Growth and quality of *Fagus sylvatica* saplings depend on seed source, site, and browsing intensity

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**Abstract.** Local climate and ungulate browsing are two major factors that affect tree regeneration and genetic adaptation in Central European forests. Owing to climate change and increasing ungulate numbers, the abiotic and biotic environments of trees are changing remarkably, making it necessary to investigate the separate and joint effects of seed source (i.e., location of tree population origin) and ungulate herbivory. We used a common garden experiment to study the growth and morphology of *Fagus sylvatica* saplings from 77 Swiss seed sources. The experiment was set up at two sites and included a clipping treatment (i.e., terminal shoot clipped at two intensities) applied before budburst to simulate winter ungulate browsing. We studied *F. sylvatica* sapling growth and morphology before and two years after clipping. Measured growth traits included sapling height, stem diameter, and biomass. Morphological traits included multi-stemming, stem and crown form, stem quality, and reaction to clipping. Seed source, test site, and simulated leader browsing were all important in determining the growth and quality of *F. sylvatica* saplings. The effects of seed source on growth and quality indicate that *F. sylvatica* possesses a large pool of diverse genotypes across Switzerland and thus has the potential to adapt to local conditions through gene flow. Growth and morphology differed significantly between the two test sites, indicating that local environments should be considered carefully when a new plantation is established. The effect of the single simulated browsing event disappeared over time for the growth traits, owing to growth compensation. However, sapling quality decreased after clipping, suggesting that browsing may lead to persistent quality losses in production forests. Neither the growth nor the morphological reaction after clipping depended on the effect of population, meaning that resilience to browsing was independent of seed source. Consequently, interactions with ungulate browsing do not have to be taken into account when selecting *F. sylvatica* populations for particular climatic and site conditions.

**Key words:** clipping experiment; European beech; *Fagus sylvatica*; genecology; herbivory; progeny test; provenance test; simulated browsing; tree regeneration; ungulate browsing.

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**INTRODUCTION**

Browsing by ungulates such as red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.), and chamois (*Rupicapra rupicapra* L.) has increased over the last decades in many parts of the world (Apollonio et al. 2010). Therefore, even tree species that are not among the most palatable species to ungulates now experience regular browsing. For example, the percentage of
European beech (Fagus sylvatica L.) saplings browsed by ungulates in southern Switzerland increased from 13% in 1993–1995 to 24% in 2009–2013 (Abegg et al. 2014, Kupferschmid et al. 2015).

Growth and morphology are key traits of forest trees. In particular, they determine (1) the period in which tree saplings are susceptible to browsing (Vacek et al. 2014), (2) the time span during which saplings are not effective in protecting against snow avalanches in winter because of complete snow coverage (Kupferschmid et al. 2006), (3) the time needed for wood production (rotation time), and (4) the quality of timber (Mitscherlich and Weise 1982). Consequently, fast- and straight-growing saplings are susceptible to ungulate browsing for a shorter period, reach tree heights and stem diameters to provide effective avalanche and rockfall protection earlier, and have a shorter rotation period than slow-growing saplings. In addition, saplings with a straight growth form provide timber of higher quality than saplings with a crooked growth form (e.g., forked, twisted, spiraled; see Fischer 2000). Thus, it is highly useful for forest managers to know the growth traits and morphological traits of sapling when selecting them as future timber trees. Three main factors are known to influence the growth and morphology of tree saplings: the genetic pre-conditions of populations (Mátyás 1996), abiotic site conditions such as climate and soil properties (Gould et al. 2012), and biotic site conditions such as ungulate browsing intensity (Gill 1992, Wallgren et al. 2014).

Due to long-term natural diversifying selection, autochthonous tree populations are often adapted to their local environments (Savolainen et al. 2007). These adaptations result in population differences that can be observed along environmental gradients in adaptive traits at the morphological, physiological, and phenological level (Alberto et al. 2013, Bussotti et al. 2015). For F. sylvatica, a previous genealogical study using the same experimental setup as in the present study demonstrated climate-driven differentiation among 77 Swiss populations (Frank et al. 2017a). In that dataset, the strongest population differentiation was found in vegetative bud phenology, that is, bud break and leaf senescence. While intra-specific differences in growth, phenology, leaf morphology, and physiology are well studied for F. sylvatica saplings (Peuke et al. 2002, Vitasse et al. 2009, 2013, Arend et al. 2016), little is known about the species’ intra-specific differences in sapling morphology. Dupré et al. (1986), for example, found differences in F. sylvatica sapling growth form among 35 populations. To our knowledge, however, nothing is known about population variation in F. sylvatica sapling resilience to ungulate browsing.

Site effects on tree growth are well known. Traditionally, multi-site planting experiments are used to study the growth potential of certain populations at different sites (Mátyás 1996). The closer the test trees are related, the more growth differences between sites can be attributed to differences in test site environments. Working with half-sibs, for example, Frank et al. (2017a) showed that F. sylvatica seedlings grew faster at a warmer and moister low-elevation planting site than at a colder and drier high-elevation planting site. Such contrasting phenotypes of genetically identical (or similar) trees at different sites are the result of phenotypic plasticity (Nicotra et al. 2010). Phenotypic plasticity has been documented, for example, in F. sylvatica radial growth (Eilmann et al. 2014), leaf anatomy (Stojnić et al. 2015), and seedling bud phenology (Vitasse et al. 2013, Frank et al. 2017a). Site conditions, in particular light regime and aboveground competition, have also been shown to influence the resilience of F. sylvatica seedlings to simulated summer browsing (Vandenbergh et al. 2008). For example, stressed F. sylvatica saplings growing with neighborhood competition in shade compensated better for biomass loss than (otherwise well-growing) saplings without competition in full sunlight (Vandenbergh et al. 2008).

Browsing not only negatively influences tree growth (Horsley et al. 2003), but also affects sapling morphology (Persson et al. 2005, Kupferschmid 2017). For example, Eiberle (1975, 1978) found a significantly reduced stem quality of F. sylvatica saplings after repeated leader shoot clipping. Likewise, Harmer (1999) found lower shoot counts in summer-clipped F. sylvatica saplings. However, in comparison with other tree species, little is known about F. sylvatica’s reaction to ungulate browsing (Kupferschmid 2017). In particular, the combined effects of seed source, site conditions, and ungulate browsing on the
growth and morphology of tree saplings are unclear, even though there is an urgent need to address such joint effects through adaptive forest management (Didion et al. 2011, Klopcić et al. 2017).

In this study, we focused on *F. sylvatica*, one of the most abundant tree species in Central Europe. This species is highly valued for the ecosystem services it provides, such as timber and fuel production, but also for contributing to rockfall protection and supporting the provision of clean drinking water. Under the influence of climate change, this species is expected to suffer at many sites in Central Europe (Gessler et al. 2007, Zimmermann et al. 2015), making it an important research subject with respect to sustainable forest management.

