Ecology, 98(1), 2017, pp. 211–227

Distinct genecological patterns in seedlings of Norway spruce and silver fir from a mountainous landscape

ALINE FRANK,[1,4] CHRISTOPH SPERISEN,[1] GLENN THOMAS HOWE,[2] PETER BRANG,[1] LORENZ WALTHERT,[1]
JOHN BRADLEY ST.CLAIR,[3] AND CAROLINE HEIRI[1]

[1]*Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, CH-8903, Birmensdorf, Switzerland*
[2]*Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, Oregon 97331-5752 USA*
[3]*Pacific Northwest Research Station, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon 97331-4401 USA*

Abstract. Understanding the genecology of forest trees is critical for gene conservation, for predicting the effects of climate change and climate change adaptation, and for successful reforestation. Although common genecological patterns have emerged, species-specific details are also important. Which species are most vulnerable to climate change? Which are the most important adaptive traits and environmental drivers of natural selection? Even though species have been classified as adaptive specialists vs. adaptive generalists, large-scale studies comparing different species in the same experiment are rare. We studied the genecology of Norway spruce (*Picea abies*) and silver fir (*Abies alba*), two co-occurring but ecologically distinct European conifers in Central Europe. For each species, we collected seed from more than 90 populations across Switzerland, established a seedling common-garden test, and developed genecological models that associate population variation in seedling growth and phenology to climate, soil properties, and site water balance. Population differentiation and associations between seedling traits and environmental variables were much stronger for Norway spruce than for silver fir, and stronger for seedling height growth than for bud phenology. In Norway spruce, height growth and second flushing were strongly associated with temperature and elevation, with seedlings from the lowlands being taller and more prone to second flush than seedlings from the Alps. In silver fir, height growth was more weakly associated with temperature and elevation, but also associated with water availability. Soil characteristics explained little population variation in both species. We conclude that Norway spruce has become an adaptive specialist because trade-offs between rapid juvenile growth and frost avoidance have subjected it to strong diversifying natural selection based on temperature. In contrast, because silver fir has a more conservative growth habit, it has evolved to become an adaptive generalist. This study demonstrates that co-occurring tree species can develop very different adaptive strategies under identical environmental conditions, and suggests that Norway spruce might be more vulnerable to future maladaptation due to rapid climate change than silver fir.

Key words: Abies alba; *adaptive genetic variation; Central Europe; climate change; common garden; conifers; evolutionary adaptation; genecology; phenotype-environment associations;* Picea abies; *quantitative genetics; soils.*

INTRODUCTION

European forests are expected to be impacted by changes in temperature and water regimes and associated increases in natural disturbances (Lindner et al. 2014). Affected species may cope with these changes via migration (i.e., colonization of new areas), phenotypic plasticity, or evolutionary adaptation (including gene flow among populations; Aitken et al. 2008). For most tree species, however, migration rates are not expected to keep pace with future climatic changes (Davis and Shaw 2001). Furthermore, although phenotypic plasticity can contribute to forest resilience in the short term (Alfaro et al. 2014), the mere existence of population-level genetic variation highlights the limits of phenotypic plasticity. Finally, evolutionary adaptation (or simply "adaptation") may improve or maintain population fitness through local changes in allele frequencies via within-population natural selection or the introduction of new alleles from other populations (Kremer et al. 2012). New mutations are expected to contribute little to the adaptive potential of tree populations in the short-run (Petit and Hampe 2006).

Genecology, the study of genetic variation in relation to the environment, is often used to investigate adaptation in forest trees (Aitken 2004, St.Clair and Howe 2007). Genecological studies allow us to (1) identify adaptive traits and selective drivers, (2) infer species' adaptive strategies, and (3) assess evolutionary potentials.

Adaptive traits are characterized by strong population differentiation and associations with environmental gradients. These traits include morphological, physiological, and phenological characteristics such as growth, foliar

Manuscript received 18 March 2016; revised 23 August 2016; accepted 6 October 2016. Corresponding Editor: John J. Battles.
[4]E-mail: aline.frank@alumni.ethz.ch

characteristics, timing of bud break and bud set, water use efficiency, photosynthetic capacity, and survival (Bussotti et al. 2015). Strong associations between trait variation and environmental variables provide evidence for natural selection, and allow us to infer the environmental drivers of population differentiation. In trees, temperature and water availability are important drivers of natural selection that have resulted in genetic adaptation on scales ranging from stands, to regions, and entire species ranges (reviewed in Howe et al. 2003, Savolainen et al. 2007, Alberto et al. 2013).

From a micro-evolutionary standpoint, tree species can be classified as adaptive specialists, adaptive generalists, or intermediate types (Rehfeldt 1994). Adaptive specialists, such as lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*), are characterized by having strong associations between adaptive traits and environmental gradients, whereas adaptive generalists, such as western white pine (*Pinus monticola*) and western redcedar (*Thuja plicata*), show weak associations between adaptive traits and environmental gradients (Aitken 2004). However, few studies have assessed two or more species in the same experiment (but see Green 2005, Vitasse et al. 2009, 2013). Comparisons of genecological patterns are particularly interesting for co-occurring species, and, thereby, a single experimental setup is key to avoid confounding effects of experimental differences. Detailed information about species' adaptive strategies is interesting per se, but can also be used to infer the potential consequences of climatic change, e.g., to assess the risk of future maladaptation (St.Clair and Howe 2007), and to develop new management strategies to adapt forests to climate change.

The evolutionary potential of species depends on both within- and among-population genetic variation. High within-population variation promotes within-population evolution (Bussotti et al. 2015), whereas high among-population variation provides a pool of diverse genotypes and alleles available via gene flow. Given sufficient gene flow, pre-adapted alleles from other populations can enhance local adaptation (Petit and Hampe 2006, Kremer et al. 2012). Gene flow, however, may also oppose adaptation, because it may lead to immigration of alleles that are, on average, less fit than existing alleles (Lenormand 2002). Detailed information about within- and among-population adaptive genetic variation is therefore fundamental for understanding climate change adaptation.

We compared the genecology of Norway spruce (referred to as "spruce;" *Picea abies* [L.] Karst.) and silver fir (referred to as "fir;" *Abies alba* Mill.), two common and widespread European conifers that often co-occur in Central Europe. Both are late-successional species, but they differ in several ecological characteristics. Fir has greater shade-tolerance than spruce (Ellenberg 2009), and spruce is more cold-tolerant but less drought-tolerant than fir (Lebourgeois et al. 2010, Zang et al. 2014). Our study focused on populations in the Swiss Alps, where both species occupy ecologically diverse habitats, extending from the wet outer Alpine chain to the dry Central Alps, and across diverse soil types (Ellenberg 2009). Although they co-occur in many areas, spruce is found in more continental climates than fir, and at higher elevations up to the tree line (Ellenberg 2009).

Studies of growth and phenology suggest that population differentiation is greater for spruce than for fir (Engler 1905, Herzog and Rotach 1990, Skrøppa and Magnussen 1993, Sagnard et al. 2002, Chmura 2006, Vitasse et al. 2009, Kapeller et al. 2012, Schueler et al. 2013). However, except for the early study of Engler (1905), these species have not been compared within the same experiment. Although large-scale provenance trials have been conducted for spruce, these tests generally assessed only a few traits (e.g., Lagercrantz and Ryman 1990, Kapeller et al. 2012). In fir, most studies included only a few populations, or only small regions (Herzog and Rotach 1990, Sagnard et al. 2002, Vitasse et al. 2009). In addition, the contribution of nonclimatic factors such as nutrient availability and site water balance to local adaptation of tree populations has received little attention so far (but see Campbell 1991, Lesser et al. 2004). Here, we used a large number of populations from diverse environments, a broad selection of phenotypic seedling traits (growth and phenology), and a variety of environmental variables representing geography, topography, climate, physical and chemical soil properties, and site water balance. Our objectives were to (1) identify adaptive traits and associated selective forces for spruce and fir populations in Switzerland, (2) compare the adaptive strategies of these two species, and (3) infer their potential for climate change adaptation.

METHODS

Population sampling and seedling cultivation

Spruce and fir in Switzerland are part of a large continuous range of the two species covering much of the Alps. Both species are abundant in Switzerland (Fig. 1), mainly in the Swiss Alps and in the Jura Mountains, located north of the Alps. Our goal was to sample native (i.e., autochthonous) stands and to cover large environmental gradients. In 2009, we sampled 72 spruce and 90 fir populations along a 25 × 25 km^2 grid throughout all biogeographic regions of Switzerland (Fig. 1). Typically, one spruce and one fir population were sampled per grid cell. More than one population per species was sampled in grid cells with high environmental heterogeneity, e.g., in mountain valleys with large differences in elevation and aspect. For each population, we selected three parent trees from an area with a relief as uniform as possible. One spruce population was represented by 10 individual trees instead of three. Selected trees were located in the same stand at least 100 m apart to minimize relatedness. For spruce, the 72 populations sampled in 2009 were complemented with 20 stored seedlots, resulting in a total of 92 populations. The stored seedlots, referred to as

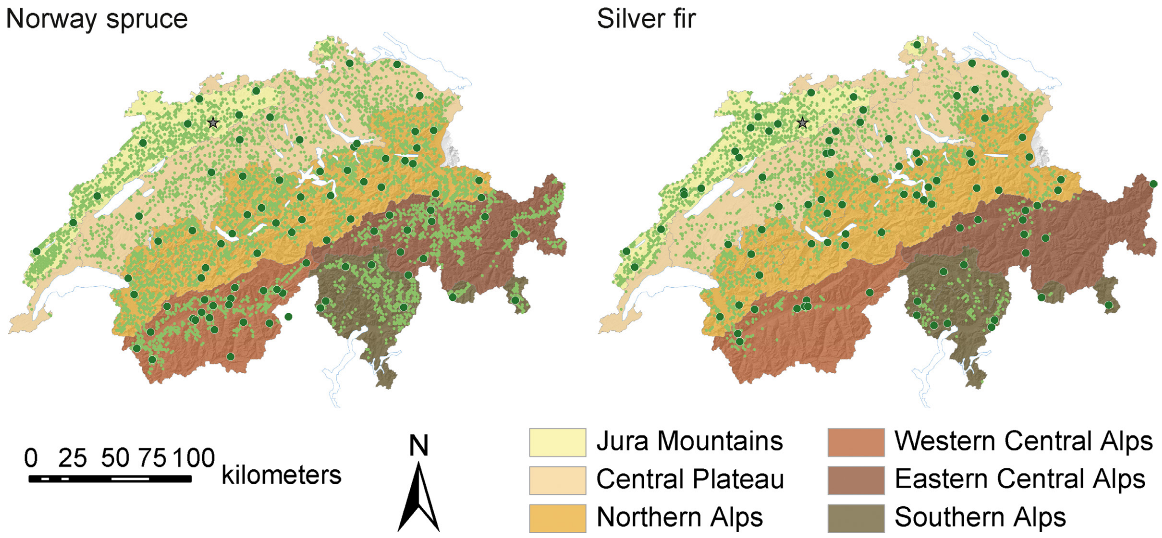

FIG. 1. Distribution of the 92 Norway spruce (*P. abies*) and 90 silver fir (*A. alba*) populations (large green dots) sampled across Switzerland. Small green dots represent the species' current distribution (WSL 2014), a star indicates the test site location. Colored regions represent the six main biogeographic regions of Switzerland (Gonseth et al. 2001).

