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Title: Recovery of silver fir (*Abies alba* Mill.) seedlings from ungulate browsing mirrors soil nitrogen availability

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Running Title: Recovery from ungulate browsing mirrors N availability

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Abstract

Abies alba has a high potential for mitigating climate change in European mountain forests, yet, its natural regeneration is severely limited by ungulate browsing. Here, we simulated browsing in a common garden experiment to study growth and physiological traits, measured from bulk needles, using a randomized block design with two levels of browsing severity and seedlings originating from 19 populations across Switzerland. Genetic factors explained most variation in growth (on average, 51.5%) and physiological traits (10.2%) under control conditions, while heavy browsing considerably reduced the genetic effects on growth (to 30%), but doubled those on physiological traits related to C storage. While browsing reduced seedling height, it also lowered seedling water use efficiency (decreased δ^{13}C) and increased their δ^{15}N. Different populations reacted differently to browsing stress, and for seedling height, starch concentration and δ^{15}N, population differences appeared to be the result of natural selection. First, we found that populations originating from the warmest regions recovered the fastest from browsing stress, and they did so by mobilizing starch from their needles, which suggests a genetic underpinning for a growth-storage trade-off across populations. Second, we found that seedlings originating from mountain populations growing on steep slopes had a higher δ^{15}N in the common garden than those originating from flat areas, indicating that they have been selected to grow on N poor, potentially drained, soils. This finding was corroborated by the fact that N concentration in adult needles was lower on steep slopes than on flat ground, strongly indicating that steep slopes are the most N poor environments. These results suggest that adaptation to climate and soil N availability, as well as ungulate browsing pressure co-determine the regeneration and range limit of silver fir.

Introduction

The forested land area in Europe has increased by 56% over the past 100 years (Fuchs *et al.*, 2015). Although climate change is partly responsible for this area gain, reforestation is also associated with management activities, such as the abandonment of agricultural land and afforestation efforts to increase timber volume and economic benefit (Seidl *et al.*, 2011). Ungulates spontaneously recolonized these new habitats and were further aided by artificial re-introductions. Until recently, due to the lack of natural predators and a decrease in big game hunting, ungulate numbers kept increasing (Apollonio *et al.*, 2010). As a result, ungulate browsing has become a major driver of forest succession in Europe, and challenges the establishment of future tree generations (Tanentzap *et al.*, 2009; Apollonio *et al.*, 2017). Since ungulates selectively browse certain tree species, such damage can have long lasting impacts on the forest species composition (Klopčič *et al.*, 2017; Ramirez *et al.*, 2019).

The most common effects of ungulate browsing are the removal of buds, thus apical meristem tissue and the removal of shoots, which reduces the photosynthesizing leaf area and alters, most often increases, the root to shoot ratio (*e.g.* McNaughton, 1983; Hoogesteger & Karlsson, 1992; Drexhage & Colin, 2003; Rhodes & Clair, 2018). Trees are often found to recover well from light to moderate browsing stress via different compensatory mechanisms at the morphological level such as increased leaf size (Lehtilä *et al.*, 2000), overcompensated growth in the leading bud (O'Reilly-Wapstra *et al.*, 2014), growing side shoots (Kupferschmid & Heiri, 2019), but also in their reproductive strategy such as increased production of female strobili (Allison, 1990). However, browsing can also severely limit growth and cause seedling mortality (Kupferschmid, 2017; Rhodes & Clair, 2018). Browsing damage and recovery depend on several factors, including the intensity and timing of browsing, but also on the stress status and the ontogenetic stage of the tree (Kupferschmid, 2017). Browsing stress generally most severely affects the early life-stages, which are already the most sensitive to environmental fluctuations and climate change related risks (Talluto *et al.*, 2017).

Early studies argued that browsing stress causes carbon (C) limitation in agreement with the C-supply-centered view of tree growth (Ericsson *et al.*, 1980; Chapin III *et al.*, 1980). However, this view has largely been challenged during the past two decades. The emerging picture is that trees

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are rarely, if at all, C limited (Körner, 2003; Millard & Grelet, 2010; Sala *et al.*, 2012; McDowell *et al.*, 2008). For example, trees have been observed to accumulate large amounts of non-structural carbohydrates (NSC) even in the presence of factors that limit their photosynthesis, such as under severe water deficit (Bréda *et al.*, 2006), defoliation (Wiley *et al.*, 2013), or light limitation (Weber *et al.*, 2018). Although seasonal fluctuations in NSC levels have been observed in seedlings, such as during bud burst or recovery from herbivory (Gill, 1992), there was no evidence for C limitation *per se* (Palacio *et al.*, 2008).

In contrast to C, nitrogen (N) is stored and seasonally remobilized; for example, N storage pools disappear after bud flushing (Millard & Grelet, 2010). In coniferous evergreen trees, N is mainly present in young needles, as RuBisCo and other photosynthetic proteins (Millard *et al.*, 2001; Camm, 1993) or as amino acids (Schneider *et al.*, 1996). Thus, ungulate browsing can drastically reduce N pools, and the recovery from browsing depends on seedling capacity to remobilize N from other tissue and on their N acquisition from the environment. Most root N uptake occurs via biotic interactions in the rhizosphere such as mycorrhizal symbiosis, associations with free-living fungi and bacteria, and endophytic bacteria that can increase the efficiency of N acquisition and assimilation (Millard & Grelet, 2010). The stable N isotope composition (δ^{15}N) of plant tissues is determined by the relative contributions of external N sources with different δ^{15}N, such as different soil N pools, symbiotic fixation of N_2, uptake of other gaseous sources (NH_3, NO_2) through stomata, different nitrogen compounds provided by mycorrhiza (Hobbie & Colpaert, 2003; Craine *et al.*, 2015), and the relationship between inorganic nitrogen influx, efflux and assimilation (Robinson *et al.*, 1998).

European silver fir (*Abies alba* Mill.) is one of the most heavily browsed species of the commercially important trees in European forests. Its browsing damage is clearly higher compared to species such as *Picea abies* and *Fagus sylvatica* (Gill, 1992; Senn & Suter, 2003). Due to its deeper rooting system, silver fir is likely superior to the latter two species to cope with drought stress (Dyderski *et al.*, 2018; Vitasse *et al.*, 2019a; Frank *et al.*, 2015; Tinner *et al.*, 2013), even though some authors debate its resistance to drought (Battipaglia *et al.*, 2009; Vitali *et al.*, 2017; George *et al.*, 2015). How silver fir can cope with changing climatic conditions may depend on the local climate and soil conditions, but also on the interaction between trees and ungulates. Several studies reported high adaptive potential and divergence among its

populations in growth, phenology and morphological traits (Hansen & Larsen, 2004; Vitasse *et al.*, 2009; Kerr *et al.*, 2015; Frank *et al.*, 2017). In addition, adult needle $\delta^{13}C$ appeared to be a good indicator of different life-history strategies related to the phenology and rate of growth: Csilléry *et al.* (2020b) found that populations that broke buds early, grew slowly and had a high water use efficiency, while those that broke buds late but grew fast and had more negative $\delta^{13}C$ values.

In this study, we assessed the physiological response of silver fir seedlings to simulated ungulate browsing two growing seasons after the treatment in an ongoing common garden experiment (Frank *et al.*, 2017; Kupferschmid & Heiri, 2019; Csilléry *et al.*, 2020b). In parallel, we assessed the same physiological traits in the source populations, whenever possible on the mother trees of the seedlings, in their home environments. Our aims were (i) gaining a deeper understanding of the physiological response to browsing stress, and (ii) detecting spatially varying selection to physiological traits that may indicate seedling capacity of recovery from browsing stress. Previous analysis of growth traits in the same common garden experiment showed that seedlings recovered from the stress caused by simulated ungulate browsing when only their terminal buds were browsed, but not after the removal of several shoots (i.e. heavy browsing; Kupferschmid & Heiri (2019)). Here, we hypothesized that the effect of simulated browsing on physiological traits related to C and N traits would be largely diminished. Further, we expected that physiological traits related to C status would be correlated with growth traits and would be heritable, while traits related to N status would have a weaker genetic component and be determined to a larger extent by the local environment. We also tested the specific hypothesis that there is a growth–storage trade–off, and if it could be triggered by browsing stress. Previous analysis of growth traits in the same common garden experiment showed that there is evidence for spatially varying selection pressure for growth and phenology traits (Csilléry *et al.*, 2020b). We hypothesized that physiological traits related to the C status would also be under spatially varying selection, and would be affected by a similar set of environmental variables as growth. In contrast, we expected that traits related to the N status would be largely environmentally determined. Finally, we hypothesized that physiological traits in seedlings in a common garden mirror the physiology of adult trees *in-situ*.

Materials and Methods

Experimental design and sampling

Our study builds on a large scale common garden experiment aimed at testing growth and phenological differences, and their potential climatic drivers, among Swiss provenances of three major tree species, including silver fir (*Abies alba* Mill.) (Frank *et al.*, 2017). The experiment started in 2010, when seeds from three dominant trees per growing site (subsequently called population) were sown in nursery beds at the premises of the Swiss Federal Research Institute WSL (Birmensdorf, Switzerland). In 2012, 16 randomly selected seedlings per mother tree were planted in the open field site near Matzendorf (Swiss Jura Mountains) in a random block design (Fig. 1A and B). In March 2015, at the start of the third field growing season, a simulated browsing experiment started to test seedling morphological response and capacity of recovery to ungulate browsing (Kupferschmid & Heiri, 2019) (Fig. 1B and C). Blocks were randomly assigned to three different treatments: the uppermost buds of the leader shoot were clipped in six blocks (Terminal bud removal), the whole leader shoot and part of the side shoots were clipped in five blocks (Heavy browsing), while the remaining five blocks were left as Controls (Kupferschmid & Heiri, 2019) (Fig. 1B and D; note that Kupferschmid & Heiri (2019) called Terminal bud removal "Light browsing").

In this study, we measured physiological traits on 19 silver fir populations out of the 90, present in the above common garden study (Table S1, Fig. 1A). Populations were selected to represent the main climatic regions of Switzerland, and were identical to those studied in Csilléry *et al.* (2020a). Needle traits were measured both on the seedlings growing in the common garden and on adult trees of the seed source populations. In September 2016, we sampled seedlings for 2016-grown, approximately 2 cm long, lateral shoots. Adult tree populations were revisited in April 2016 to collect needles from ten trees per site, including the three mother trees, if they could be identified, and other dominant trees from the stand (Csilléry *et al.*, 2020b). Approximately 200 m distance was kept between sampled trees to capture the environmental heterogeneity of each site, averaging over the local growing conditions of individual trees. 2015-grown needles from sunlit outer branches were selected to assure homogeneity of sampling among trees (Brendel

et al., 2003). Needles were stored in plastic bags at 5°C and lyophilized for at least 48 hrs within 24 hrs of their collection.

Growth traits in seedlings

Growth traits were measured yearly from 2012 to 2016 after growth cessation, and have been analyzed across 90 provenances in Frank *et al.* (2017) and Kupferschmid & Heiri (2019). We re-analysed the 2015 and 2016 growth traits here from the selected 19 populations (i) to check if the effect of browsing using 19 vs 90 populations agrees, and (ii) to assess the relationship between growth and physiological traits. Height was measured from the ground to the highest point of the tree in mm (Height; all trait names are capitalized) or to the tip of the terminal shoot in mm (Terminal Height). Diameter was measured 2 cm above the soil surface in mm. Needle samples were collected in 2016, after growth cessation, between 17 September and 7 October. In February 2017, all seedlings were cut 2 cm above the soil surface and their Fresh Weight was determined using a hanging scale (Kern HDBH 5K5N) with a precision of 5 g. Additionally, the weight of 1000 seeds from each mother tree in g and the diameter at breast height (DBH) of each mother tree in mm were measured to account for potential maternal effects (see details in Csilléry *et al.* (2020b)).

Sugar, Starch and NSC in seedlings

We measured Sugar concentrations in the harvested needles, i.e. the amount of low molecular weight sugars (glucose, fructose and sucrose) by converting them to glucose following the protocol of Wong (1990) and Hoch *et al.* (2002). 8-10 mg of dried ground needles were boiled in 2 ml distilled water for 30 minutes. An aliquot of 200 µl was treated with invertase and isomerase from baker's yeast (Sigma-Aldrich, St. Louis, MO, USA) to degrade sucrose and convert fructose into glucose. The total amount of glucose was determined photometrically at 340 nm in a 96-well microplate photometer (HR 7000, Hamilton, Reno, NE, USA) after enzymatic conversion to gluconate-6-phosphate (hexokinase reaction, hexokinase from Sigma Diagnostics, St. Louis, MO, USA). NSC (Non Structural Carbohydrates) is the sum of low molecular weight sugars and starch. We measured NSC concentrations by digesting all starch

into glucose, and determined the amount of glucose photometrically. To digest the starch, we used a 500 µl aliquot of the boiled material and incubated with a fungal amyloglucosidase from *Aspergillus niger* (Sigma-Aldrich, St. Louis, MO, USA) for 15 h at 49°C. Starch concentrations were derived as the difference between NSC and Sugar concentrations. Pure starch and glucose, fructose and sucrose solutions were used as standards, and a standard plant powder (Orchard leaves, Leco, St. Joseph, MI, USA) as a control. NSC concentrations were expressed on a percent of dry matter basis. All samples were analyzed in the same laboratory and by the same person at the Swiss Federal Institute WSL using the same protocol for processing samples in order to minimize biases (Quentin *et al.*, 2015). Sugar, Starch and NSC were expressed as percentages.

Stable isotope traits in adult trees and seedlings

δ^{13}C, δ^{15}N, and C and N concentrations were measured in the lyophylized needle tissue following the same protocol in adult trees and seedlings. Approximately 80 mg of lyophilized needle material was milled in 2 ml polypropylene tubes equipped with a glass ball (diameter of 5 mm) for 4 min at 30 Hz. Milled samples were directly weighed into small tin capsules (approx. 5 mg, XPR2 microbalance from Mettler Toledo), and combusted in an elemental analyzer (Flash EA by Thermo Finnigan, Bremen, Germany) coupled to an isotope ratio mass spectrometer (Delta XP by Thermo Finnigan, Bremen, Germany) by a Conflo II interface (Thermo Finnigan, Bremen, Germany). C isotope values are expressed as ‰ relative to Vienna-Pee Dee Belemnite (V-PDB) standard, and N isotope values relative to N_2 in air. Both C and N isotope values are reported using the δ-notation (Werner & Brand, 2001).

Environmental conditions

We characterized the environmental conditions at the seed source sites of the 19 populations, and the soil of the common garden site. First, a soil profile was taken at each of the 19 seed source sites and soil N and C concentrations (expressed as percentages) were determined from the uppermost part of the A horizon (see Frank *et al.* (2017) for more details). We also placed soil profiles at several locations at the common garden site (see Fig. 1B) and determined the C and N concentrations across different depths. Second, we determined the latitude, longitude, elevation,

slope, and aspect of each site from a 90m resolution digital terrain model (DTM) from EarthEnv (Robinson *et al.*, 2014), and the topographic wetness index (TWI) using the SAGA Wetness Index on a 10m aggregation of the SwissAlti3D DTM (Conrad *et al.*, 2015). Third, we extracted raw climate time series from CHELSAcruts (http://chelsa-climate.org/chelsacruts/), which is a time series version of the CHELSA data (Karger *et al.*, 2017). Several climatic indices were calculated across the 1901-1979 period, thus excluding the recent years that are affected by climate warming and did not affect the establishment of current adult trees.

Statistical analyses

Seedlings that died during the experiment or were damaged by frost or insect herbivory were omitted (N=15). We also excluded outlier observations that were not consistent with the treatments as well as suggested observation errors. In particular, we excluded control seedlings that had a height loss between 2014 autumn and 2015 spring (N=3), seedlings with Terminal Bud removal that had a height loss greater than 20% (N=7), and seedlings in the Heavy Browsing treatment that exhibited no height loss due to the treatment (N=2), leading to a total of 224 seedlings in the Control, 271 in the Terminal bud removal, 218 in the Heavy browsing treatments. The concentration of Starch was calculated based on NSC minus free sugars, which led to some negative values. For the sake of easier interpretation of the effects, we added ten to all Starch values to assure that all observations are non-negative. Starch, Height, Terminal Height, and Fresh Weight were log-transformed to achieve a close to normal distribution. All other traits were normally distributed based on visual evaluation of histograms. We also calculated a derived trait from the different height measures to check the homogeneity of the treatments on the targeted seedlings (eq. 1):

$$HeightLoss(\%) = 100 \times \frac{(Height_{2014autumn} - Height_{2015springafterclipping})}{Height_{2014autumn}} \qquad (1)$$

First, we used a linear mixed-effects model, so-called animal model (Henderson, 1975), implemented in the R package ASReml-R that uses ASReml version 4.0 (Butler *et al.*, 2009) to estimate the proportion of the trait variance explained by the treatment, block, population of origin, and genetic (family) effects. We fitted a separate model to Control and Terminal bud

removal together, and Control and Heavy browsing together for two reasons. First, a treatment variance component would have been difficult to interpret with the two treatments together in one model. Second, we wanted to quantify the effect of Terminal bud removal and Heavy browsing separately on the growth and physiology of the seedlings. We used the following model (eq. 2):

$$\mathbf{y} = \mathbf{X_{sw}}sw + \mathbf{X_{dbh}}dbh + \mathbf{Z_t}\mathbf{t} + \mathbf{Z_b}\mathbf{b} + \mathbf{Z_p}\mathbf{p} + \mathbf{Z_a}\mathbf{a} + \mathbf{e} \qquad (2)$$

where $\mathbf{y}$ is a vector of observations for a trait on all seedlings, and $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices relating the covariates and random effects to the observations, respectively. sw and dbh are covariates for the maternal effects Seed Weight and Diameter at Breast Height, respectively. The random effects were $\mathbf{t}$ for treatment (Terminal bud removal or Heavy browsing), $\mathbf{b}$ for block, $\mathbf{p}$ for populations, while $\mathbf{a}$ is a vector of individual breeding values with variance $Var(a) = A \times V_A$. A is the inverse kinship matrix constructed based on half-sib family relationships using the function *ainverse* and V_A is the additive genetic variance, i.e. part of trait variance that is due to heritable genetic factors. Finally, $\mathbf{e}$ is the vector of residuals following $E \sim N(0, V_E)$, where V_E is the error variance. In order to evaluate the significance of the covariates, we compared models with and without these using a Wald-test (wald.asreml function). We also compared models with and without random effects using a likelihood ratio test (p-values based on the χ^2 distribution are reported). All variance components, including treatment, block, population and genetic, were expressed as proportions to the total phenotypic variance, V_T. The proportion of the trait variance due to genetic factors is the heritability of the trait, denoted as $h^2 = V_A/V_T$ (Falconer & Mackay, 1996). The significance of variance components was assessed using z-scores with z>2 indicating a non-zero variance component.

