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Competitive ability of natural Douglas fir regeneration in central European close-to-nature forests

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ABSTRACT

Douglas fir (*Pseudotsuga menziesii*) has regenerated naturally in European forests since the middle of the 20th century. Some cases of an invasive character of the species have been reported under specific site conditions, but systematic data on the extent of natural regeneration and spread of Douglas fir across different forest communities are largely lacking. Due to its potential tolerance to increasing summer droughts, Douglas fir has been suggested as a sustainable future tree species for Central European forests. In this study, we investigated natural regeneration of Douglas fir in comparison to native tree species in 39 forest stands in Switzerland belonging to different forest communities. We analyzed the regeneration success of Douglas fir, Norway spruce (*Picea abies*), silver fir (*Abies alba*), and European beech (*Fagus sylvatica*) with respect to ecological site conditions. The proportion of Douglas fir seedlings (<130 cm height) was <5% in the majority of stands; but in four stands, Douglas fir was the most abundant species among seedlings. In most other stands, Norway spruce (occurring in 37 stands/dominant in 10 stands), silver fir (38/2 stands) and beech seedlings (35/10 stands) were more abundant than Douglas fir seedlings. Saplings (≥130 cm height but <12 cm diameter at breast height) of Douglas fir were observed in five stands with proportions between 10% and 23% and in eight stands with proportions of <10%, in particular in stands with a high proportion of Douglas fir seed trees. Beech saplings occurred in 28 stands and were most abundant in eleven stands. Saplings of silver fir (24/3 stands) and Norway spruce (19/6 stands) were less frequent. The abundance of Douglas fir seedlings correlated positively with the proximity to seed trees and light transmission of the canopy, but negatively with understory vegetation cover and litter abundance. Ungulate browsing did not significantly affect the regeneration of any tree species in the study stands. On the Central Plateau, Douglas fir was mainly planted in productive beech forest communities where it is strongly limited due to its low competitiveness compared to beech and other fast-growing deciduous tree species. On dry and less productive sites, where the canopy is not closed, Douglas fir is able to establish successfully. On such sites, a close monitoring of Douglas fir regeneration and the potential implementation of control measures is recommended.

1. Introduction

Coast Douglas fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) has been grown in Europe since the end of the 19th century due to its growth performance and wood properties (Hermann and Lavender, 1990; Spellmann et al., 2015). In Switzerland, Douglas fir is the second most abundant alien tree species after black locust (*Robinia pseudoacacia* L.) with an average proportion of 0.18% of stems per hectare (Brändli et al., 2020). It has most frequently been planted in close-to-nature beech and silver fir-beech forest communities at lower elevations on the Central Plateau and in the Jura (Bürgi and Diez, 1986; Bégin, 1992). In some locations, Douglas fir has also been planted as protective forest in montane conifer communities. Commonly, Douglas fir grows in mixture with other tree species and, occasionally, it forms larger groups or even stands of a few hectares. In Germany and France, the average proportion of Douglas fir stems per hectare is 10 to 15 times higher than in Switzerland because the species is of relatively high economic importance in these countries and has also been planted in monocultures, particularly in France (van Loo et al., 2019; Pötzelsberger et al., 2020b; Bindewald et al., 2021). Douglas fir has been appreciated by European foresters because of its productivity and wood quality for decades. In light of climate change, Norway spruce (*Picea abies*) is

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currently on the decline in Central European forests due to its drought sensitivity, which is further amplified by its susceptibility to bark beetle attacks (Temperli et al., 2013; Seidl et al., 2016; Schuldt et al., 2020). For this reason, there is increasing interest in Douglas fir and also silver fir (*Abies alba* Mill.) as potential replacement species that better cope with summer drought, making them potentially sustainable under future climate change (Lévesque et al., 2014; Vitali et al., 2017). While several studies compared the growth of adult trees of these potential alternative species, less attention has been paid to natural regeneration, which is crucial for establishing sustainable forests.

Douglas fir has regenerated naturally in Europe since the middle of the 20th century (e.g., OECD, 2008; Schmid et al., 2014; van Loo et al., 2019). By that time Douglas fir, introduced at the end of the 19th century, had reached an age, at which it produced abundant numbers of seeds (Rohmeder, 1972; Annen, 1998). Therefore, the species may eventually extend its range and increase its abundance in European forests (Bindewald et al., 2021). The spread of an introduced non-native species combined with negative effects on biodiversity is considered as invasion (Nehring et al., 2013; Schwarz et al., 2016), which is a major cause of global biodiversity loss (Rejmanek and Richardson, 1996; Schmid et al., 2014). In several reviews, Douglas fir was reported to have fewer negative ecological impacts on European forest ecosystems than other introduced species such as black locust (Schmid et al., 2014; Vor et al., 2015; Brang et al., 2016; Pötzelsberger et al., 2020a; Wohlgemuth et al., 2021). Herbaceous understory vegetation in Douglas fir stands shows a similar or even greater number of species than in native forest stands and is generally more affected by silvicultural interventions than by tree species composition (Augusto et al., 2003; Budde, 2006). Furthermore, cultivation of Douglas fir has similar effects on soil chemistry as native tree species (Schmid et al., 2014; Wohlgemuth et al., 2021). However, pure Douglas fir stands provide less favorable habitats for many animal and fungal species in comparison to pure and mixed native forest stands (Wohlgemuth et al., 2021).

Whether natural regeneration of Douglas fir will lead to uncontrolled spread into European forests has been debated among conservationists, foresters and scientists for some time (Richardson and Rejmánek, 2004; Schmid et al., 2014), e.g. in the European-wide COST Action NNEXT ('Non-native Tree Species for European Forests', Spiecker et al., 2019). Field surveys in the Black Forest, Germany, showed that Douglas fir successfully regenerates on dry, acidic and nutrient-poor forest sites where it might become the dominant tree species (Knoerzer, 1999). Although such sites are not frequent in the Black Forest, this finding fueled conservation debates because it demonstrated that – under specific environmental conditions – Douglas fir has the potential to outcompete native species (Höltermann et al., 2008). In Germany, Douglas fir has therefore been classified as invasive by the Federal Agency for Nature Conservation (Nehring et al., 2013). In neighboring Switzerland, Douglas fir is currently not listed as an invasive species (Schwarz et al., 2016) and guidelines generally accept an admixture of Douglas fir in common forest communities (Wohlgemuth et al., 2021). A fundamental problem in the discussion and subsequent assessments of invasiveness is that systematic data on the extent of natural regeneration and therefore the spread of Douglas fir are largely lacking. For Germany, analyses of inventory data revealed that natural Douglas fir regeneration occurred in 1.7% of the survey plots of the national forest inventory and on 0.3% of the area of forest habitats of high conservation value in the German state of Baden-Württemberg (Bindewald et al., 2021).