"pooled seedlots", consisted of mixed seed from 10 trees per population. In April (fir) and May (spruce) 2010, approximately 2000 seeds from each tree (referred to as a "family") were sown directly into nursery beds at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL in Birmensdorf, Switzerland, where the seedlings were grown for two years. The nursery beds were permanently shaded by slats (50% permeable for sunlight) during the first 3 months, and as necessary until end of August (spruce) or September (fir), to protect seedlings from high solar radiation. Because families and populations were not replicated or randomized in the nursery, we used seedling height after the third, i.e., 2012 growing season (H0) as a covariate to account for possible growth differences in the nursery.

Field test

We transplanted a random selection of viable seedlings with present terminal buds from the nursery to the open field test site in spring 2012, where they were allowed to acclimate for a year before measurements started in spring 2013. The field test was located at Brunnersberg, a former pasture on a south facing slope (20–24% incline) in the Jura Mountains in Switzerland (47°19′35″ N, 7°36′42″ E, 1,090 m a.s.l.; Fig. 1). The site is characterized by a mean annual temperature of 6°C, mean annual precipitation sum of 1400 mm, and shallow rendzic soil. For the growing seasons 2013 and 2014, mean spring temperatures (March–May) were 4°C and 7°C, respectively, and the top soil was predominantly moist. The average soil water potential at 15 cm was −23 (±64) kPa in 2013 and −11 (±25) kPa in 2014, as measured from June to September using 12 MPS-2 sensors (Decacon Devices, Pullman, Washington, USA). The site was watered when the soil water potential reached −500 kPa during one extremely dry period in July 2013.

For each species, the seedlings (i.e., the offspring of 90–92 populations with mostly three families each) were planted at a 30 cm × 40 cm spacing in 16 blocks. Within blocks, each family was represented by one seedling, whereas each pooled seedlot was represented by three seedlings. All seedlings were randomized within blocks without regard to population origin. For families that had fewer than 16 seedlings in the nursery, we set a threshold of at least 12 seedlings for being included in the field experiment. Mortality during the first (acclimation) year in the field was minor. Thus, there were at least 10 live trees per seedlot when measurements began in spring 2013, resulting in 4245 spruce and 4033 fir seedlings that were included in the analyses.

Measurements and derived traits

Growth.—Seedling height (H) and stem diameter (D) were measured at the end of the third (H0, D0; 2012) and fourth (H, D; 2013) growing seasons (Table 1). Derived traits included slenderness ratio (H/D; a measure for growth partitioning potentially related to competitive status and drought tolerance) and fourth-year height and stem diameter increments (HIncr, DIncr) as H − H0 and D − D0, respectively. During the fourth growing season, height was measured twice a week, and height growth curves were fitted for every seedling as described in Appendix S1. Based on these growth curves, the following traits were derived for each seedling. The date of height growth cessation (GrowthCess) was estimated as the date at which 95% of the total height growth was achieved. Mean daily height growth rate (GrowthRate) was estimated as the mean first derivative of the growth curve

Table 1. Phenotypic traits measured on Norway spruce (*P. abies*) and silver fir (*A. alba*) seedlings grown in a common environment.

					Norway spruce		Silver fir	
Trait group	Trait	Abbreviation	Description	Unit	Mean	SD	Mean	SD
Growth	Early height†; covariate	H0	Early seedling height from ground surface to uppermost needle tip (spruce) or bud base (fir)	mm				
	Height‡	H	Seedling height from ground surface to uppermost needle tip (spruce) or bud base (fir)	mm	214.3	63.8	132.4	24.8
	Height increment	HIncr	H minus H0	mm	57.9	28.1	28.4	12.1
	Stem diameter‡	D	Stem diameter 2 cm above ground surface	mm	7.9	2.2	5.6	1.2
	Stem diameter increment	DIncr	D minus early stem diameter 2 cm above ground surface (D0†)	mm	4.2	1.4	2.5	0.9
	Height growth rate§	GrowthRate	Mean first derivative of growth curve	mm/d	1.5	0.6	0.9	0.3
	Height growth duration§	GrowthDur	Time from BudBreakT4 to GrowthCess	d	41.3	7.9	29.6	6.6
	Slenderness ratio	H/D	Ratio of H to D	cm/mm	2.7	0.6	2.4	0.4
Phenology	Fourth-year terminal bud break§	BudBreakT4	Membrane below bud scales broken, first green needles visible (fir); bud scales broken circularly, revealing green needles at the bud tip (spruce); refers to terminal buds	JD$^{\#}$	149	11	141	6
	Fourth-year lateral bud break§	BudBreakL4	Membrane below bud scales broken, first green needles visible (fir); bud scales broken circularly, revealing green needles at the bud tip (spruce); refers to lateral buds, i.e., adjacent to terminal buds	JD$^{\#}$	145	11	133	4
	Fifth-year terminal bud break¶	BudBreakT5	Membrane below bud scales broken, first green needles visible (fir); bud scales broken circularly, revealing green needles at the bud tip (spruce); refers to terminal buds	JD$^{\#}$	137	13	129	5
	Height growth cessation§	GrowthCess	Date at which 95% of terminal leader height growth was achieved	JD$^{\#}$	191	10	171	4
	Second flushing§	SecFlush	Occurrence of second flushing anywhere on the seedling (but not on terminal or adjacent lateral buds; spruce)	1, 0	31%	46%	–	–

† Measured after growing season 3 (2012).
‡ Measured after growing season 4 (2013).
§ Measured or observed during growing season 4 (2013).
¶ Measured or observed during growing season 5 (2014).
# Julian Day (day of the year).

between terminal bud break and GrowthCess. Height growth duration (GrowthDur) was estimated as the number of days from terminal bud break to GrowthCess.

Bud phenology and second flushing.—We measured bud phenology twice weekly on terminal and directly adjacent lateral buds in the fourth growing season, and once weekly on terminal buds in the fifth growing season. The Julian Days (JD) of three predefined phenological stages were recorded: bud swelling, bud break, and shoot emergence. Because these three stages were correlated (r = 0.65–0.91 for spruce and r = 0.55–0.71 for fir), only the dates of the second phenological stage, i.e., bud break, were used to analyze terminal and lateral bud phenology in both species (BudBreakT4, BudBreakT5 and BudBreakL4; Table 1). Missing bud break values were estimated as described in Appendix S1. During the fourth growing season, the presence or absence of second flushing (SF) was recorded. Thereby, we distinguished between SF of terminal buds, SF of adjacent lateral buds, and SF anywhere else on the seedling (SecFlush). For analysis, only SecFlush was used (Table 1).

Seed source environments

Each seed source (i.e., population origin) was characterized by 114 environmental variables (Appendix S2: Table S1), which were assigned to six environmental subgroups: (1) geography and topography, (2) physical and chemical soil properties, (3) temperature, (4) precipitation, (5) site water balance, and (6) clear sky radiation. Geographic and topographic data (subgroup 1) were recorded at every site. Prior to analysis, aspect (ASP) was transformed to a continuous variable (Appendix S2: Table S2). Physical and chemical soil properties (subgroup 2) were derived from local soil pits that were located within a few meters of one of the parent trees as described in Appendix S1. To estimate climate variables (subgroups 3–6), we used climate data from 1931 to 1960, the time period that was associated with the establishment of the seed trees sampled for this study. Daily air temperature (mean, minimum, maximum), precipitation, relative humidity, and clear sky radiation were available from a representative network of climate stations across Switzerland (Remund et al. 2014, data provided by the Federal Office of Meteorology and Climatology MeteoSwiss). These data were spatially interpolated for every population using Shepard's Gravity Interpolation method (Zelenka et al. 1992, Remund et al. 2011). We then used site-specific estimates of precipitation, evapotranspiration, and plant available water capacity (AWC) to calculate site water balance (SWB) on a monthly basis according to Grier and Running (1977).

Data analysis

All analyses were done using the statistical computing environment R (v3.0.3 and v3.1.3; R Core Team 2014).

Variance components and quantitative genetic parameters.—We analyzed each trait except SecFlush using the R lmer function in the "lme4" package (Bates et al. 2015). Prior to the final analyses, we used a linear mixed-effects model (Eq. 1 without covariate H0) to identify outliers separately for each species. For each trait, observations whose residuals exceeded three standard deviations were removed from the final dataset (0.7% of all observations in both species). Subsequently, we applied the linear mixed-effects model (Eq. 1 including covariate H0) to estimate variance components, and to obtain population and family-within-population effects, i.e., Best Linear Unbiased Predictions (BLUPs) of population and family-within-population means. Pooled seedlots were not used to estimate variance components, but were used to obtain BLUPs. General diagnostic plots produced for every seedling trait revealed no obvious violations of model assumptions.

$$Y_{ijk} = \mu + \mathrm{H0} + B_i + P_j + F(P)_k + B \times P_{ij} + \varepsilon. \qquad (1)$$

Y_{ijk} is the value of the k^{th} family (F) from the j^{th} population (P) in the i^{th} block (B); μ is the overall mean; H0 is the fixed effect of early seedling height (covariate); B, P, and $F(P)$ are the random effects of block, population, and family-within-population; $B \times P$ is the interaction of block and population; and ε is the residual error, which represents the interaction of block and family-within-population ($B \times F(P)$). We analyzed the binary trait, SecFlush, using a generalized linear mixed-effects model (R function glmer, package "lme4", binomial model, link = "logit", optimizer = "bobyqa") without the covariate H0, since this led to very large eigenvalues, which made the model nearly unidentifiable. We set the error variance for SecFlush to $\pi^2/3 = 3.29$ as suggested by Gilmour et al. (1985) and Frampton et al. (2013).

We tested for the effect of population, and used the variance components to estimate the following quantitative genetic parameters for every seedling trait (for details see Appendix S1: Quantitative genetics and Appendix S2: Table S2): within-population phenotypic variance ($\sigma^2_{\mathrm{t(p)}}$), total and within-population additive genetic variances (σ^2_{a}, $\sigma^2_{\mathrm{a(p)}}$), population differentiation (Q_{st}), heritability among all families (i.e., across populations, h^2_{i}), within-population individual-tree heritability ($h^2_{\mathrm{i(p)}}$), the additive genetic coefficient of variation within populations ($\mathrm{AGCV}_{\mathrm{i(p)}}$), and within-population evolutionary potential ($\mathrm{EP}_{\mathrm{i(p)}}$) were estimated. To account for potential environmental differences between the spruce and fir populations, we re-estimated population differentiation for each species on a subset of matched populations (Appendix S1). Population and family-within-population effects (BLUPs, see previous text) were extracted using the R function ranef (package "lme4"). In addition, we calculated across-population genetic correlations (r_{a}) for selected pairs of traits (Appendix S1: Quantitative genetics).