Second, the model including the Control and Terminal bud removal groups revealed that including the treatment did not improve the model fit (with the exception of Terminal Height in 2015 and 2016, and C concentration), and even when it did, treatment did not explain a significant part of the trait variance (with the exception of Terminal Height in 2015). Thereby, we applied a simpler model excluding treatment effect for a data set pooling the Control and Terminal bud

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removal groups (eq 3).

$$\mathbf{y} = \mathbf{X_{sw}}sw + \mathbf{X_{dbh}}dbh + \mathbf{Z_b}\mathbf{b} + \mathbf{Z_p}\mathbf{p} + \mathbf{Z_a}\mathbf{a} + \mathbf{e} \tag{3}$$

We used this model to estimate the amount of population differentiation that is due to genetic factors, defined as $Q_{ST} = V_P/(V_P + 2V_A)$, where V_P is the population variance (Whitlock, 2008). Estimating Q_{ST} requires a large sample size, so we benefited from being able to pool together the two treatment groups to obtain more reliable estimates. Previous analyses of this common garden experiment have already estimated Q_{ST} for several growth and phenology traits from 2013 and 2014 (Frank *et al.*, 2017; Csilléry *et al.*, 2020b). We took advantage of having the full time series of growth traits from 2012 to 2016 to assess the evolution of Q_{ST} in time, and to contrast Q_{ST} between growth and physiological traits. Additionally, we used the genetic marker data available from Csilléry *et al.* (2020b) to test if trait divergence between populations was significantly higher than that at genetic markers (F_{ST}) using the R package *QstFstComp* (Gilbert & Whitlock, 2015). Finally, we also attempted to use the pooled data set to estimate genetic correlations. However, due to our limited sample size, these models were unstable (see more details in Supplementary results and Table S7).

Third, we assessed the role of environment in driving trait divergence between populations in seedlings. We only used traits that expressed a Q_{ST} significantly higher than zero, i.e. Height, Starch and δ^{15}N. Although the effects of environmental variables on Height have been assessed by earlier studies (Frank *et al.*, 2017; Kupferschmid & Heiri, 2019; Csilléry *et al.*, 2020b), we repeated these analyses for the sake of completeness and also to see if findings of earlier studies were confirmed despite the reduced sample size. For these tests, we extracted the population effects from the pooled model (i.e. Control + Terminal bud removal) and correlated these with the environmental variables using a Spearman correlation test (see details below). Additionally, we explicitly tested if there was a growth–storage trade–off by correlating the Height in 2015 with the difference in Starch concentration between Control and Heavy Browsing treatment (population means). Finally, we also tested the correlation between traits measured in adult trees *in-situ* and environmental variables. In order to do so, we first tested if traits were significantly different among populations, and since they were (Kruskal-Wallis tests

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trait-by-trait: $\chi^2 > 44.86$, df=18, p-value<0.001, see Fig. S2 for details), we could use all five traits measured in adult trees, i.e. C concentration, δ^{13}C, N concentration, δ^{15}N, and C/N for this analysis. Note that the same test was already performed for δ^{13}C by Csilléry *et al.* (2020b).

In order to reveal the potential environmental drivers of adaptation, we correlated the population effects of seedlings traits extracted from the pooled model (eq. 3) and the population means of adult traits with a total of 37 environmental variables, including topographic and bio-climatic variables, drought and frost indices, and soil variables extracted from local soil pits (Table S5 and S6). We used a correction for multiple testing that accounts for the correlation among variables, thereby for the non-independence of tests. A Principal Component (PC) analysis of all environmental variables (*prcomp* function in R using scale=TRUE) revealed that nine PC axes explained 95% of the total variance (94.75%), thus we adjusted the p-values using a Bonferroni correction as if we performed nine independent tests for each trait. Further, we used an even more strict correction: we accounted for testing seven traits (in seedlings) and five traits (in adult trees), which could be considered as two and four independent tests based on the same argument as above (i.e. two axes explained 99.9% and four axes 99.64% of the total variance in seedlings and adult trees, respectively). Thereby, we adjusted for 18 and 36 independent tests in seedlings and adult trees, respectively.

Results

Response to simulated browsing

Terminal bud removal affected the growth of seedlings one growing season after the clipping experiment (i.e. in 2015 autumn): their Terminal Height was reduced, but not their Height or Diameter (Table S2, Fig. S1 and 2). In contrast, Terminal bud removal did not explain a significant part of the variation, neither in growth traits nor in physiological traits two growing seasons after the clipping experiment (i.e. in 2016 autumn) (Fig. 2), although the model fit still improved by including the Terminal bud removal treatment for Terminal height and C concentration (Table S2). In contrast, Heavy browsing had a long-lasting effect on most traits: both Height and Terminal Height decreased (Fig. S1), and in 2015 and 2016, over 40% of the

trait variation was explained by the treatment (Fig. 2). In contrast, Heavy browsing did not explain trait variation in 2015 Diameter and 2016 Diameter and Fresh Weight (Fig. 2). Among the physiological traits, only δ^{13}C and δ^{15}N were affected by the Heavy browsing treatment: over 40% of the trait variation was explained by browsing stress, even though the standard error of this variance component was high (Fig. 2 and 3). On average, δ^{13}C decreased with 0.86 ‰ as a result of the Heavy browsing treatment, with the greatest decrease observed in population POS, with 1.39 ‰ (before last population on Fig. 3). δ^{15}N increased, on average, with 1.07 ‰ as a consequence of Heavy browsing, with an increase being as high as 1.79 ‰ in SIG (fifth population on Fig. 3).

Local environmental variation may have interfered with the treatment within the common garden, and was quantified using Block effects. Including Block significantly improved the model fit for all traits but C concentration (Table S2). Block explained the highest proportion of trait variation in Fresh weight (10.8%, SE: 5.0%) among the growth traits, and in Sugar concentration (18.6%, SE: 7.6%) among the physiological traits. Block variance was, on average, higher than Population variance for growth traits (Fig. 2), suggesting that the local growing conditions were just as important as the population of origin.

Genetic and population effects on trait variation

Genetic effects explained the most variation in both growth and most physiological traits, and with or without Heavy browsing stress (Fig. 2, Table S3). The heritability of growth traits varied between 0.65 (Diameter 2015) and 0.38 (Terminal Height 2015). The genetic variance component was also significant for Diameter in 2016 (h^2=0.47, SE: 0.21) when the Terminal bud removal treatment was removed from the model (unlike in the model shown on Fig. 2). Among the physiological traits, the highest heritability was observed for NSC concentration (h^2=0.21, SE: 0.16) and δ^{13}C (h^2=0.18, SE: 0.15). Interestingly, the genetic effects became stronger under the Heavy browsing treatment, especially for storage related traits, thus NSC, Starch, Sugar and C concentration (Fig. 2, Table S3). In contrast, the genetic effects decreased under stress for δ^{13}C (Fig. 2). Among the two proxies for maternal effects, Seed weight had a significant effect on all growth traits and a marginally significant effect on C concentration (Table S2). In contrast, the size of the mother tree (DBH) did not affect seedling performance in any way

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(Table S2).

Population of origin explained a significant part of the trait variance only for Terminal height among the growth traits, however, under Heavy browsing stress, the population differences became stronger and significant for all growth traits, except for Diameter and Fresh weight (Fig. 2). Taking together the high genetic and low population effects (without browsing stress, using equation 3), Q_{ST}s were not significantly different from a neutral expectation derived from genetic markers for the 2015 and 2016 growth traits (see Fig. 4 for Height, and Table S4 for other traits). Note that higher Q_{ST} values were detected for Height in previous years by previous studies: Q_{ST} was significantly different from zero for 2013 Height using 90 populations in Frank *et al.* (2017) and Q_{ST} was significantly larger than F_{ST} for 2013 and 2014 Height using 19 populations in Csilléry *et al.* (2020b). These trends were also confirmed herein despite the reduced sample size due to mortality and the browsing experiment (Fig. 4 and Table S4).

A higher proportion of the trait variation was due to population of origin in physiological than in growth traits (Fig. 2). Further, all population effects for physiological traits were significant except for C concentration and C/N (Table S2 and Fig. 2). δ^{15}N had an exceptionally high proportion of trait variance explained by population (19.7%, SE: 6.7%). Some of these population differences might have been the result of spatially varying selection at the source populations. Indeed, the Q_{ST} of Starch and δ^{15}N were significantly different from zero (Fig. 4). When comparing Q_{ST} to a neutral expectation derived from genetic markers based on F_{ST}, we found evidence for selection on Height 2013 and C concentration, and tendencies for Height on other years, δ^{15}N and Starch (Table S4). However, note that the mixed effects model used by *QstFstComp* did not include Block and covariates for maternal effects, which may have altered the results.

Environmental drivers of population divergence and response to browsing

Several environmental variables related to the temperature of the seed source sites were correlated with seedling growth in the common garden (Table S5). Generally speaking, warmer

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and more thermally stable seed source sites were related to faster growth, as it has been shown by previous analyses of data from this experiment (Frank *et al.*, 2017; Kupferschmid & Heiri, 2019; Csilléry *et al.*, 2020b). More interestingly, we found evidence for a growth–storage trade–off at the level of populations mediated by browsing stress: seedlings from fast growing populations, which often came from warm places, tended to decrease their storage (Starch concentration) in response to Heavy browsing stress, while seedlings from slow growing populations, often originating from cold places, tended to increase their Starch concentrations when heavily browsed (Fig. 5). Note that the correlation was also significant for family means (Pearson correlation, r=0.33, p-value=0.018), suggesting a potential genetic underpinning for this trade–off. Finally, the population effects for Starch concentration under non-stressed conditions (model equation 3) did not reveal correlations with any of the environmental variables (Table S5), suggesting that the growth–storage trade–off is triggered only under Heavy browsing stress.

The common garden site was within the species distribution range, and it was climatically close to the seed source environments (Frank *et al.*, 2017). However, using soil samples from the common garden site and *in-situ*, we found that the soil N concentration was higher and the C/N (mean=10.6) was lower in Matzendorf than in any of the 19 seed source sites (mean C/N of 16.4, Fig. S3). Further, we found that forest soils across the 19 sites had a large variation in their N concentration (Fig. S3). The most N poor soils were observed in mountain populations (top four sites: PRA, TSC, BON, SIR), and the most N rich soils were at the Swiss Plateau (top four sites: VAZ, COR, BEI, GRB) (Fig. S3 and Fig. 6). The greater between-site environmental variation *in-situ* was reflected by a higher coefficient of variation (CV) in the population medians of traits measured in adult trees in comparison to the CV of the seedling population effects (Fig. 6 and Fig. S4). Interestingly, Heavy browsing stress also increased the variation across populations: the CV for C/N and δ^{15}N were almost as high for heavily browsed seedlings as for adult trees *in-situ* (Fig. 6).

Although soil composition may vary considerably within short distances, we found that the analysis of samples from a single soil profile *in-situ* explained the variation in traits measured in adult trees. Soil C/N was strongly and positively correlated with the population median C/N from adult tree needles (Fig. 6, Table S6). Population median C/N and N concentration in adult

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tree needles were significantly associated with the Slope (and the Topographic wetness index), such that steeper terrain led to lower N concentration, thus higher C/N in needles. Additionally, higher temperature stability (T seasonality) and higher annual precipitation (MAP) were also associated with higher N concentration (and lower C/N) (Fig. 6, Table S6). Further, seedling population effects for δ^{15}N were correlated with principally the same environmental variables as N concentration and C/N in adult trees (Tables S5 and S6), such as with the Slope, the Topographic wetness index, temperature seasonality and precipitation variables (Fig. 6, Table S5). Thus, it appeared that descendants of populations that came from steep terrains with less developed soils had a higher δ^{15}N in the common garden (Fig. 6).

Discussion

Heritability and browsing stress in growth and physiological traits

Multi−site experiments or experiments involving different treatments allow to detect genotype−environment or genotype−treatment interactions, but often lead to reduced heritability estimates or significant heritability in one site or under one treatment only (Grattapaglia *et al.*, 2018). Here, we performed a simulated browsing experiment with two treatment levels, which allowed us to explore how the genetic component of trait variation is altered by stress. Genetic factors explained most variation in growth traits (on average, 51.5%), but only 10.2%, on average, in physiological traits under control conditions (Fig. 2, Table S3). In contrast, Heavy browsing stress considerably reduced the genetic effects on growth (to 30%, on average), but doubled those on physiological traits related to storage (Fig. 2).

In this study, the relatively low heritability in physiological traits could be attributed to factors that reduce the additive genetic variance or those that increase the environmental variance. First, some physiological traits might be more closely related to fitness, thus natural selection might have removed much of the additive genetic variance (Merilä & Sheldon, 2000; Hansen *et al.*, 2011; Hoffmann *et al.*, 2016). Little information is available on how closely physiological traits are related to fitness in trees, but there is experimental evidence that the survival and long-term growth in trees is dependent on C availability and in capacity of storage (Sala *et al.*, 2012). Nevertheless, some previous studies found that traits directly related to reproductive success, such as seed production, had a higher heritability than that of growth traits (Caignard *et al.*, 2019). Second, some physiological traits are less integrative than growth traits, and they change on shorter time scales (Millard & Grelet, 2010). Indeed, the most integrative physiological traits had the largest part of the trait variation explained by genetic effects, such as NSC and Starch concentration, and δ^{13}C (Fig. 2). Finally, physiological traits appeared to be more affected by micro-environmental variation, as suggested by the relatively high Block effects, for example for Sugar concentration (Fig. 2).

Several previous common garden studies estimated the heritability of growth traits and found moderate to high heritabilities (Cornelius, 1994), even though, it is well known that these values

are inflated and likely much lower in natural settings (*e.g.* Latreille & Pichot, 2017). Fewer studies estimated the heritability of physiological traits, and most of them concentrated on δ^{13}C or water use efficiency (WUE), and usually from wood, and not from needles. For example, in Maritime pine, Brendel *et al.* (2002) found a moderate heritability for δ^{13}C based on a bulk sample across several tree rings (0.17), and Marguerit *et al.* (2014) found a higher heritability for δ^{13}C (0.29), compared to circumference and height. Here, we found a heritability of 0.18 (SE: 0.15) for δ^{13}C under control conditions (Table S3), but the genetic effects vanished for seedlings under Heavy browsing stress (Fig. 2).

Traits related to the N status are often considered principally environmentally determined, and, as a result, very few studies assessed the genetic factors that may influence them. Li *et al.* (1991) assessed the so-called nitrogen use efficiency (NUE) in a fertilization experiment, defined as added N per stem biomass. They found that NUE traits were under a moderate to high genetic control in Loblolly pine: families with higher NUE had greater root length and stem height at low N concentrations, but not at high N concentrations. Xu *et al.* (2003) evaluated the heritability of δ^{15}N in hoop pine; the first study assessing the genetics of this trait in forest trees. They found that under water stress, δ^{15}N was higher and had a moderate heritability, but there were no significant genetic effects at the wet site. The same trends were confirmed for European beech in a watering experiment, i.e. higher δ^{15}N (and also lower δ^{13}C) under water stress, and a family treatment interaction for traits related to N concentration (Aranda *et al.*, 2017). Finally, most recently, Hu *et al.* (2021) found both genetic and latitudinal, population variation for N isotope discrimination in heart-leaved willow. In agreement with these studies, here we found a significant genetic (family) variation for δ^{15}N only under browsing stress. Our results also showed that under stress, seedlings had a higher δ^{15}N (Fig. 3). Thus, we join Hu *et al.* (2021), and suggest that genetic studies of δ^{15}N could enhance our understanding of N acquisition and metabolism in forest trees. Finally, trees may also influence the composition of microbial communities, thereby the N concentration of the microbial biomass beneath them. Schweitzer *et al.* (2008) found that individual genotypes in *Populus* explained up to 70% of the variation in soil microbial community composition. Thus, part of the genetic variance for N related traits might reflect a dynamic interaction between the trees and soil microbial communities.