Bindewald and Michiels (2018) found that Douglas fir regeneration was only weakly affected by browsing. In contrast, the successful establishment of several native tree species, such as silver fir, can be constrained by high browsing pressure from wild ungulates (Kupferschmid et al., 2013; Kupferschmid et al., 2014). Light availability and vegetation cover are other important drivers of tree regeneration under canopy (Lieffers et al., 1999; Scherrer et al., 2021). In comparison with wide-spread European beech (*Fagus sylvatica* L.), silver fir, and sycamore maple (*Acer pseudoplatanus* L.), Douglas fir is clearly less shade tolerant (Niinemets and Valladares, 2006). Besides direct competition, also indirect effects of understory vegetation, such as the promotion of post-dispersal predation by creating preferred microhabitats and foraging areas for seed predators and herbivores, play an important role in driving natural tree regeneration in general (Royo and Carson, 2008) and also particularly in Douglas fir recruitment (Caccia and Ballare, 1998). Moreover, management practices such as thinning, clearing or grazing have been shown to facilitate natural regeneration of Douglas fir in plantations in Northern Europe (Jonášová et al., 2006) as well as in close-to-nature Mediterranean montane forests (Broncano et al., 2005). However, such studies on drivers and mechanisms of natural Douglas fir regeneration in European Forests are still scarce.

This study presents one of the first systematic assessments of the extent of natural Douglas fir regeneration in Central Europe across different forest communities. Specifically, we investigated the presence of Douglas fir seedlings and saplings and their competitors in the natural regeneration in 39 close-to-nature forest stands with varying abundance of seed producing trees. Based on multiple ecological factors assessed in the field, we analyzed potential driving factors of regeneration. Specifically, we asked the following questions: (1) How frequently and how abundantly does Douglas fir naturally regenerate in comparison with Norway spruce, silver fir, beech and other tree species? (2) To which extent do ecological factors, such as local climate, seed source, litter, soil conditions and the presence of competing vegetation, promote or limit natural regeneration of Douglas fir in comparison with Norway spruce, silver fir, beech and other species? (3) To which extent does forest community predict Douglas fir regeneration? (4) To which extent does browsing affect the regeneration of Douglas fir in comparison to Norway spruce, silver fir and beech?

2. Materials and methods

2.1. Stand selection and characterization

We based this study on a comprehensive inventory of exotic tree species plantations in Switzerland listing 1026 stands, where Douglas fir was planted mostly in mixture with native broadleaved or coniferous species (Fig. 1; Bürgi and Diez, 1986). From this inventory, all 65 plantations were selected that contained at least ten Douglas fir trees with a minimum age of 55 years at the time of the inventory because this is the maximum age for them to reach maturity in stands (Annen, 1998). Thus, in theory, they should have repeatedly produced seed to allow the species to establish naturally. These 65 stands were visited for a first assessment of Douglas fir regeneration in 2015, when they had reached an age of 85–130 years (Hafner and Wohlgemuth, 2016). In this study that aims at comparing the regeneration of Douglas fir with common native tree species, only stands with Douglas fir seedlings and/or saplings were considered. To prevent spatial autocorrelation, the sample was reduced to one stand per 10 km × 10 km grid cell using random selection, which resulted in a final sample of 39 stands (Frei et al., 2021).

The 39 stands covered a wide climatic range with annual mean temperatures between 5.3 °C and 10.2 °C and annual precipitation sums between about 1000 mm and 2000 mm (Table S1). According to the Swiss habitat classification TypoCH, which mostly corresponds with the level of phytosociological alliances (Delarze et al., 2015), 23 stands were classified as submontane beech forests (*Galio-* and *Luzulo-Fagenion*), nine stands as montane beech forests (*Lonicero-Fagenion*), and five stands as upper montane silver fir-beech forests (*Abieti-Fagenion*). Two other stands were assigned to mountain conifer forests (one *Ononido-Pinion* and one *Vaccinio-Piceion*; Table S1).

2.2. Field survey

Each stand was delineated by the outermost Douglas fir trees present. The points of a 25 m × 25 m grid based on the national LV95 coordinate system located within each stand were numbered and six to eight of the

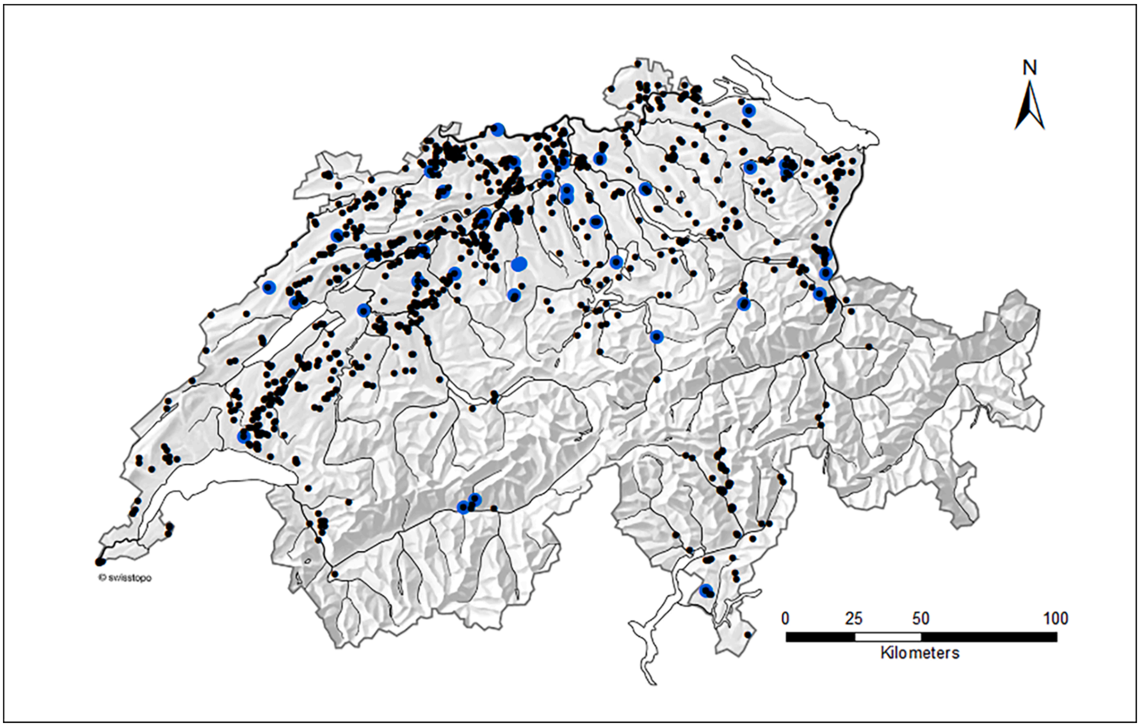

Fig. 1. Map of Switzerland showing the locations of the 1026 forest stands, where Douglas fir was planted mostly in mixture with native broadleaved or coniferous species (small black dots; Bürgi and Diez, 1986) and the 39 stands with seed producing Douglas fir, in which natural regeneration was assessed (large blue dots). For stand names refer to Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