The aim of this study was to investigate if and how *F. sylvatica* sapling growth and morphology is influenced by (1) genetic differences among populations, that is, among saplings from different seed sources, (2) test site conditions (abiotic environment), (3) terminal shoot loss due to ungulate browsing (biotic environment), and (4) combined effects of (1–3). The outcome of this study will be useful for understanding *F. sylvatica* sapling growth and morphology in more detail. In addition, it will help refine forest managers’ criteria for selecting populations for plantations in regions with high ungulate browsing and for selecting future crop trees of good quality from *F. sylvatica* saplings.

**Materials and Methods**

**Plant material and experimental setup**

We used 77 autochthonous *F. sylvatica* populations from across Switzerland (Frank et al. 2017a). The area covered by the populations used extended to 197 × 264 km (Frank et al. 2017a). It represents the species’ range in Switzerland and a central part of the species’ distribution in Europe (Pluess et al. 2016). The seed sources covered large environmental gradients, for example, elevations from 338 to 1440 m a.s.l. Seeds were collected in fall 2011 from three maternal trees per seed source and were sown in winter (January 2012) into nursery beds at the Swiss Federal Research Institute WSL in Birmensdorf, Switzerland. Originally, 80 seed sources had been sampled, but the seeds from three locations did not germinate properly, resulting in a total of 77 populations used in this study. Seedlings of all three mother trees were at our disposal for 59 seed sources. Thirteen seed sources were represented by two mother trees and five seed sources by one mother tree (Pop. no. 225, 227, 239, 246, and 268). Throughout the paper, the term “population” refers to individuals whose seeds were collected at the same place of origin. The term “seed source” refers to the location of population origins.

After the seedlings had been cultivated for one year (for details, see Frank et al. 2017a), they were transferred as bare-root seedlings to the two test sites, Birmensdorf (47°21′44″ N, 8°27′22″ E, 550 m a.s.l., garden of WSL) and Matzendorf (47°19′35″ N, 7°36′42″ E, 1090 m a.s.l.) in spring 2013. The two sites represent diverse environments, with Birmensdorf being generally warmer and moister than Matzendorf (Frank et al. 2017a). The seedlings were planted in 16 plots per site (Appendix S1: Fig. S1a), with each plot containing one seedling from each mother tree, that is, three seedlings per population, randomly distributed within plots in six rows (Appendix S1: Fig. S1b). In total, the 32 plots at both sites contained 6628 live seedlings at beginning of the measurements in spring 2014 (Frank et al. 2017a).

**Simulated browsing treatment**

Before budburst in spring 2015, the three-year-old saplings were clipped to simulate a single winter browsing event by roe deer (light clipping) or by red deer (heavy clipping), resulting in three treatments. No clipping represented the control treatment. Light clipping included removal of the uppermost bud of all the terminal but no lateral shoots (Appendix S1: Fig. S1c). Heavy clipping included removal of the complete shoots formed in the previous year (2014), that is, the terminal shoots from the first and all additional flushes in 2014, and the complete removal of the uppermost lateral shoot (Appendix S1: Fig. S1c). Treatments were applied at the plot level (no and heavy clipping: 5 plots; light clipping: 6 plots) according to a random treatment assignment (Appendix S1: Fig. S1a). Clipping was performed using pruning shears (Type Felco 2; FELCO SA, Les Geneveyss-sur-Coffraneo, Switzerland).
**Sapling trait measurements**

For this study, growth and morphological traits of *F. sylvatica* saplings were assessed in 2014, before clipping, and in autumn 2015 and 2016, that is, one and two growing seasons after clipping (Table 1). Reaction type after clipping (ReactType) was used to describe whether new leader shoots originated from existing buds or were formed by flagging, that is, upward bending of existing lateral shoots (Kupferschmid 2017). The place of reaction (ReactPlace) was defined as the number of buds or twigs between the clipping location and the origin of the new terminal shoot.

In 2014, we assessed sapling quality directly using the crown classification of Ott et al. (2003), but combining Ott’s levels 1 (fine branches) and 2 (rough branches) to form the good quality class (representing silviculturally desirable trees; Appendix S1: Fig. S3). In 2016, we refined the quality assessment by judging stem form (StemForm16, Table 1) and crown form separately. Sapling crown form (CrownForm16) was classified using five levels, as done by Ott et al. (2003), except that level 2 differed from that of Ott et al. (2003) and from level 1 in that it had a more branched treetop (Fig. 1). We ultimately used the classes strictly monocorm (i.e., monocorm with clear apical dominance), branched monocorm (i.e., monocorm with a tendency of proleptic branching in the upper crown), steep branches, forked branches, and bushy form (Fischer 2000, Leonhardt and Wagner 2006). The combination of StemForm16 and CrownForm16 was then used to assign each sapling to one of four quality levels (Quality16, Fig. 1; analogous to the approach of Brodowski 2015). Further details of growth and morphological trait measurements are described in Appendix S1 timing in Appendix S1: Fig. S2.

In order to estimate sapling biomass, dry weight was measured for 50 saplings originating from two control plots at each site (100 saplings in total) that were harvested at the end of the experiment in February 2017. Each of these saplings was cut 2 cm above the soil surface, crushed, placed in a paper bag, oven-dried for 75 h (until mass constancy) at 70°C, and weighed to an accuracy of 1 mg.

**Data analysis**

We used the statistical computing environment R v3.3.3 for data analysis (R Core Team 2017).

**Biomass modeling.**—Sapling biomass (Biom), that is, sapling dry weight, was estimated as an allometric function of diameter and height. The linear regression model (Eq. 1; multiple $R^2$: 0.9727, p-value: <2.2e-16) was calibrated using data from the 100 harvested *F. sylvatica* saplings:

$$\log(\text{Biom}) = -5.639 \pm 0.205 + 1.956 \pm 0.121 \times \log(D) + 0.977 \pm 0.093 \times \log(H)$$

(1)

Biomass in 2014 (Biom14) and 2016 (Biom16) was then predicted for all saplings using their diameter and height measurements.

**Analysis of variance—basic models.**—Analysis of variance for the growth and morphological traits was performed using different R functions for the three different data types. For the continuous traits (Table 1), we applied a linear mixed-effects model using the R function lmer (package lme4; Bates et al. 2015). For the binary traits, we applied a generalized linear mixed-effects model and used the R function glmer (package lme4, binomial model, link = logit, optimizer = bobyqa). For the ordinal traits, we applied a cumulative link mixed model using the R function clmm (package ordinal; Christensen 2015).