Response to simulated browsing

Loosing the terminal bud, thus the apical meristem tissue, did not have long-term impacts on growth, C and N storage, and re-mobilization in seedlings: two growing seasons after the loss, they did not differ from control seedlings in the measured traits, with the exception of Terminal height (Table S2 and Fig. 2). In contrast, Heavy browsing had three long lasting effects on seedlings affecting their (i) growth and storage, (ii) water use efficiency, and (iii) N status. We discuss these one by one in the following paragraphs.

First, seedlings had a reduced height growth, but interestingly, seedling Diameter and Fresh weight were not affected, suggesting that the overall growth of the seedlings had recovered two vegetative seasons after the stress. This is because seedlings altered their growth form: they became shorter, but grew more side shoots (multi-stemmed growth), which is a typical reaction to browsing in silver fir (Kupferschmid & Heiri, 2019), but also in other tree species (*e.g.* Lehtilä *et al.*, 2000; Kupferschmid, 2017). Additionally, we found that the fastest growing populations, originating from the warmest regions, decreased their Starch concentration the most as a reaction to Heavy browsing stress (Fig. 5). This result is in agreement with previous studies showing that NSC accumulation may occur at the expense of growth under stress (Wiley & Helliker, 2012; Wiley *et al.*, 2013; Palacio *et al.*, 2014; Puri *et al.*, 2015). C storage can be a priority over growth, because survival depends more on C demands for metabolism than for growth (Sala *et al.*, 2012). Our results support this literature, and taken together with the significant heritability of storage traits (Fig. 2), suggest a potential genetic underpinning for a growth–storage trade–off.

Second, seedlings that suffered from simulated Heavy browsing had an, on average, 0.86 ‰ lower $\delta^{13}C$ two vegetative seasons after the treatment. This reduced water use efficiency might be due to an increase in stomatal conductance, which would increase photosynthesis, and therefore compensate for the loss of photosynthesizing needle surface. Stomatal opening has been shown as a compensatory reaction in plants to a reduction in leaf surface by browsing or leaf detachment (Welker & Menke, 1990). The loss of branches also increased the root to shoot ratio, but $\delta^{13}C$ was measured two growing seasons later. Using this same experiment, Kupferschmid & Heiri (2019) showed that browsed seedlings grew more lateral shoots and recovered their above

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surface biomass two vegetative seasons after the treatment, thus they likely re-established their root to shoot ratio at the time when $\delta^{13}C$ was measured. Another simulated browsing experiment in *Abies*, combined with C labelling, showed that while browsing increased C allocated to the fine roots, the phenology of trees was the main determinant of the C allocation from shoots to roots and not browsing stress (Endrulat *et al.*, 2016).

Third, simulated heavy browsing increased $\delta^{15}N$ (Fig. 2 and 3). This might be related to the above mentioned increase in transpiration, which could also have increased the transport of nitrate, or ammonium, to the needles, even though we did only observe a slight but not significant increase in needle N concentration as a result of Heavy browsing. Although gymnosperms are known to have low nitrate reductase in the leaves, it has also been shown that this enzyme can be induced by providing nitrate (Smirnoff *et al.*, 1984), which suggests that nitrogen rich soils, such as the common garden site, might increase the nitrate concentration in needles (Smirnoff & Stewart, 1985). As inorganic N is enriched compared to assimilated, organic nitrogen (Pritchard & Guy, 2005; Cui *et al.*, 2020; Hu *et al.*, 2021), inorganic nitrate in needles may explain the shift to a more ^{15}N enriched N isotope composition under the Heavy browsing treatment. The increased N demand for compensatory growth might also lead to increased root nitrate assimilation capacities and, thus a decrease in the efflux of enriched non-assimilated nitrate.

Comparison of physiological traits between seedlings and adult trees

Comparison of physiological traits between life stages can enhance our understanding of acclimation and adaptation to the environment (McDowell *et al.*, 2013; Donohue, 2014). Differences in gas exchange characteristics between seedlings and adults can be related to changes during the development in light availability, hydraulic conductance, and carbon allocation (Steppe *et al.*, 2011; Day & Greenwood, 2011; McDowell *et al.*, 2011). Additionally, environmental differences between life-stages in our study were imposed by the fact that seedlings grew in a common garden and adult trees *in-situ*. While the common garden setting removed the environmental variation among populations present at the seed source sites, it also created a different environment than what could have been available for seedlings at their seed source sites. In particular, the common garden was likely too sun exposed for the shade

tolerant *Abies* seedlings (Ellenberg, 1988), which created stress for all seedlings, including the controls. Further, the common garden had a higher N supply in comparison to the seed source sites due to the fact that it was established on a former pasture that had been fertilized in the past (Fig. S3). Bearing in mind these effects, we attempt to interpret the differences in physiological traits between seedlings and adult trees at the population level.

Using the same 19 populations and common garden experiment as herein, Csilléry *et al.* (2020b) found that the population mean δ^{13}C in adult trees *in-situ* was a good predictor of the adaptive growth strategies. In particular, Csilléry *et al.* (2020b) showed that the timing and rate of growth evolved towards two extreme strategies, "start early and grow slowly" or "start late and grow fast", and populations following the "start early and grow slowly" strategy had higher water use efficiency. In this study, we additionally measured δ^{13}C in seedlings, but found that the population mean δ^{13}C in seedlings and adult trees were not correlated with one another (Pearson correlation, r=0.019, p-value=0.94). We also found the coefficient of variation of δ^{13}C across adult tree populations was nearly four times higher than in seedlings in the pooled control group (Fig. S4). These results are in agreement with the lack of significant population variation for δ^{13}C in control seedlings (Fig. 2). Although we cannot exclude the possibility that seedlings and adults have inherently different δ^{13}C, we argue that in our experiment δ^{13}C in seedlings was predominantly determined by the sun exposed setting of our common garden, which likely prohibited detecting population differences.

Seedling needle N concentrations were higher, C/N ratios were lower, and δ^{15}N were higher than the respective values in the adult trees, and to an extent that the ranges of seedling and adult population means did not even overlap (Fig. 6). These results are in agreement with the N rich soil of the common garden site and the poor N supply of the forest soils at the seed source sites. The low δ^{15}N values from needles of adult trees could indicate strong mycorrhizal activity, which is typical in N poor forest soils (Hobbie & Colpaert, 2003; Hobbie & Högberg, 2012; Craine *et al.*, 2015). While the high needle δ^{15}N values for seedlings likely reflect the past use of fertilizers at the common garden site, it could also indicate that a lower portion of N was obtained from mycorrhizal fungi. Indeed, it has been reported that a reduced dependence on mycorrhiza can enrich plants in ^{15}N by reducing the depletion associated with N transfers from mycorrhizal fungi (Högberg *et al.*, 2011).

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Evidence for spatially varying selection

Population differences for Height, Starch concentration and δ^{15}N appeared to be the result of natural selection (Fig. 4, Table S4). In this study, we were able to analyse the full time series of growth traits from 2012 to 2016. Even though our data set was reduced in comparison to previous analyses of the 2012 and 2013 data by Frank *et al.* (2017) and Csilléry *et al.* (2020b), we were able to confirm the Q_{ST} values reported by these studies, suggesting that our results are not limited by sample size. Overall, we found that the population differentiation diminished with time, and by 2016, none of the growth traits showed significant population genetic differentiation (Fig. 4). This decrease in Q_{ST} principally stems from a decrease in the within population variance, while the genetic variance component stayed relatively stable over time. The temporal stability of family effects is also supported by the fact that our proxy for maternal effects, seed weight, was still significant in 2016 for growth traits (Table S2). In contrast, populations might have become more similar to each other with time because all seedlings were, to some extent, stressed at the common garden site, as suggested by the small range of δ^{13}C (Fig. S4).

A surprisingly strong correlation was detected between seedling δ^{15}N and N concentration with the slope of the terrain, and, a slightly weaker but still significant correlation with temperature stability and precipitation (Fig. 6, Table S6 and S5). Seedlings coming from mountain populations growing on steep slopes, great temperature fluctuation and low amounts of precipitation, had a significantly higher needle δ^{15}N in the common garden. This finding, along with the significant Q_{ST}-F_{ST} tests, indicate that silver fir populations from mountainous regions across Switzerland have been selected to grow on N poor, potentially less developed and/or drained, soils. This finding was further corroborated by the fact that N concentration in needles of adult trees was lower on steep slopes than on flat ground, indicating that steep slopes are the most N poor environments (Fig. 6).

Forest soils can have a great variation in nitrogen mineralization, which leads to variation in nitrate and ammonium supplies. Topographic factors such as slope position and aspect have already been documented as key determinants of local N transformations. For example, higher levels of nitrification have been found at the bottom of slopes than towards the ridge of slopes (Zak *et al.*, 1989; Hirobe *et al.*, 1998), where the density of macro-invertebrates is also higher

(Hishi *et al.*, 2014). In contrast, it is also possible that seedlings originating from steep slopes have a different degree of mycorrhization also at the common garden site, or have different root architecture affecting soil N exploration, or have a preference to N forms with higher δ^{15}N such as nitrate compared to ammonium (Kahmen *et al.*, 2008). Moreover, the higher δ^{15}N might indicate higher N uptake efficiency, for example, due to reduced root efflux of non-assimilated inorganic nitrogen (Robinson *et al.*, 1998).

Conclusions and outlook

Conifers remain dominant only in the most hardy habitats across the globe: they are the most drought and frost resistant trees that can grow on nutrient poor soils (*e.g.* Sakai & Larcher, 2012; Lupi *et al.*, 2013; Moran *et al.*, 2017). N is considered the most important element in plant nutrition and its acquisition and assimilation have been shown to play a key role in growth, and recovery from drought stress (Li *et al.*, 1991; Gessler *et al.*, 2017; Millard & Grelet, 2010). In coniferous evergreen trees, N is obtained from the environment via ectomycorrhizal partners and stored mainly in needles, which can be easily mobilized (Millard & Grelet, 2010). In this study, we join the few existing studies (Li *et al.*, 1991; Xu *et al.*, 2003; Aranda *et al.*, 2017; Hu *et al.*, 2021), and show evidence for adaptation in δ^{15}N in silver fir across Switzerland. First, we show that silver fir seedlings from cold habitats (mountain populations) had a low growth rate and high storage levels, and they did not mobilize their carbohydrates to recover their photosynthesizing tissue loss due to browsing stress, as opposed to fast growing provenances from warm environments, such as the Swiss plateau. Second, we also show that population variation in needle N concentration in adult trees and δ^{15}N in seedlings is a results of adaptation to spatially varying selection pressure driven by soil N availability. Since the highest elevation habitats have the shortest vegetative season and are more likely to have less developed soils, it is likely that the evolution of populations occupying these most extreme habitats is influenced by multiple stresses. The positive genetic correlation between Starch and δ^{15}N suggests that the two adaptive strategies related to the climate and soil may co-evolve (Supplementary Results, Table S7), which could play an important role in the ongoing colonization of high elevation habitats in silver fir (Vitasse *et al.*, 2019b; Major *et al.*, 2021).

Data and Materials Availability

Phenotypic traits from seedlings including growth and physiological traits, stable isotope traits from adult trees, and C and N concentrations from top layer soil of the soil profiles *in-situ* and in the common garden are available at `10.5281/zenodo.5083749`.

Supplementary Data

Table S1 Names, political and geographic situation of the 19 silver fir (*Abies alba* Mill.) populations.

Table S2 Model comparisons.

Table S3 Trait heritabilities under Control conditions (pooled model).

Table S4 Q_{ST}-F_{ST} tests.

Table S5 Correlation between traits measured in seedlings and environmental variables.

Table S6 Correlation between traits measured in adult trees and environmental variables.

Figure S1 Height loss due to Terminal bud removal and Heavy browsing treatments per block.

Figure S2 Physiological trait values in adult trees *in-situ* per populations and Kruskal-Wallis test of population differences.

Figure S3 C/N ratio of the top mineral soil layer at the common garden site in Matzendorf and at the seed source populations.

Figure S4 Coefficient of variation in C concentration and $\delta^{13}C$, and correlation between population medians in adult trees (and seedling population effects) and environmental variables.

Supplementary Results Genetic correlations among growth and physiological traits

Conflict of Interest

None declared.

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Authors' Contributions

ADK, KC, NB and A. Gessler conceived the ideas, acquired funding, and designed the methodology. KC carried out the needle and A. Glauser the soil sampling. KC and NB measured the stable isotope traits. A. Glauser measured the starch, sugar and NSC. KC, ADK and A. Glauser analyzed the data, and all authors interpreted the results. KC and ADK wrote the first draft of the manuscript and all authors contributed to the final version.

