

Root architecture might account for contrasting establishment success of *Pseudotsuga menziesii* var. *menziesii* and *Pinus sylvestris* in Central Europe under dry conditions

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Abstract

• **Key message** *Pinus sylvestris* seedlings quickly expand their roots to deeper soil layers while *Pseudotsuga menziesii* concentrates its root system in the topsoil, thereby running the risk of desiccation during long dry spells, as indicated by lower survival after simulated summer drought.

• **Context** *Pseudotsuga menziesii* (Douglas-fir) is regarded as a promising species to maintain the productivity of Central European lowland forests given the projected increase of long dry spells.

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Contribution of the coauthors T. Wohlgemuth, B. Moser, C. Bachofen and M. Metslaid developed the idea and designed the experiment. The field work was carried out by C. Bachofen, M. Metslaid and J. Müller, supported by T. Wohlgemuth and B. Moser. C. Bachofen and J. Müller analysed the data; B. Moser, J. Müller and T. Wohlgemuth wrote the manuscript with editorial advice by the coauthors.

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• **Aims** Will the species be able to regenerate from seed and spread outside plantations in a drier temperate Europe?
• **Methods** We measured the relative growth rate, biomass allocation, root architecture, and phenotypic plasticity of *Pseudotsuga menziesii* seedlings sown in a common garden and grown under current precipitation and prolonged drought, respectively. The species' competitive ability with respect to *Pinus sylvestris* L., the most drought-tolerant native conifer in Central Europe, was assessed during three growing seasons.
• **Results** *Pinus sylvestris* seedlings had higher relative growth rates than did *Pseudotsuga menziesii* seedlings, first in terms of aboveground biomass and later in terms of shoot height. This resulted in heavier and taller seedlings after three growing seasons under both moist and dry conditions. Shorter vertical roots corresponded with lower survival of *Pseudotsuga menziesii* seedlings under dry conditions.
• **Conclusion** Fast root proliferation allows *Pinus sylvestris* seedlings to reach deeper water pools that are less rapidly depleted during transient drought. By contrast, the shallow root system might put *Pseudotsuga menziesii* seedlings at the risk of desiccation during prolonged dry spells.

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1 Introduction

Projections of climatic change have amplified the debate on whether tree species composition in European forests has to be actively managed in order to guarantee forest continuation, protection against natural hazards and economically important timber production in the coming century (Bussotti et al. 2015; Lindner et al. 2014; Wohlgemuth 2015). Foresters have long been studying non-native tree species that could enhance wood production under current climatic conditions. As such, *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) was first introduced to increase wood production (González-García et al. 2013). Today, about 2 % of the German and 3 % of the French forest area, respectively, are stocked with *Pseudotsuga menziesii*, and the species is expected to become the third most important conifer in Europe after *Picea abies* (L.) H. Karst. (Norway spruce) and *Pinus sylvestris* L. (Scots pine; Schmid et al. 2014). It is regarded as a promising alternative to *Picea abies* in commercial lowland forests under future climatic conditions (Brang et al. 2008; Fischer 2008). More recently, it has even been suggested that *Pseudotsuga menziesii* might be able to grow in regions as dry as the Central Alpine valleys (Chen et al. 2010; Eilmann and Rigling 2012), although such drought tolerance is still up for debate (Littell et al. 2008; Sergent et al. 2014). The expansion of *Pseudotsuga menziesii* in Central European forests is, however, increasingly criticised by nature conservationists, who fear negative effects of non-native species on biodiversity and forest functioning (Schmid et al. 2014). Taking such concerns into account, the question of how well exotic tree species will be adapted to future climatic conditions and might be able to outcompete native species gains importance (Schüler et al. 2014).

The most drought-resistant native conifer in Central Europe is *Pinus sylvestris* (Braun-Blanquet 1961; Ozenda 1985). In particular, Central Alpine populations are known for their high phenotypic plasticity, which enables them to grow in changing environments (Richter et al. 2012). Nevertheless, *Pinus sylvestris* has suffered high mortality in dry Alpine valleys after the exceptional summer drought in 2003, for instance in the Valais, Switzerland (Bigler et al. 2006; Rigling et al. 2013) and the Aosta valley, Italy (Vacchiano et al. 2012). As a result, adequate management measures (Vacchiano and Motta 2015) and potential alternatives to *Pinus sylvestris*, such as *Pseudotsuga menziesii*, have been investigated (Eilmann and Rigling 2012). These studies have, however, focused on planted seedlings, which until now are common practice in Central Europe but are costly and may necessitate irrigation, especially in dry years. Planted *Pseudotsuga menziesii* seedlings are known