Overall, we used the following mixed-effects model Eq. 2:

$$Y_{ijklm} = \mu + LT_{ij} + S_i + T(S)_{ij} + B(S)_{ik} + P_l + F(P)_{im} + T_j \times S_i + e_{ijklm}$$

(2)

where $Y_{ijkl}$ was the value of the $m$th family ($F$) from the $l$th population ($P$) in the $j$th block ($B$) under the $i$th treatment at the $j$th site ($S$), and $\mu$ was the overall mean. LT$_{ij}$ was included as a fixed effect to account for potential growth differences that already developed in the nursery. $S$ was the fixed effect of site; $T(S)$ was the fixed effect of clipping within the sites; $B(S)$, $P$, and $F$ ($P$) were the random effects of block-within-site, population, and family-within-population; and $T \times S$ was the fixed effect of the interaction between treatment and site. The models did not converge if the 16 plots per site were used as block in the mixed-effects models. To still account for differences between lower and upper parts of the site (at site Matzendorf), and outer and inner parts (at site Birmensdorf), we
Table 1. Description of the growth and morphological traits measured on *Fagus sylvatica* saplings before (2014) and after (2015 and 2016) simulated browsing.

| Traits            | Units/levels | Data type | TF | Year | Season | Description                                                                 |
|-------------------|--------------|-----------|----|------|--------|----------------------------------------------------------------------------|
| **Growth traits** |              |           |    |      |        |                                                                            |
| H14               | cm           | Continuous| Sqrt| 2014 | Fall   | Sapling height (vertical distance to the base of the uppermost terminal bud after growing season 2014) |
| HaT14             | cm           | Continuous| Sqrt| 2015 | Spring | Sapling height after growing season 2014, after clipping in spring 2015 |
| H15               | cm           | Continuous| Sqrt| 2015 | Fall   | Sapling height after growing season 2015                                |
| H16               | cm           | Continuous| Sqrt| 2016 | Fall   | Sapling height after growing season 2016                                |
| LTot13            | cm           | Continuous| Sqrt| 2013 | Spring | Total sapling length along the stem axis after growing season 2012; used as covariate for ANOVA |
| LTot15            | cm           | Continuous| Sqrt| 2015 | Fall   | Total sapling length along the stem axis after growing season 2015      |
| LTot16            | cm           | Continuous| Sqrt| 2016 | Fall   | Total sapling length along the stem axis after growing season 2016      |
| LLead14           | cm           | Continuous| Sqrt| 2014 | Fall   | Length of terminal shoot along the stem axis from growing season 2014   |
| LLead15           | cm           | Continuous| Sqrt| 2015 | Fall   | Length of terminal shoot along the stem axis from growing season 2015   |
| LLead16           | cm           | Continuous| Sqrt| 2016 | Fall   | Length of terminal shoot along the stem axis from growing season 2016   |
| SecFlush14        | 0, 1         | Binary    |     | 2014 | Fall   | Occurrence of second (and additional) flushes during growing season 2014 |
| SecFlush16        | 0, 1         | Binary    |     | 2016 | Fall   | Occurrence of second (and additional) flushes during growing season 2016 |
| LSecFlush14       | cm           | Continuous| Sqrt| 2014 | Fall   | Length of second and potential additional flushes in 2014               |
| LSecFlush16       | cm           | Continuous| Sqrt| 2016 | Fall   | Length of second and potential additional flushes in 2016               |
| RelGr14           | cm/cm        | Continuous| None| 2014 |        | Relative annual growth in 2014 = LLead14/H14                            |
| RelGr15           | cm/cm        | Continuous| None| 2015 |        | Relative annual growth in 2015 = LLead15/LTot15                         |
| RelGr16           | cm/cm        | Continuous| None| 2016 |        | Relative annual growth in 2016 = LLead16/LTot16                         |
| D14               | mm           | Continuous| Sqrt| 2014 | Fall   | Sapling stem diameter 2 cm above the ground after growing season 2014   |
| D15               | mm           | Continuous| Sqrt| 2015 | Fall   | Sapling stem diameter 2 cm above the ground after growing season 2015   |
| D16               | mm           | Continuous| Sqrt| 2016 | Fall   | Sapling stem diameter 2 cm above the ground after growing season 2016   |
| Biom14            | g            | Continuous| Log | 2014 |        | Sapling biomass after growing season 2014                               |
| Biom16            | g            | Continuous| Log | 2016 |        | Sapling biomass after growing season 2016                               |
| **Morphological traits** |        |           |    |      |        |                                                                            |
| ReactType         | 0, 1         | Binary    | None| 2015 | Fall   | Reaction type one season after clipping. 0: building new shoot from bud, 1: bending up existing lateral shoot |
| ReactPlace        | 0, 1         | Binary    | None| 2015 | Fall   | Reaction place one season after clipping. One or more buds between clipping place and new bud/twig |
| MultiStem14       | 1, 2, 3      | Ordinal   | None| 2014 | Fall   | Number of vertically growing stems in 2014 that reach 2/3 of terminal leader length, in three classes: 1, 2, >2 |
| MultiStem16       | 1, 2, 3      | Ordinal   | None| 2016 | Fall   | Number of vertically growing stems in 2016 that reach 2/3 of terminal leader length, in three classes: 1, 2, >2 |
| FormLead14        | 1, 2, 3, 4   | Ordinal   | None| 2014 | Fall   | Growth form of first flush on the 2014 terminal shoot. 1: vertical; 2: bent (<25° to <65°); 3: horizontal growth; 4: no shoot |
| FormSecFlush14    | 1, 2, 3, 4   | Ordinal   | None| 2014 | Fall   | Growth form of additional flushes on the 2014 terminal shoot. Same levels as for FormLead14 |
### Table 1. Continued.