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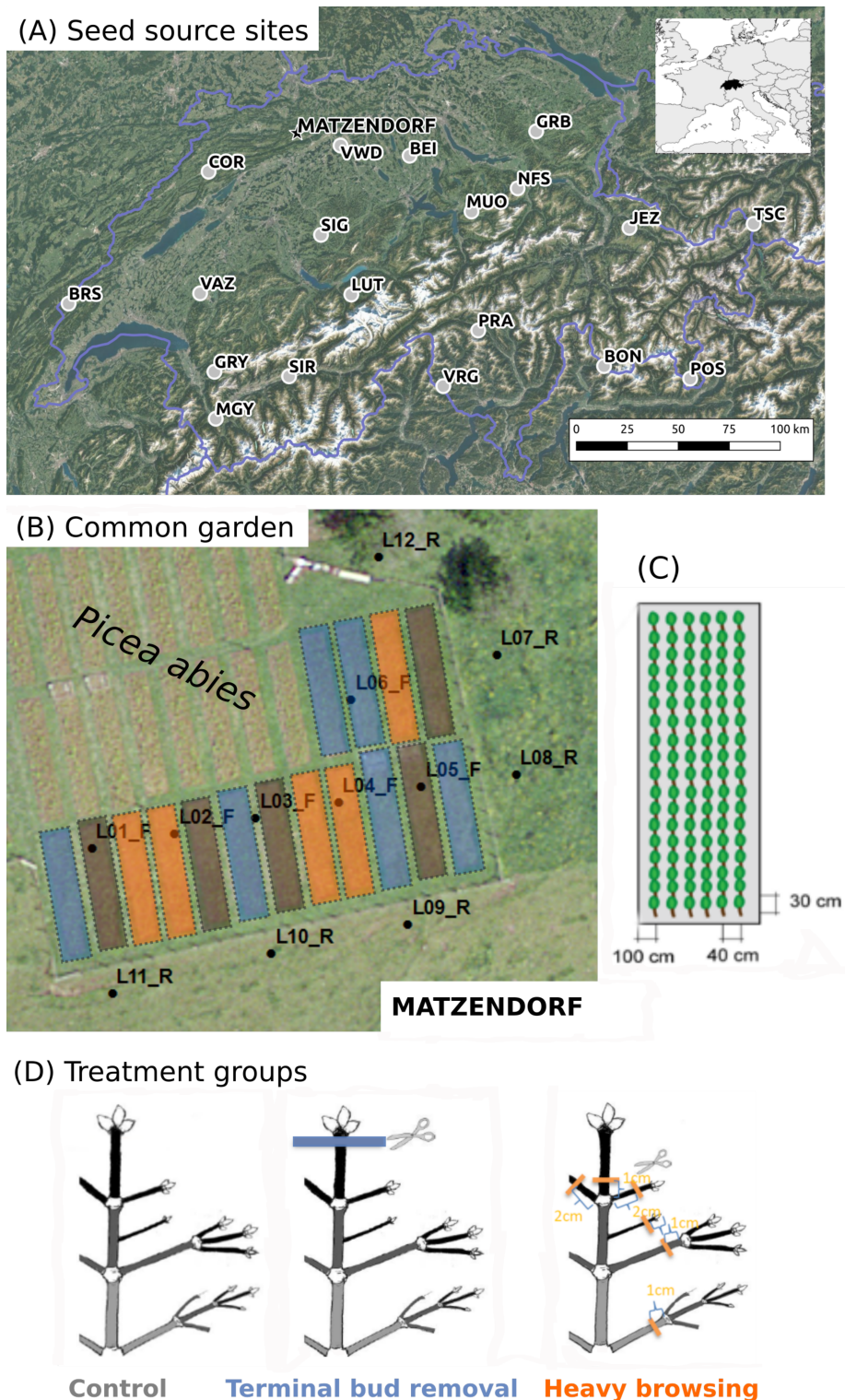
Figure 1: (A) Situation of the 19 seed source populations and the common garden in Matzendorf. (B) Areal photo of the common garden site. Silver fir blocks are highlighted in colors according to the treatment applied (Control - grey, Terminal bud removal - blue, Heavy clipping - orange). Black points labelled starting with "L" indicate the location of the soil samples within and outside of the experimental area. (C) Arrangement of seedlings in a single block. (D) Graphical illustration of the different treatments.
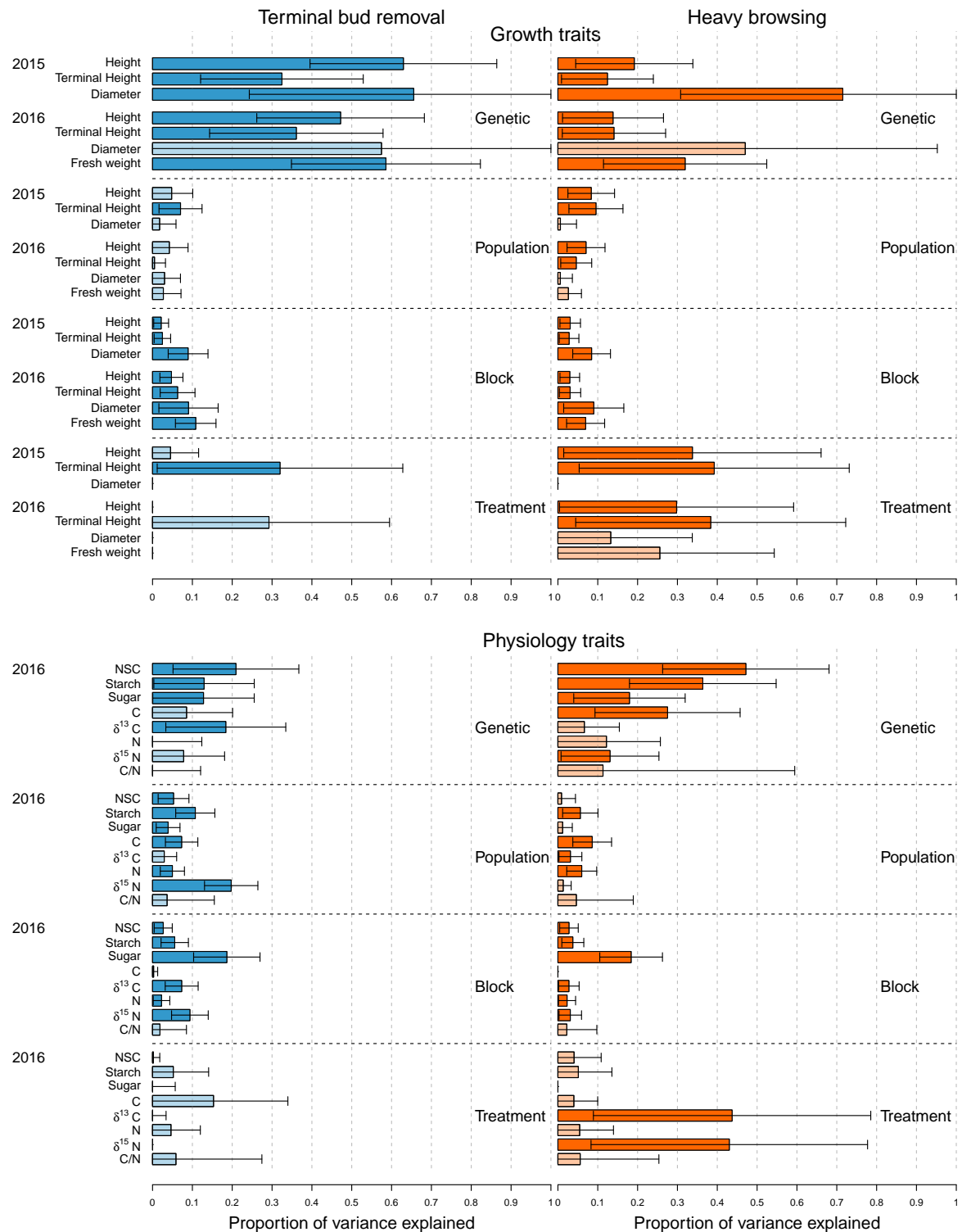
Figure 2: Variance components from the mixed effects models described in equation 2 expressed as proportions of the total variance. The first column in blue shows the model including the Control and the Terminal bud removal groups, and Treatment shows the trait variance explained due to Terminal bud removal. The second column in orange shows the model including the Control and the Heavy browsing groups, and Treatment shows the trait variance explained due to Heavy browsing. Dark color bars indicate that a significant part of the trait variance was explained by the given factor (Genetic etc.), while light color bars indicate non-significant variance components.
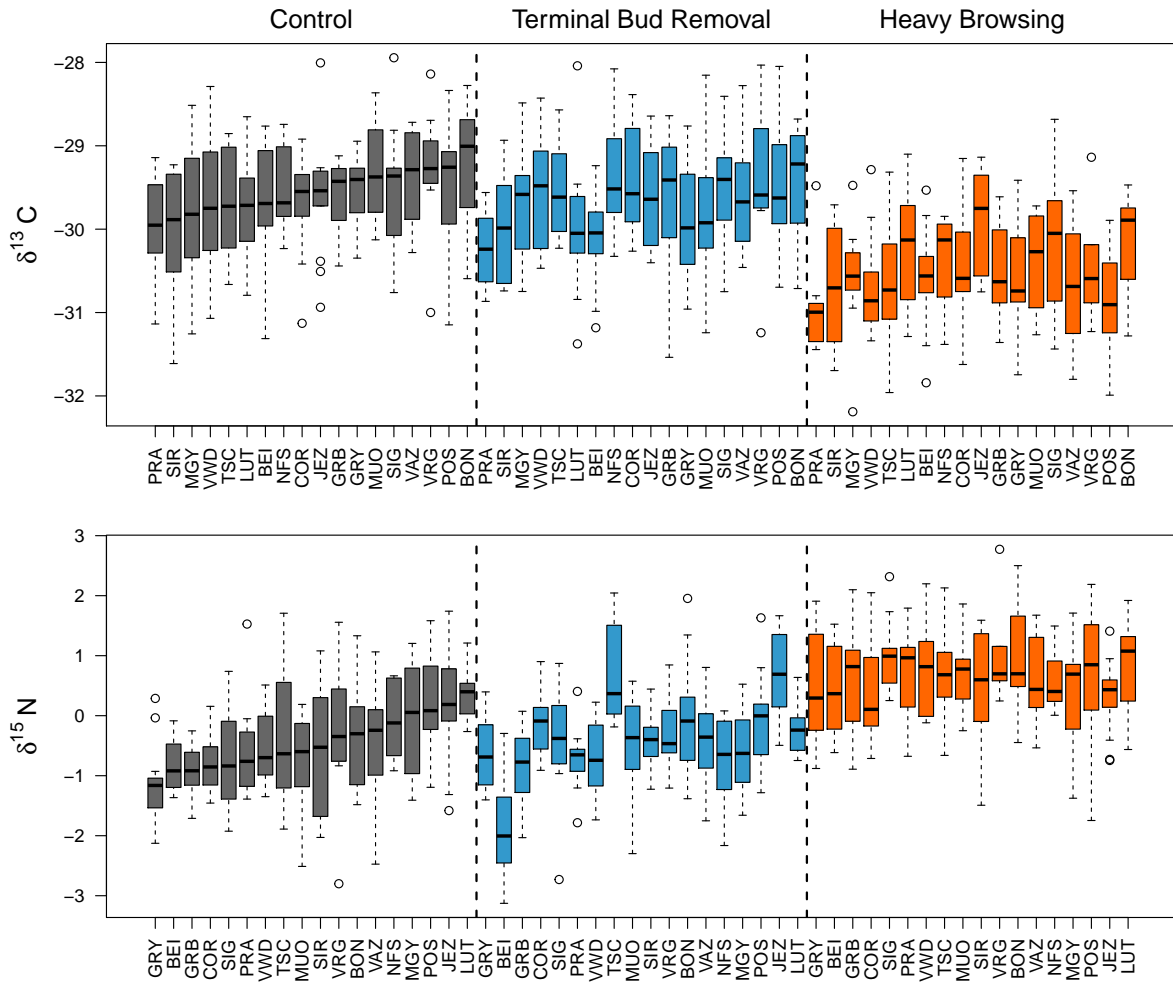
Figure 3: Boxplots of the raw δ^{13}C and δ^{15}N values per population across the three treatment groups: Control, Terminal bud removal, and Heavy browsing (see Fig. 1). Populations are ordered according to their medians in the Control group.
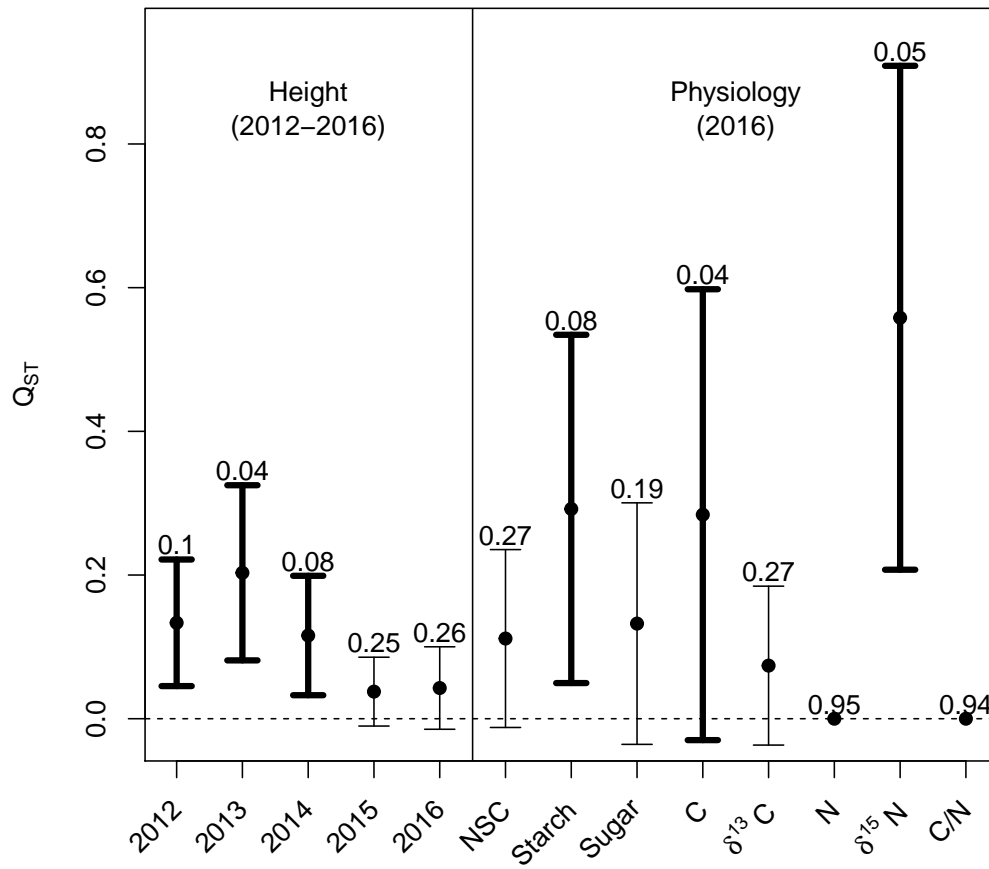
Figure 4: Population genetic differentiation (Q_{ST}) estimated from the pooled model (equation 3), combining data from the Control and Terminal bud removal groups for Height from 2012 to 2016, and for physiological traits measured in 2016. The numbers above each bar show the p-values from the Q_{ST}-F_{ST} test (see full test results in Table S4). Traits that showed evidence for spatially varying selection shown in bold.
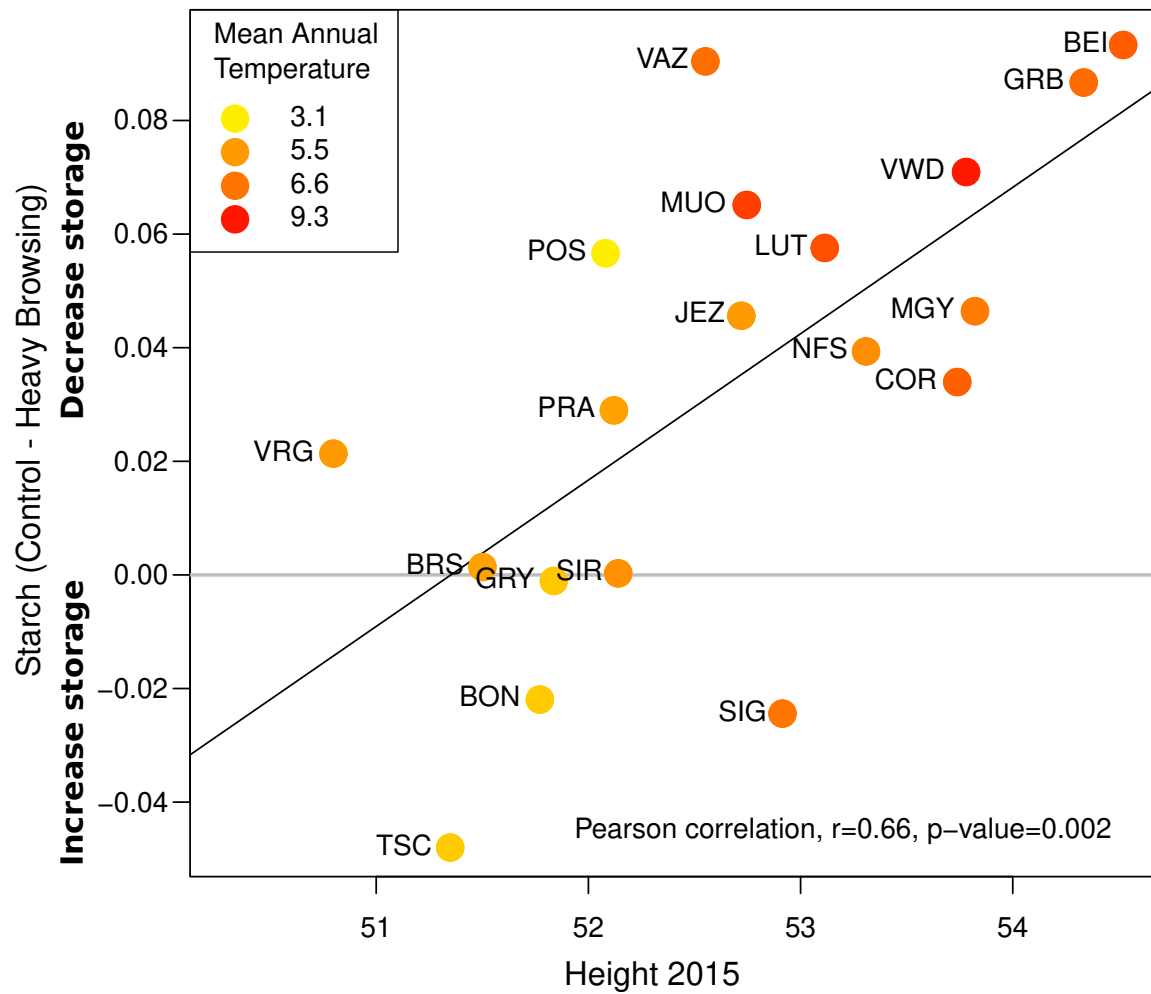
Figure 5: Growth–storage trade–off according to climate origin. Each point shows the difference between population means for Control and Heavy browsing treatments against the mean Height of the population in 2015, after the browsing treatment. Color code corresponds to the mean annual temperature of the seed source sites. See Table S5 for correlation between Height and climatic variables.
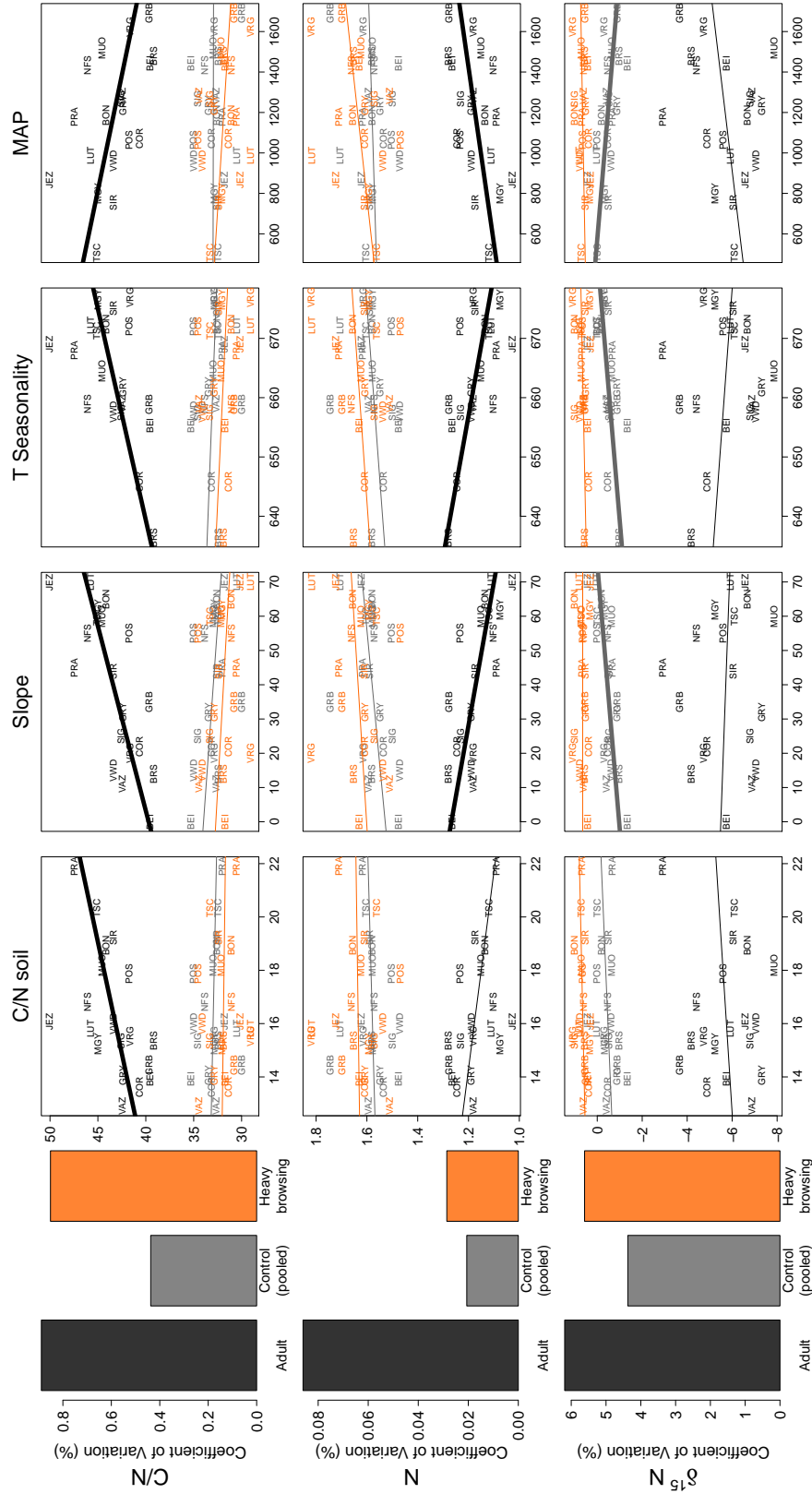
Figure 6: The strongest significant correlations between environmental variables (x axes) and mean trait values (y axes) in seedlings (orange and grey lines) and in adult trees (black lines). Barplots in the first column show the coefficient of variation among populations. Slope of the terrain is expressed as a percentage. T stands for temperature and measured in °C. MAP stands for Mean annual precipitation (in mm). All correlation tests between environmental variables and trait values with correction for multiple testing are shown in Tables S5 and S6. Thick lines indicate significant correlations while thin lines indicate non-significant relations. For simplicity, MAP is shown instead of other precipitation variables that had more significant correlations with trait values. Note that for seedlings, correlation tests were performed on population effects extracted from mixed-effects models, while this figure shows simple population means for an easier comparison with adult values.