Phenotype-environment associations.—We studied phenotype-environment associations using simple correlations, simple linear models, and multivariate models using the population effects (BLUPs) from analyses of variance and a subset of site-specific environmental variables. For each seedling trait, population outliers were removed if the population effect exceeded 1.5 interquartile range (maximum number of effects removed per trait was 2 for spruce and 3 for fir; Emerson and Strenio 1983).

To investigate linear relationships, we calculated Pearson correlation coefficients between the population effects for each seedling trait and 23 environmental variables. These 23 variables consisted of 13 uncorrelated variables that were also used in multiple regression (variance inflation factor VIF < 10, maximum $r = 0.77$ for spruce and 0.70 for fir) and another 10 variables that were of particular interest (Table 2; Appendix S2: Table S3). We

TABLE 2. Environmental variables from six environmental subgroups used to describe 92 Norway spruce (*P. abies*) and 90 silver fir (*A. alba*) population origins.

			Norway spruce				Silver fir					
Code	Unit	Description	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Test site¶	Use of variable#
(1) Geography and topography												
LAT	m	Latitude based on the Swiss grid system	93,527	278,260	174,246	44,943	104,921	289,740	188,374	44,679	241,735	d,e
LONG	m	Longitude based on the Swiss grid system	503,145	801,328	662,112	66,658	503,145	831,601	658,818	72,341	613,085	d,e
ELEV	m a.s.l.	Elevation	440	2,032	1,264	394	391	1,681	989	289	1,090	e
SLOPE	%	Slope	0	95	45	22	0	85	41	23	22	d,e
ASP	Gon	Aspect	0	390	210	129	0	390	220	143	150	d,e
(2) Physical and chemical soil properties												
CLAY	%	Clay content of lower soil (ca. 45–55 cm)	1.6	66.9	16.2	14	2.2	66.9	22.6	15	na	b,c,d,e
C/N	–	Ratio org. C to tot. N of top soil (ca. 5–15 cm)	10.1	31	16.6	4.3	9.7	30.5	16.3	3.2	na	b,c,d,e
pH	–	pH of top soil (ca. 5–15 cm)	2.8	7.6	4.8	1.3	2.8	7.6	5.1	1.5	6.9	b,c,d,e
AWC	mm	Plant available water capacity of 1 m soil depth (Teepe et al. 2003)	31.5	242.2	143.8	41.7	24	242.6	149.1	43	na	e
(3) Temperature†‡												
MAT	°C	Mean annual temperature	0.5	9	5.5	1.9	2.4	9.2	6.6	1.4	6	e
MTwarm	°C	Mean temperature of warmest month	9.9	18.7	14.9	2	11.7	18.8	16.1	1.4	15.2	e
MTcold	°C	Mean temperature of coldest month	−9.8	−1.7	−4.8	1.8	−7.7	−1.7	−3.9	1.5	−4.4	e
MTsp	°C	Mean spring temperature (March–May)	−0.3	9.1	5	2.1	1.7	9.2	6.4	1.5	5.6	a,b,d,e
DTAsp	°C	Maximum diurnal temp. amplitude in spring (March–May)	13.3	20.8	16.9	1.5	14.1	21.1	17.7	1.4	18.9	e
MATvar	°C	Variance of mean annual temp. among years	0.3	0.7	0.4	0.1	0.3	0.6	0.4	0.1	0.4	a,b,d,e
CONT	°C	Continentality (inter-annual temp. variance)	48.5	63.8	55	3.6	49.1	66.1	56.3	3.2	56.2	a,b,d,e
(4) Water availability†‡												
PRCan	mm	Annual precipitation sum	712.4	1999.4	1339.7	322.5	832.7	2056.5	1304.8	286.1	1421.4	a,b,d,e
PRCsu	mm	Summer precipitation sum	198.5	633.7	427.5	104.3	252.2	609.2	433.5	85.7	431	e
PRCwi	mm	Winter precipitation sum	157.2	468.1	292.6	70.7	167	428.5	269.2	59	340.5	e
PRCPETveg§	mm	Precipitation minus potential evapotranspiration of March–November	−159	968.9	441.5	316.4	−146.3	1020.9	412.3	277.7	561.8	e
DRYPsu	d	Absolute maximum drought (prec. ≤1 mm) period length in summer (June–August)	14	34	21.6	3.8	14	34	22.2	5	33	a,b,d,e
(5) Site water balance†§												
SWBmin	mm	Minimum site water balance (Grier and Running 1977)	−169.1	124.7	44.6	72.7	−152.2	133.9	48.6	58.1	67.3	a,b,d,e
(6) Radiation†‡												
RADveg	W/m^2	Mean clear sky radiation during March–November	190.9	280	250.1	15.8	190	272.5	244.9	17.1	na	e

† Values calculated per year and then averaged across the time period, if not otherwise stated.

‡ Calculations based on 1931–1960 daily data, if not otherwise stated.

§ Calculations based on 1931–1960 monthly data.

¶ Average field site climate (variable groups 3–5) based on 1931–1960 climate data interpolated for a Swiss National Forest Inventory plot 2.1 km and 69 m away.

Variables used for the Climate models (a), for the Climate & Soil models (b), for the Soil models (c), for the Complete models (d), and/or for single correlations (e).

also calculated simple linear regressions between H and SecFlush vs. mean spring temperature (March–May; MTsp), annual precipitation sum (PRCan), and elevation, i.e., three representative variables for important environmental gradients. Also quadratic relationships between traits and environmental variables were tested, but differed on average only by 0.03 R^2 from linear models.

To study relationships between population effects and several environmental variables, we built four multivariate genecological models by multiple linear regressions. For these models, we used only the 13 uncorrelated environmental variables that had been chosen as described in Appendix S1. The "Climate" model included six climate variables from subgroups 3–5 as independent variables. The "Climate & Soil" model included three additional soil variables from subgroup 2. The "Soil" model included only the three soil variables. Finally, the "Complete" model included all variables from the Climate & Soil model, plus four geographic and topographic variables from subgroup 1. For each variable, linear and quadratic terms were tested to account for non-linear relationships. We compared regression models using the all-subsets variable reduction approach (R function regsubsets, package "leaps") and selected the best smallest models using Mallow's C_p, a multimodel inference statistic that is closely related to AIC for a Gaussian normal distribution (Mallows 1973, Boisbunon et al. 2014). Model performance was assessed using adjusted coefficients of determination (R^2_{adj}) and Bonferroni-corrected P values (P_{Bonf}, where n indicates the number of traits).

Geographic population variation.—To study geographic patterns of genetic variation, we mapped the population effects (BLUPs) for H and BudBreakT4, and also compared these to the population effects predicted from the genecological models.

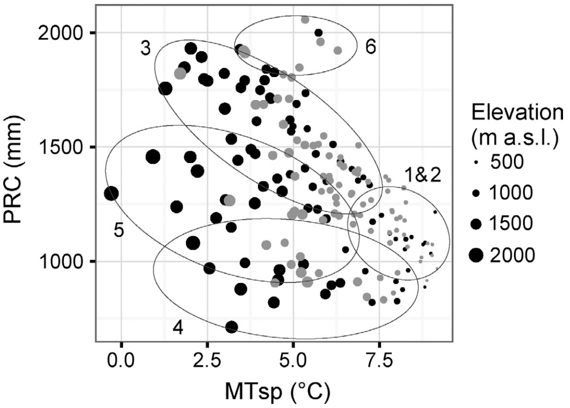

Fig. 2. Population origins of Norway spruce (*P. abies*; $n = 92$, black) and silver fir (*A. alba*; $n = 90$, gray) within the environmental gradients of annual precipitation sum (PRCan), mean spring temperature (March–May; MTsp), and elevation (point size). Circles group populations according to the six main biogeographic regions of Switzerland (Gonseth et al. 2001): (1) Jura Mountains, (2) Central Plateau, (3) Northern Alps, (4) Western Central Alps, (5) Eastern Central Alps, (6) Southern Alps. Climate data represent mean values for the period 1931–1960.

Results

Environment of sampled populations

Among-population variation was considerable for most environmental variables, and comparable for spruce and fir (Table 2, Fig. 2). The spruce populations extended into colder areas (MAT = 0.5–9.0°C) compared to fir (MAT = 2.4–9.2°C). This was primarily due to the larger elevational range of spruce (440–2,032 m a.s.l.) compared to fir (391–1681 m a.s.l.). We accounted for these differences by matching spruce and fir populations on key environmental variables for some analyses (see below).

Species' phenotypic characteristics

Spruce seedlings exhibited on average greater height growth than did fir seedlings (Table 1). Compared to fir, spruce seedlings grew faster (GrowthRate), had twice the height increment (HIncr), and were 62% taller (H) by the end of the fourth growing season. Bud break (BudBreakT4, BudBreakL4 and BudBreakT5) occurred 8–12 d later in spruce than in fir. Height growth duration (GrowthDur) was 11 d longer and height growth cessation (GrowthCess) occurred 20 d later in spruce than in fir. Second flushing was only observed on spruce, with 31% of seedlings exhibiting second flushing anywhere on the plant (except on terminal or adjacent lateral buds; SecFlush). Terminal buds second flushed on only 3% of spruce seedlings, representing too few observations for analysis of variance. There was a high genetic correlation between SecFlush and H ($r_a = 0.82$), which indicates that families with SecFlush tended to have greater height growth, and suggests that seedling height may have been influenced by second flushing in previous years.

Genetic variation

Among-population genetic variation.—Population differentiation was greater for height growth than for phenological traits, and greater for spruce than for fir (Figs. 3a–c and 4; Appendix S2: Tables S4 and S5). For spruce, significant among-population differences ($P_{Bonf} < 0.05$) were found for all traits except for stem diameter and stem diameter increment (D, DIncr). For fir, significant among-population differences were found for all traits, except for GrowthRate, fifth-year terminal bud break (BudBreakT5), and GrowthCess. Percentages of total phenotypic variation attributed to populations ($\% \sigma^2_p$) were larger in spruce than in fir for most traits, but not for D, DIncr, and GrowthDur. Across all traits and species, population differentiation (Q_{st}) was greatest for SecFlush in spruce ($Q_{st} = 0.53$). Among the traits measured in both species, Q_{st} values were greatest for H and

HIncr. For these traits, and for GrowthRate, Q_{st} values for spruce (0.48, 0.46, and 0.21) were at least twice as high as those for fir (0.22, 0.21, and 0.09). This was also true when populations matched on environmental variables were used to compare Q_{st} values between spruce and fir (e.g., H and HIncr; Table 3; Appendix S2: Table S6). For the remaining traits, Q_{st} was similar for the two species, and generally higher for growth than for phenology. Q_{st} values of phenological traits ranged from 0.10 to 0.13 for bud break and 0.15 to 0.17 for GrowthCess. For both species, real and modeled population effects indicate that seedlings from the lowlands north of the Alps (Central Plateau) were taller than those from the Alps (Fig. 4; Appendix S2: Fig. S1). Nonetheless, populations varied considerably in the Central Plateau, particularly in spruce. No distinct geographic pattern was observed for BudBreakT4 in either species.