| Traits          | Units/levels | Data type | TF      | Year | Season | Description                                                                 |
|-----------------|--------------|-----------|---------|------|--------|----------------------------------------------------------------------------|
| FormLat14       | 1, 2, 3, 4   | Ordinal   | None    | 2014 | Fall   | Average growth form of lateral shoots formed in 2012 and 2013. Same levels as for FormLead14 |
| FormProI14      | 1, 2, 3, 4   | Ordinal   | None    | 2014 | Fall   | Average growth form of proleptic shoots on the 2014 terminal shoot. Same levels as for FormLead14 |
| FormLead16      | 1, 2, 3, 4   | Ordinal   | None    | 2016 | Fall   | Growth form of the full 2016 terminal shoot. Same levels as for FormLead14 |
| Quality14       | 1, 2, 3, 4   | Ordinal   | None    | 2014 | Fall   | Quality in four classes adapted from the five classes presented by Ott et al. (2003) (Appendix S1: Fig. S3) |
| Quality16       | 1, 2, 3, 4   | Ordinal   | None    | 2016 | Fall   | Quality in four classes as a combination of StemForm16 and CrownForm16 (Fig. 1) |
| StemForm16      | 1, 2, 3      | Ordinal   | None    | 2016 | Fall   | Sapling stem form. 1: straight; 2: bent (deviation from vertical line 22.5–45°); 3: heavily bent (Fig. 1) |
| CrownForm16     | 1, 2, 3, 4, 5| Ordinal   | None    | 2016 | Fall   | Sapling crown form. Five levels (Fig. 1) |
| Dominance16     | 1, 2, 3      | Ordinal   | None    | 2016 | Fall   | Dominance of a sapling compared to its neighbors. 1: dominant; 2: intermediate; 3: suppressed |
| ApiDomOcc14     | 0, 1         | Binary    | None    | 2014 | Fall   | Occurrence of proleptic lateral buds (min. 0.5 cm) at uppermost part of 2014 terminal shoot |
| ApiDomOcc16     | 0, 1         | Binary    | None    | 2016 | Fall   | Occurrence of proleptic lateral buds (min. 0.5 cm) at uppermost part of 2016 terminal shoot |
| ApiDomNum16     | n            | Continuous| Log     | 2016 | Fall   | Number of meristems along the 2016 terminal shoot until proleptic sprouting |
| ApiDomRatio16   | mm/n         | Continuous| Log     | 2016 | Fall   | Ratio of terminal leader length to number of apical buds, that is, LLead16/ApiDomNum16 |

**Notes:** Transformation (TF) indicates the type of transformation applied to the trait for statistical analysis. Derived traits are given in italics.

**Fig. 1.** Scheme for the assessment of *Fagus sylvatica* sapling quality according to stem and crown form. Sapling quality was derived as four classes (Quality16) from StemForm16 (stem form classes 1–3) and CrownForm16 (crown form classes 1–5). White boxes represent very good quality; light gray, good quality; gray, bad quality; and dark gray, very bad quality.
summarized the 16 plots to 2 blocks per site for analysis of variance (Appendix S1: Fig. S1a). After square-root- or log-transformations were completed for all continuous traits except for RelGr (no transformation; Table 1), there were no violations of model assumptions for any trait.

To evaluate the effect of treatment, we included $T(S)$ and its interaction with $S$ only for the traits that were measured after the treatment was applied. A Tukey post hoc test was used to distinguish between the effects of the three treatment levels (R function glht, incl. Bonferroni correction of p-values, package multcomp; Hothorn et al. 2008).

We used parametric bootstrapping for the continuous traits to test for the significance of all factors in our mixed-effects model Eq. 2. This was done using the R function PBmodcomp with nsim = 1000 (package pbkrtest; Halekoh and Højsgaard 2014). The final p-values for the continuous traits were calculated as the average of three bootstrapping repetitions per trait. For the binary and ordinal traits, it was not possible to use parametric bootstrapping. Instead, we used likelihood ratio tests that compared the full model to the same model without the terms that should be tested (R function ANOVA). All p-values were corrected for multiple comparisons, package multcomp; Hothorn et al. 2008).

Population differentiation.—We used the variance components from the full mixed-effects model (Eq. 2) for population ($\sigma^2_p$) and family ($\sigma^2_{f|p}$) to calculate population differentiation ($Q_{\text{st}}$) as $\sigma^2_p / (\sigma^2_p + 2\sigma^2_{f|p})$ (Spitze 1993) with $\sigma^2_{f|p} = 3\sigma^2_{f|p}$ (Campbell 1979). $Q_{\text{st}}$ is based on the amount of population variation relative to the within-population additive genetic variation and represents the degree of population differentiation as a number between 0 and 1 (Spitze 1993).

Trait–environment relations.—We analyzed linear relationships between sapling phenotypes and seed source environments by Pearson correlations and simple linear models (lm(trait ~ environmental variable)), both based on the population random effects obtained from analyses of variance and a subset of site-specific environmental variables. The population random effects were extracted from the results of the mixed-effect models using the R function ranef (package lme4). These values represent best linear unbiased predictions of population means (Frank et al. 2017b). The environmental variables included temperature variables, such as mean annual temperature (MAT), and precipitation variables for the time period 1931–1960 that were approximated for each seed source (Frank et al. 2017b: Table A1). In addition, elevation was recorded at each seed source. To account for multiple comparisons, p-values for Pearson correlation coefficients were corrected after Bonferroni using $n = \text{number of environmental variables} \times \text{number of traits per group}$, that is, $n = 7 \times 21$ for the growth traits and $n = 7 \times 18$ for the morphological traits. We explored sapling phenotypes in relation to elevation at seed source for both study sites using box plots for each elevation class.

Submodels for testing relationships between morphology and growth after clipping.—We tested for relationships between morphological and growth traits after clipping. These submodels included the same factors as in Eq. 2, but excluding F(I), as well as an additional fixed factor for the morphological trait of interest. We tested (1) the effect of multi-stemming in 2016 (MultiStem16) on sapling height after clipping (H16) and (2) the effect of growth form before clipping (FormLead14) on terminal leader growth after clipping (LLead15 and LLead16).

RESULTS

Population differences

We found a significant effect of population ($p < 0.05$) for 12 out of 21 growth traits and 4 out of 18 morphological traits (Fig. 2). Population differentiation ($Q_{\text{st}}$) for the growth traits was between 0.07 (RelGr16) and 0.46 (RelGr15), with an average of 0.15 per trait (Fig. 2). For the morphological traits, $Q_{\text{st}}$ was generally higher than for the growth traits and ranged from 0.00 (for the traits for which population variance was zero) to 0.49 (FormLat14), with an average of 0.18 per trait. Overall, largest population differentiation ($Q_{\text{st}} > 0.3$) was found for RelGr15, FormLat14, FormLead16, Quality14, Quality16, and CrownForm16 (Fig. 2).

Correlations of population random effects with past temperature variables and with the elevation
at seed source were significant for the growth traits SecFlush14 ($r = 0.44$ with all temperature variables and $-0.43$ with elevation), LSecFlush16 ($r = 0.42$ with MAT), and RelGr15 ($r = -0.53$ to $-0.56$ with temperature variables and $0.5$ with elevation), and for the morphology traits StemForm16 ($r = 0.39-0.41$ with temperature variables and $r = -0.41$ with elevation; Appendix S1: Table S1). Further significant correlations were found for the morphology traits FormLead14 ($r = 0.45–0.47$ with temperature variables and $r = 0.44$ with elevation) and(ApiDomNum16 ($r = -0.4$ with MAT and MTSp and $r = 0.42$ with elevation; Appendix S1: Table S1). For the precipitation variables, only total winter precipitation (PRWi) was significantly negatively correlated with LSecFlush16 ($r = -0.42$) and positive with RelGr15 ($r = 0.44$; Appendix S1: Table S1).