Supplementary Data

Title: Recovery of silver fir (*Abies alba* Mill.) seedlings from ungulate browsing mirrors soil nitrogen availability

The following Supplementary Data are available for this article:

Table S1 Names, political and geographic situation of the 19 silver fir (*Abies alba* Mill.) populations.

Table S2 Model comparisons.

Table S3 Trait heritabilities under Control conditions (pooled model).

Table S4 Q_{ST}-F_{ST} tests.

Table S5 Correlation between traits measured in seedlings and environmental variables.

Table S6 Correlation between traits measured in adult trees and environmental variables.

Figure S1 Height loss due to Terminal bud removal and Heavy browsing treatments per block.

Figure S2 Physiological trait values in adult trees *in-situ* per populations and Kruskal-Wallis test of population differences.

Figure S3 C/N ratio of the top mineral soil layer at the common garden site in Matzendorf and at the seed source populations.

Figure S4 Coefficient of variation in C concentration and $\delta^{13}C$, and correlation between population medians in adult trees (and seedling population effects) and environmental variables.

Supplementary Results Genetic correlations among growth and physiological traits

Table S1: Abbreviations of the population names, their longitude and latitude, elevation in meters, and names of the nearby village (all in Switzerland) from which the abbreviations were derived. Identical to Table S1 of Csilléry *et al.* (2020b).

Population code	Latitude	Longitude	Elevation	Nearby village
BEI	$47.230°N$	$8.318°E$	843	Beinwil
BON	$46.324°N$	$9.541°E$	1334	Bondo
BRS	$46.595°N$	$6.175°E$	1221	Le Chenit (Le Brassus)
COR	$47.162°N$	$7.055°E$	840	Cormoret
GRB	$47.334°N$	$9.114°E$	922	Oberhelfenschwil (Graben)
GRY	$46.299°N$	$7.091°E$	1433	Gryon
JEZ	$46.921°N$	$9.700°E$	1158	Jenaz
LUT	$46.634°N$	$7.952°E$	817	Lütschental
MGY	$46.095°N$	$7.100°E$	1022	Martigny
MUO	$46.991°N$	$8.708°E$	691	Muotatal
NFS	$47.090°N$	$8.997°E$	1152	Näfels
POS	$46.270°N$	$10.082°E$	1602	Poschiavo (Le Prese)
PRA	$46.479°N$	$8.750°E$	1180	Prato (Leventina)
SIG	$46.891°N$	$7.761°E$	938	Signau
SIR	$46.280°N$	$7.560°E$	1149	Sierre
TSC	$46.938°N$	$10.481°E$	1284	Tschlin
VAZ	$46.639°N$	$7.002°E$	965	Maules
VRG	$46.237°N$	$8.530°E$	1149	Vergeletto
VWD	$47.273°N$	$7.884°E$	481	Vordemwald

Table S2: Likelihood ratio tests (LRT) comparing models of different complexity. The full model included all variables listed in the column headings as random effects. This model was compared to a model without the variables in the column headings one by one. If the log likelihood of the full model was greater, the p-value of the LRT is given. p-values less than 0.05 indicate that the model is better including the given random effect. Note however that while the model can be significantly better with a given random effect, the variance component associated with it is not always different from zero (see Fig. 2). If the log likelihood of the reduced model was greater, NA is given.

Year	Trait	Seed Weight	DBH	Treatment	Block	Population	Pedigree
Terminal bud removal							
Growth traits							
2015	Height	0.010	0.904	0.093	0.064	0.369	0.000
	Terminal Height	0.007	0.899	0.000	0.006	0.078	0.000
	Diameter	0.002	0.229	0.998	0.000	0.680	0.000
2016	Height	0.002	0.592	0.997	0.001	0.376	0.001
	Terminal Height	0.000	0.729	0.004	0.000	0.873	0.000
	Diameter	0.003	0.444	NA	0.000	0.487	0.000
	Fresh weight	0.003	0.502	0.999	0.000	0.544	0.000
Physiological traits							
2016	NSC [%]	0.496	0.386	0.888	0.055	0.104	0.103
	Starch [%]	0.655	0.421	0.199	0.000	0.002	0.227
	Sugar [%]	0.505	0.370	NA	0.000	0.120	0.254
	C [%]	0.055	0.483	0.000	0.773	0.012	0.376
	δ^{13}C	0.278	0.526	NA	0.000	0.298	0.145
	N [%]	0.524	0.255	0.106	0.095	0.007	NA
	δ^{15}N	0.200	0.202	NA	0.000	0.000	0.377
	C/N	0.301	0.386	0.057	0.153	0.028	NA
Heavy browsing							
Growth traits							
2015	Height	0.038	0.966	0.001	0.002	0.015	0.025
	Terminal Height	0.111	0.765	0.000	0.001	0.004	0.099
	Diameter	0.005	0.325	0.997	0.000	0.889	0.000
2016	Height	0.032	0.860	0.001	0.005	0.021	0.155
	Terminal Height	0.011	0.796	0.000	0.002	0.076	0.107
	Diameter	0.005	0.493	0.095	0.000	0.846	0.000
	Fresh weight	0.046	0.729	0.013	0.000	0.382	0.005
Physiological traits							
2016	NSC [%]	0.568	0.061	0.174	0.042	0.787	0.001
	Starch [%]	0.271	0.064	0.159	0.008	0.132	0.005
	Sugar [%]	0.519	0.181	NA	0.000	0.593	0.109
	C [%]	0.156	0.737	0.030	0.998	0.028	0.030
	δ^{13}C	0.202	0.733	0.000	0.003	0.065	0.316
	N [%]	0.814	0.066	0.094	0.092	0.040	0.285
	δ^{15}N	0.559	0.563	0.000	0.002	0.432	0.073
	C/N	0.575	0.079	0.090	0.103	0.077	0.316

Table S3: Heritability estimates under control conditions (i.e. no browsing stress) estimated from the pooled model (equation 3) for all traits measured in seedlings in the common garden. Sugar, Starch, NSC, C, N are concentrations and expressed as %, and δ traits as ‰.

Trait	h^2	SE
Growth traits		
Height 2015	0.642	0.235
Height 2016	0.472	0.210
Terminal Height 2015	0.375	0.169
Terminal Height 2016	0.415	0.183
Diameter 2015	0.656	0.413
Diameter 2016	0.575	0.602
Fresh weight 2016	0.586	0.237
Physiology traits (2016)		
NSC	0.210	0.158
Starch	0.134	0.129
Sugar	0.128	0.127
C	0.094	0.124
$\delta^{13}C$	0.184	0.150
N	0.000	0.126
$\delta^{15}N$	0.078	0.103
C/N	0.000	0.124

Table S4: Test of spatially divergent selection based on the comparison between population genetic divergence at traits (Q_{ST}) and genetic divergence at neutral genetic markers (F_{ST}) for all traits measured in seedlings in the common garden. Calculations were performed using the R package *QstFstComp* (Gilbert & Whitlock, 2015). Note that slightly different Q_{ST} values are reported in Fig. 4 because the calculations are based on a mixed effects model that includes the covariates Seed weight and DBH of mother trees, and random effects block and population. Note also that Csilléry *et al.* (2020b) reported the same test results for 2013 and 2014 Height and Diameter, but their test results were different (higher Q_{ST} and smaller p-values) because the sample size was larger. The tests reported herein are based on a sample size roughly 40% less due to mortality and because the Heavy browsing blocks are excluded. Sugar, Starch, NSC, C, N are concentrations and expressed as %, and δ traits as ‰.

Trait	Q_{ST}	F_{ST}	Q_{ST}-F_{ST}	CI low	CI high	p-value
Height 2012	0.132	0.0453	0.086	−0.0643	0.1605	0.096
Height 2013	0.193	0.0453	0.148	−0.0667	0.1795	0.039
Height 2014	0.143	0.0453	0.097	−0.0653	0.1689	0.079
Height 2015	0.084	0.0453	0.039	−0.0669	0.1884	0.250
Height 2016	0.086	0.0453	0.041	−0.0718	0.2366	0.262
Diameter 2012	−0.002	0.0453	−0.047	−0.0613	0.1362	0.911
Diameter 2013	0.044	0.0453	−0.002	−0.0627	0.1487	0.508
Diameter 2014	0.033	0.0453	−0.013	−0.0623	0.1440	0.606
Diameter 2015	0.031	0.0453	−0.014	−0.0648	0.1634	0.616
Diameter 2016	0.042	0.0453	−0.003	−0.0670	0.1784	0.517
Fresh weight	0.055	0.0453	0.010	−0.0684	0.1966	0.421
NSC	0.100	0.0453	0.055	−0.5611	0.7839	0.269
Starch	0.349	0.0453	0.304	−1.0825	1.0532	0.077
Sugar	0.132	0.0453	0.087	−1.0223	1.0548	0.186
C	0.487	0.0453	0.442	−0.9589	0.8590	0.044
δ^{13}C	0.085	0.0453	0.040	−0.9246	0.9766	0.271
N	−0.312	0.0453	−0.357	−0.6628	0.6552	0.954
δ^{15}N	0.508	0.0453	0.463	−1.0619	0.9839	0.051
C/N	−0.250	0.0453	−0.295	−0.7229	0.6866	0.938

Table S5: Spearman correlation (uncorrected p-value) between seedling population effects extracted from the pooled model (equation 3) and environmental variables. Starch is a concentration and expressed ‰, and $\delta^{15}N$ as ‰ Correlations that are significant (p-value < 0.05) after a correction for 18 independent tests are marked in **_bold italic_**, while those significant with correction for nine independent tests are marked in **bold**. Abbreviations: TWI: topographic wetness index, T: temperature, P: precipitation, Mon: month, Qtr: quarter, PET: potential evapotranspiration, AWC: available water capacity

	Height 2012	Height 2013	Seedlings (population effects) Height 2014	Height 2015	Height 2016	Starch	δ^{15}N
			Spearman correlation (p-value)				
Topographic variables							
Long	-0.1 (0.673)	-0.21 (0.381)	-0.17 (0.494)	-0.15 (0.531)	-0.22 (0.373)	0.3 (0.209)	0.43 (0.066)
Lat	0.49 (0.037)	0.46 (0.048)	0.46 (0.051)	0.54 (0.018)	0.47 (0.046)	0.25 (0.292)	-0.32 (0.18)
Elevation	**-0.63 (0.005)**	**-0.66 (0.003)**	-0.59 (0.009)	-0.56 (0.013)	-0.51 (0.028)	-0.28 (0.243)	0.18 (0.466)
Slope	-0.03 (0.898)	-0.06 (0.805)	0.04 (0.886)	-0.05 (0.847)	-0.11 (0.649)	0.1 (0.697)	**_0.66 (0.002)_**
TWI	0.15 (0.541)	0.16 (0.503)	0.14 (0.565)	0.22 (0.354)	0.32 (0.188)	-0.17 (0.489)	**-0.66 (0.003)**
Aspect	-0.11 (0.659)	-0.12 (0.628)	-0.16 (0.505)	-0.19 (0.429)	-0.11 (0.664)	0.29 (0.221)	0.24 (0.33)
Bioclimatic variables							
Annual Mean T	**_0.7 (0.001)_**	**_0.73 (0.001)_**	**_0.66 (0.003)_**	**0.63 (0.005)**	0.6 (0.008)	0.26 (0.278)	-0.27 (0.262)
Mean Diurnal Range	-0.35 (0.137)	-0.32 (0.182)	-0.3 (0.214)	-0.44 (0.06)	-0.35 (0.145)	-0.1 (0.689)	0.36 (0.131)
Isothermality	**-0.65 (0.003)**	**-0.65 (0.003)**	-0.61 (0.007)	**_-0.66 (0.003)_**	-0.56 (0.014)	-0.14 (0.565)	0.45 (0.056)
T Seasonality	-0.27 (0.262)	-0.27 (0.262)	-0.27 (0.269)	-0.43 (0.07)	-0.36 (0.127)	0.06 (0.815)	**0.62 (0.005)**
Max T of Warmest Mon	**0.66 (0.003)**	**_0.68 (0.002)_**	0.61 (0.007)	0.56 (0.014)	0.55 (0.016)	0.21 (0.389)	-0.25 (0.299)
Min T of Coldest Mon	0.6 (0.007)	**0.64 (0.004)**	0.56 (0.013)	0.56 (0.015)	0.54 (0.02)	0.19 (0.423)	-0.34 (0.152)
T Annual Range	0.25 (0.302)	0.38 (0.112)	0.32 (0.177)	0.11 (0.646)	0.16 (0.498)	-0.02 (0.934)	0.01 (0.986)
Mean T of Wettest Qtr	0.44 (0.058)	0.42 (0.077)	0.34 (0.152)	0.32 (0.18)	0.28 (0.247)	0.31 (0.193)	0.08 (0.748)
Mean T of Driest Qtr	**0.65 (0.003)**	0.57 (0.012)	0.5 (0.03)	0.52 (0.023)	0.43 (0.069)	0.38 (0.105)	-0.18 (0.457)
Mean T of Warmest Qtr	**_0.71 (0.001)_**	**_0.73 (0.001)_**	**0.65 (0.003)**	0.62 (0.006)	0.61 (0.007)	0.28 (0.253)	-0.25 (0.295)
Mean T of Coldest Qtr	0.6 (0.008)	**0.62 (0.005)**	0.56 (0.014)	0.54 (0.018)	0.5 (0.032)	0.32 (0.188)	-0.18 (0.462)

Seedlings (population effects)

Spearman correlation (p-value)

	Height 2012	Height 2013	Height 2014	Height 2015	Height 2016	Starch	δ^{15}N
Annual P	0.1 (0.689)	0.08 (0.754)	0.01 (0.974)	0.05 (0.837)	0.04 (0.877)	-0.07 (0.781)	-0.57 (0.012)
P of Wettest Mon	-0.03 (0.911)	-0.03 (0.917)	-0.09 (0.71)	-0.04 (0.888)	-0.07 (0.781)	-0.09 (0.721)	-0.51 (0.026)
P of Driest Mon	-0.3 (0.206)	-0.34 (0.152)	-0.31 (0.19)	-0.33 (0.165)	-0.23 (0.339)	-0.19 (0.431)	-0.3 (0.209)
P Seasonality	-0.37 (0.118)	-0.31 (0.201)	-0.36 (0.135)	-0.35 (0.139)	-0.38 (0.114)	-0.04 (0.871)	0.32 (0.177)
P of Wettest Qtr	-0.03 (0.9)	-0.07 (0.787)	-0.09 (0.705)	-0.05 (0.843)	-0.09 (0.705)	-0.16 (0.522)	-0.49 (0.036)
P of Driest Qtr	0.39 (0.104)	0.44 (0.063)	0.45 (0.053)	0.51 (0.028)	0.48 (0.041)	-0.13 (0.595)	**-0.79 (<0.001)**
P of Warmest Qtr	0.08 (0.732)	0.01 (0.98)	-0.01 (0.963)	0.04 (0.877)	-0.01 (0.957)	0.21 (0.393)	-0.22 (0.365)
P of Coldest Qtr	0.33 (0.163)	0.42 (0.077)	0.36 (0.131)	0.41 (0.082)	0.41 (0.083)	-0.19 (0.427)	**-0.75 (<0.001)**
Drought and frost indices							
PET (Thornthwaite)	**0.71 (0.001)**	**0.73 (0.001)**	**0.66 (0.003)**	**0.64 (0.004)**	0.59 (0.009)	0.28 (0.243)	-0.23 (0.339)
PET (Hargreaves)	0.38 (0.109)	0.42 (0.074)	0.39 (0.099)	0.33 (0.165)	0.31 (0.19)	0.14 (0.56)	0.09 (0.699)
AWC	-0.5 (0.032)	-0.54 (0.019)	-0.45 (0.057)	-0.52 (0.023)	-0.48 (0.041)	-0.3 (0.214)	0.39 (0.1)
Late frost	*0.71 (<0.001)*	*0.74 (<0.001)*	*0.67 (0.002)*	**0.64 (0.004)**	0.6 (0.008)	0.26 (0.289)	-0.26 (0.275)
Soil variables from local soil pits							
Sand [%]	-0.45 (0.055)	-0.42 (0.074)	-0.39 (0.099)	-0.46 (0.049)	-0.49 (0.037)	0.09 (0.705)	0.52 (0.023)
Silt [%]	*0.74 (<0.001)*	*0.69 (0.001)*	*0.66 (0.002)*	**0.65 (0.003)**	**0.75 (<0.001)**	0.17 (0.494)	-0.25 (0.302)
Clay [%]	0.26 (0.289)	0.27 (0.262)	0.26 (0.278)	0.34 (0.15)	0.3 (0.214)	-0.1 (0.694)	-0.53 (0.022)
Total N [%]	-0.21 (0.393)	-0.25 (0.306)	-0.16 (0.498)	-0.12 (0.626)	-0.11 (0.662)	-0.28 (0.253)	0.02 (0.945)
Total C [%]	-0.22 (0.354)	-0.31 (0.193)	-0.22 (0.373)	-0.17 (0.48)	-0.2 (0.402)	-0.3 (0.209)	0.02 (0.945)
Organic C [%]	-0.27 (0.262)	-0.37 (0.123)	-0.27 (0.262)	-0.23 (0.346)	-0.26 (0.285)	-0.32 (0.18)	0 (0.991)
Organic C/Total N	-0.36 (0.129)	-0.46 (0.049)	-0.36 (0.127)	-0.43 (0.068)	-0.52 (0.023)	0.11 (0.662)	0.33 (0.17)
pH (upper limit)	0.11 (0.652)	0.16 (0.517)	0.23 (0.342)	0.26 (0.275)	0.19 (0.436)	-0.15 (0.527)	-0.25 (0.306)
AWC (1m)	-0.06 (0.794)	-0.04 (0.884)	-0.04 (0.884)	-0.09 (0.705)	0 (0.991)	0.27 (0.266)	-0.08 (0.732)