grid points were randomly chosen as centers of 50 m^2 circular survey plots ($r = 4$ m), resulting in a total of 238 sampling plots. From July to November 2017, standardized regeneration surveys were conducted in each sampling plot by counting the individuals of each woody species in the two height classes seedlings (<130 cm height) and saplings (≥130 cm total height but <12 cm diameter at breast height (DBH)). The proportion of individuals damaged by browsing was estimated for each species and the overall browsing damage in each plot was determined as the weighted average of the browsing damage to all individual species. For this reason, only ungulate browsing but no other types of damage from animals such as debarking were considered. In Central Europe, mainly roe deer (*Capreolus capreolus*) browses on Douglas fir (Spellmann et al., 2015). Abundances of vascular plant and moss species in the understory vegetation were assessed by applying the Braun-Blanquet approach (Braun-Blanquet, 1964; Küchler et al., 2015). From these relevés, total vegetation cover and the averaged (abundance-weighted) nutrient indicator value (Landolt et al., 2010) were derived. The nutrient indicator value indicates the soil nutrient availability experienced by the herbaceous vegetation (Diekmann, 2003). In addition, the following parameters were assessed in the field: the proportion of mature Douglas fir, silver fir, Norway spruce, and beech trees, i.e. the percentage of stems of the respective species of the total number of stems with DBH >12 cm within 9 m from the plot center; the distance from the plot center to the nearest Douglas fir seed tree, i.e., a tree with DBH >30 cm; the leaf area index (LAI), i.e. the leaf area per ground surface, determined from hemispherical photos of the canopy (Digital Plant Canopy Imager CI-110; CID Inc., Camas, Washington, USA; images taken from 1.0 m above ground, i.e., generally above the herbaceous vegetation); and litter thickness determined as the average of three measurements per plot (in the plot center, at half of its radius, and at the plot edge). In every second plot, soil samples of 0.5 dm^3 from 10 cm and 30 cm depth were taken, oven-dried, and ground in the laboratory. The pH of individual samples dissolved in $CaCl_2$ was measured and the average pH of each stand determined. As meteorological co-variates we used annual mean temperature and annual precipitation sum for each stand based on interpolated temperature and precipitation data for the norm period 1981–2010 (Source: MeteoSwiss).

2.3. *Data analysis*

The influence of explanatory variables on regeneration was investigated by multiple regression analyses. We fitted generalized linear mixed models (GLMMs) to plot level data using the R package ‘glmmTMB’ (Brooks et al., 2017). Stand was included in the models as random effect to account for spatial correlation among the 6–8 sampling plots per stand. Two plots had to be excluded from the analyses because LAI measurements were missing. We defined the seedling respectively sapling stem density per hectare of Douglas fir, silver fir, Norway spruce, and beech as response variables. The modelling followed the concept of a hurdle model, which accounts for the presence or absence of regeneration in a plot with a first model, the so-called occurrence model, and with a second model, the abundance model, accounts for the number of seedlings in plots where regeneration was present (Zuur and Ieno, 2016). If the pairwise correlation coefficient R between two explanatory variables was $R > 0.5$, the variable that was considered less biologically relevant was dropped. The initial models included the explanatory variables ‘Annual mean temperature’, ‘Annual precipitation sum’, ‘Soil pH’, ‘LAI’, ‘Litter thickness’, ‘Vegetation cover’, ‘Nutrient indicator value’, ‘Proportion of mature trees’ (referring to conspecific mature trees) and ‘Distance to seed producing Douglas fir’ (for Douglas fir models only). Occurrence models additionally included ‘Overall browsing damage’ for all species, while abundance models included ‘Browsing damage’ for the respective tree species. Continuous explanatory variables were standardized to zero mean and unit variance using the ‘decostand’ function in R package ‘vegan’ (Oksanen et al., 2019). The occurrence models were fitted using binomial distributions. Subsequently, abundance of individuals in plots with non-zero regeneration was fitted with truncated negative binomial models. The R package ‘DHARMa’ (Hartig, 2020) was used to check whether models fulfilled assumptions about homogeneity of residuals.

For each dependent variable, the function ‘dredge’ in R package ‘MuMiN’ (Bartoń, 2019) was used to find the most parsimonious models, i.e., those with the smallest Akaike information criterion (AIC) among the models with all possible combinations of explanatory variables. The final model reported was the average of all models whose AIC differed by <2 from the best model (Burnham and Anderson, 2002). All analyses were performed using R 4.0.3 statistical software (R Development Core Team, 2020).

3. Results

3.1. Regeneration of Douglas fir compared to native tree species

3.1.1. Seedlings

The total seedling density of all tree species (young growth-stage; <130 cm) was on average over all 39 stands 18,177 ± 3092 stems/ha. Among all tree species, beech grew most abundantly accounting for 29% (5,204 ± 2221 stems/ha) and silver fir for 17% (3,025 ± 663 stems/ha) of the seedlings (Fig. 2a). Seedling densities of ash (*Fraxinus excelsior* L.*;* 17%; 3,158 ± 798 stems/ha) and sycamore maple (15%; 2,683 ± 639 stems/ha) were also greater than those of Douglas fir (10%; 1,850 ± 797), which ranked on fifth position. Norway spruce (6%; 1,034 ± 274 stems/ha) and the 27 species classified as ’other broadleaved species’ (5%; 854 ± 190 stems/ha) each produced about half as many seedlings as Douglas fir. ‘Other conifers’ were a marginal group accounting for 0.1% of seedlings.

3.1.2. Saplings

The average sapling density of all species (thicket-stage: ≥130 cm, DBH <12 cm) amounted with 1,741 ± 281 stems/ha to approximately one tenth of the average number of seedlings. Similar as for seedlings, beech was also the most abundant tree species among saplings (48%; 832 ± 224 stems/ha; Fig. 2b). Sycamore maple was the second most abundant species (15%; 264 ± 61 stems/ha), followed by ‘other broadleaved species’ (11%; 190 ± 51 stems/ha). Silver fir accounted for 10% (167 ± 48 stems/ha) and Norway spruce for 9% (159 ± 54 stems/ha) of all saplings. Douglas fir ranked sixth among saplings, with a proportion of 3% (59 ± 24 stems/ha), whereas ‘other conifers’ were negligible (0.1%).

3.2. Regeneration density by stand and forest community

3.2.1. Seedlings

Douglas fir seedlings were found in 108 of 238 plots (45%) and in 36 of 39 stands (92%; Fig. 3a, Table S2). In half of the plots with Douglas fir seedlings and in more than half of the stands (21 of 39) the proportion of Douglas fir was below 5%. Douglas fir seedlings accounted for up to 25% in 11 stands and dominated in four stands. Beech seedlings occurred in 139 of 238 plots in 35 stands. It was the most abundant species in seven stands with proportions between 44% and 83%, and it was present in an additional 13 stands with lower proportions between 5% and 33%. Silver fir seedlings occurred in 168 of 238 plots in 38 stands, dominating in ten stands with proportions >43%. Norway spruce seedlings were found in 119 plots in 37 stands and dominated in two of these stands. In the remaining 16 stands, other species dominated as seedlings, mainly ash and sycamore maple.

In the *Fagenion* communities, the average proportion of Douglas fir saplings ranged between 3% and 13% (Fig. 4a, Table S4). Generally, the most abundant species among seedlings in these communities were either beech (*Luzulo-Fagenion*) or ‘other broadleaved species’ (*Galio-Fagenion* and *Lonicero-Fagenion*. and *Abieti-Fagenion*). In the two conifer dominated communities, where beech was absent and silver fir rare (1% of seedlings), Douglas fir seedlings dominated with 67% (*Vaccinio-Piceion*) and 69% (*Ononido-Pinion*).