Focusing further on MAT at seed sources, we found significant linear relationships with relative growth (RelGr) in 2014 (increasing growth with increasing temperature at seed source) and 2015 (increasing growth with decreasing temperature at seed source), but no linear relationship in 2016 (Fig. 3a–c). In addition, FormLead14, FormLead16, and StemForm16 were all positively related to MAT. This means that saplings belonging to populations from warmer environments (i.e., lower elevations) showed generally higher values for terminal leader growth form and stem form, that is, lower quality (Fig. 3d–f).

Site differences

We found significant differences between the two test sites for 12 out of 21 growth traits ($p < 0.05$; Table 2). For these traits, fixed effect estimates for the Matzendorf site were negative, meaning that growth was greater at the lower-elevation Birmensdorf site than at the higher-elevation Matzendorf site. A clear difference between the sites in sapling growth can be found, for example, in height and terminal shoot length (Fig. 4). Site differences for most growth traits increased over time: While the effect of site was not significant for most traits in 2014, it became significant in 2015 and/or 2016, and the fixed effect estimates increased over time for several traits (Table 2). Site differences were larger for sapling height, shoot growth, and biomass compared to stem diameter.

In addition, we found significant site effects for nine morphological traits (Table 2). The coefficient estimates of the Matzendorf site were positive for MultiStem16, FormLead14, FormSecFlush14, and StemForm16, indicating lower quality at the Matzendorf site than at the Birmensdorf site (Table 2). Exceptions were found for FormLat14 and FormProl14, for which growth form values were higher at the Birmensdorf site than at the Matzendorf site, and thus, these twigs grew more horizontally at the Birmensdorf site.
In 2014, there were more saplings with proleptic shoots on terminal shoots (ApiDomNum16) at the Matzendorf site than at the Birmensdorf site, but the opposite was true in 2016 (Table 2). Trait variation was generally greater at the Birmensdorf site than at the Matzendorf site (see standard deviations in Table 2 and Fig. 4). For most traits, saplings from low-elevation seed sources did not perform better at the low-elevation study site Birmensdorf relative to saplings from high-elevation seed sources, and saplings from high-elevation seed sources did not perform better at the high-elevation study site Matzendorf relative to saplings from the low-elevation seed sources; that is, there was no cross-effect (see, e.g., H15, Appendix S1: Fig. S4). In contrast, for LLead15 we found indications of such a cross-effect (Appendix S1: Fig. S4).

**Simulated browsing**

The fixed effect of clipping (i.e., simulated browsing) was significant for all traits measured after the treatment, with the exceptions of RelGr16, FormLead16, and Dominance16 (Table 3). Growth reactions after simulated browsing differed between clipping intensities: There was no difference between the light clipping treatment and the control for any growth trait (except LTot15), that is, saplings grew equally with or without light simulated browsing (Table 3 and Fig. 4). Fixed effect estimates for all growth traits (except RelGr15 and LLead15) were more negative for the heavy than for the light treatment, meaning that growth decreased with increasing clipping intensity (Table 3). A significant negative effect of heavy clipping was found, for example, for sapling height (Fig. 4a). In contrast, a significant positive effect of heavy clipping was found for RelGr15 (Fig. 4b). The fixed effect of clipping was significant for FormLead16 (Fig. 4c) and Dominance16 (Fig. 4d). For RelGr15, FormLead16, and Dominance16, there were no significant effects of clipping (Table 3). The fixed effect of clipping was significant for LLead15 (Fig. 4e) and RelGr15 (Fig. 4f). For LLead15, there was a significant positive effect of heavy clipping (Fig. 4e). For RelGr15, there was a significant negative effect of heavy clipping (Fig. 4f).
Table 2. Differences between sites (B, Birmensdorf; M, Matzendorf) for 21 growth traits and 18 morphological traits of *Fagus sylvatica* saplings.