to grow faster (Nabel et al. 2013) and have different root morphologies (Preisig et al. 1979) than seedlings grown from seed. Relying on natural regeneration or direct seeding might be more cost-efficient if the species should be managed at larger scales in the future. Assessing the ability of *Pseudotsuga menziesii* to establish from seed under future climatic conditions will further allow to evaluate its potential to spread outside managed forests and invade habitats where it is undesirable, as e.g. in nature reserves. This is important since *Pseudotsuga menziesii* has a high reproductive potential once it reaches maturity (Richardson and Rejmánek 2004). As in all plant species, the competitive ability of tree seedlings is determined by their ability to acquire resources such as light, water and nutrients (Rewald and Leuschner 2009; Schulte et al. 2013). Seedling establishment and successful regeneration are thus to a large extent driven by the soil exploitation strategy of a species and its belowground interaction with neighbouring species (Messier et al. 2009). High rates of root extension (Zhang et al. 2012) and the ability to quickly occupy a large soil volume seem to be major attributes of competitive species (Mommer et al. 2011; Rajaniemi 2007). The competitive hierarchy of coexisting species may change with resource availability, depending on the plasticity of a species' root system in response to stress (Fort et al. 2014; Zhang et al. 2012). Consequently, the morphology and plasticity of the root system are crucial parameters to assess a species' ability to successfully establish and compete under current and future climatic conditions. Like most pines species, *Pinus sylvestris* produces a taproot already during the earliest seedling stages (Wilcox 1968), reaching up to 40-cm soil depth within 6 months after germination (Moser et al. 2015) and allowing it to acquire water from deeper soil layers that are less rapidly depleted during drought events (Ryel et al. 2008). By contrast, little is known about the root architecture of *Pseudotsuga menziesii* seedlings during early establishment (but see Preisig et al. 1979 for 5–8-year-old seedlings), while 10–80-year-old *Pseudotsuga menziesii* were shown to have a superficial root system (Mauer and Palatova 2012), which only slowly advances to deeper soil layers (Domec et al. 2004).

The aim of the present study was to assess the relative competitive abilities of *Pseudotsuga menziesii* and *Pinus sylvestris* seedlings in Central European lowland forests under current climatic conditions and aggravated, climate change-type drought. Both species were sown in a common garden in the presence of interspecific and intraspecific competition and grown for 3 years either under current summer precipitation or 4 months of summer drought during the second and third growing season. The competitive ability of the two species was assessed in terms of relative growth rate, and their establishment success was related to biomass allocation, root architecture and phenotypic plasticity.

2 Material and methods

2.1 Species and seed material

Pseudotsuga menziesii (Mirb.) Franco is a widespread tree species in western North America ranging from Canada to Mexico (Little 1971). Two subspecies are distinguished, var. *glauca* and var. *menziesii*. The latter was introduced to Europe in 1827 and first cultivation trials took place in Central Europe by the end of the nineteenth century (Kowarik and Rabitsch 2010; Tschopp et al. 2015). *Pseudotsuga menziesii* var. *glauca*—the more drought-resistant inland variety native to the Rocky Mountains—occurs in a wide range of mesic to xeric sites (Ferrell and Woodard 1966). This variety has been shown to be very susceptible to *Rhabdocline pseudotsugae*, a fungal needle cast present in North America (Blada 1971; Hoff 1987), which has spread to Europe starting in 1914 causing a huge damage in Douglas-fir plantations (Bürgi and Diez 1986; Stimm and Dong 2001). Therefore, the coastal variety (var. *menziesii*) is now grown almost exclusively in European forests. In our experiment, we used seeds from commercial harvests of two *Pseudotsuga menziesii* var. *menziesii* populations, one from the west coast of the USA and one from a population introduced to Germany in the nineteenth century (Table 1). According to Eilmann et al. (2013), coastal populations of *Pseudotsuga menziesii* in the USA increase their productivity and, concomitantly, decrease their drought resistance along the latitudinal gradient from south to north. Consequently, the US population included in our experiment may be considered as both intermediately productive and intermediately drought tolerant. Unfortunately, we were not able to trace the origin of the German population, but we expect a potential adaptation to European environmental conditions since its introduction in the nineteenth century.