3.2.2. Saplings

Douglas fir saplings occurred in 19 of 238 plots (8%) and in 13 of 39 stands (33%) (Fig. 3b, Table S3). In eight stands their proportion was <10% and in the other 5, they amounted to 23% at most. In contrast, beech saplings were found in 106 plots (45%) in 28 stands (72%) with proportions between 2% and 100%. In 11 of these stands, beech saplings dominated. Silver fir saplings occurred in 52 plots (22%) in 24 stands

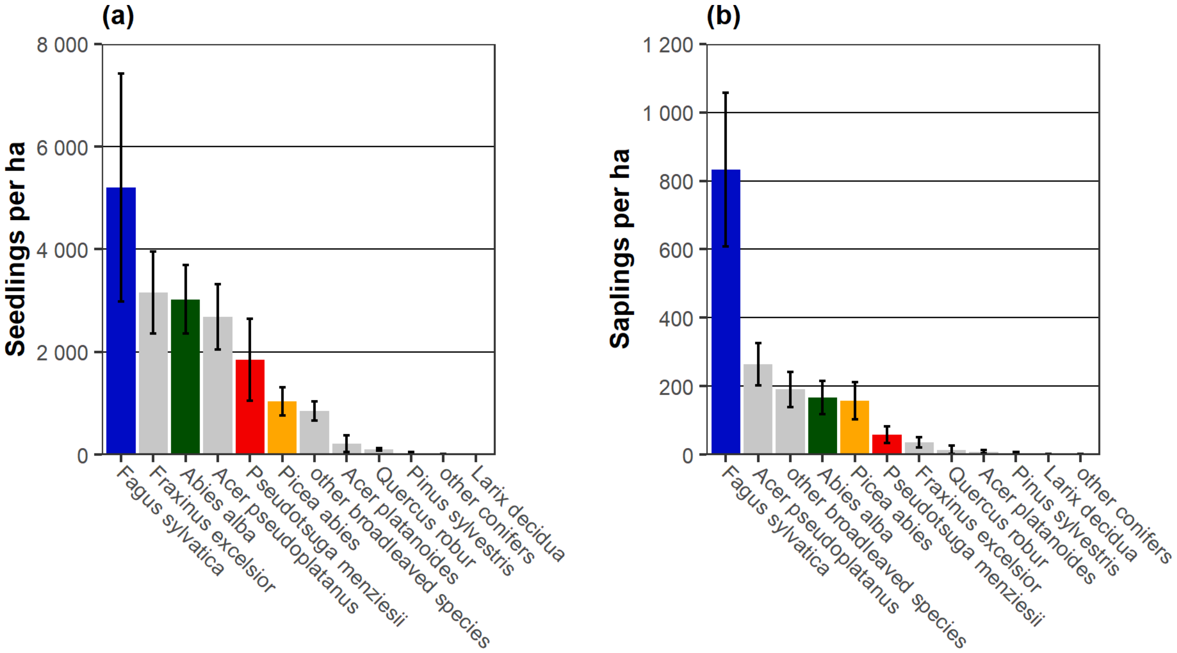

Fig. 2. Natural regeneration by tree species in the 238 plots for (a) seedlings (height <130 cm) and (b) saplings (height ≥130 cm). Error bars represent standard errors among plots. The category ‘other broadleaved species’ contains 23 tree species (*Acer campestris, A. opalus, Alnus glutinosa, Betula pendula, Carpinus betulus, Castanea sativa, Ilex aquifolium, Juglans regia, Ostrya carpinifolia, Populus tremula, Prunus avium, Pyrus pyraster, Quercus petraea, Q. pubescens, Q. rubra, Robinia pseudoacacia, Salix caprea, Sorbus aria, S. aucuparia, Tilia cordata, T. platyphyllos, Trachycarpus fortunei, Ulmus glabra*) and the category ‘other conifers’ contains the four species *Abies nordmanniana, Pinus strobus, Taxus baccata, Thuja* spp.