Within-population genetic variation.—The amounts of within-population genetic variation were similar for the growth traits of spruce and fir, but clearly higher for the phenological traits of spruce compared to fir (Fig. 3d–f; Appendix S2: Tables S4 and S5). The additive genetic coefficient of variation ($AGCV_{i(p)}$) was very high for SecFlush of spruce (55.4%) and moderate for five out of seven growth traits in both species (13.8–25.5%). $AGCV_{i(p)}$ was relatively low for GrowthDur and H/D (6.9–11.5%) of spruce and fir, and very low for the phenological traits (0.50–6.9; except SecFlush). Within-population heritabilities ($h^2_{i(p)}$) were much higher for bud break than for the other traits, and higher in spruce (max. $h^2_{i(p)}$ = 0.74 for BudBreakL4) than in fir (maximum $h^2_{i(p)}$ = 0.36 for BudBreakT4). Evolutionary potential ($EP_{i(p)}$) was used to assess the relative potential for within-population natural selection. $EP_{i(p)}$ was largest for SecFlush of spruce (17.5%), followed by GrowthRate in both species (11.0–12.3%). Relatively low $EP_{i(p)}$ values (<5%) were recorded for GrowthDur, BudBreakT4 and GrowthCess of spruce, and for all phenological traits of fir. The large difference in $AGCV_{i(p)}$ and $EP_{i(p)}$ between SecFlush and the other traits should be interpreted with caution because of the differences in the distributions of the measured traits (i.e., binary vs. continuous).

Phenotype-environment associations

Differences among seedling traits.—Across species, H and HIncr had the largest correlations with environmental variables, and also had the Climate models with the largest R^2_{adj} (Tables 4 and 5). Similar results were found for SecFlush, which occurred only in spruce. Other traits were weakly associated with environmental variables, including D in spruce, GrowthRate and slenderness ratio (H/D) in fir, and BudBreakT4, BudBreakL4, BudBreakT5, and GrowthCess in both species. Geographic variation in H and BudBreakT4 are shown in Fig. 4; Appendix S2: Fig. S1.

Differences among environmental variables.—Correlations between seedling traits and environmental variables (Table 4) were generally higher for temperature variables

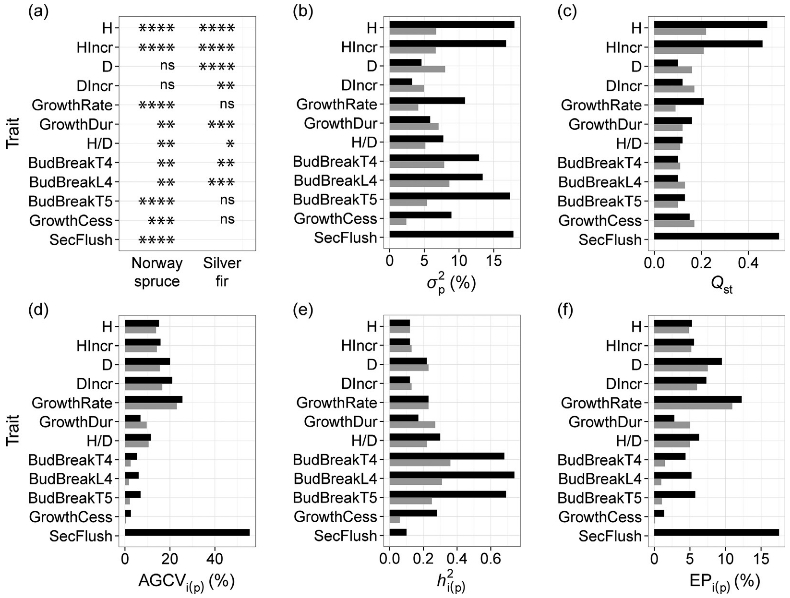

FIG. 3. Quantitative genetic estimates for all seedling traits of Norway spruce (*P. abies*; black) and silver fir (*A. alba*; gray). (a) Differences among populations (ns: non-significant, *: $P_{Bonf} < 0.05$, **: $P_{Bonf} < 0.01$, ***: $P_{Bonf} < 0.001$, ****: $P_{Bonf} < 0.0001$), (b) proportions of among-population phenotypic variance σ^2_p, (c) population differentiation (Q_{st}), (d) additive genetic coefficient of variation ($AGCV_{i(p)}$), (e) individual-tree narrow-sense heritability ($h^2_{i(p)}$), and (f) evolutionary potential ($EP_{i(p)}$). Compare Table 1 for seedling trait codes and descriptions.

TABLE 3. Population differentiation (Q_{st}) of 58 Norway spruce (*P. abies*) and 62 silver fir (*A. alba*) populations that were matched based on 13 environmental variables.

	Q_{st}			
	H		HIncr	
Analysis†	Norway spruce	Silver fir	Norway spruce	Silver fir
1	0.44	0.17	0.40	0.14
2	0.32	0.16	0.25	0.14
Mean	0.38	0.17	0.33	0.14

† Analysis 1 was conducted using Norway spruce as the "treatment" and silver fir as the "control." Analysis 2 was conducted using silver fir as the "treatment" and Norway spruce as the "control."

(subgroup 3) than for water availability (subgroups 4 and 5). In spruce, SecFlush and all growth traits except D were strongly correlated with temperature. In fir, H, HIncr, and DIncr were moderately correlated with temperature. Compared to temperature, water availability had fewer strong correlations with seedling traits in both species. In addition, R^2 values of simple linear regressions between H and SecFlush vs. mean spring temperature (MTsp) were larger than those including annual precipitation sum (PRCan; Fig. 5).

Soil characteristics, clear sky radiation, and variables of geograpy and topography explained little among-population variation. Among the soil properties, only CLAY was significantly associated with any of the seedling traits, being correlated with H, HIncr, and SecFlush in spruce (Table 4). Soil variables did not significantly improve model fit for either species when added to the climate variables in the genecological models – the mean R^2_{adj} of the Climate & Soil model did not increase for spruce, and only increased by 0.02 for fir (Appendix S2: Table S7). The Soil model explained little among-population variation in both species (mean R^2_{adj} = 0.08–0.10; Appendix S2: Table S8). No significant correlations were found between clear sky radiation (RADveg, subgroup 6) and seedling traits (Table 4). Among the geographic and topographic variables (subgroup 1), elevation (ELEV) and latitude (LAT) were highly correlated with seedling traits in both species. When added to the Climate & Soil model, however, these variables (excluding ELEV due to high collinearity) did not enhance mean R^2_{adj} (+0.04 for spruce, and +0.02 for fir; Complete models, data not shown).

Differences between species.—Environmental variables explained more population-level variation in spruce than in fir (Figs. 4 and 5, Tables 4 and 5; Appendix S2: Fig. S1, Tables S7 and S8). The correlations between seedling traits and environmental variables were generally stronger for spruce than for fir, and similarly, Climate model R^2_{adj} was greater for spruce than for fir (mean = 0.40 vs. 0.28). In spruce, temperature variables were most strongly correlated with seedling traits, with a maximum correlation of 0.81 between SecFlush and MTsp. In fir, both temperature and water availability had strong correlations with seedling traits. For example, the correlation between HIncr and maximum diurnal temperature amplitude during spring (DTAsp) was 0.49, and the correlation between H and maximum summer drought period length (DRYPsu) was 0.53. Climate models for spruce retained twice as many temperature variables than water availability variables (37 vs. 18 variables), but models for fir retained equal numbers of variables related to both temperature and water availability (26 vs. 27 variables).

DISCUSSION

Adaptive trait variation

Height growth and second flushing are key adaptive traits.—Height growth and second flushing (in spruce) had the greatest population differentiation and strongest associations with environmental variables and thus appear to be key adaptive traits. Height growth is the most widely measured trait in genecological studies of forest trees, and is often used as a proxy for productivity and fitness (Savolainen et al. 2007, Kapeller et al. 2012). Indeed, tree height has been used to describe adaptive genetic variation in many conifers, such as Norway spruce (Kapeller et al. 2012), Scots pine (*Pinus sylvestris*; Rehfeldt et al. 2002), western larch (*Larix occidentalis*; Rehfeldt and Jaquish 2010), lodgepole pine (Rehfeldt et al. 1999), and Douglas-fir (St.Clair et al. 2005). Similarly, second flushing, a key component of early height growth, has been highlighted as an adaptive trait in several woody species, including spruce (Holzer 1993, Hannerz et al. 1999, Cline and Harrington 2007).

The low population differentiation we found for the phenological traits seems atypical, especially for spruce. In other studies, bud set of spruce was strongly differentiated along latitudinal and altitudinal gradients (Chen et al. 2012, Alberto et al. 2013). Here, we measured growth cessation (not bud set per se) because bud set is difficult to detect on older seedlings that have needles tightly clustered around the developing buds. In addition, our spruce seedlings were older than those used in other studies. Holzer (1993), for example, studied the phenology of very young spruce seedlings growing under controlled conditions. Bud set is largely controlled by photoperiod and temperature in young conifer seedlings (e.g., Chen et al. 2012), but endogenous signals become increasingly important as seedlings mature (Clapham et al. 2001, and references therein). This typically results in a decrease in population differentiation over time, which may at least in part explain the low differentiation we found in spruce growth cessation.

TABLE 4. Pearson correlation coefficients (*r*) between seedling trait population effects (BLUPs) and environmental variables for Norway spruce (*P. abies*) and silver fir (*A. alba*).