Pinus sylvestris L. is the most drought-tolerant conifer in Central Europe ranging from the Mediterranean to Siberia (<http://www.euforgen.org/distribution-maps/>). In Central Alpine valleys, it forms stands between 500 and 1500 m a.s.

l. We collected seeds from a low elevation (Leuk) and a high elevation (Visperterminen) population in the Central Alpine Rhone valley (Table 1), the driest regions in Switzerland. In both populations, seeds were collected from five maternal lineages in winter 2011/2012.

2.2 Experimental setup

Pseudotsuga menziesii and *Pinus sylvestris* were grown in mesocosms (200 cm × 80 cm × 50 cm) in a common garden near Leuk (Valais, Switzerland; 46° 18' 33" N, 07° 41' 10" E; 610 m a.s.l.). The mesocosms were filled with 30 cm of sand and gravel from the local Rhone riverbed (subsoil), covered by 15 cm of humus (Oekohum GmbH, Herrenhof, Switzerland; topsoil), similar to the two-layered forest soils of the Rhone valley with a parent material horizon and an organic surface horizon (Richter et al. 2012). All mesocosms were shaded with white knitted polypropylene shade cloth that blocked out 22 % of the sunlight, generating light to medium shade conditions optimal for *Pseudotsuga menziesii* seedling establishment (Brodie and DeBell 2013; Mailly and Kimmins 1997). The mesocosms were arranged in a split-plot design with five blocks (whole plots), each containing two mesocosms (split plots) exposed to differing watering regimes (control and drought, respectively; Online Resource 1a). Each mesocosm was divided into two half-mesocosms, which represents a second level of blocking to minimise the effect of unknown nuisance factors. Each half-mesocosm consisted of 70 squares of 10 cm × 10 cm, which were sown with 15 seeds of one of the 2 *Pinus sylvestris* populations (either Leuk or Visperterminen) or 20 seeds of one of the 2 *Pseudotsuga menziesii* populations (either Germany or USA) between March 20 and 23, 2012. Each population was sown in 5 squares per half-mesocosm, i.e. a total of 20 squares. The remaining 50 squares contained Mediterranean populations of *Pinus sylvestris*, *Pinus nigra* Arnold and *Pinus halepensis* Mill., which are not part of the present study (details in Online Resource 1b). We used a higher seed density in *Pseudotsuga*

Table 1 Origin of *Pinus sylvestris* and *Pseudotsuga menziesii* seeds sown in the common garden at Leuk (Switzerland) and climatic conditions at the seed origin (average annual temperature and annual precipitation sum; means 1950–2000)

Species	<i>Pinus sylvestris</i>		<i>Pseudotsuga menziesii</i>	
	Leuk Switzerland	Visperterminen Switzerland	Snoqualmie USA	Tauberbischofsheim Germany
Status	Autochthonous	Autochthonous	Autochthonous	Introduced
Latitude	46.29	46.27	47.53	49.63
Longitude	46.29	46.27	−121.82	9.65
Elevation (m a.s.l.)	570	1360	500	370
Temperature (°C)	9	5.1	10.1	9.4
Precipitation (mm)	812	1317	1608	674

Climatic data provided by MeteoSwiss (*Pinus sylvestris*) and www.worldclim.org (*Pseudotsuga menziesii*; Hijmans et al. 2005)

menziesii to balance its inferior seed quality (Online Resource 2). After sowing, all mesocosms were watered regularly until May 31, 2012, to maximise emergence. Starting from June 1, 2012, automatic transparent rain shelters were used to intercept natural rainfall during the growing season (June–September 2012, end of March–end of September 2013 and 2014). During these periods, the mesocosms were irrigated automatically in two consecutive nights per week (Richter et al. 2012). In the control treatment, 151 % of the average April–September precipitation in the Rhone valley, i.e. 416 mm from the end of March to the end of September, was applied to individual mesocosms. This corresponds to the top decile of the long-term rainfall measured at the nearby MeteoSwiss station in Sion from 1864 to 2011. The drought treatment consisted of the same irrigation treatment as the controls in 2012 as well as from the end of March until the end of May 2013 and 2014, but it included a complete summer drought without irrigation from the beginning of June to the end of September 2013 and 2014 (Online Resource 3). This represents an increase in long dry spells as projected for Central Europe by the end of the century (Lindner et al. 2014). Mesocosms were subjected to natural rainfall from the end of September to the end of March. Volumetric soil water content was recorded in both treatments with EC-5 soil moisture sensors (Decagon, Pullman, USA) installed at 5- and 40-cm soil depths (Online Resource 3). Although the soil water content was considerably lower in the subsoil than in the topsoil, this does not correspond to plant available water because soil texture differed substantially between the two layers. The permanent wilting point of humus exceeds 20 % (Zuber 2007) whereas that of a sandy/gravelly soil lies between 2 and 4 % (Singer and Munns 2006). In the topsoil, the permanent wilting point was therefore reached approximately within 1 month after the onset of the drought (cf. Online Resource 3). By contrast, it is difficult to define when plant available water reached critical levels in the subsoil because the accuracy of EC-5 soil moisture sensors is about 1–2 % even after soil-specific calibration.