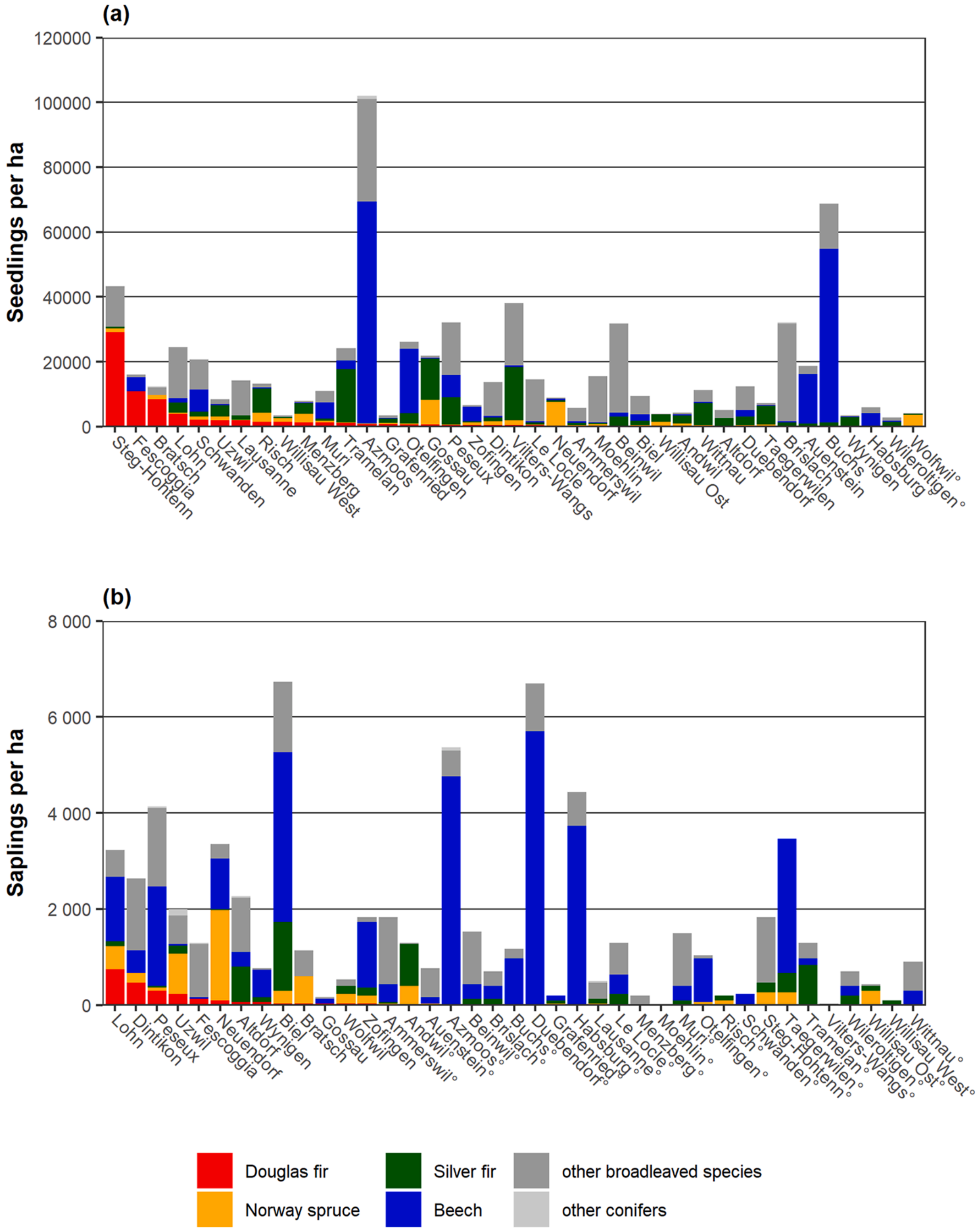

Fig. 3. Number of seedlings (a) and saplings (b) of Douglas fir, Norway spruce, silver fir, beech, 'other broadleaved species' and 'other conifers' in the 39 stands. The stands are sorted by number of Douglas fir stems. The symbol '°' indicates stands without Douglas fir regeneration. The category 'other broadleaved species' contains the 23 species listed in the caption of Fig. 2 plus *Acer pseudoplatanus, A. platanoides, Fraxinus excelsior,* and *Quercus robur*. 'Other conifers' stands for the four conifer species listed in the caption of Fig. 2 plus *Larix decidua* and *Pinus sylvestris*.

(62%), with proportions between 1% and 100%. In 3 stands they were the most abundant species. Norway spruce saplings were found in 45 plots (19%) in 19 stands (49%), dominating in 6 stands.

In all forest communities the proportion of Douglas fir saplings was ≤8% on average (Fig. 4b, Table S4). Except for stands of the *Lonicero-Fagenion* community, the proportion of Douglas fir was smaller among saplings than among seedlings. In contrast, the beech sapling proportions in the *Fagenion* communities exceeded the one for seedlings except for the *Lonicero-Fagenion* communities. Silver fir sapling proportions were smaller than seedling proportions except for the mountain conifer forests. The proportion of Norway spruce saplings increased in comparison to seedling proportions except for the *Abieti-Fagenion* communities.

3.3. Ecological factors influencing seedling and sapling occurrence and abundance

The occurrence model revealed that the odds for finding Douglas fir seedlings were greater on plots with smaller herbaceous vegetation cover, thinner litter cover, in proximity to seed trees, and under open canopy, indicated by low LAI values (Table 1A). In plots where Douglas fir seedlings were found, their number was negatively related to herbaceous vegetation cover (Table 1B). Douglas fir saplings were more abundant in stands with a higher proportion of adult Douglas fir trees

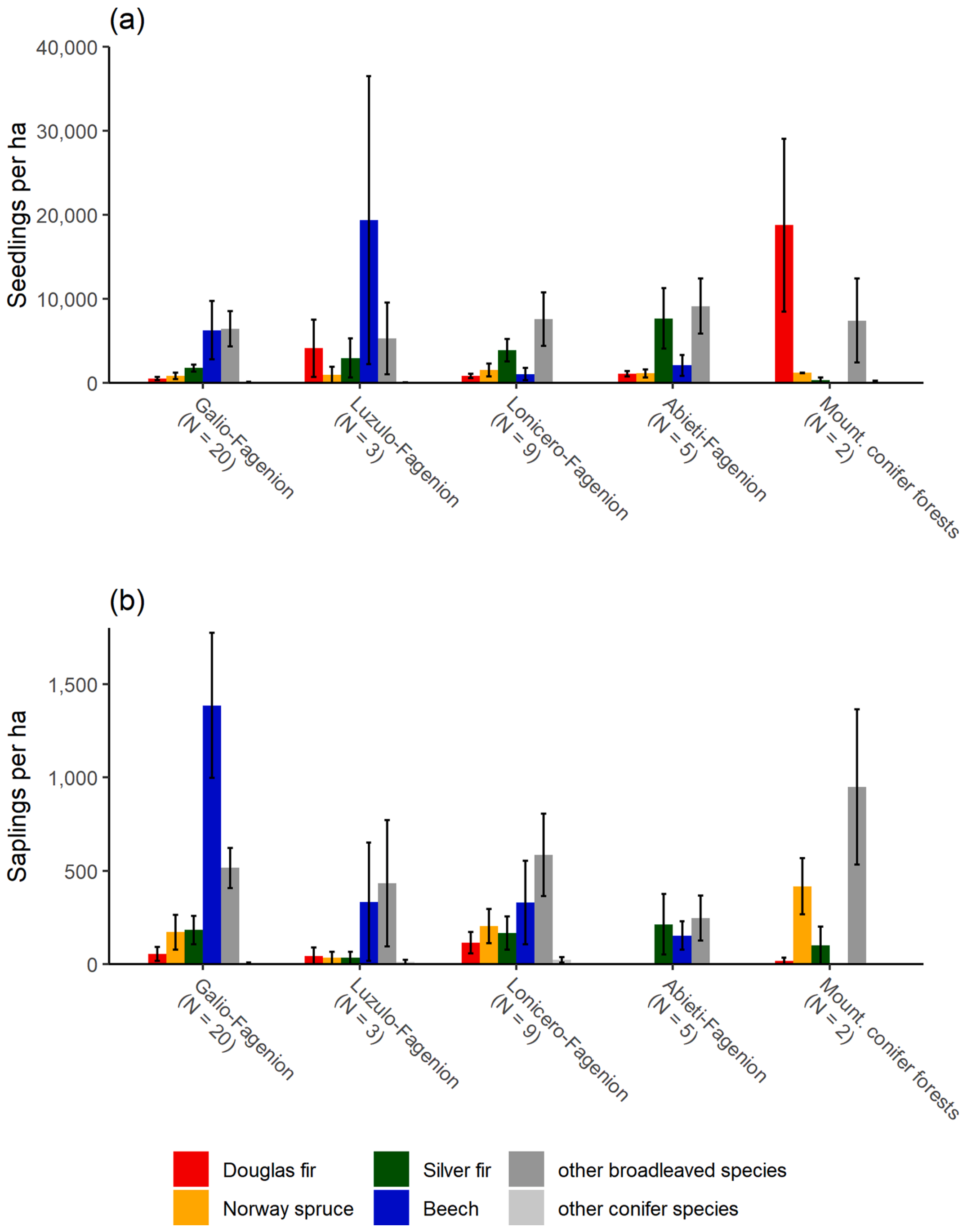

Fig. 4. Number of seedlings (a) and saplings (b) of Douglas fir, Norway spruce, silver fir, beech, 'other broadleaved species', and 'other conifers' in the 39 stands classified in five forest communities (TypoCH classification, Delarze et al., 2015): Mountain conifer forests: *Vaccinio-Piceion* (N = 1), *Ononido-Pinion* (N = 1). For the species summarized in the categories 'other broadleaved species' and 'other conifers' refer to the caption of Fig. 3. Error bars represent standard errors among stands.

(Table 2A). Due to the low number of plots with Douglas fir saplings, significant influences could not be detected in the abundance models.

The odds for finding beech seedlings were greater in stands with higher mean annual temperature and larger annual precipitation sum (Table 1A). It was also more likely to find beech seedlings in stands with a higher proportion of adult beeches. Conversely, more herbaceous vegetation cover reduced the likelihood for the presence of beech seedlings. Similarly, beech seedling abundance was higher in stands with a greater proportion of adult beeches and on plots where the herbaceous vegetation indicated lower nutrient availability (Table 1B). The likelihood of finding beech saplings increased with mean annual temperature and soil pH, and decreased with herbaceous vegetation cover (Table 2A). Likewise, beech sapling abundance increased with pH and decreased with vegetation cover (Table 2B).