| Trait                  | Birmensdorf | Matzendorf | FE  | pS  | Interpretation                                      |
|------------------------|-------------|------------|-----|-----|-----------------------------------------------------|
| **Growth**             |             |            |     |     |                                                     |
| H14                    | 61.8 (25.4) | 51.1 (16.3) | -0.59 | ns | No difference in sapling height                     |
| HaT14                  | 57.0 (24.6) | 47.3 (16.2) | -0.54 | *  | Greater height of trees in B than in M              |
| H15                    | 98.1 (33.1) | 72.7 (18.0) | -1.24 | *  | Greater height in B than in M                       |
| H16                    | 151.6 (51.9) | 105.0 (27.4) | -1.88 | *  | Greater height in B than in M                       |
| LTot15                 | 101.8 (35.7) | 75.9 (18.0) | -1.24 | *  | Greater total length of trees in B than in M        |
| LTot16                 | 151.7 (51.7) | 105.6 (27.3) | -1.86 | *  | Greater total length of trees in B than in M        |
| LLead14                | 29.2 (20.1) | 22.1 (12.2) | -0.52 | ns | No difference in terminal leader length             |
| LLead15                | 42.5 (15.9) | 24.0 (8.9)  | -1.55 | *  | Greater terminal leader length in B than in M       |
| LLead16                | 52.1 (24.5) | 32.2 (15.8) | -1.47 | *  | Greater terminal leader length in B than in M       |
| SecFlush14             | 91.3 [28.2] | 88.2 [32.3] | -0.29 | *** | More frequent 2nd flushes in B than in M            |
| LSecFlush14            | 21.7 (15.2) | 13.9 (9.0)  | -0.80 | ns | No difference in length of second flushes           |
| LSecFlush16            | 26.5 (18.1) | 18.3 (11.1) | -0.73 | *  | Greater length of 2nd flush in B than in M          |
| RelGr14                | 0.4 (0.2)   | 0.4 (0.1)   | -0.04 | ns | No difference in relative growth                    |
| RelGr15                | 0.4 (0.1)   | 0.3 (0.1)   | -0.10 | *  | Greater relative growth in B than in M              |
| RelGr16                | 0.3 (0.1)   | 0.3 (0.1)   | -0.04 | ns | No difference in relative growth                    |
| D14                    | 11.3 (2.8)  | 10.9 (2.3)  | -0.04 | ns | No difference in stem diameter                      |
| D15                    | 15.8 (3.8)  | 14.1 (2.8)  | -0.19 | ns | No difference in stem diameter                      |
| D16                    | 20.6 (5.9)  | 18.4 (3.7)  | -0.21 | *  | Greater stem diameter in B than in M                |
| Biom14                 | 27.9 (24.0) | 20.1 (13.7) | -0.18 | ns | No difference in modeled biomass                    |
| Biom16                 | 218.2 (180.3) | 110.9 (67.0) | -0.48 | *  | Greater modeled biomass in B than in M              |
| **Morphology**         |             |            |     |     |                                                     |
| ReactType              | 34.5 [47.5] | 33.7 [47.3] | -0.07 | ns | No difference in reaction type                      |
| ReactPlace             | 35.0 [47.7] | 29.6 [45.6] | -0.20 | ** | More trees with only one bud or a twig between clipping place and origin of new 2015 leader shoot in M than in B |
| MultiStem14            | 1.4 (0.7)   | 1.5 (0.8)   | 0.33 | ns | No difference in multi-stemming                    |
| MultiStem16            | 1.1 (0.4)   | 1.2 (0.5)   | 0.56 | *  | More multi-stemmed trees in M than in B             |
| FormLead14             | 1.8 (0.8)   | 2.0 (0.4)   | 0.95 | ** | More trees with bent growth form (= lower quality) of terminal shoot in M than in B |
| FormSecFlush14         | 1.7 (1)     | 1.8 (0.9)   | 0.31 | *  | More trees with bent growth form (= lower quality) of terminal 2nd flush shoot(s) in M than in B |
| FormLat14              | 3.0 (0.3)   | 2.9 (0.4)   | -0.74 | *  | More trees with bent growth form (= lower quality) of older lateral shoots in B than in M |
| FormProl14             | 3.6 (0.8)   | 2.6 (1)     | -2.26 | *** | More trees with bent growth form (= lower quality) of proleptic shoots in B than in M |
| FormLead16             | 1.1 (0.3)   | 1.1 (0.4)   | 0.36 | ns | More trees with bent growth (= lower quality) of terminal and 2nd flush shoots in M than in B |
| Quality14              | 2.4 (1.4)   |             |     |     | Data only for B                                    |
| Quality16              | 1.5 (0.9)   | 1.6 (0.9)   | 0.35 | ns | No difference in quality index                      |
| StemForm16             | 1.6 (0.7)   | 1.7 (0.7)   | 0.29 | *** | More trees with bent stem form (= lower quality) in M than in B |
| CrownForm16            | 1.9 (1)     | 2.1 (1)     | 0.31 | ns | More trees with awkward crown form (= lower quality) in M than in B |
| Dominance16            | 2.3 (0.7)   | 2.2 (0.6)   | -0.36 | ns | No difference in sapling dominance                  |
| ApiDomOcc14            | 21.4 [41.1] | 69.5 [46.1] | 2.33 | *** | More trees with proleptic shoots on terminal shoot in M than in B |
| ApiDomOcc16            | 96.2 [19.1] | 84.9 [35.8] | -1.46 | *** | More trees with proleptic shoots on terminal shoot in B than in M |
| ApiDomNum16            | 4.3 (2.3)   | 4.9 (2.5)   | 0.14 | ns | No difference in apical dominance                   |
| ApiDomRatio16          | 17.2 (15.9) | 10.2 (10.9) | -0.61 | ns | No difference in apical dominance ratio             |

Notes: For each trait, results include mean values ± standard deviation (SD) for continuous and ordinal traits (not transformed) or percentages ± SD for binary traits (italicized) per site, coefficients of the fixed effect estimated for site Matzendorf (FE), significances of the site effect (pS), and an interpretation of the effect. Trait codes, units, and descriptions are provided in Table 1.

***p < 0.001; **p < 0.01; *p < 0.05; ns = non-significant at $\alpha = 0.05$. 

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clipping on sapling growth was found one year after the treatment for RelGr15 (Table 3) and LLead15 (Fig. 4b). Several growth traits measured in 2016, such as LLead16, SecFlush16, RelGr16, and D16, did not differ significantly between clipping treatments (Table 3).

For the morphological traits, MultiStem16, Quality16, StemForm16, and CrownForm16 showed increasing fixed effect estimates for the light and heavy clipping treatment, that is, more multi-stemmed saplings and lower quality with increasing clipping intensity (Table 3). The percentage of sapling with very good quality in 2016 was highest in the control (no clipping) and lowest in the heavy clipping treatment (Fig. 5). The majority of trees retained good quality even after clipping. Heavily and lightly clipped saplings were more likely to become multi-stemmed if they were single-stemmed before the treatment, or to stay multi-stemmed if they were already multi-stemmed (Table 4).

In addition, we found relationships between morphology and growth after clipping. In 2016, for example, multi-stemmed saplings were able to compensate for shoot loss after clipping if they became single-stemmed but compensated to a lesser extent if they stayed multi-stemmed ($p < 0.001$ for the effect of binary MultiStem16 in the mixed-effects model for H16). Furthermore, saplings with a vertical growth form compensated better for shoot loss than saplings with a horizontal growth form. LLead15 and LLead16 of saplings that grew vertically before the clipping treatment (FormLead14) exceeded LLead15 and LLead16 of saplings that had a bent growth form before the clipping treatment ($p < 0.001$ for the effect of FormLead14 in the mixed-effects models for LLead15 and LLead16; Appendix S1: Fig. S5).

Saplings that were lightly clipped reacted mostly by forming a new shoot through elongation growth of an existing bud (81%, see ReactType in Table 3), but in about one-third of all cases this was not the uppermost bud (ReactPlace). In contrast, about half of the heavily clipped saplings reacted with upward bending of an existing twig (so-called “flagging”), and this reaction usually occurred in the uppermost bud of these saplings (Table 3). Saplings with vertically growing lateral twigs reacted more often with flagging than saplings with bent lateral shoots at the Birmensdorf site, but not at the Matzendorf site.

**Combined effects of seed source, site, and simulated browsing**

We found combined effects, that is, interactions between treatment and site ($T \times S$). This interaction was significant for all 14 growth traits measured after the browsing treatment in 2015, except for D15 (Appendix S1: Table S2). In contrast, of the 11 morphological traits measured, $T \times S$ was significant for only StemForm16, ApiDomOcc16, and ApiDomRatio16 (Appendix S1: Table S2).

The interaction between population and treatment ($P \times T$) was not significant for any of the 25 traits, and the interaction between population and site ($P \times S$) was only significant for 5 of the 25 traits (LLead15, LLead16, RelGr15, RelGr16, and D14; data not shown). In addition, including $P \times S$ did not allow models to converge properly, which was also the case for the interaction between block and population ($B(S) \times P$). Consequently, these three interactions were not retained in the final mixed-effects models (see Eq. 2 in section *Analysis of variance—basic models*).