Table S6: Spearman correlation (uncorrected p-value) between traits measured in adult trees *in-situ* (population means) and environmental variables. C and N are concentrations and expressed as %, and δ traits as ‰. Correlations that are significant (p-value < 0.05) after a correction for 36 independent tests are marked in ***bold italic***, while those significant with correction for nine independent tests are marked in **bold**. Abbreviations: TWI: topographic wetness index, T: temperature, P: precipitation, Mon: month, Qtr: quarter, PET: potential evapotranspiration, AWC: available water capacity

	Adult trees in-situ (population median)				
	C	δ^{13}C	N	δ^{15}N	C/N
	Spearman correlation (p-value)				
Topographic variables					
Longitude	-0.6 (0.008)	-0.13 (0.604)	-0.38 (0.108)	0.11 (0.657)	0.32 (0.182)
Latitude	-0.14 (0.58)	-0.33 (0.163)	0.33 (0.161)	-0.01 (0.957)	-0.34 (0.15)
Elevation	-0.02 (0.94)	0.45 (0.051)	-0.15 (0.529)	0.18 (0.471)	0.16 (0.508)
Slope	-0.49 (0.034)	-0.05 (0.839)	*-0.81 (<0.001)*	-0.1 (0.683)	*0.78 (<0.001)*
TWI	0.47 (0.045)	-0.11 (0.665)	**0.61 (0.005)**	-0.25 (0.295)	-0.56 (0.015)
Aspect	0.46 (0.049)	0.34 (0.15)	-0.12 (0.617)	-0.27 (0.264)	0.12 (0.623)
Bioclimatic variables					
Annual Mean T	0.02 (0.945)	-0.4 (0.087)	0.16 (0.522)	-0.2 (0.402)	-0.17 (0.48)
Mean Diurnal Range	-0.12 (0.621)	0.18 (0.466)	-0.46 (0.047)	-0.19 (0.423)	0.42 (0.073)
Isothermality	-0.1 (0.689)	0.29 (0.228)	-0.31 (0.201)	-0.06 (0.809)	0.3 (0.211)
T Seasonality	-0.28 (0.247)	0.04 (0.87)	**-0.65 (0.003)**	-0.07 (0.776)	0.59 (0.009)
Max T of Warmest Mon	0.11 (0.667)	-0.37 (0.116)	0.13 (0.61)	-0.21 (0.385)	-0.12 (0.631)
Min T of Coldest Mon	0.17 (0.48)	-0.33 (0.17)	0.26 (0.288)	-0.19 (0.444)	-0.24 (0.324)
T Annual Range	0.06 (0.809)	-0.28 (0.244)	-0.23 (0.351)	-0.41 (0.082)	0.17 (0.48)
Mean T of Wettest Qtr	-0.22 (0.358)	-0.59 (0.008)	0.11 (0.643)	-0.3 (0.217)	-0.1 (0.689)
Mean T of Driest Qtr	-0.24 (0.313)	-0.34 (0.148)	-0.04 (0.869)	-0.06 (0.809)	-0.03 (0.9)
Mean T of Warmest Qtr	0.03 (0.905)	-0.37 (0.119)	0.1 (0.675)	-0.22 (0.369)	-0.11 (0.641)
Mean T of Coldest Qtr	0.12 (0.631)	-0.38 (0.113)	0.13 (0.605)	-0.26 (0.272)	-0.11 (0.641)
Annual P	0.04 (0.871)	-0.12 (0.637)	0.52 (0.022)	0.16 (0.503)	-0.6 (0.008)
P of Wettest Mon	0.11 (0.667)	-0.08 (0.748)	0.58 (0.009)	0.12 (0.616)	**-0.64 (0.004)**
P of Driest Mon	**0.63 (0.005)**	0.09 (0.705)	0.08 (0.747)	-0.25 (0.295)	-0.01 (0.968)
P Seasonality	-0.04 (0.865)	-0.07 (0.762)	0.47 (0.043)	0.05 (0.854)	-0.43 (0.068)
P of Wettest Qtr	0.08 (0.748)	-0.07 (0.778)	0.46 (0.048)	0.26 (0.285)	-0.51 (0.027)
P of Driest Qtr	0.28 (0.24)	-0.04 (0.878)	0.46 (0.048)	0.02 (0.928)	-0.47 (0.043)
P of Warmest Qtr	-0.2 (0.414)	0.02 (0.943)	0.21 (0.389)	0.09 (0.705)	-0.29 (0.231)
P of Coldest Qtr	0.18 (0.457)	-0.1 (0.692)	0.53 (0.018)	0.01 (0.968)	-0.57 (0.012)
Drought and frost indices					
PET (Thornthwaite)	-0.04 (0.877)	-0.43 (0.064)	0.1 (0.68)	-0.19 (0.431)	-0.11 (0.641)
PET (Hargreaves)	0.19 (0.431)	-0.26 (0.286)	-0.2 (0.42)	-0.35 (0.145)	0.25 (0.299)
late.frost2	-0.01 (0.974)	-0.44 (0.061)	0.13 (0.597)	-0.19 (0.427)	-0.14 (0.556)
Soil variables from local soil pits					
Sand [%]	-0.06 (0.815)	0.13 (0.584)	-0.18 (0.455)	0.18 (0.471)	0.2 (0.402)
Silt [%]	-0.11 (0.652)	-0.1 (0.684)	-0.1 (0.691)	-0.35 (0.147)	0.06 (0.804)
Clay [%]	-0.12 (0.616)	-0.13 (0.596)	0.25 (0.296)	-0.12 (0.61)	-0.3 (0.217)
Total N [%]	0.12 (0.631)	-0.04 (0.881)	0.11 (0.656)	0.25 (0.306)	-0.12 (0.636)
Total C [%]	0.1 (0.683)	-0.06 (0.792)	0.08 (0.755)	0.36 (0.133)	-0.06 (0.809)
Total Organic C [%]	0.09 (0.71)	-0.09 (0.726)	0.04 (0.864)	0.33 (0.163)	-0.03 (0.9)
Organic C/Total N	-0.13 (0.595)	-0.02 (0.935)	-0.58 (0.009)	0.03 (0.911)	**0.63 (0.005)**
pH (upper limit)	-0.04 (0.888)	0.08 (0.756)	0.06 (0.799)	0.08 (0.754)	-0.07 (0.776)
AWC (1m)	0.02 (0.935)	-0.02 (0.949)	0.04 (0.855)	-0.57 (0.011)	0 (0.991)

Figure S1: Height loss per block. See Fig/ 1 for the spatial arrangement of the blocks.

Figure S2: Traits measured in adult trees *in-situ* across the 19 populations and Kruskal-Wallis test of differences between population medians.

Figure S3: C/N ratio of the top mineral soil layer at the common garden site in Matzendorf and at the seed source populations. Boxplots at the common garden site represent variation of C/N across three to four replicate measures between layers 0 to 15 cm depth. A single measure was taken *in-situ*.

Figure S4: Coefficient of variation in C concentration and $\delta^{13}C$, and correlation between adult population medians (and seedling population effects) and environmental variables. Note that these are the strongest correlations that have unadjusted p-values < 0.05 (see Table S6), but none of them passed the correction for multiple testing.

Genetic correlations among growth and physiological traits

We fitted a multivariate version of equation 3 to estimate the additive genetic covariance between all pairs of seedling traits (COV_A) and the genetic correlations between traits as

$$r_g = \frac{COV_A(i,j)}{\sqrt{(V_A(i)V_A(j)}},$$

where i and j are indices for two different traits. Only traits measured in 2016 were compared. Significant genetic correlations were detected when the absolute value of the Z score was higher than two.

Due to the limited sample size, convergence was achieved only if we used population as a fixed and not a random effect, as opposed to the pooled model that was used to estimate Q_{ST}. Even with this model, 15 out of the 55 trait pairs did not reach convergence (Table S7). Among the other 40 trait pairs we were able to identify several significant additive genetic trait correlations between pairs of growth or physiological traits, as well as between a growth and a physiological trait. However, these estimates also have to be interpreted with caution because population differences for some traits may have created spurious correlations. In the below paragraph, we attempt to interpret some of the significant correlations.

Not surprisingly, we detected a strong genetically based character integration between Height and Diameter and between Height and Fresh weight (Table S7). Physiological traits were largely independent from one another with the exception of derived traits with their original traits (Starch vs NSC, C/N vs C, C/N vs N). Although Starch and Sugar were not derived from one another, the significant negative correlation between them could be partly due to the measurement method. We detected a strong positive genetic correlation between δ^{15}N and Starch (r_g=0.65, z-score=3.03). Although the heritability of δ^{15}N did not differ significantly from zero, our data revealed that seedlings from the same family that had a high Starch concentration also had a high δ^{15}N. We also detected a significant positive genetic correlation between δ^{13}C and C concentration, thus higher water use efficiency was genetically associated with higher bulk C concentration. Finally, several physiological traits were genetically correlated with growth traits. Needle Starch was positively correlated with Diameter, Sugar with all growth traits, though weakly. δ^{13}C was positively correlated with growth traits, needle C concentration had a negative genetic correlation with growth. δ^{15}N also showed a significant negative genetic character integration with Height and Fresh Weight, indicating that families that had a higher δ^{15}N grew less and/or had a lower biomass.

Table S7: Genetic correlations (r_g) between growth and physiological traits measured in 2016 and the z-scores from the model. Sugar, Starch, NSC, C, N are concentrations and expressed as %, and δ traits as ‰. nc indicates that the model did not converge to the maximum likelihood solution with ASReml. z-scores > 2 indicate a non-zero additive genetic covariance between traits.

Trait 1	Trait 2	r_g	z-score
δ^{15}N	δ^{13}C	−0.013	2.029
δ^{15}N	N	nc	nc
δ^{15}N	C	−0.013	2.029
δ^{15}N	C/N	−0.013	2.029
δ^{15}N	Sugar	0.081	2.150
δ^{15}N	Starch	0.655	3.032
δ^{15}N	NSC	0.523	2.481
δ^{15}N	Diameter	−0.013	2.029
δ^{15}N	Height	−0.800	3.470
δ^{15}N	Fresh weight	−0.726	3.610
δ^{13}C	N	0.355	1.084
δ^{13}C	C	0.331	2.557
δ^{13}C	C/N	0.111	0.727
δ^{13}C	Sugar	0.000	2.239
δ^{13}C	Starch	nc	nc
δ^{13}C	NSC	nc	nc
δ^{13}C	Diameter	0.430	3.580
δ^{13}C	Height	0.167	3.482
δ^{13}C	Fresh weight	0.521	3.624
N	C	−0.013	2.029
N	C/N	−0.943	0.739
N	Sugar	−0.204	1.213
N	Starch	nc	nc
N	NSC	nc	nc
N	Diameter	−0.013	2.029
N	Height	nc	nc
N	Fresh weight	−0.013	2.029
C	C/N	−0.482	0.852
C	Sugar	nc	nc
C	Starch	−0.541	1.290
C	NSC	−0.848	1.739
C	Diameter	−0.535	3.550
C	Height	−0.757	2.430
C	Fresh weight	−0.672	3.165
C/N	Sugar	−0.613	1.090
C/N	Starch	0.621	1.150
C/N	NSC	0.245	1.353
C/N	Diameter	nc	nc
C/N	Height	−0.178	2.105
C/N	Fresh weight	−0.945	2.456

Trait 1	Trait 2	r_g	z-score
Sugar	Starch	−0.391	2.430
Sugar	NSC	0.742	2.699
Sugar	Diameter	0.060	3.574
Sugar	Height	0.151	3.356
Sugar	Fresh weight	0.120	3.592
Starch	NSC	0.874	1.565
Starch	Diameter	0.280	3.575
Starch	Height	−0.078	3.205
Starch	Fresh weight	0.008	3.573
NSC	Diameter	0.259	3.568
NSC	Height	0.023	3.053
NSC	Fresh weight	0.089	3.542
Diameter	Height	0.944	2.746
Diameter	Fresh weight	nc	nc
Height	Fresh weight	0.956	3.429

Supplementary Data

Title: Recovery of silver fir (*Abies alba* Mill.) seedlings from ungulate browsing mirrors soil nitrogen availability

The following Supplementary Data are available for this article:

Table S1 Names, political and geographic situation of the 19 silver fir (*Abies alba* Mill.) populations.

Table S2 Model comparisons.

Table S3 Trait heritabilities under Control conditions (pooled model).

Table S4 Q_{ST}-F_{ST} tests.

Table S5 Correlation between traits measured in seedlings and environmental variables.

Table S6 Correlation between traits measured in adult trees and environmental variables.

Figure S1 Height loss due to Terminal bud removal and Heavy browsing treatments per block.

Figure S2 Physiological trait values in adult trees *in-situ* per populations and Kruskal-Wallis test of population differences.

Figure S3 C/N ratio of the top mineral soil layer at the common garden site in Matzendorf and at the seed source populations.

Figure S4 Coefficient of variation in C concentration and $\delta^{13}C$, and correlation between population medians in adult trees (and seedling population effects) and environmental variables.

Supplementary Results Genetic correlations among growth and physiological traits

Table S1: Abbreviations of the population names, their longitude and latitude, elevation in meters, and names of the nearby village (all in Switzerland) from which the abbreviations were derived. Identical to Table S1 of Csilléry *et al.* (2020b).

Population code	Latitude	Longitude	Elevation	Nearby village
BEI	$47.230°N$	$8.318°E$	843	Beinwil
BON	$46.324°N$	$9.541°E$	1334	Bondo
BRS	$46.595°N$	$6.175°E$	1221	Le Chenit (Le Brassus)
COR	$47.162°N$	$7.055°E$	840	Cormoret
GRB	$47.334°N$	$9.114°E$	922	Oberhelfenschwil (Graben)
GRY	$46.299°N$	$7.091°E$	1433	Gryon
JEZ	$46.921°N$	$9.700°E$	1158	Jenaz
LUT	$46.634°N$	$7.952°E$	817	Lütschental
MGY	$46.095°N$	$7.100°E$	1022	Martigny
MUO	$46.991°N$	$8.708°E$	691	Muotatal
NFS	$47.090°N$	$8.997°E$	1152	Näfels
POS	$46.270°N$	$10.082°E$	1602	Poschiavo (Le Prese)
PRA	$46.479°N$	$8.750°E$	1180	Prato (Leventina)
SIG	$46.891°N$	$7.761°E$	938	Signau
SIR	$46.280°N$	$7.560°E$	1149	Sierre
TSC	$46.938°N$	$10.481°E$	1284	Tschlin
VAZ	$46.639°N$	$7.002°E$	965	Maules
VRG	$46.237°N$	$8.530°E$	1149	Vergeletto
VWD	$47.273°N$	$7.884°E$	481	Vordemwald

Table S2: Likelihood ratio tests (LRT) comparing models of different complexity. The full model included all variables listed in the column headings as random effects. This model was compared to a model without the variables in the column headings one by one. If the log likelihood of the full model was greater, the p-value of the LRT is given. p-values less than 0.05 indicate that the model is better including the given random effect. Note however that while the model can be significantly better with a given random effect, the variance component associated with it is not always different from zero (see Fig. 2). If the log likelihood of the reduced model was greater, NA is given.