Environmental variable	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	AWC	MAT	MTwarm	MTcold	**MTsp**	DTAsp	**MATvar**	**CONT**	**PRCan**	PRCsu	PRCwi	PRCPETveg	**DRYPsu**	**SWBmin**	RADveg
Subgroup			1				2						3						4			5	6
Norway spruce																							
H	*0.42*	−0.18	*−0.78*	−0.30	0.11	*0.40*	−0.22	0.03	0.16	*0.74*	*0.76*	*0.62*	*0.76*	*0.61*	−0.25	*0.46*	−0.27	−0.08	*−0.47*	−0.25	*0.42*	−0.11	−0.10
HIncr	*0.44*	−0.15	*−0.77*	−0.31	0.11	*0.40*	−0.24	0.03	0.16	*0.72*	*0.74*	*0.60*	*0.75*	*0.63*	−0.23	*0.47*	−0.27	−0.08	*−0.48*	−0.25	*0.43*	−0.10	−0.10
D	0.00	−0.02	−0.19	0.09	0.12	0.13	0.01	0.06	−0.01	0.23	0.25	0.21	0.24	0.14	−0.07	0.12	−0.04	0.00	−0.11	−0.06	0.07	−0.07	−0.18
DIncr	0.04	−0.09	−0.36	0.09	0.17	0.23	−0.07	0.08	0.03	*0.41*	*0.43*	0.37	*0.42*	0.28	−0.09	0.21	−0.20	−0.12	−0.28	−0.22	0.15	−0.21	−0.21
GrowthRate	0.28	−0.08	*−0.58*	−0.14	0.12	0.30	−0.14	0.01	0.11	*0.56*	*0.58*	*0.46*	*0.58*	*0.51*	−0.20	*0.40*	−0.18	−0.04	−0.35	−0.17	0.27	−0.10	−0.16
GrowthDur	*0.59*	0.02	*−0.62*	−0.32	0.19	0.27	−0.22	0.00	0.13	*0.50*	*0.53*	*0.40*	*0.54*	*0.42*	−0.23	*0.40*	−0.14	0.06	−0.31	−0.11	0.38	0.02	−0.05
H/D	0.32	−0.14	*−0.55*	−0.29	0.05	0.20	−0.18	−0.03	0.26	*0.48*	*0.49*	*0.41*	*0.50*	*0.46*	−0.15	0.31	−0.18	−0.07	−0.30	−0.17	0.34	−0.03	0.00
BudBreakT4	*−0.44*	−0.16	0.10	0.24	−0.21	−0.01	0.12	0.16	−0.10	−0.01	−0.02	0.05	−0.03	−0.14	−0.04	−0.24	0.07	−0.04	0.12	0.02	−0.22	−0.08	−0.19
BudBreakL4	−0.38	−0.13	0.10	0.18	−0.20	0.02	0.13	0.16	−0.13	−0.03	−0.05	0.02	−0.05	−0.10	−0.07	−0.22	0.15	0.04	0.17	0.10	−0.25	0.00	−0.10
BudBreakT5	−0.31	−0.22	−0.09	0.17	−0.19	0.12	0.06	0.21	−0.12	0.18	0.16	0.21	0.16	0.00	−0.13	−0.14	0.06	−0.01	0.06	0.00	−0.13	−0.10	−0.21
GrowthCess	−0.07	−0.11	−0.30	−0.02	−0.14	0.22	0.00	0.13	−0.05	0.30	0.31	0.28	0.31	0.16	−0.26	0.07	−0.01	0.03	−0.11	−0.03	−0.05	−0.07	−0.14
SecFlush	0.31	−0.24	*−0.80*	−0.25	0.01	*0.41*	−0.16	0.14	0.13	*0.79*	*0.80*	*0.69*	*0.81*	*0.59*	−0.26	0.38	−0.31	−0.15	*−0.47*	−0.32	*0.43*	−0.24	−0.23
Silver fir																							
H	*0.63*	−0.16	*−0.49*	−0.34	0.02	0.34	−0.28	0.07	−0.09	0.37	*0.39*	0.28	*0.39*	*0.47*	0.10	0.30	−0.25	−0.14	−0.25	−0.17	*0.53*	0.01	0.21
HIncr	*0.64*	−0.15	*−0.51*	−0.34	0.02	0.34	−0.30	0.06	−0.08	0.37	*0.39*	0.27	*0.40*	*0.49*	0.08	0.31	−0.24	−0.12	−0.26	−0.15	*0.52*	0.05	0.22
D	*0.49*	−0.11	−0.22	−0.19	−0.01	0.36	−0.30	0.16	−0.10	0.10	0.11	0.05	0.11	0.32	0.16	0.17	−0.01	0.03	0.02	0.05	0.38	0.22	0.28
DIncr	*0.53*	−0.16	−0.39	−0.28	0.02	0.38	−0.26	0.09	−0.05	0.25	0.27	0.18	0.27	*0.43*	0.01	0.24	−0.10	0.00	−0.13	−0.01	*0.45*	0.20	0.30
GrowthRate	*0.43*	0.03	−0.25	−0.17	0.02	0.17	−0.17	0.02	−0.08	0.13	0.16	0.06	0.16	0.31	0.03	0.23	0.01	0.09	−0.06	0.07	0.20	0.21	0.18
GrowthDur	0.17	−0.14	−0.14	−0.11	−0.15	0.23	−0.05	0.17	−0.05	0.15	0.16	0.14	0.15	0.00	0.26	0.07	*−0.40*	*−0.41*	−0.28	*−0.39*	0.38	−0.31	0.07
H/D	−0.30	0.05	0.04	0.06	0.01	−0.26	0.20	−0.14	0.05	0.07	0.06	0.08	0.07	−0.16	−0.14	−0.05	−0.13	−0.13	−0.16	−0.18	−0.21	−0.33	−0.25
BudBreakT4	−0.01	0.13	−0.03	0.00	0.06	−0.07	−0.12	−0.19	0.19	−0.03	−0.02	−0.06	−0.01	0.13	−0.31	0.04	0.33	0.38	0.17	0.35	−0.28	0.38	−0.08
BudBreakL4	−0.16	0.10	0.09	0.12	0.06	−0.11	−0.03	−0.19	0.13	−0.06	−0.05	−0.04	−0.05	0.03	−0.31	−0.09	0.27	0.31	0.15	0.27	−0.38	0.29	−0.06
BudBreakT5	−0.03	0.06	0.07	−0.02	0.19	0.01	−0.18	−0.11	−0.05	−0.10	−0.09	−0.11	−0.09	0.07	−0.28	0.02	0.31	0.34	0.21	0.33	−0.18	0.29	0.01
GrowthCess	0.21	−0.04	−0.37	−0.17	−0.02	0.15	−0.27	−0.07	0.18	0.34	0.36	0.26	0.37	0.21	−0.21	0.20	−0.24	−0.16	−0.32	−0.22	0.15	−0.13	−0.09

Notes: Significant correlations ($P_{\mathrm{Bonf}} < 0.05$) are highlighted in italics; highly significant correlations ($P_{\mathrm{Bonf}} < 0.001$) are highlighted in bold italics. The environmental variables used in final multivariate genecological models (Table 5) are indicated in bold. Abbreviations are described in Tables 1 and 2.

Table 5. Climate models for Norway spruce (*P. abies*) and silver fir (*A. alba*) that describe population effects (BLUPs) for seedling traits (Trait) as a function of seed source climate variables (Model coefficients).

				Model coefficients											
				Temperature						Water availability					
Trait	R^2_{adj}	P_{Bonf}	Intercept	MTsp	MTsp^2	MATvar	MATvar^2	CONT	CONT^2	PRCan	PRCan^2	DRYPsu	DRYPsu^2	SWBmin	SWBmin^2
Norway spruce															
H	0.72	0.0000	−143.297	4.756		41.794		1.005				3.696	−0.075	0.057	
HIncr	0.72	0.0000	−94.786	4.086			39.318		0.009			3.176	−0.062	0.051	
D	0.09	0.0605	−0.504	0.191	−0.015										
DIncr	0.20	0.0003	−0.312	0.102	−0.007										
GrowthRate	0.45	0.0000	−0.698	0.095	−0.006		0.355		9.8E−05					3.7E−04	
GrowthDur	0.44	0.0000	−8.740		0.061	5.533			0.001					0.009	
H/D	0.35	0.0000	−0.976	0.049		0.604		0.008			−4.3E−08			0.001	6.6E−06
BudBreakT4	0.26	0.0002	25.317	3.003	−0.315	−15.636			−0.002	−0.024	8.1E−06				
BudBreakL4	0.23	0.0003	11.966	2.935	−0.265			−0.257				−0.223			
BudBreakT5	0.31	0.0000	6.289	4.773	−0.406			−0.252				−0.201			
GrowthCess	0.27	0.0000	8.502	2.326	−0.192	−57.123	53.373								
SecFlush	0.73	0.0000	−6.521	0.521	−0.025				4.8E−04		1.2E−07	0.227	−0.004		
Silver fir															
H	0.48	0.0000	−62.581	0.509		91.322	−94.305	0.271		0.025	−8.4E−06	0.210			8.0E−05
HIncr	0.49	0.0000	−145.303	0.345		84.131	−87.544	3.459	−0.028	0.021	−7.0E−06	0.175			
D	0.32	0.0000	−11.630			0.744		0.326	−0.003	0.002	−6.7E−07		3.6E−04		
DIncr	0.43	0.0000	−8.786					0.271	−0.002	0.001	−3.6E−07		2.0E−04		
GrowthRate	0.17	0.0114	−1.715					0.058	−4.9E−04				2.7E−05	1.6E−04	−1.4E−06
GrowthDur	0.22	0.0002	−0.809			4.825				−0.001			0.001		
H/D	0.20	0.0008	0.136			−0.191							−7.2E−05	−4.5E−04	
BudBreakT4	0.23	0.0003	1.198		0.014	−3.842							−0.001	0.008	
BudBreakL4	0.24	0.0004	3.998		0.010	−3.506		−0.043					−0.001	0.004	
BudBreakT5	0.16	0.0052	−1.858			−4.398				0.005	−1.3E−06				
GrowthCess	0.18	0.0022	−1.292	0.092					1.9E−04						1.5E−05

Notes: R^2_{adj} and P_{Bonf} describe model performance. Abbreviations are explained in Tables 1 and 2.