**DISCUSSION**

**Population differences**

We expected to find genetic differences among populations in potentially adaptive sapling traits, such as growth and morphology, for *F. sylvatica* at different sites and under different simulated browsing regimes. In addition, we expected these differences to be related to environments at seed source because of past natural diversifying selection (Alberto et al. 2013). Indeed, population differentiation values ($Q_a$) and trait–environment correlations indicated climate-driven population variation. $Q_a$ values and trait–environment correlations were within the range of those found for *F. sylvatica* seedling growth and phenology in a previous study by Frank et al. (2017a). The slightly higher $Q_a$ values found in the present study for sapling height and diameter in 2014 (traits analyzed in both studies) can be attributed to differences in data preparation (with vs. without outlier analysis), block arrangement (2 blocks summarizing 16 plots), mortality ($N = 5786$ saplings were still alive in 2016 vs. $N = 6356$ for H14...
in 2014), and mixed-model structure. Overall, our results appear to be very stable and not highly sensitive to analytical details.

Interestingly, we found higher $Q_{st}$ in *F. sylvatica* sapling morphology than in its growth (this study) or phenology (Frank et al. 2017a). This indicates higher genetic differentiation between populations for morphological traits than for growth and phenological traits. Considering resource allocation and architectural constraints, it is reasonable to assume that morphological traits are particularly important for juvenile *F. sylvatica* trees to withstand the juvenile stage. Consequently, these traits may be under stronger selection than growth and phenological traits, leading to higher population differentiation in *F. sylvatica* sapling morphology. In particular, the fact that *Fagus* primarily builds plagiotropic shoots that become secondarily orthotropic by bending upward (architectural model by Troll; Bartels 1993) leads to large differences in the structure of individual trees (Millet et al. 1998) and, thus, to large variation in morphological traits.

The differentiation patterns of several traits in this study changed over time, that is, increased (e.g., for second flush length) or decreased (e.g., for leader shoot length) between 2014 and 2016. The lack of population × clipping treatment interactive effects indicates that the simulated browsing treatment did not drive these changes in $Q_{st}$ over time. Instead, the particularly warm and dry weather in summer 2015 (Meteo-Schweiz 2016) likely caused different growing conditions among years. A particularly strong effect of the 2015 growing conditions can be found in relative growth (RelGr15), which showed a much higher $Q_{st}$ value (Fig. 2) and a linear relationship with MAT that was the inverse of that found for RelGr14 and RelGr16 (Fig. 3). The dry and hot weather in 2015 likely caused lower growth variation within populations, and, therefore, higher variation among populations (Appendix S1: Figs. S6, S7). However, the inverse trait–environment pattern was probably caused by saplings from cold seed.

Fig. 4. Sapling height and terminal shoot length of *Fagus sylvatica* saplings at the two planting sites Birmensdorf (a, c) and Matzendorf (b, d) in relation to simulated browsing treatment (no, light, and heavy clipping). Measurements took place before the treatment was applied in fall 2014 (white boxes), directly after the treatment in spring 2015 (light gray boxes; only for sapling height), one vegetation period after the treatment in fall 2015 (gray boxes), and two vegetation periods after the treatment in fall 2016 (dark gray boxes). Box plots were drawn using the ggplot2 package in R. Thick vertical line: median; bottom and top of each box: first and third quartiles; whiskers: quartiles ± 1.5 × interquartile range (IQR); circles: outliers, that is, more extreme values exceeding 1.5 × IQR.
sources that grew better than saplings from warmer seed sources during 2015 (Fig. 3). Consequently, saplings from colder seed sources might profit more from warmer and drier conditions than the offspring of trees from warmer seed sources. A second explanation for the observed changes in differentiation patterns over time could be the effect of age. As trees mature,
different traits become important, which may alter differentiation patterns (White and Ching 1985, Howe et al. 2006). However, the time span of this study was likely too short to cause relevant age effects, even if the saplings roughly doubled in size during the experimental period.

Are the population differences shown in this study sufficient to guide seed source selection, for example, for establishing new plantations? The notably high population differentiation values show that the choice of population is indeed important, in particular for sapling quality, since we found highest $Q_{st}$ values for these traits. Seed source selection seems to be more important for the less favorable growing site Matzendorf, as population differentiation at this site had previously been shown to be stronger than at the more favorable growing site Birmensdorf (Frank et al. 2017a). Yet, as this study assessed overall population differentiation using two single test sites, but not single population differences using multiple reciprocal test sites, we cannot suggest to use specific populations for plantations at specific sites. Further studies should, therefore, be directed to compare a subset of $F. sylvatica$ populations at multiple test sites.

**Site differences**

Our results showed that the planting environment had an effect on the growth and quality of $F. sylvatica$ saplings. They grew significantly more and were of better quality at the Birmensdorf than at the Matzendorf site. Growing conditions were more favorable and less extreme at the lower-elevation Birmensdorf site, with deeper soil, warmer temperatures, and longer growing seasons (shown in detail by Frank et al. 2017a). These conditions seem to positively affect not only $F. sylvatica$ sapling growth (found in this study and by Frank et al. 2017a), but also morphology and quality (found in this study), which were generally worse at the less favorable study site Matzendorf. Height and diameter of $F. sylvatica$ saplings have also been found to be significantly affected by the microsite level, where patches with high-temperature fluctuation featured high mortality and represented the least suitable environments (Gömöry et al. 2011). According to Dupré et al. (1986), the effect of site can be strong enough to mask population variability, in particular on poor soils and at heterogeneous sites.

The differences found in $F. sylvatica$ sapling growth and morphology between the two study sites can be interpreted as a high potential for

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Fig. 5. Numbers of *Fagus sylvatica* saplings at Birmensdorf (a) and Matzendorf (b) showing very good quality (light gray), good quality (gray), bad quality (dark gray), and very bad quality (very dark gray) for different intensities of simulated browsing (no, light, and heavy clipping). Percentages per treatment and site are shown. Quality definitions are provided in Fig. 1. Note that sapling numbers per treatment differ because the 16 plots at each site could not be equally assigned to the three treatments, resulting in six plots for light clipping and five plots each for no and heavy clipping.
phenotypic plasticity of this species; that is, a high capacity of similar genotypes to show different phenotypes in different environments such as different growing sites (Vitasse et al. 2013, Stojnić et al. 2015). Phenotypic plasticity counteracts population differentiation, yet both factors can usually be observed in forest trees (Nicotra et al. 2010). Our results confirm the importance of considering the effect of planting site as an additional factor influencing F. sylvatica sapling growth and quality, particularly when establishing a new plantation, for example, after wind fall (Kramer et al. 2014).