While the occurrence of silver fir seedlings was negatively related to herbaceous vegetation cover and soil pH, the abundance of seedlings was negatively related only to vegetation cover (Table 1). For silver fir saplings, no significant relations to any of the explanatory variables resulted (Table 2). Norway spruce seedling occurrence was positively related to annual precipitation but negatively to herbaceous vegetation cover and litter thickness. No significant relations were found for Norway spruce seedling abundance. Sapling occurrence of Norway spruce was negatively related to annual precipitation and sapling abundance resulted in no significant relations.

Table 1

Model selection results for the presence or absence (occurrence models) (A) and for the abundance (abundance models) (B) for seedlings ($<$130 cm height) of Douglas fir, Norway spruce, silver fir, and beech. The average of all top models with ΔAICc < 2 is presented, i.e. 5 top models for occurrence (TMO) resp. 38 top models for abundance (TMA) of Douglas fir (N = 238 resp. N = 108), 17 TMO resp. 55 TMA of Norway spruce (N = 238 resp. N = 119), 9 TMO resp. 16 TMA of silver fir (N = 238 resp. N = 168), and 8 TMO resp. 7 TMA of beech (N = 238 resp. N = 139). The significant variables (**in bold**) were included in all best models, the non-significant variables only in single best models. Factors that were dropped during model reduction are indicated with 'NA', factors that were not included in full model are indicated with '-'.

	Douglas fir			*Norway spruce*			*Silver fir*			*Beech*		
Explanatory variable	Est.	SE	*P*	Est.	SE	*P*	Est.	SE	*P*	Est.	SE	*P*
(A) Occurrence models												
Vegetation cover	−0.55	0.19	**0.005**	−0.63	0.18	**0.001**	−0.78	0.20	**<0.001**	−0.44	0.19	**0.021**
Litter thickness	−0.50	0.18	**0.007**	−0.39	0.14	**0.017**	0.01	0.06	0.929	−0.03	0.11	0.751
Distance to mature Douglas fir	−0.48	0.19	**0.010**	–	–	–	–	–	–	–	–	–
LAI	−0.44	0.18	**0.013**	−0.29	0.19	0.119	0.03	0.11	0.774	−0.01	0.06	0.884
Annual precipitation sum	0.37	0.24	0.130	−0.44	0.21	**0.032**	NA	NA	NA	0.65	0.30	**0.028**
Soil pH	0.29	0.26	0.275	0.01	0.07	0.841	−0.60	0.30	**0.042**	0.36	0.40	0.368
Annual mean temperature	−0.15	0.24	0.530	−0.19	0.22	0.400	−0.14	0.26	0.571	1.00	0.38	**0.009**
Nutrient indicator value	−0.04	0.12	0.731	−0.04	0.11	0.733	NA	NA	NA	0.01	0.08	0.879
Proportion of mature trees	NA	NA	NA	0.21	0.19	0.277	0.08	0.16	0.639	0.44	0.21	**0.039**
Overall browsing damage	NA	NA	NA	0.11	0.16	0.482	0.27	0.24	0.265	0.04	0.12	0.715
(B) Abundance models												
Vegetation cover	−0.74	0.20	**<0.001**	−0.12	0.21	0.559	−0.43	0.14	**0.002**	−0.41	0.27	0.134
Annual mean temperature	−0.17	0.25	0.504	−0.21	0.31	0.506	−0.18	0.23	0.439	0.54	0.44	0.217
Browsing damage	0.12	0.16	0.445	0.16	0.18	0.391	0.01	0.06	0.819	−0.02	0.08	0.835
Litter thickness	−0.08	0.15	0.591	−0.29	0.22	0.181	−0.05	0.11	0.651	NA	NA	NA
LAI	−0.07	0.14	0.619	0.00	0.02	0.948	−0.01	0.05	0.872	−0.02	0.10	0.862
Distance to mature Douglas fir	−0.03	0.10	0.780	–	–	–	–	–	–	–	–	–
Soil pH	0.03	0.11	0.811	−0.24	0.31	0.435	−0.02	0.09	0.852	0.68	0.44	0.127
Proportion of mature trees	0.11	0.15	0.479	0.09	0.15	0.529	0.18	0.15	0.239	0.86	0.18	**<0.001**
Annual precipitation sum	NA	NA	NA	−0.01	0.06	0.915	−0.01	0.06	0.925	0.03	0.13	0.834
Nutrient indicator value	NA	NA	NA	−0.15	0.22	0.497	−0.01	0.07	0.841	−0.61	0.28	**0.026**

Annual mean temperature, annual precipitation sum: interpolated temperature and precipitation data for the period 1981–2010 (Source: MeteoSwiss); Soil pH: average of pH measurements at 10 cm and 30 cm depth; Nutrient indicator value: average Landolt indicator value for nutrient availability, abundances weighted; indicator values range between 1 and 5 (Landolt et al., 2010). Proportion of mature trees: the proportion of conspecific mature trees.

Table 2

Model selection results for the presence or absence (occurrence models) (A) and for the abundance (abundance models) (B) for saplings ($\geq$130 cm height and $<$12 cm DBH) of Douglas fir, Norway spruce, silver fir and beech. The average of all top models with ΔAICc < 2 is presented, i.e. 6 TMO resp. no TMA of Douglas fir (N = 238 resp. N = 19), 19 TMO resp. 11 TMA of Norway spruce (N = 238 resp. N = 45), 24 TMO resp. no TMA of silver fir (N = 238 resp. N = 52) and 10 TMO resp. 5 TMA of beech (N = 238 resp. N = 106). The significant variables (**in bold**) were included in all best models, the non-significant variables only in single best models. Factors that were dropped during model reduction are indicated with 'NA', factors that were not included in full model are indicated with '-'.