		Terminal bud removal					
Year	Trait	Seed Weight	DBH	Treatment	Block	Population	Pedigree
Growth traits							
2015	Height	0.010	0.904	0.093	0.064	0.369	0.000
	Terminal Height	0.007	0.899	0.000	0.006	0.078	0.000
	Diameter	0.002	0.229	0.998	0.000	0.680	0.000
2016	Height	0.002	0.592	0.997	0.001	0.376	0.001
	Terminal Height	0.000	0.729	0.004	0.000	0.873	0.000
	Diameter	0.003	0.444	NA	0.000	0.487	0.000
	Fresh weight	0.003	0.502	0.999	0.000	0.544	0.000
Physiological traits							
2016	NSC [%]	0.496	0.386	0.888	0.055	0.104	0.103
	Starch [%]	0.655	0.421	0.199	0.000	0.002	0.227
	Sugar [%]	0.505	0.370	NA	0.000	0.120	0.254
	C [%]	0.055	0.483	0.000	0.773	0.012	0.376
	δ^{13}C	0.278	0.526	NA	0.000	0.298	0.145
	N [%]	0.524	0.255	0.106	0.095	0.007	NA
	δ^{15}N	0.200	0.202	NA	0.000	0.000	0.377
	C/N	0.301	0.386	0.057	0.153	0.028	NA
		Heavy browsing					
Year	Trait	Seed Weight	DBH	Treatment	Block	Population	Pedigree
Growth traits							
2015	Height	0.038	0.966	0.001	0.002	0.015	0.025
	Terminal Height	0.111	0.765	0.000	0.001	0.004	0.099
	Diameter	0.005	0.325	0.997	0.000	0.889	0.000
2016	Height	0.032	0.860	0.001	0.005	0.021	0.155
	Terminal Height	0.011	0.796	0.000	0.002	0.076	0.107
	Diameter	0.005	0.493	0.095	0.000	0.846	0.000
	Fresh weight	0.046	0.729	0.013	0.000	0.382	0.005
Physiological traits							
2016	NSC [%]	0.568	0.061	0.174	0.042	0.787	0.001
	Starch [%]	0.271	0.064	0.159	0.008	0.132	0.005
	Sugar [%]	0.519	0.181	NA	0.000	0.593	0.109
	C [%]	0.156	0.737	0.030	0.998	0.028	0.030
	δ^{13}C	0.202	0.733	0.000	0.003	0.065	0.316
	N [%]	0.814	0.066	0.094	0.092	0.040	0.285
	δ^{15}N	0.559	0.563	0.000	0.002	0.432	0.073
	C/N	0.575	0.079	0.090	0.103	0.077	0.316

Table S3: Heritability estimates under control conditions (i.e. no browsing stress) estimated from the pooled model (equation 3) for all traits measured in seedlings in the common garden. Sugar, Starch, NSC, C, N are concentrations and expressed as %, and δ traits as ‰.

Trait	h^2	SE
Growth traits		
Height 2015	0.642	0.235
Height 2016	0.472	0.210
Terminal Height 2015	0.375	0.169
Terminal Height 2016	0.415	0.183
Diameter 2015	0.656	0.413
Diameter 2016	0.575	0.602
Fresh weight 2016	0.586	0.237
Physiology traits (2016)		
NSC	0.210	0.158
Starch	0.134	0.129
Sugar	0.128	0.127
C	0.094	0.124
δ^{13}C	0.184	0.150
N	0.000	0.126
δ^{15}N	0.078	0.103
C/N	0.000	0.124

Table S4: Test of spatially divergent selection based on the comparison between population genetic divergence at traits (Q_{ST}) and genetic divergence at neutral genetic markers (F_{ST}) for all traits measured in seedlings in the common garden. Calculations were performed using the R package *QstFstComp* (Gilbert & Whitlock, 2015). Note that slightly different Q_{ST} values are reported in Fig. 4 because the calculations are based on a mixed effects model that includes the covariates Seed weight and DBH of mother trees, and random effects block and population. Note also that Csilléry *et al.* (2020b) reported the same test results for 2013 and 2014 Height and Diameter, but their test results were different (higher Q_{ST} and smaller p-values) because the sample size was larger. The tests reported herein are based on a sample size roughly 40% less due to mortality and because the Heavy browsing blocks are excluded. Sugar, Starch, NSC, C, N are concentrations and expressed as %, and δ traits as ‰.

Trait	Q_{ST}	F_{ST}	Q_{ST}-F_{ST}	CI low	CI high	p-value
Height 2012	0.132	0.0453	0.086	-0.0643	0.1605	0.096
Height 2013	0.193	0.0453	0.148	-0.0667	0.1795	0.039
Height 2014	0.143	0.0453	0.097	-0.0653	0.1689	0.079
Height 2015	0.084	0.0453	0.039	-0.0669	0.1884	0.250
Height 2016	0.086	0.0453	0.041	-0.0718	0.2366	0.262
Diameter 2012	-0.002	0.0453	-0.047	-0.0613	0.1362	0.911
Diameter 2013	0.044	0.0453	-0.002	-0.0627	0.1487	0.508
Diameter 2014	0.033	0.0453	-0.013	-0.0623	0.1440	0.606
Diameter 2015	0.031	0.0453	-0.014	-0.0648	0.1634	0.616
Diameter 2016	0.042	0.0453	-0.003	-0.0670	0.1784	0.517
Fresh weight	0.055	0.0453	0.010	-0.0684	0.1966	0.421
NSC	0.100	0.0453	0.055	-0.5611	0.7839	0.269
Starch	0.349	0.0453	0.304	-1.0825	1.0532	0.077
Sugar	0.132	0.0453	0.087	-1.0223	1.0548	0.186
C	0.487	0.0453	0.442	-0.9589	0.8590	0.044
δ^{13}C	0.085	0.0453	0.040	-0.9246	0.9766	0.271
N	-0.312	0.0453	-0.357	-0.6628	0.6552	0.954
δ^{15}N	0.508	0.0453	0.463	-1.0619	0.9839	0.051
C/N	-0.250	0.0453	-0.295	-0.7229	0.6866	0.938

Table S5: Spearman correlation (uncorrected p-value) between seedling population effects extracted from the pooled model (equation 3) and environmental variables. Starch is a concentration and expressed ‰, and $\delta^{15}N$ as ‰ Correlations that are significant (p-value < 0.05) after a correction for 18 independent tests are marked in **bold italic**, while those significant with correction for nine independent tests are marked in **bold**. Abbreviations: TWI: topographic wetness index, T: temperature, P: precipitation, Mon: month, Qtr: quarter, PET: potential evapotranspiration, AWC: available water capacity

	Height 2012	Height 2013	Height 2014	Height 2015	Height 2016	Starch	$\delta^{15}N$
Seedlings (population effects)							
	Spearman correlation (p-value)						
Topographic variables							
Long	-0.1 (0.673)	-0.21 (0.381)	-0.17 (0.494)	-0.15 (0.531)	-0.22 (0.373)	0.3 (0.209)	0.43 (0.066)
Lat	0.49 (0.037)	0.46 (0.048)	0.46 (0.051)	0.54 (0.018)	0.47 (0.046)	0.25 (0.292)	-0.32 (0.18)
Elevation	**-0.63 (0.005)**	**-0.66 (0.003)**	-0.59 (0.009)	-0.56 (0.013)	-0.51 (0.028)	-0.28 (0.243)	0.18 (0.466)
Slope	-0.03 (0.898)	-0.06 (0.805)	0.04 (0.886)	-0.05 (0.847)	-0.11 (0.649)	0.1 (0.697)	***0.66 (0.002)***
TWI	0.15 (0.541)	0.16 (0.503)	0.14 (0.565)	0.22 (0.354)	0.32 (0.188)	-0.17 (0.489)	**-0.66 (0.003)**
Aspect	-0.11 (0.659)	-0.12 (0.628)	-0.16 (0.505)	-0.19 (0.429)	-0.11 (0.664)	0.29 (0.221)	0.24 (0.33)
Bioclimatic variables							
Annual Mean T	***0.7 (0.001)***	***0.73 (0.001)***	***0.66 (0.003)***	**0.63 (0.005)**	0.6 (0.008)	0.26 (0.278)	-0.27 (0.262)
Mean Diurnal Range	-0.35 (0.137)	-0.32 (0.182)	-0.3 (0.214)	-0.44 (0.06)	-0.35 (0.145)	-0.1 (0.689)	0.36 (0.131)
Isothermality	**-0.65 (0.003)**	**-0.65 (0.003)**	-0.61 (0.007)	***-0.66 (0.003)***	-0.56 (0.014)	-0.14 (0.565)	0.45 (0.056)
T Seasonality	-0.27 (0.262)	-0.27 (0.262)	-0.27 (0.269)	-0.43 (0.07)	-0.36 (0.127)	0.06 (0.815)	**0.62 (0.005)**
Max T of Warmest Mon	**0.66 (0.003)**	***0.68 (0.002)***	0.61 (0.007)	0.56 (0.014)	0.55 (0.016)	0.21 (0.389)	-0.25 (0.299)
Min T of Coldest Mon	0.6 (0.007)	***0.64 (0.004)***	0.56 (0.013)	0.56 (0.015)	0.54 (0.02)	0.19 (0.423)	-0.34 (0.152)
T Annual Range	0.25 (0.302)	0.38 (0.112)	0.32 (0.177)	0.11 (0.646)	0.16 (0.498)	-0.02 (0.934)	0.01 (0.986)
Mean T of Wettest Qtr	0.44 (0.058)	0.42 (0.077)	0.34 (0.152)	0.32 (0.18)	0.28 (0.247)	0.31 (0.193)	0.08 (0.748)
Mean T of Driest Qtr	**0.65 (0.003)**	0.57 (0.012)	0.5 (0.03)	0.52 (0.023)	0.43 (0.069)	0.38 (0.105)	-0.18 (0.457)
Mean T of Warmest Qtr	***0.71 (0.001)***	***0.73 (0.001)***	**0.65 (0.003)**	0.62 (0.006)	0.61 (0.007)	0.28 (0.253)	-0.25 (0.295)
Mean T of Coldest Qtr	0.6 (0.008)	**0.62 (0.005)**	0.56 (0.014)	0.54 (0.018)	0.5 (0.032)	0.32 (0.188)	-0.18 (0.462)

	Height 2012	Height 2013	Height 2014	Height 2015	Height 2016	Starch	δ^{15}N
			Seedlings (population effects)				
			Spearman correlation (p-value)				
Annual P	0.1 (0.689)	0.08 (0.754)	0.01 (0.974)	0.05 (0.837)	0.04 (0.877)	-0.07 (0.781)	-0.57 (0.012)
P of Wettest Mon	-0.03 (0.911)	-0.03 (0.917)	-0.09 (0.71)	-0.04 (0.888)	-0.07 (0.781)	-0.09 (0.721)	-0.51 (0.026)
P of Driest Mon	-0.3 (0.206)	-0.34 (0.152)	-0.31 (0.19)	-0.33 (0.165)	-0.23 (0.339)	-0.19 (0.431)	-0.3 (0.209)
P Seasonality	-0.37 (0.118)	-0.31 (0.201)	-0.36 (0.135)	-0.35 (0.139)	-0.38 (0.114)	-0.04 (0.871)	0.32 (0.177)
P of Wettest Qtr	-0.03 (0.9)	-0.07 (0.787)	-0.09 (0.705)	-0.05 (0.843)	-0.09 (0.705)	-0.16 (0.522)	-0.49 (0.036)
P of Driest Qtr	0.39 (0.104)	0.44 (0.063)	0.45 (0.053)	0.51 (0.028)	0.48 (0.041)	-0.13 (0.595)	**-0.79 (<0.001)**
P of Warmest Qtr	0.08 (0.732)	0.01 (0.98)	-0.01 (0.963)	0.04 (0.877)	-0.01 (0.957)	0.21 (0.393)	-0.22 (0.365)
P of Coldest Qtr	0.33 (0.163)	0.42 (0.077)	0.36 (0.131)	0.41 (0.082)	0.41 (0.083)	-0.19 (0.427)	**-0.75 (<0.001)**
Drought and frost indices							
PET (Thornthwaite)	**0.71 (0.001)**	**0.73 (0.001)**	**0.66 (0.003)**	**0.64 (0.004)**	0.59 (0.009)	0.28 (0.243)	-0.23 (0.339)
PET (Hargreaves)	0.38 (0.109)	0.42 (0.074)	0.39 (0.099)	0.33 (0.165)	0.31 (0.19)	0.14 (0.56)	0.09 (0.699)
AWC	-0.5 (0.032)	-0.54 (0.019)	-0.45 (0.057)	-0.52 (0.023)	-0.48 (0.041)	-0.3 (0.214)	0.39 (0.1)
Late frost	*0.71 (<0.001)*	*0.74 (<0.001)*	*0.67 (0.002)*	*0.64 (0.004)*	0.6 (0.008)	0.26 (0.289)	-0.26 (0.275)
Soil variables from local soil pits							
Sand [%]	-0.45 (0.055)	-0.42 (0.074)	-0.39 (0.099)	-0.46 (0.049)	-0.49 (0.037)	0.09 (0.705)	0.52 (0.023)
Silt [%]	*0.74 (<0.001)*	*0.69 (0.001)*	*0.66 (0.002)*	**0.65 (0.003)**	*0.75 (<0.001)*	0.17 (0.494)	-0.25 (0.302)
Clay [%]	0.26 (0.289)	0.27 (0.262)	0.26 (0.278)	0.34 (0.15)	0.3 (0.214)	-0.1 (0.694)	-0.53 (0.022)
Total N [%]	-0.21 (0.393)	-0.25 (0.306)	-0.16 (0.498)	-0.12 (0.626)	-0.11 (0.662)	-0.28 (0.253)	0.02 (0.945)
Total C [%]	-0.22 (0.354)	-0.31 (0.193)	-0.22 (0.373)	-0.17 (0.48)	-0.2 (0.402)	-0.3 (0.209)	0.02 (0.945)
Organic C [%]	-0.27 (0.262)	-0.37 (0.123)	-0.27 (0.262)	-0.23 (0.346)	-0.26 (0.285)	-0.32 (0.18)	0 (0.991)
Organic C/Total N	-0.36 (0.129)	-0.46 (0.049)	-0.36 (0.127)	-0.43 (0.068)	-0.52 (0.023)	0.11 (0.662)	0.33 (0.17)
pH (upper limit)	0.11 (0.652)	0.16 (0.517)	0.23 (0.342)	0.26 (0.275)	0.19 (0.436)	-0.15 (0.527)	-0.25 (0.306)
AWC (1m)	-0.06 (0.794)	-0.04 (0.884)	-0.04 (0.884)	-0.09 (0.705)	0 (0.991)	0.27 (0.266)	-0.08 (0.732)

Table S6: Spearman correlation (uncorrected p-value) between traits measured in adult trees *in-situ* (population means) and environmental variables. C and N are concentrations and expressed as %, and δ traits as ‰. Correlations that are significant (p-value < 0.05) after a correction for 36 independent tests are marked in ***bold italic***, while those significant with correction for nine independent tests are marked in **bold**. Abbreviations: TWI: topographic wetness index, T: temperature, P: precipitation, Mon: month, Qtr: quarter, PET: potential evapotranspiration, AWC: available water capacity