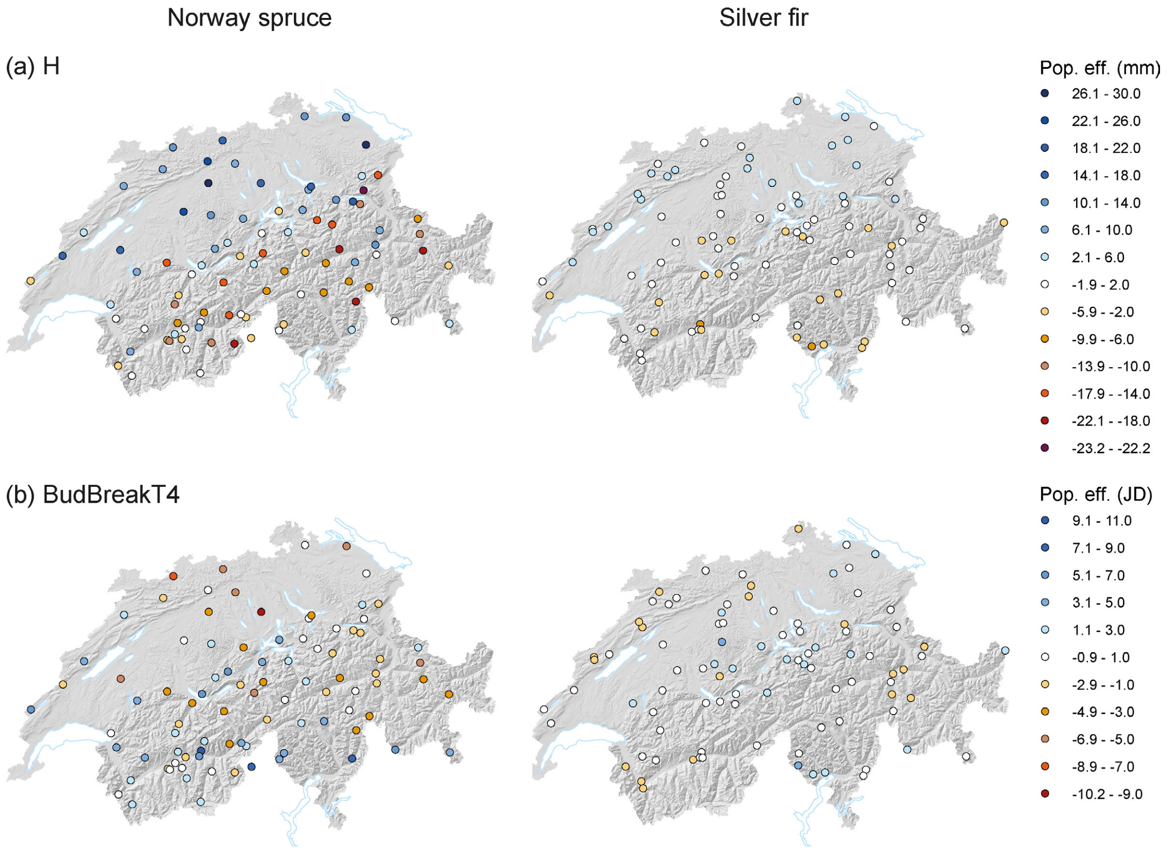

FIG. 4. Geographic variation in real population effects (BLUPs) of seedling height (H; a) and bud break (BudBreakT4; b) among 92 and 90 populations of Norway spruce (*P. abies*) and silver fir (*A. alba*) in Switzerland. Positive values represent above-average population performance, negative values represent below-average population performance.

Differentiation results from natural selection by the environment.—Population differentiation is generally enhanced by (1) random genetic drift in small populations, (2) low gene flow, (3) high among-population environmental variability, and (4) high among-population diversifying selection (Savolainen et al. 2007, Leinonen et al. 2008). In the spruce and fir populations we studied, genetic drift was presumably low due to sufficiently large population size. Neutral gene flow among spruce and fir populations in Switzerland is assumed to be high in both species, as indicated by low levels of neutral population differentiation (F_{st}), which were estimated for comparable populations of spruce and fir in Switzerland using 13 and 18 isozyme markers (Finkeldey et al. 2000). Both species are wind-pollinated; thus, genes may be transferred over large distances and elevational gradients (Petit and Hampe 2006, King et al. 2013). Among-population environmental variability is high, and both species inhabit similar climatic regimes.

In summary, two lines of evidence suggest that the differentiation we found was driven by among-population diversifying selection. First, Q_{st} was much higher than F_{st} (Finkeldey et al. 2000), indicating that population differentiation has been enhanced by diversifying (natural) selection (McKay and Latta 2002). The traits we measured had Q_{st} values that were 4–23 times the F_{st} values of spruce (F_{st} = 0.023) and 3–6 times the F_{st} values of fir (F_{st} = 0.034). Second, variation in many of the traits was strongly associated with environmental variables. For example, correlations between height growth traits and climate variables were as high as 0.78 in spruce and 0.64 in fir, and multivariate genecological models explained as much as 72% of the height growth variation in spruce, and 49% in fir. This indicates that large parts of the among-population genetic variation resulted from selective forces imposed by local climates.

Temperature and water availability are key selective forces.—Temperature explained the greatest amount of among-population variation in height growth and second flushing, especially in spruce. Temperature is one of the most important selective forces leading to local adaptation in plants, especially in regions with strong elevational gradients (Stöcklin et al. 2009, Vitasse et al. 2013). Indeed, many genecological studies have shown steep genetic clines for adaptive traits of forest trees in relation to temperature (Howe et al. 2003). In our study, spruce and fir seedlings from warm,

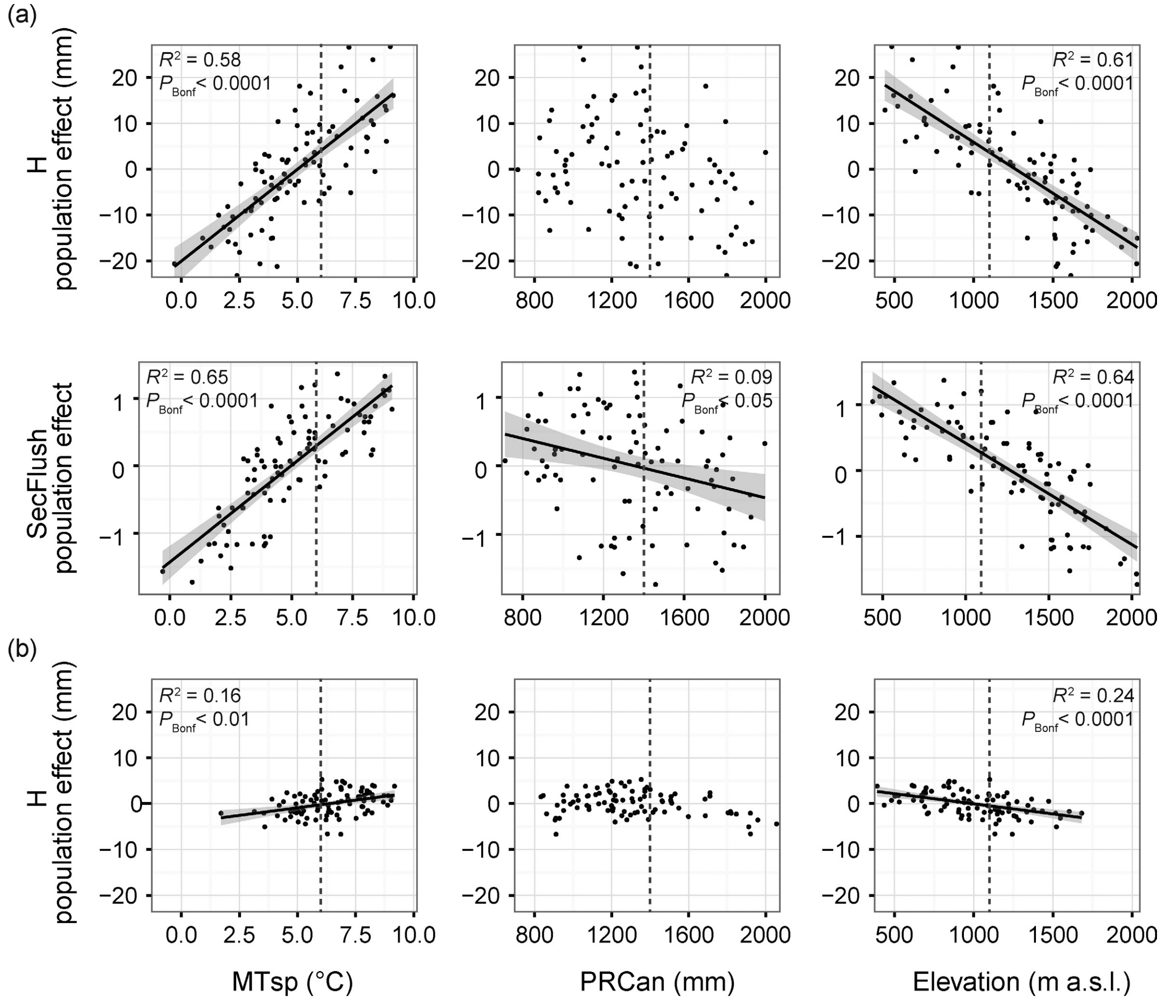

FIG. 5. Linear relations of population effects (BLUPs) for (a) Norway spruce (*P. abies*) seedling height and second flushing (H, SecFlush; n = 92) and (b) silver fir (*A. alba*) seedling height (H; n = 90) with mean spring temperature (March–May; MTsp), annual precipitation sum (PRCan) and elevation. Performance of significant models is displayed with P_{Bonf}, R^2 and standard error (gray surface). Regression lines of non-significant models ($P_{\text{Bonf}} \geq 0.05$) are not displayed. Climate data represent mean values for the period 1931–1960. Dashed lines indicate environment of test site (Table 2).

low-elevation populations grew faster than those from cold, high-elevation populations. Strong associations between height growth vs. temperature and elevation were previously found for juvenile spruce in the Swiss Alps (Engler 1905), Austria (Kapeller et al. 2012), and Eastern and Northern Europe (Skrøppa and Magnussen 1993). Height growth is also strongly associated with local temperature regimes in other conifers, such as Douglas-fir in North America (St.Clair et al. 2005). Additionally, spruce populations from warmer and lower-elevation environments had a stronger tendency to second flush. These results match those of Holzer (1993), who reported that second flushing occurred in low-elevation, but not in high-elevation spruce populations. He concluded that second flushing is a key trait for local adaptation to elevation. Indeed, the relation of second flushing with elevation and local temperature regimes seems to be the result of a strong trade-off between maximizing growth and minimizing frost damage (discussed below).

We found that water availability explained much less variation in height growth and second flushing than did temperature and elevation – and the same has been observed in other species (Mátyás 1996). Compared to temperature and elevation, precipitation variables were only weakly correlated with growth traits in whitebark pine (*Pinus albicaulis*) populations from the Rocky Mountains (Bower and Aitken 2008) and in black spruce (*Picea mariana*) from Quebec (Beaulieu et al. 2004).

Soil factors are important aspects of a species' autecology (Walthert et al. 2013) but are rarely considered in genecological studies. Campbell (1991) attempted to relate genetic variation in Douglas-fir to several soil types, and Lesser et al. (2004) studied the existence of limestone ecotypes in white spruce (*Picea glauca*). However, the soil factors included in these studies did not explain much population variation in the two species. Here, we used more precise soil and climatic variables to describe seed sources environments, including soil texture (clay content), nutrients (C/N), pH, and minimum site water balance (SWBmin). Nevertheless, physical and chemical soil characteristics explained little adaptive genetic variation in spruce and fir, and only SWBmin improved the genecological models to a small extent. This variable may have had a measureable effect because it integrates the effects of soil, precipitation, and evapotranspiration, and may be even more important where water is more limiting than in Switzerland. Finally, we had only one soil pit per population, which may have obscured associations with soil variables.