	Douglas fir			*Norway spruce*			*Silver fir*			*Beech*		
Explanatory variable	Est.	SE	*P*	Est.	SE	*P*	Est.	SE	*P*	Est.	SE	*P*
(A) Occurrence models												
Proportion of mature trees	0.65	0.29	**0.023**	0.06	0.16	0.688	0.14	0.19	0.468	0.02	0.10	0.821
Overall browsing damage	−0.61	0.44	0.166	−0.07	0.18	0.692	NA	NA	NA	−0.02	0.09	0.857
Litter thickness	−0.06	0.19	0.738	0.00	0.05	0.950	0.01	0.06	0.866	NA	NA	NA
LAI	−0.02	0.13	0.851	−0.01	0.08	0.885	0.35	0.23	0.118	0.06	0.15	0.691
Soil pH	0.01	0.12	0.917	0.14	0.28	0.613	0.10	0.21	0.638	1.22	0.54	**0.025**
Nutrient indicator value	0.01	0.11	0.904	−0.01	0.07	0.901	0.01	0.06	0.900	0.21	0.27	0.442
Annual precipitation sum	−0.01	0.15	0.908	−1.06	0.53	**0.046**	−0.01	0.07	0.903	0.03	0.16	0.856
Vegetation cover	NA	NA	NA	0.00	0.05	0.947	−0.12	0.21	0.549	−0.57	0.24	**0.016**
Annual mean temperature	NA	NA	NA	−0.20	0.34	0.556	−0.26	0.28	0.365	1.24	0.51	**0.015**
Distance to mature Douglas fir	NA	NA	NA	–	–	–	–	–	–	–	–	–
(B) Abundance models												
Soil pH	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.69	0.21	**<0.001**
Vegetation cover	NA	NA	NA	−0.10	0.22	0.632	NA	NA	NA	−0.53	0.15	**<0.001**
Annual mean temperature	NA	NA	NA	−0.01	0.08	0.881	NA	NA	NA	0.23	0.34	0.508
Annual precipitation sum	NA	NA	NA	NA	NA	NA	NA	NA	NA	−0.50	0.34	0.142
LAI	NA	NA	NA	−0.11	0.21	0.613	NA	NA	NA	−0.02	0.08	0.781
Litter thickness	NA	NA	NA	−0.35	0.27	0.189	NA	NA	NA	−0.01	0.07	0.830
Nutrient indicator value	NA	NA	NA	−0.01	0.07	0.865	NA	NA	NA	NA	NA	NA
Proportion of mature trees	NA	NA	NA	0.04	0.12	0.742	NA	NA	NA	NA	NA	NA
Distance to mature Douglas fir	NA	NA	NA	–	–	–	–	–	–	–	–	–
Browsing damage	NA	NA	NA	−0.01	0.09	0.881	NA	NA	NA	NA	NA	NA

Variable explanations see Table 1.

Browsing intensity varied substantially among tree species, but did not significantly influence the seedling or sapling abundances of Douglas fir, Norway spruce, silver fir, or beech (Table 1). On average, browsing damage on seedlings and saplings of Douglas fir (3.2%), beech and Norway spruce (each $<$ 1%) was small in comparison to silver fir (21.3%; Fig. 5). In ash (31.9%), Norway maple (*Acer platanoides* L.;

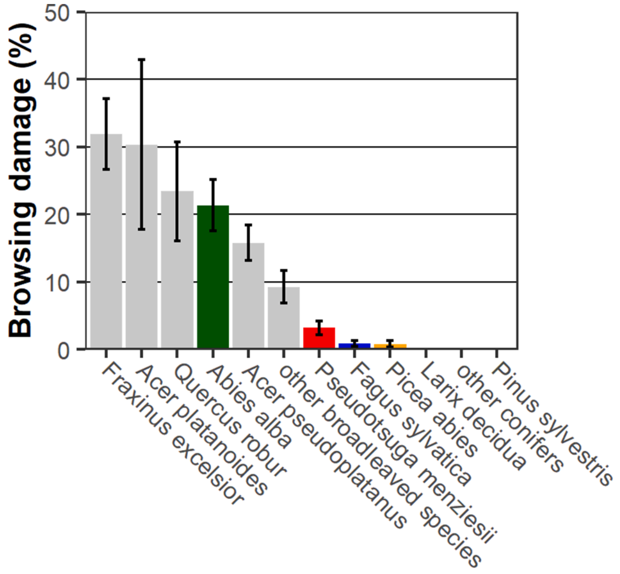

Fig. 5. Percentage of seedlings and saplings per tree species damaged by browsing. For the species contained in the categories 'other broadleaved species' and 'other conifers' refer to the caption of Fig. 2. Error bars represent standard errors among plots.

30.3%), pedunculate oak (*Quercus robur* L., 23.4%), sycamore maple (15.8%) and other species (9.6%) the proportions of seedlings and saplings damaged by browsing were also greater than in Douglas fir. Larch (*Larix decidua* Mill.) and pine (*Pinus sylvestris* L.) were free of browsing damage in the study plots.

4. Discussion

The quantitative assessment of natural regeneration in forest stands with Douglas fir in Switzerland revealed that Douglas fir regenerated in the majority of the studied stands. While Douglas fir seedlings were present in 45% of the plots and in 90% of the stands, its abundance was mostly subordinate. Douglas fir saplings were found in 8% of the plots and in one third of the stands. They did not dominate the regeneration of any stand. In contrast, silver fir and beech saplings occurred in almost all stands and dominated the regeneration in half of them. Norway spruce saplings were found in only half of the stands but still were the most abundant species in six stands. Our results show that Douglas fir, Norway spruce, silver fir, and beech seedlings were limited by abundant understory vegetation. Douglas fir and Norway spruce were also limited by thick litter layers. Distance to seed source and shade (LAI) reduced Douglas fir seedling occurrence, while unfavorable climatic conditions limited beech occurrence. However, we did not find that browsing affected natural regeneration in the studied species.

4.1. Extent of natural Douglas fir regeneration

More than 90% of the forest stands considered in this study grow on sites that are naturally dominated by beech or silver fir. They belong to the forest communities *Galio-* and *Luzulo-Fagenion* (i.e. submontane beech forests), *Lonicero-Fagenion* (montane beech forests) and *Abieti-Fagenion* (fir-beech forests). In these communities, Douglas fir is not competitive in comparison to rapidly growing broad-leaved tree species, in particular beech, unless tending measures reduce competitors and improve light conditions (Bianchi et al., 2018; Eberhard and Hasenauer, 2018). It is unlikely that Douglas fir will spread in these forest communities under current environmental conditions due to its low competitive strength during early life-stages (Devine and Harrington, 2008; Moser et al., 2021). Disturbances of the top soil facilitate natural Douglas fir regeneration due to partial removal of the litter layer. On weakly acidic sites, beech and other deciduous tree species grow so vigorously that tending in favor of Douglas fir is hardly successful or at least not economical (Ammann, 2020). On calcareous sites with lime present in the topsoil, Douglas fir regeneration regularly suffers from chlorosis and often fails (Perakis et al., 2006; Mainwaring et al., 2014).

