, soil characteristics, such as pH, affect bud phenology in beech (Arend et al., 2016). Yet, we do not know how soil characteristics and site water balance may have influenced population differentiation. Finally, phenotypic plasticity of beech was insufficiently addressed in previous genecological studies (but see, Eilmann et al., 2014; Vitasse et al., 2013).

Here, we present results from a common garden study using two field sites and 77 beech populations from Switzerland. Our objectives were to answer the following questions: (1) Do beech populations show genetic differentiation in quantitative traits within a small, environmentally heterogeneous region? (2) Are

there phenotype-environment associations that indicate potential environmental drivers of population differentiation? (3) What is the extent of phenotypic plasticity in potentially adaptive traits?, and (4) Does phenotypic plasticity vary along environmental gradients?

This study will help us understand the adaptive character of seedling phenotypic traits, the effect of seed source environments on population differentiation, and the potential for climate change adaptation in beech.

2. Methods

2.1. Population sampling

Seeds were collected in fall 2011 from 77 natural populations (i.e., autochthonous provenances) of beech from an area of 197 km \times 264 km in Switzerland. This represents a central part of the species' distribution. The selected populations were located in the colline to the lower subalpine forest zones and in all six main biogeographic regions of Switzerland (Fig. 1). Populations were chosen to sample large environmental gradients, whereas topography and aspect were as uniform as possible within populations (Table 1; for details see Pluess et al., 2016). Each population was represented by three single-tree seedlots (families) collected from trees at least 100 m apart. Sampled seed trees were part of the upper canopy layer.

2.2. Seedling cultivation and field test

Approximately 600 seeds from each tree were sown into nursery beds at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL in Birmensdorf, Switzerland, during January 2012, and cultivated for one year. The seedlings were permanently shaded by slats (50% permeable for sunlight) for the first three months, and occasionally as necessary thereafter until the end of August, to protect them from solar radiation.

Two common gardens, i.e., field test sites (referred to as “sites”), were established in contrasting environments (Fig. 1). The first site was located at WSL in Birmensdorf (47°21'44" N, 8°27'22" E) at an elevation of 550 m a.s.l. (“low elevation site”), and the second site was located at Brunnersberg (47°19'35" N, 7°36'42" E) in the Jura Mountains at an elevation of 1090 m a.s.l. (“high elevation site”). The two sites differed in their environmental conditions (Table 2). The low elevation site faced west and was nearly flat. The soil was a Gley that was limited by a water-impermeable horizon at approximately 45–70 cm depth. The high elevation site faced southeast with an incline of 22%. The soil was a Rendzina with a rooting depth of approximately 40 cm limited by bedrock. Top soils of both sites showed neutral pH and appeared to be equally well penetrable by plant roots. Average spring and summer air and soil temperatures during the measurement year 2014 at the low elevation site were consistently 3 °C above the values at the high elevation site. Although less precipitation was recorded at the low elevation site in 2014, soil water potential during summer reached less negative values compared to the high elevation site. At the high elevation site, soil water potential was generally lower and more variable than at the low elevation site, reaching almost –400 kPa during one drought event in June 2014.

The one-year-old seedlings were planted in spring 2013 into 16 blocks per site at a 30 cm \times 40 cm spacing, with every family being represented by one offspring in every block. There were at least 24 live seedlings per family and a total of 6628 live seedlings when field measurements began in spring 2014.

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