Adaptive strategies of spruce and fir

Spruce is an adaptive specialist and fir is an adaptive generalist.—The contrasting genecological patterns we found for spruce and fir – strong climate-related differentiation in spruce vs. modest differentiation in fir – suggest that spruce is an adaptive specialist and fir is an adaptive generalist (Rehfeldt 1994). Even for populations from comparable environments that were matched on key environmental variables, differentiation in height growth was twice as high for spruce as for fir. Therefore, different levels of among-population variation seem to reflect real differences in the ways these species respond to climate-based natural selection. Earlier studies also suggested that spruce is more differentiated than fir. European provenance studies generally found substantial differentiation in spruce (Engler 1905, Bossel 1983, Holzer 1993, Fouvy and Jeantet 1997, Hannerz et al. 1999, Kapeller et al. 2012, Schueler et al. 2013). In contrast, variation was generally low among populations of fir in Europe (Engler 1905, Herzog and Rotach 1990, Larsen and Mekic 1991, Sagnard et al. 2002, Vitasse et al. 2009, Alberto et al. 2013). Spruce also seems to be an adaptive specialist relative to other species – having Q_{st} values for height increment much larger than the mean Q_{st} of 0.32 for 29 tree species (Table 2; Table S1 in Alberto et al. 2013). Likewise, fir is more of a generalist, exhibiting below-average differentiation for height growth.

Spruce and fir differ in early height growth.—On average, spruce seedlings were much taller than fir by the end of the fourth growing season. Early height growth is generally determined by the timing of bud break, growth rate, and timing of growth cessation (Skrøppa and Magnussen 1993, Green 2005). Although spruce flushed about a week later than fir, spruce seedlings grew twice as fast, and stopped growing more than two weeks later than fir. Differences in early growth rate and growth duration between spruce and fir species were also found in studies of Norway spruce, hybrid white spruce (*P. glauca* × *Picea engelmannii*), silver fir, and subalpine fir (*Abies lasiocarpa*) (Engler 1905, Green 2005). In addition, second flushing extended the growth period in spruce, but not in fir. The high genetic correlation between second flushing and total seedling height (r_a = 0.82) indicates that second flushing is an important component of early seedling growth in spruce. In contrast, we did not observe second flushing in fir, and indeed, this trait has rarely been reported for this species (but see Dolnicki and Nawrot-Chorabik 2003).

Early height growth of spruce subjects the species to strong diversifying selection.—Spruce and fir populations in Switzerland probably have comparable levels of genetic drift, gene flow, and climatic variability. However, because spruce inhabits somewhat higher elevations with colder temperatures (Brändli 1998), we also conducted analyses on subsets of populations that were climatically matched. These analyses still revealed much greater differentiation for spruce, particularly for early height growth (Table 3). Considering their ecological characteristics, we conclude that spruce has been exposed to much greater diversifying selection than has fir (Savolainen et al. 2007, Leinonen et al. 2008).

Spruce is considered a late-successional, shade-tolerant species (Motta 2003), but it can also establish and grow on open sites, e.g., after clear-felling or wind throw (Ellenberg 2009, Kramer et al. 2014). Under these conditions, fast height growth presumably helps spruce rapidly occupy disturbed sites and newly formed gaps in the canopy. Important components of early height growth in spruce are second flushing and late height growth cessation, which enable the species to take full advantage of the growing season. However, in cold areas, this involves a trade-off between maximizing early height growth, in particular by second flushing, and avoiding damage from early fall frosts (Aitken and Hannerz 2001, Green 2005, St.Clair et al. 2005). It is this trade-off that leads to strong diversifying selection between populations inhabiting warmer and colder areas. That is, phenotypes that are adaptive in one area are maladaptive in another. Compared to spruce, fir has greater shade tolerance (Ellenberg 2009) and a limited capacity to exploit high-light conditions at a young age (Fairbairn and Neustein 1970, Grassi and Bagnaresi 2001). Fir has, therefore, a more conservative growth strategy. Its juvenile height growth is slow, does not include second flushing, and only starts to increase from ages 7 to 10 (Engler 1905). Compared to spruce, the early growth pattern of fir leads to less pronounced adaptive trade-offs and weaker diversifying selection for height growth and closely related traits.

Potential for climate change adaptation

Genecological studies that incorporated climate change projections have found that substantial genetic change is needed to maintain local adaptation in several tree species (Rehfeldt et al. 2002, Wang et al. 2006, St.Clair and Howe 2007). The contrasting adaptive strategies of spruce and fir suggest that the amount of genetic change needed will probably differ between these species. The adaptive specialist, spruce, with its strong temperature-related differentiation, is likely more vulnerable to climate-related maladaptation than fir.

The evolvability of local populations can be inferred from estimates of gene flow, within-population genetic variation, and the heritability of adaptive traits (Houle 1992, Bussotti et al. 2015). For conifers, gene flow is assumed to be high (Savolainen et al. 2007), although its extent may be constrained by population fragmentation and physical barriers, such as mountain ranges. The results of isozyme analyses mentioned previously (Finkeldey et al. 2000) indicate that gene flow is high for both species in Switzerland, despite the complex topography of the country. This might facilitate the immigration of pre-adapted genes and promote the adaptation to climate change (Petit and Hampe 2006, Kremer et al. 2012). However, the high degree of environmental specialization of spruce may locally lead to adaptational lags and, as a consequence, to maladaptation (St.Clair and Howe 2007). Therefore, gene flow may be relatively more important for spruce than for fir. Furthermore, our estimates of within-population genetic variation, heritability, and evolutionary potential of the measured traits indicate that both species have some potential to adapt via *in situ* evolution. Obviously, regardless if adaptation is driven by gene flow or *in situ* evolution, this potential will depend on the extent of climate change itself.

Phenotypic plasticity and epigenetic memory effects may also play a role in the response of local tree populations to climate change (Nicotra et al. 2010, Bräutigam et al. 2013). Our study was designed as a short-term, single-site experiment that included seeds from one single year and therefore did not allow us to assess these effects. Long-term and multi-site experiments using a subset of the populations and focusing on the most informative traits in spruce and fir seedlings, i.e., height growth and second flushing, would be particularly valuable to study phenotypic plasticity and to assess trait variation over time. In addition, multi-site experiments would enable to substantiate the existence of local adaptation (Blanquart et al. 2013), and to specify heritability estimates that are probably biased upwards in a single-site field test due to among-site G × E interaction variance. Thereby, multi-site tests could improve our understanding of climate change adaptation of the two species.

Management implications

The stronger phenotype-environment associations in spruce suggest that this species is of much higher priority for management actions concerning climate change than fir. Potential management implications might be (1) to intermix seed sources from warmer climates into current reforestation plans (see below), even if those plans rely primarily on natural regeneration; (2) to consider planting "genetic outposts" in locations adjacent to native stands to promote assisted gene flow (see St.Clair and Howe 2011); and (3) to consider targeted gene conservation activities for conserving unique genetic variation in stands that are particularly threatened by climate change (e.g., *ex-situ* collections). Furthermore, the multivariate genecological models used in this paper might be exploited to delineate climate-based seed zones or seed transfer guidelines, and to ultimately develop strategies for preparing forests to climate change, e.g., by guiding assisted gene flow (Aitken and Whitlock 2013). These guidelines should not only consider the status quo of genecological relations, but also integrate the expected amount of climate change. This might be done using the approach of relative risk of maladaptation (St.Clair and Howe 2007).

ACKNOWLEDGMENTS

The authors thank the large team of field workers for seed harvest, soil profile analyses, chemical analyses of soil characteristics, plantation of seedlings, trait assessments, and site maintenance. A special thank goes to A. Burkart and his team of gardeners at WSL for support during seed harvest, seedling management, and common garden procedures. The authors further thank G. Schneiter, P. Jakob and P. Waldner for technical support, and D. Steiner and B. Büttler for providing the experimental site at Brunnersberg and their helping hands. In addition, the authors are grateful for the statistical advice provided by J. Wunder (WSL), J. Zell (WSL), A.R. Pluess (WSL), and M. Tanadini (statistic consulting ETH Zurich). Thanks also to the Swiss Long-term Forest Ecosystem Research Programme (LWF) for providing soil data of one seed source. This work was funded by the research program "Forests and Climate Change" of FOEN and WSL.

LITERATURE CITED

Aitken, S. N. 2004. Genetics and genetic resources: genecology and adaptation of forest trees. Pages 197–204 *in* J. Burley, editor. Encyclopedia of forest sciences. Elsevier, Oxford, UK.

Aitken, S. N., and M. Hannerz. 2001. Genecology and gene resource management strategies for conifer cold hardiness. Pages 23–53 *in* F. J. Bigras and S. J. Colombo, editors. Conifer cold hardiness. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Aitken, S. N., and M. C. Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. Annual Review of Ecology, Evolution, and Systematics 44:367–388.

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95–111.

Alberto, F. J., et al. 2013. Potential for evolutionary responses to climate change – evidence from tree populations. Global Change Biology 19:1645–1661.

Alfaro, R. I., et al. 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. Forest Ecology and Management 333:76–87.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beaulieu, J., M. Perron, and J. Bousquet. 2004. Multivariate patterns of adaptive genetic variation and seed source transfer in *Picea mariana*. Canadian Journal of Forest Research 34:531–545.

Blanquart, F., O. Kaltz, S. L. Nuismer, and S. Gandon. 2013. A practical guide to measuring local adaptation. Ecology Letters 16:1195–1205.

Boisbunon, A., S. Canu, D. Fourdrinier, W. Strawderman, and M. T. Wells. 2014. Akaike's information criterion, C_p and estimators of loss for elliptically symmetric distributions. International Statistical Review 82:422–439.

Bossel, F. 1983. Tests comparatifs de provenances vaudoises d'épicéa. Schweizerische Zeitschrift für Forstwesen 134: 339–360.

Bower, A. D., and S. N. Aitken. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). American Journal of Botany 95:66–76.

Brändli, U.-B. 1998. Die häufigsten Waldbäume der Schweiz. Ergebnisse aus dem Landesforstinventar 1983–85: Verbreitung, Standort und Häufigkeit von 30 Baumarten. Ber. Eidg. Forsch.anst. Wald Schnee Landsch. 342:279.

Bräutigam, K., et al. 2013. Epigenetic regulation of adaptive responses of forest tree species to the environment. Ecology and Evolution 3:399–415.

Bussotti, F., M. Pollastrini, V. Holland, and W. Brüggemann. 2015. Functional traits and adaptive capacity of European forests to climate change. Environmental and Experimental Botany 111:91–113.

Campbell, R. K. 1991. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southwestern Oregon. Forest Science 37:973–986.

Chen, J., et al. 2012. Disentangling the roles of history and local selection in shaping clinal variation of allele frequencies and gene expression in Norway spruce (*Picea abies*). Genetics 191:865–881.