**Simulated browsing treatments**

It is well known that biotic effects, such as single (simulated) browsing events, have an impact on the growth and morphology of many tree species (Gill 1992, Hester et al. 2006). Furthermore, the direct impact of browsing, that is, the growth reduction due to browsing, typically increases with browsing intensity (Wallgren et al. 2014, Kupferschmid 2017). However, browsing can stimulate certain deciduous tree species to produce more aboveground biomass (Persson et al. 2007) and larger height increments (Danell et al. 1994). For F. sylvatica, a lower tolerance to browsing compared to other deciduous tree species has been described (Kupferschmid 2017). Still, it is suited as a hedge plant because its branching is stimulated by cutting (Pfisterer 1999).

Therefore, we expected the F. sylvatica saplings studied here to show a plastic growth reaction upon simulated browsing and to show partial height compensation, that is, no reduction in height growth after light clipping. This was true for most growth traits, in that the one-time loss of terminal buds was compensated by increased sapling growth during the year after clipping. Consequently, light single browsing events in winter are unlikely to stunt F. sylvatica sapling growth. This might be the reason why ungulate browsing had a minor impact on F. sylvatica growth in several earlier studies (van Hees et al. 1996, Schulze et al. 2014).

Upon heavy simulated browsing, we even found overcompensation in two growth traits, that is, greater relative growth and longer terminal leader length, one season after heavy clipping (RelGr15 and LLead15). For most other growth traits, however, the heavy simulated browsing treatment caused significant growth reduction, in particular in height and total length of the saplings (Table 3). Under a repeated heavy browsing treatment, F. sylvatica saplings have been shown to decrease in height (Eiberle 1978). Likewise, in nature, repeated heavy browsing may result in saplings half the height of unbrowsed ones, as shown in a comparison of unfenced and fenced sites (Olesen and Madsen 2008). The negative effect of the single heavy browsing event on F. sylvatica sapling growth shown in this study may not persist in the long term, as it was no longer significant in four out of eight growth traits two seasons after the clipping treatment (Table 3).

As cutting can stimulate the branching of F. sylvatica (Pfisterer 1999), we expected the saplings to become bushy after leader shoot loss (like Pinus sylvestris and Betula pubescens/pendula; Persson et al. 2005) and, thus, sapling quality to decrease after simulated browsing. In fact, most morphological traits indicated reduced quality after the single clipping treatment (Table 3). For multi-stemming (MultiStem), quality (Quality), and crown form (CrownForm), even the light

Table 4. Percentages of Fagus sylvatica saplings per clipping treatment that changed in number of stems after clipping.

| Change in number of stems | Total | Birmensdorf | Matzendorf |
|---------------------------|-------|-------------|------------|
|                           | No    | Light | Heavy  | No    | Light | Heavy | No    | Light | Heavy |
| Remained single-stemmed   | 63.6  | 60.2  | 54.1   | 69.3  | 64.7  | 58.9  | 57.8  | 55.5  | 49.5  |
| Became multi-stemmed      | 7.9   | 9.8   | 13.6   | 6.9   | 7.6   | 10.8  | 9.0   | 12.0  | 16.3  |
| Remained multi-stemmed    | 4.5   | 4.7   | 6.2    | 2.1   | 3.6   | 4.9   | 7.0   | 5.8   | 7.5   |
| Became single-stemmed     | 24.0  | 25.4  | 26.1   | 21.8  | 24.1  | 25.3  | 26.3  | 26.7  | 26.7  |

**Note:** Percentages were derived for all saplings at both sites (Total) and separately for the saplings at each planting site (Birmensdorf, Matzendorf).
clipping treatment was sufficient to impair sapling quality. However, most lightly clipped saplings reacted to leader bud removal by forming a new shoot from one of the uppermost distal, regularly formed lateral buds. Thus, stem forms of lightly clipped saplings were significantly less affected than those of heavily clipped saplings. Heavy browsing that affects several but not all branches (as our heavy clipping treatment) often leads to twigs bending upwards (flagging) and thus to multi-stemming. Consequently, ungulate browsing of saplings represents an important threat to commercial *F. sylvatica* timber production, for which straight, single-stemmed high-quality trees are key.

**Combined effects of seed source, site, and simulated browsing**

Somewhat surprisingly, we found that neither the growth nor the morphological reactions of *F. sylvatica* saplings to clipping depended on seed source, as there was no interaction between population and clipping treatment. On the one hand, we found higher *Qst* values in *F. sylvatica* sapling morphological traits than in its growth traits. On the other hand, saplings with vertical growth compensated for terminal shoot loss better than saplings with horizontal growth, and saplings with multiple stems compensated worse than saplings with single stems. These results indicate that the ability to compensate height loss after browsing depended on the growth form and shape of the saplings (quality). Thus, morphology was important for determining the resilience to browsing.

Nonetheless, population differences for most traits were maintained at similar levels after browsing (see, e.g., H and RelGr in Appendix S1: Figs. S6, S7). This finding is in line with results for the offspring of Scots pine (*P. sylvestris*) families that showed significant differences in morphological growth traits regardless of browsing treatments (O’Reilly-Wapstra et al. 2014). We conclude that population and browsing effects on sapling growth and morphology can be treated as two independent but probably additive factors.

Theoretically, the lack of population-specific reaction after browsing might be a consequence of planting shock after transplanting the saplings to the two study sites, as they first had to build new roots. Consequently, they may not have been able to show their full growth potential (von Wuehlisch 2004). The saplings of this study, however, were growing for two full years at the two study sites before being exposed to simulated browsing. In addition, 8 out of 14 traits clearly differed between populations before clipping (e.g., H14, D14, and FormLead14, see Fig. 2). Many of these population differences may have vanished due to the stress induced by our simulated winter browsing.

Virtually all response patterns to browsing in our study were site-specific, as we found significant interactions between site and clipping treatment (*T × S*). This result has implications not only for climatic differences between sites (this study), but also for differences within sites, for example, differences in shading (Harmer 1999) and/or neighborhood vegetation (Vandenberghe et al. 2008). This finding is not surprising, as the vigor or stress status of trees appears to be crucial in determining the recovery pattern after browsing (Kupferschmid 2017).

**Conclusions**

Population differences indicate that a large pool of genetically diverse populations is available across Switzerland. Therefore, there is potential for adaptation processes through gene flow. Site differences indicate that the abiotic environment of a planting site should be considered carefully when establishing a new plantation, such as after wind fall, forest fires, or for assisted migration. *Fagus sylvatica* sapling growth appears to be resilient to a single browsing event, owing to the species’ high level of phenotypic plasticity. Nevertheless, the negative effect of simulated browsing on sapling quality poses a risk to *F. sylvatica* production forests because timber quality traits directly influence forest profitability. Seed source, planting site, and leader browsing are all important in determining the growth and morphology of *F. sylvatica* saplings. However, the reaction after browsing does not depend on population, so browsing resilience seems to be independent of seed source. Therefore, commercial *F. sylvatica* production can be optimized for growth and quality without considering browsing susceptibility.
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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2580/full