Nevertheless, on three dry or nutrient poor sites, the abundance of Douglas fir seedlings was rather high. In the semi-open southern Alpine stand Fescoggia at 840 m a.s.l. (*Luzulo-Fagenion*), Douglas fir seedlings dominated (68%), but saplings were subordinate. In two stands in the central Alpine Valais, Bratsch at 1340 m a.s.l. (*Ononido-Pinion*) and Steg-Hohtenn at 1150 m a.s.l. (*Vaccinio-Piceion*), Douglas fir seedlings even reached highest stem numbers of the entire sample. These stands were characterized by small herbaceous cover on shallow, nutrient poor soils with a pH of around 7, and a semi-open stand structure. In the three stands, high mean ecological indicator values for light confirm high light transmission. Potentially, this may have provided favorable conditions for Douglas fir regeneration. Although these communities were underrepresented in the sample, our findings suggest that Douglas fir may successfully regenerate under these environmental conditions. An additional explanation for the regeneration success observed on such sites may be the ability of Douglas fir to resist repeated drought phases, both as an adult tree (Eilmann and Rigling, 2012) and as seedling and sapling, similar as in Mediterranean Douglas fir stands at higher elevations in Spain (Broncano et al., 2005). In contrast, Norway spruce faces bark beetle attacks under summer drought conditions (Temperli et al., 2013; Seidl et al., 2016; Schuldt et al., 2020) and Scots pine declines after repeated long-lasting droughts (Rigling et al., 2013). Our observations are in line with findings from the Black Forest in Germany and from Austria, where Douglas fir was reported to successfully regenerate in large numbers under dry, nutrient-poor conditions (Knoerzer and Reif, 1996; Essl, 2005). Further studies including additional stands belonging to these communities are important to gain a better understanding of the conditions for massive natural regeneration of Douglas fir and the effectiveness of control measures. An experimental study also showed that Douglas fir seedlings thrive better than oak, silver fir, Norway spruce and Scots pine under dry and nutrient-poor conditions (Moser et al., 2021). This was explained, among other factors, by the finely branched roots of Douglas fir, which extend mainly superficially at seedling age (Calvaruso et al., 2011; Lei et al., 2012; Moser et al., 2016). This root structure allows Douglas fir seedlings to efficiently take up nutrients from the topsoil, which seems to be particularly beneficial on poor, drying soils. While Douglas fir seedlings were occasionally highly abundant, Douglas fir saplings were only scarcely present in contrast to saplings of Norway spruce, silver fir, and various broadleaved species. In some stands, the low number of Douglas fir saplings may be due to silvicultural interventions as suggested by signs of such measures in several stands. Interventions to control the establishment on new sites are relatively easy because Douglas fir regenerates only generatively and generation times are between 15 and 40 years (Spellmann et al., 2015). The absence of vegetative regeneration largely prevents an uncontrolled spread of the species. Recommendations for controlling undesired establishment of Douglas fir regeneration include the early harvest of potential seed trees and the removal of naturally occurring seedlings and saplings (Spellmann et al., 2015). Recommendations in Germany also include a buffer zone of up to two kilometers around sensitive habitats, such as particularly vulnerable forest communities and open, nutrient poor sites, which is permanently kept free of Douglas fir (Fischer, 2008).

4.2. Drivers of natural regeneration

Our results demonstrate that seedlings were more likely to be found when herbaceous vegetation cover was low. For Douglas fir and silver fir, seedling abundance was also higher if the ground was only loosely covered by vegetation. Dense herbaceous vegetation, which spreads on productive soils immediately after opening the canopy, negatively affects germination and establishment of tree seedlings. This may be due to direct competition for light, water, and nutrients, but may also be related to a higher presence of predators, such as mice, under herbaceous vegetation (Caccia and Ballare, 1998; Vandenberghe et al., 2006; Royo and Carson, 2008). It strongly depends on the tree species, which of these factors is most important. Studies from southwestern Germany confirmed that a dense herbaceous layer reduced emergence of Douglas fir seedlings (Guntermann, 1989; Knoerzer et al., 1995). After successful establishment, however, further development of the seedlings was not affected by the herbaceous vegetation (Knoerzer et al., 1995). A thick litter layer corresponded to a lower probability of finding Douglas fir seedlings, which was probably due to unfavorable germination conditions because litter may act as a mechanical barrier and make it difficult for seedlings to access sufficient water (Caccia and Ballare, 1998; Tschopp et al., 2014). Knoerzer (1999) showed this for Douglas fir germination, especially on sites with a thick needle litter layer.

In the present analysis, Douglas fir seedlings were more frequently found close to seed trees, which can be explained by limited seed dispersal in this species. Douglas fir seeds weigh only about 20% of silver fir seeds, but twice as much as seeds of Norway spruce, larch, and Scots pine (Burkart, 2018). Douglas fir seeds are rarely carried further than 100 m by wind, even in the main wind direction (Roy, 1960), which limits their dispersal. Furthermore, Douglas fir requires 20 to 40% of open-sky light intensity for both establishment and growth (Mailly and Kimmins, 1997; Drever and Lertzman, 2003; Harrington, 2006), whereas beech and other broad-leaved species are more shade tolerant in comparison (Niinemets and Valladares, 2006). Our survey confirmed that Douglas fir requires more light than beech for successful regeneration. Such light-rich conditions, favorable for Douglas fir growth, often occur as a result of disturbances such as windthrow or silvicultural interventions (Bindewald et al., 2021; Scherrer et al., 2021). In contrast, shade-tolerant beech establishes and can even thrive under closed canopy but is also more competitive than Douglas fir in gaps (Knoerzer and Reif, 1996; Spellmann et al., 2015).

The percentage of seedlings and saplings damaged by browsing was higher in several deciduous tree species and silver fir than in Douglas fir (Fig. 5), but lower in beech and Norway spruce. The ranking of browsing frequencies among species in our survey was comparable to the findings of Kupferschmid et al. (2020) who reported highest browsing frequencies in Swiss forests in oak, maple, and ash, followed in descending order by silver fir, beech, and Norway spruce. Despite the substantial differences in damage proportions among species in our study, browsing did not significantly influence seedling and sapling abundances of Douglas fir, Norway spruce, silver fir, and beech (Table 1). The low browsing frequency in Douglas fir seedlings and saplings corresponds well to the findings of a study in southwestern Germany, which reported that Douglas fir in comparison to oak was only weakly affected by browsing providing the species with a competitive advantage on dry, nutrient-poor sites with high light availability (Bindewald and Michiels, 2018). These observations suggest that browsing is generally not an important factor influencing Douglas fir regeneration. However, to gain a conclusive picture about the importance of browsing, controlled field studies using fences or other protection measure to prevent ungulate browsing are required.

Beech saplings were more abundant in stands with little herbaceous vegetation cover, on sites with higher soil pH, and at locations with higher mean annual temperature (Table 2). Norway spruce saplings were slightly more abundant in stands with less precipitation. In contrast, no significant correlation with environmental factors was found for Douglas fir and silver fir saplings. In four stands on the northern side of the Alps Douglas fir accounted for ≥200 stems/hectare. However, Douglas fir saplings never dominated the regeneration in these stands, even though clear indications of recent silvicultural measures to promote Douglas fir were found in three of these four stands.

5. Conclusions and management implications

Douglas fir has regenerated naturally in Europe for several decades. It has been shown to potentially become invasive by its spread to nutrient poor soils in open forests (Knoerzer 1999, Essl 2005) and can also negatively impact biodiversity (reviewed in Schmid et al., 2014; Wohlgemuth et al., 2021). Our quantitative assessment of natural Douglas fir regeneration in Swiss forest stands, where the species has been planted 85–130 years ago, shows that Douglas fir cannot competitively establish in productive beech forest communities on the Central Plateau. Thus, the successful promotion of Douglas fir in productive communities requires specific tending measures (Jonášová et al., 2006) to control rapidly growing native broadleaved tree species, in particular beech, and vigorously spreading understory vegetation. However, our results also suggest that on dry, nutrient poor sites, where fast-growing deciduous trees are nutrient-limited and naturally substituted by conifers, Douglas fir may find a regeneration niche. Therefore, monitoring of regeneration dynamics is strongly recommended to prevent uncontrolled spread of Douglas fir on such sites.

CRediT authorship contribution statement

Esther R. Frei: Data curation, Formal analysis, Validation, Visualization, Writing – original draft, Writing – review & editing. **Barbara Moser:** Conceptualization, Formal analysis, Methodology, Writing – review & editing. **Thomas Wohlgemuth:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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