Chmura, D. J. 2006. Phenology differs among Norway spruce populations in relation to local variation in altitude of maternal stands in the Beskidy Mountains. New Forests 32:21–31.

Clapham, D., I. Ekberg, C. Little, and O. Savolainen. 2001. Molecular biology of conifer frost tolerance and potential applications to tree breeding. Pages 187–219 *in* F. J. Bigras and S. J. Colombo, editors. Conifer cold hardiness. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Cline, M. G., and C. A. Harrington. 2007. Apical dominance and apical control in multiple flushing of temperate woody species. Canadian Journal of Forest Research 37:74–83.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292: 673–679.

Dolnicki, A., and K. Nawrot-Chorabik. 2003. Preliminary studies on dynamics of frost-hardiness in silver fir (*Abies alba* Mill.) from the Beskid Slaski Mountains. Acta Agraria et Silvestria series Silvestris 41:3–13.

Ellenberg, H. 2009. Coniferous woodland and mixed woods dominated by conifers. Pages 191–242. Vegetation ecology of Central Europe. Cambridge University Press, Cambridge, UK.

Emerson, J. D., and J. Strenio. 1983. Boxplots and batch comparison. Pages 58–96 *in* D. C. Hoaglin, F. Mosteller, and J. W. Tukey, editors. Understanding robust and exploratory data analysis. John Wiley & Sons, New York, New York, USA.

Engler, A. 1905. Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. Erste Mitteilung. Mitteilungen der Schweizerischen Centralanstalt für das forstliche Versuchswesen 8:81–236.

Fairbairn, W. A., and S. A. Neustein. 1970. Study of response of certain coniferous species to light intensity. Forestry 43:57–71.

Finkeldey, R., G. Mátyás, C. Sperisen, and P. Bonfils. 2000. Strategien zur Auswahl forstlicher Genreservate in der Schweiz. Forest Snow and Landscape Research 75:137–152.

Fouvy, P., and G. Jeantet. 1997. Provenances vaudoises d'épicéa: bilan de 30 ans de tests comparatifs. Schweizerische Zeitschrift für Forstwesen 148:103–130.

Frampton, J., F. Isik, and D. M. Benson. 2013. Genetic variation in resistance to *Phytophthora cinnamomi* in seedlings of two Turkish *Abies* species. Tree Genetics and Genomes 9:53–63.

Gilmour, A. R., R. D. Anderson, and A. L. Rae. 1985. The analysis of binomial data by a generalized linear mixed model. Biometrika 72:593–599.

Gonseth, Y., T. Wohlgemuth, B. Sansonnens, and A. Buttler. 2001. Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. Umwelt Materialien Nr. 137 Bundesamt für Umwelt, Wald und Landschaft, Bern, Switzerland.

Grassi, G., and U. Bagnaresi. 2001. Foliar morphological and physiological plasticity in *Picea abies* and *Abies alba* saplings along a natural light gradient. Tree Physiology 21:959–967.

Green, D. S. 2005. Adaptive strategies in seedlings of three co-occurring, ecologically distinct northern coniferous tree species across an elevational gradient. Canadian Journal of Forest Research 35:910–917.

Grier, C. G., and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology 58:893–899.

Hannerz, M., J. Sonesson, and I. Ekberg. 1999. Genetic correlations between growth and growth rhythm observed in a short-term test and performance in long-term field trials of Norway spruce. Canadian Journal of Forest Research 29: 768–778.

Herzog, M., and P. Rotach. 1990. Trockenresistenz und Immissionshärte der Weisstanne (*Abies alba* Mill.). Frühtestuntersuchungen mit vier Provenienzen. Schweizerische Zeitschrift für Forstwesen 141:989–1010.

Holzer, K. 1993. The evolution of Alpine Norway spruce during immigration into high altitudes and its consequences. Pages 68–78 *in* Proceedings of IUFRO (S2.2-11) symposium, Latvia, Wien.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics 130:195–204.

Howe, G. T., S. N. Aitken, D. B. Neale, K. D. Jermstad, N. C. Wheeler, and T. H. H. Chen. 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. Canadian Journal of Botany 81:1247–1266.

Kapeller, S., M. J. Lexer, T. Geburek, J. Hiebl, and S. Schueler. 2012. Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: selecting appropriate provenances for future climate. Forest Ecology and Management 271:46–57.

King, G. M., F. Gugerli, P. Fonti, and D. C. Frank. 2013. Tree growth response along an elevational gradient: climate or genetics? Oecologia 173:1587–1600.

Kramer, K., P. Brang, H. Bachofen, H. Bugmann, and T. Wohlgemuth. 2014. Site factors are more important than salvage logging for tree regeneration after wind disturbance in Central European forests. Forest Ecology and Management 331:116–128.

Kremer, A., et al. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. Ecology Letters 15:378–392.

Lagercrantz, U., and N. Ryman. 1990. Genetic structure of Norway spruce (*Picea abies*): concordance of morphological and allozymic variation. Evolution 44:38–53.

Larsen, J. B., and F. Mekic. 1991. The geographic variation in European silver fir (*Abies alba* Mill.). Gas exchange and needle cast in relation to needle age, growth rate, dry matter partitioning and wood density by 15 different provenances at age 6. Silvae Genetica 40:188–198.

Lebourgeois, F., C. B. K. Rathgeber, and E. Ulrich. 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). Journal of Vegetation Science 21:364–376.

Leinonen, T., R. B. O'Hara, J. M. Cano, and J. Merilä. 2008. Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. Journal of Evolutionary Biology 21:1–17.

Lenormand, T. 2002. Gene flow and the limits to natural selection. Trends in Ecology and Evolution 17:183–189.

Lesser, M. R., M. Cherry, and W. H. Parker. 2004. Investigation of limestone ecotypes of white spruce based on a provenance test series. Canadian Journal of Forest Research 34:1119–1127.

Lindner, M., et al. 2014. Climate change and European forests: what do we know, what are the uncertainties, and what are the implications for forest management? Journal of Environmental Management 146:69–83.

Mallows, C. L. 1973. Some comments on Cp. Technometrics 15:661–675.

Mátyás, C. 1996. Climatic adaptation of trees: rediscovering provenance tests. Euphytica 92:45–54.

McKay, J. K., and R. G. Latta. 2002. Adaptive population divergence: markers, QTL and traits. Trends in Ecology and Evolution 17:285–291.

Motta, R. 2003. Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. Forest Ecology and Management 181:139–150.

Nicotra, A. B., et al. 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15:684–692.

Petit, R. J., and A. Hampe. 2006. Some evolutionary consequences of being a tree. Annual Review of Ecology, Evolution, and Systematics 37:187–214.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt, G. E. 1994. Evolutionary genetics, the biological species, and the ecology of the interior cedar-hemlock forests. Pages 91–100 *in* D. M. Baumgartner, J. E. Lotan, and J. R. Tonn, editors. Proceedings of the interior cedar-hemlock-white pine forests: ecology and management, Spokane, WA. Washington State University Extension, Pullman, Washington, USA.

Rehfeldt, G. E., and B. C. Jaquish. 2010. Ecological impacts and management strategies for western larch in the face of climate-change. Mitigation and Adaptation Strategies for Global Change 15:283–306.

Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecological Monographs 69:375–407.

Rehfeldt, G. E., N. M. Tchebakova, Y. I. Parfenova, W. R. Wykoff, N. A. Kuzmina, and L. I. Milyutin. 2002. Intraspecific responses to climate in *Pinus sylvestris*. Global Change Biology 8:912–929.

Remund, J., M. Frehner, L. Walthert, M. Kägi, and B. Rihm. 2011. Schätzung standortspezifischer Trockenstressrisiken in Schweizer Wäldern. Schlussbericht Version 2.3. Meteotest, Bern, Switzerland. 56.

Remund, J., B. Rihm, and B. Huguenin-Landl. 2014. Klimadaten für die Waldmodellierung für das 20. und 21. Jahrhundert. Meteotest, Bern, Switzerland. 38.

Sagnard, F., C. Barberot, and B. Fady. 2002. Structure of genetic diversity in *Abies alba* Mill. from southwestern Alps: multivariate analysis of adaptive and non-adaptive traits for conservation in France. Forest Ecology and Management 157:175–189.

Savolainen, O., T. Pyhäjärvi, and T. Knürr. 2007. Gene flow and local adaptation in trees. Annual Review of Ecology, Evolution, and Systematics 38:595–619.

Schueler, S., et al. 2013. Adaptive genetic diversity of trees for forest conservation in a future climate: a case study on Norway spruce in Austria. Biodiversity and Conservation 22:1151–1166.

Skrøppa, T., and S. Magnussen. 1993. Provenance variation in shoot growth components of Norway spruce. Silvae Genetica 42:111–120.

St.Clair, J. B., and G. T. Howe. 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Global Change Biology 13:1441–1454.

St.Clair, J. B., and G. T. Howe. 2011. Strategies for conserving forest genetic resources in the face of climate change. Turkish Journal of Botany 35:403–409.

St.Clair, J. B., N. L. Mandel, and K. W. Vance-Borland. 2005. Genecology of Douglas-fir in western Oregon and Washington. Annals of Botany 96:1199–1214.

Stöcklin, J., P. Kuss, and A. R. Pluess. 2009. Genetic diversity, phenotypic variation and local adaptation in the alpine landscape: case studies with alpine plant species. Botanica Helvetica 119:125–133.

Teepe, R., H. Dilling, and F. Beese. 2003. Estimating water retention curves of forest soils from soil texture and bulk density. Journal of Plant Nutrition and Soil Science 166: 111–119.

Vitasse, Y., S. Delzon, C. C. Bresson, R. Michalet, and A. Kremer. 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Canadian Journal of Forest Research 39:1259–1269.

Vitasse, Y., G. Hoch, C. F. Randin, A. Lenz, C. Kollas, J. F. Scheepens, and C. Körner. 2013. Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. Oecologia 171:663–678.

Walthert, L., E. Graf Pannatier, and E. S. Meier. 2013. Shortage of nutrients and excess of toxic elements in soils limit the distribution of soil-sensitive tree species in temperate forests. Forest Ecology and Management 297:94–107.

Wang, T., A. Hamann, A. Yanchuk, G. A. O'Neill, and S. N. Aitken. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology 12:2404–2416.

WSL. 2014. Swiss National Forest Inventory (NFI). Data of the third survey 2004/06 (NFI3). Fabrizio Cioldi 08.12.2014. Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland.

Zang, C., C. Hartl-Meier, C. Dittmar, A. Rothe, and A. Menzel. 2014. Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. Global Change Biology 20:3767–3779.

Zelenka, A., G. Czeplak, V. D'Agostino, W. Josefsson, E. Maxwell, R. Perez, M. Noia, C. Ratto, and R. Festa. 1992. Techniques for supplementing solar radiation network data. IEA Report IEASHCP-9D-1. Swiss Meteorological Institute, Zurich, Switzerland. 261.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1632/suppinfo