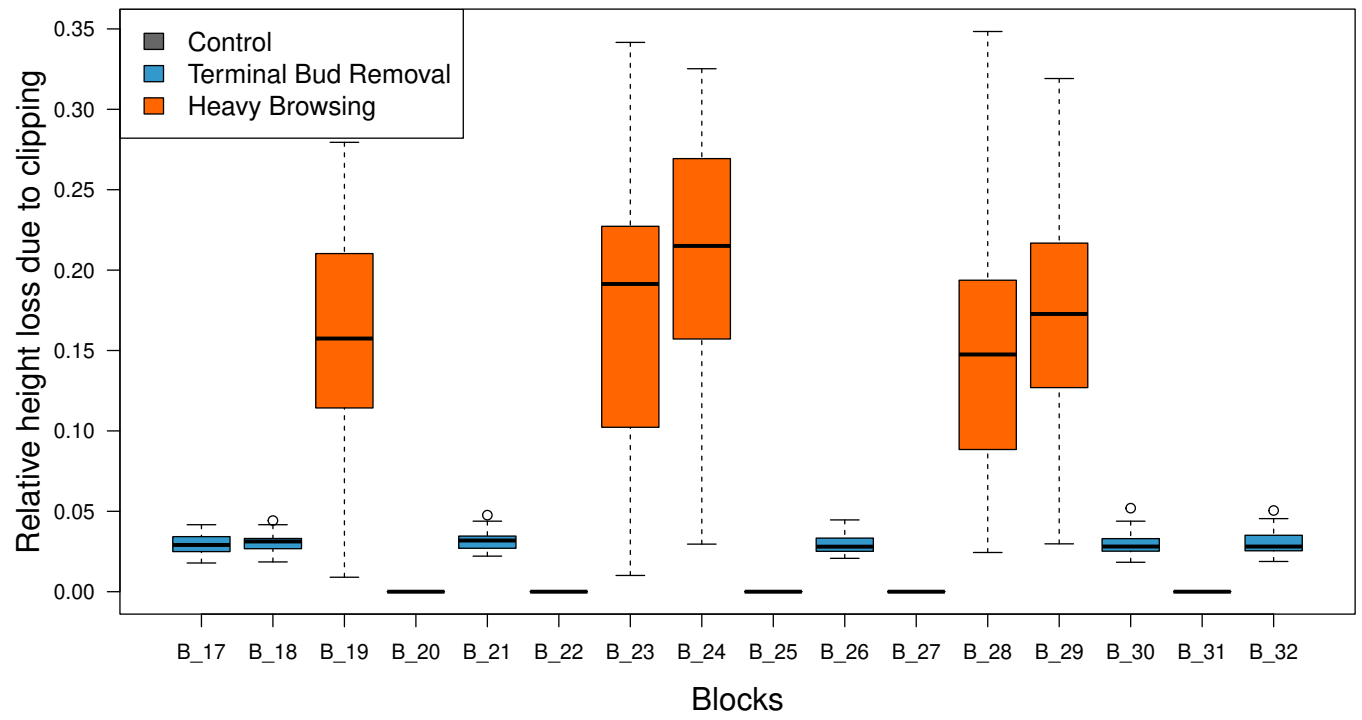|	Adult trees in-situ (population median)				
	C	δ^{13}**C**	**N**	δ^{15}**N**	**C/N**
	Spearman correlation (p-value)				
Topographic variables					
Longitude	-0.6 (0.008)	-0.13 (0.604)	-0.38 (0.108)	0.11 (0.657)	0.32 (0.182)
Latitude	-0.14 (0.58)	-0.33 (0.163)	0.33 (0.161)	-0.01 (0.957)	-0.34 (0.15)
Elevation	-0.02 (0.94)	0.45 (0.051)	-0.15 (0.529)	0.18 (0.471)	0.16 (0.508)
Slope	-0.49 (0.034)	-0.05 (0.839)	*-0.81 (<0.001)*	-0.1 (0.683)	*0.78 (<0.001)*
TWI	0.47 (0.045)	-0.11 (0.665)	**0.61 (0.005)**	-0.25 (0.295)	-0.56 (0.015)
Aspect	0.46 (0.049)	0.34 (0.15)	-0.12 (0.617)	-0.27 (0.264)	0.12 (0.623)
Bioclimatic variables					
Annual Mean T	0.02 (0.945)	-0.4 (0.087)	0.16 (0.522)	-0.2 (0.402)	-0.17 (0.48)
Mean Diurnal Range	-0.12 (0.621)	0.18 (0.466)	-0.46 (0.047)	-0.19 (0.423)	0.42 (0.073)
Isothermality	-0.1 (0.689)	0.29 (0.228)	-0.31 (0.201)	-0.06 (0.809)	0.3 (0.211)
T Seasonality	-0.28 (0.247)	0.04 (0.87)	**-0.65 (0.003)**	-0.07 (0.776)	0.59 (0.009)
Max T of Warmest Mon	0.11 (0.667)	-0.37 (0.116)	0.13 (0.61)	-0.21 (0.385)	-0.12 (0.631)
Min T of Coldest Mon	0.17 (0.48)	-0.33 (0.17)	0.26 (0.288)	-0.19 (0.444)	-0.24 (0.324)
T Annual Range	0.06 (0.809)	-0.28 (0.244)	-0.23 (0.351)	-0.41 (0.082)	0.17 (0.48)
Mean T of Wettest Qtr	-0.22 (0.358)	-0.59 (0.008)	0.11 (0.643)	-0.3 (0.217)	-0.1 (0.689)
Mean T of Driest Qtr	-0.24 (0.313)	-0.34 (0.148)	-0.04 (0.869)	-0.06 (0.809)	-0.03 (0.9)
Mean T of Warmest Qtr	0.03 (0.905)	-0.37 (0.119)	0.1 (0.675)	-0.22 (0.369)	-0.11 (0.641)
Mean T of Coldest Qtr	0.12 (0.631)	-0.38 (0.113)	0.13 (0.605)	-0.26 (0.272)	-0.11 (0.641)
Annual P	0.04 (0.871)	-0.12 (0.637)	0.52 (0.022)	0.16 (0.503)	-0.6 (0.008)
P of Wettest Mon	0.11 (0.667)	-0.08 (0.748)	0.58 (0.009)	0.12 (0.616)	**-0.64 (0.004)**
P of Driest Mon	**0.63 (0.005)**	0.09 (0.705)	0.08 (0.747)	-0.25 (0.295)	-0.01 (0.968)
P Seasonality	-0.04 (0.865)	-0.07 (0.762)	0.47 (0.043)	0.05 (0.854)	-0.43 (0.068)
P of Wettest Qtr	0.08 (0.748)	-0.07 (0.778)	0.46 (0.048)	0.26 (0.285)	-0.51 (0.027)
P of Driest Qtr	0.28 (0.24)	-0.04 (0.878)	0.46 (0.048)	0.02 (0.928)	-0.47 (0.043)
P of Warmest Qtr	-0.2 (0.414)	0.02 (0.943)	0.21 (0.389)	0.09 (0.705)	-0.29 (0.231)
P of Coldest Qtr	0.18 (0.457)	-0.1 (0.692)	0.53 (0.018)	0.01 (0.968)	-0.57 (0.012)
Drought and frost indices					
PET (Thornthwaite)	-0.04 (0.877)	-0.43 (0.064)	0.1 (0.68)	-0.19 (0.431)	-0.11 (0.641)
PET (Hargreaves)	0.19 (0.431)	-0.26 (0.286)	-0.2 (0.42)	-0.35 (0.145)	0.25 (0.299)
late.frost2	-0.01 (0.974)	-0.44 (0.061)	0.13 (0.597)	-0.19 (0.427)	-0.14 (0.556)
Soil variables from local soil pits					
Sand [%]	-0.06 (0.815)	0.13 (0.584)	-0.18 (0.455)	0.18 (0.471)	0.2 (0.402)
Silt [%]	-0.11 (0.652)	-0.1 (0.684)	-0.1 (0.691)	-0.35 (0.147)	0.06 (0.804)
Clay [%]	-0.12 (0.616)	-0.13 (0.596)	0.25 (0.296)	-0.12 (0.61)	-0.3 (0.217)
Total N [%]	0.12 (0.631)	-0.04 (0.881)	0.11 (0.656)	0.25 (0.306)	-0.12 (0.636)
Total C [%]	0.1 (0.683)	-0.06 (0.792)	0.08 (0.755)	0.36 (0.133)	-0.06 (0.809)
Total Organic C [%]	0.09 (0.71)	-0.09 (0.726)	0.04 (0.864)	0.33 (0.163)	-0.03 (0.9)
Organic C/Total N	-0.13 (0.595)	-0.02 (0.935)	-0.58 (0.009)	0.03 (0.911)	**0.63 (0.005)**
pH (upper limit)	-0.04 (0.888)	0.08 (0.756)	0.06 (0.799)	0.08 (0.754)	-0.07 (0.776)
AWC (1m)	0.02 (0.935)	-0.02 (0.949)	0.04 (0.855)	-0.57 (0.011)	0 (0.991)

Figure S1: Height loss per block. See Fig/ 1 for the spatial arrangement of the blocks.
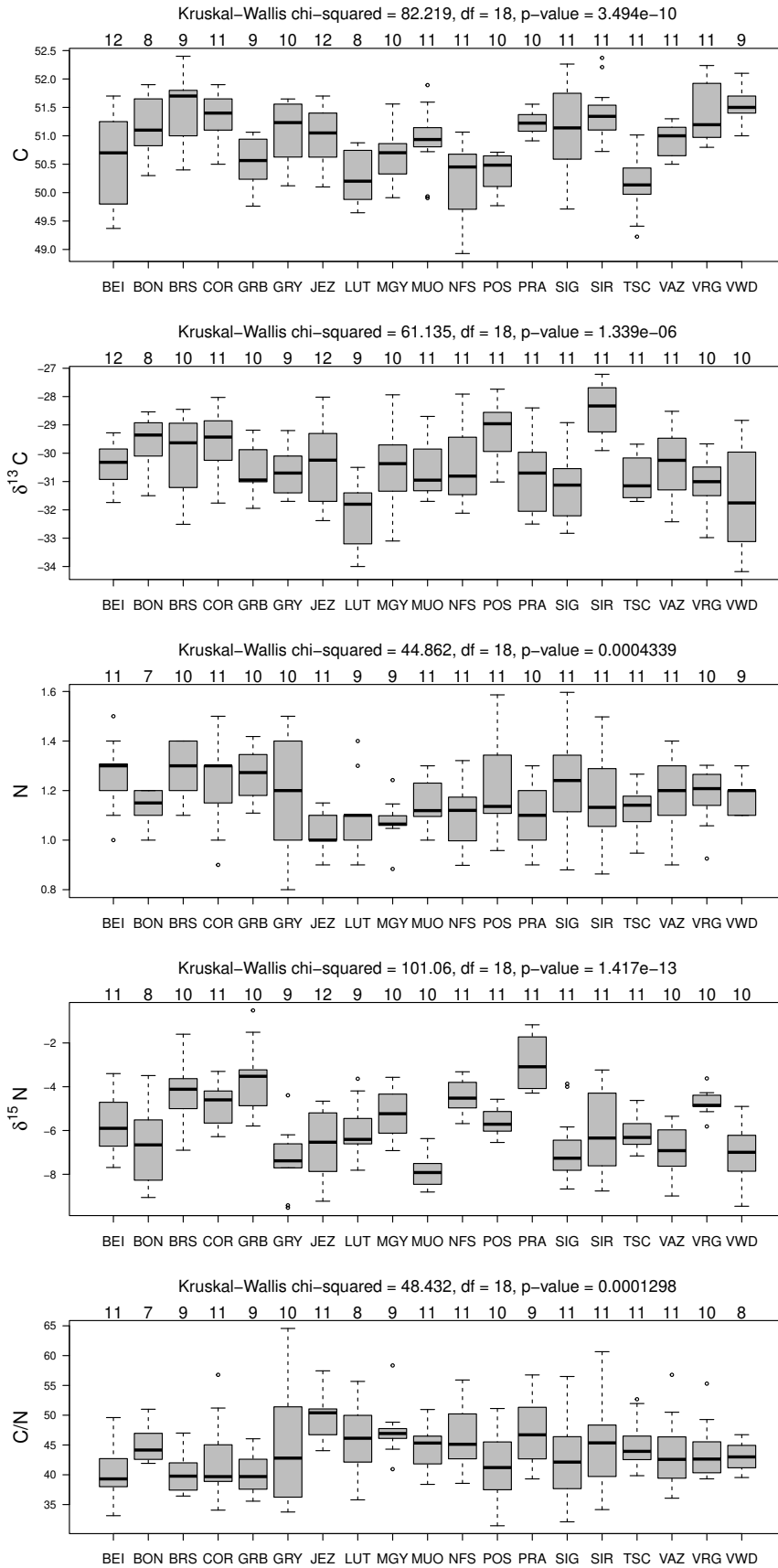
Figure S2: Traits measured in adult trees *in-situ* across the 19 populations and Kruskal-Wallis test of differences between population medians.
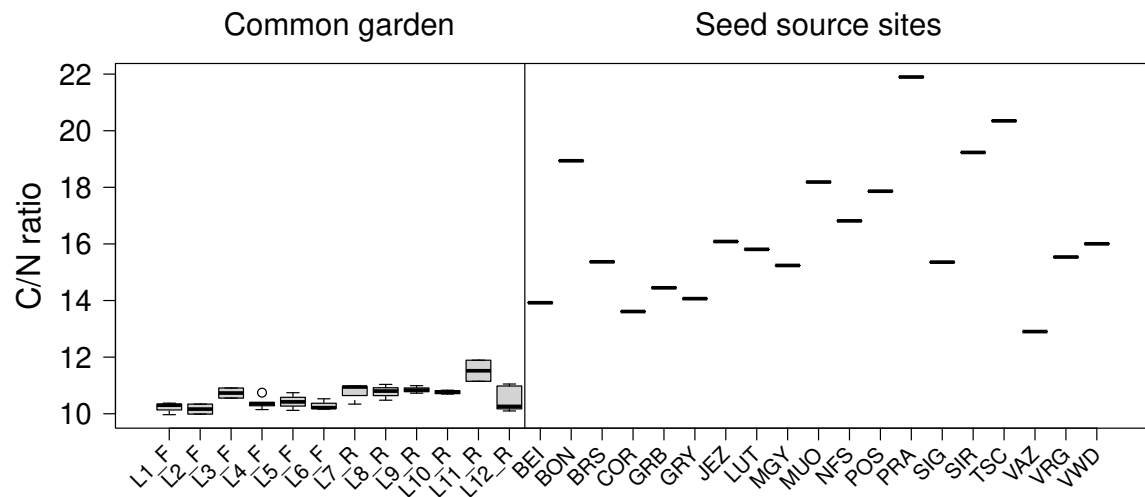
Figure S3: C/N ratio of the top mineral soil layer at the common garden site in Matzendorf and at the seed source populations. Boxplots at the common garden site represent variation of C/N across three to four replicate measures between layers 0 to 15 cm depth. A single measure was taken *in-situ*.

Figure S4: Coefficient of variation in C concentration and $\delta^{13}C$, and correlation between adult population medians (and seedling population effects) and environmental variables. Note that these are the strongest correlations that have unadjusted p-values < 0.05 (see Table S6), but none of them passed the correction for multiple testing.

Genetic correlations among growth and physiological traits

We fitted a multivariate version of equation 3 to estimate the additive genetic covariance between all pairs of seedling traits (COV_A) and the genetic correlations between traits as

$$r_g = \frac{COV_A(i,j)}{\sqrt{(V_A(i)V_A(j)}},$$

where i and j are indices for two different traits. Only traits measured in 2016 were compared. Significant genetic correlations were detected when the absolute value of the Z score was higher than two.

Due to the limited sample size, convergence was achieved only if we used population as a fixed and not a random effect, as opposed to the pooled model that was used to estimate Q_{ST}. Even with this model, 15 out of the 55 trait pairs did not reach convergence (Table S7). Among the other 40 trait pairs we were able to identify several significant additive genetic trait correlations between pairs of growth or physiological traits, as well as between a growth and a physiological trait. However, these estimates also have to be interpreted with caution because population differences for some traits may have created spurious correlations. In the below paragraph, we attempt to interpret some of the significant correlations.

Not surprisingly, we detected a strong genetically based character integration between Height and Diameter and between Height and Fresh weight (Table S7). Physiological traits were largely independent from one another with the exception of derived traits with their original traits (Starch vs NSC, C/N vs C, C/N vs N). Although Starch and Sugar were not derived from one another, the significant negative correlation between them could be partly due to the measurement method. We detected a strong positive genetic correlation between δ^{15}N and Starch (r_g=0.65, z-score=3.03). Although the heritability of δ^{15}N did not differ significantly from zero, our data revealed that seedlings from the same family that had a high Starch concentration also had a high δ^{15}N. We also detected a significant positive genetic correlation between δ^{13}C and C concentration, thus higher water use efficiency was genetically associated with higher bulk C concentration. Finally, several physiological traits were genetically correlated with growth traits. Needle Starch was positively correlated with Diameter, Sugar with all growth traits, though weakly. δ^{13}C was positively correlated with growth traits, needle C concentration had a negative genetic correlation with growth. δ^{15}N also showed a significant negative genetic character integration with Height and Fresh Weight, indicating that families that had a higher δ^{15}N grew less and/or had a lower biomass.

Table S7: Genetic correlations (r_g) between growth and physiological traits measured in 2016 and the z-scores from the model. Sugar, Starch, NSC, C, N are concentrations and expressed as %, and δ traits as ‰. nc indicates that the model did not converge to the maximum likelihood solution with ASReml. z-scores > 2 indicate a non-zero additive genetic covariance between traits.

Trait 1	Trait 2	r_g	z-score
δ^{15}N	δ^{13}C	−0.013	2.029
δ^{15}N	N	nc	nc
δ^{15}N	C	−0.013	2.029
δ^{15}N	C/N	−0.013	2.029
δ^{15}N	Sugar	0.081	2.150
δ^{15}N	Starch	0.655	3.032
δ^{15}N	NSC	0.523	2.481
δ^{15}N	Diameter	−0.013	2.029
δ^{15}N	Height	−0.800	3.470
δ^{15}N	Fresh weight	−0.726	3.610
δ^{13}C	N	0.355	1.084
δ^{13}C	C	0.331	2.557
δ^{13}C	C/N	0.111	0.727
δ^{13}C	Sugar	0.000	2.239
δ^{13}C	Starch	nc	nc
δ^{13}C	NSC	nc	nc
δ^{13}C	Diameter	0.430	3.580
δ^{13}C	Height	0.167	3.482
δ^{13}C	Fresh weight	0.521	3.624
N	C	−0.013	2.029
N	C/N	−0.943	0.739
N	Sugar	−0.204	1.213
N	Starch	nc	nc
N	NSC	nc	nc
N	Diameter	−0.013	2.029
N	Height	nc	nc
N	Fresh weight	−0.013	2.029
C	C/N	−0.482	0.852
C	Sugar	nc	nc
C	Starch	−0.541	1.290
C	NSC	−0.848	1.739
C	Diameter	−0.535	3.550
C	Height	−0.757	2.430
C	Fresh weight	−0.672	3.165
C/N	Sugar	−0.613	1.090
C/N	Starch	0.621	1.150
C/N	NSC	0.245	1.353
C/N	Diameter	nc	nc
C/N	Height	−0.178	2.105
C/N	Fresh weight	−0.945	2.456

Trait 1	Trait 2	r_g	z-score
Sugar	Starch	−0.391	2.430
Sugar	NSC	0.742	2.699
Sugar	Diameter	0.060	3.574
Sugar	Height	0.151	3.356
Sugar	Fresh weight	0.120	3.592
Starch	NSC	0.874	1.565
Starch	Diameter	0.280	3.575
Starch	Height	−0.078	3.205
Starch	Fresh weight	0.008	3.573
NSC	Diameter	0.259	3.568
NSC	Height	0.023	3.053
NSC	Fresh weight	0.089	3.542
Diameter	Height	0.944	2.746
Diameter	Fresh weight	nc	nc
Height	Fresh weight	0.956	3.429