2.3 Seedling emergence and survival

Emergence rate in the mesocosms exceeded 75 % in *Pseudotsuga menziesii* from the USA and both *Pinus sylvestris* populations, which is slightly lower than the germination rate under lab conditions (Online Resource 2). The quality of *Pseudotsuga menziesii* seeds from Germany was poor: while 46 % of the seeds were germinated under lab conditions, only 27 % emerged in the mesocosms. In order to ensure similar levels of competition among seedlings, the number of seedlings per square was reduced to four in April 2013, to two in October 2013 and to one in May 2014 by randomly selecting seedlings to be harvested/removed. According to Poorter et al. (2012), plant growth in container or pot experiments is likely to be reduced when the total biomass exceeds 1 g L⁻¹ soil volume. In our experiment, total plant biomass per mesocosm amounted

to 0.4 g L⁻¹ in September 2012, to 1.1 (control) and 0.7 (drought) g L⁻¹ in September 2013 and to 3.6 (control) and 1.6 (drought) g L⁻¹ in September 2014. This suggests that mesocosm size potentially limited the growth of control seedlings in 2014 but not in 2012 and 2013. Bigger mesocosms might have resulted in higher biomass of control seedlings and thus more pronounced treatment effects in 2014.

Due to the large number of replicates in the overall experiment (5 blocks × 2 mesocosms × 2 half-mesocosms × 70 squares = 1400 squares; cf. Online Resource 1), it was not feasible to regularly count the number of seedlings per square. The number of squares with living seedlings was recorded instead, although not for all the treatments and half-mesocosms at the same time (details in Online Resource 4). Direct calculations of seedling mortality are thus impossible and the proportion of squares with at least one living seedling was used as a surrogate of seedling survival. We are aware that this is a very rough estimate of survival, which underestimates mortality rates of individual seedlings. Nevertheless, we consider it crucial to have an approximate measure of survival in order to evaluate regeneration success.

2.4 Biomass allocation, plant architecture and relative growth rate

Plant architecture and biomass allocation were assessed in September 2013 and 2014 by excavating the seedlings of one randomly selected block. The following parameters were measured on one randomly selected seedling per square (two half-mesocosms per treatment × five squares per population = ten replicates per treatment and population): the longest vertical root, the longest lateral root (Online Resource 5), shoot height (from the root collar to the insertion of the bud), shoot and root biomass (after drying to constant weight). In the non-excavated blocks, shoot biomass was measured at the end of each growing season, i.e. at the end of September 2012, 2013 and 2014, by randomly selecting five squares per mesocosm and population and harvesting one random seedling per square. Details on sample sizes are given in Online Resource 4. Relative growth rates (V_{2013}/V_{2012} and V_{2014}/V_{2013}) were calculated on an annual basis (September–September) for shoot and root biomass, shoot height and vertical and lateral root length.

2.5 Data analyses

Effects of the drought treatment, species and populations on shoot and root biomass, vertical and lateral root length and relative growth rates were tested with linear mixed effects models using the statistics program R (R Core Team 2015) and the lmer function of the lme4 package. Blocks were treated as a random effect and treatment, species and population as fixed effects with populations being nested in species. Since the lmer function does not provide *P* values for the fixed effects,

we calculated *P* values using the lmerTest package. A simultaneous test for multiple comparisons of means using Holm adjustment was conducted with the glht function from the multcomp package (Hothorn et al. 2008). In 2013, only one

seedling of the German *Pseudotsuga menziesii* population was present in the drought-stressed container of the block selected for the root harvest, thus statistical tests of root parameters neglect this population (cf. Figs. 1, 2 and 3).

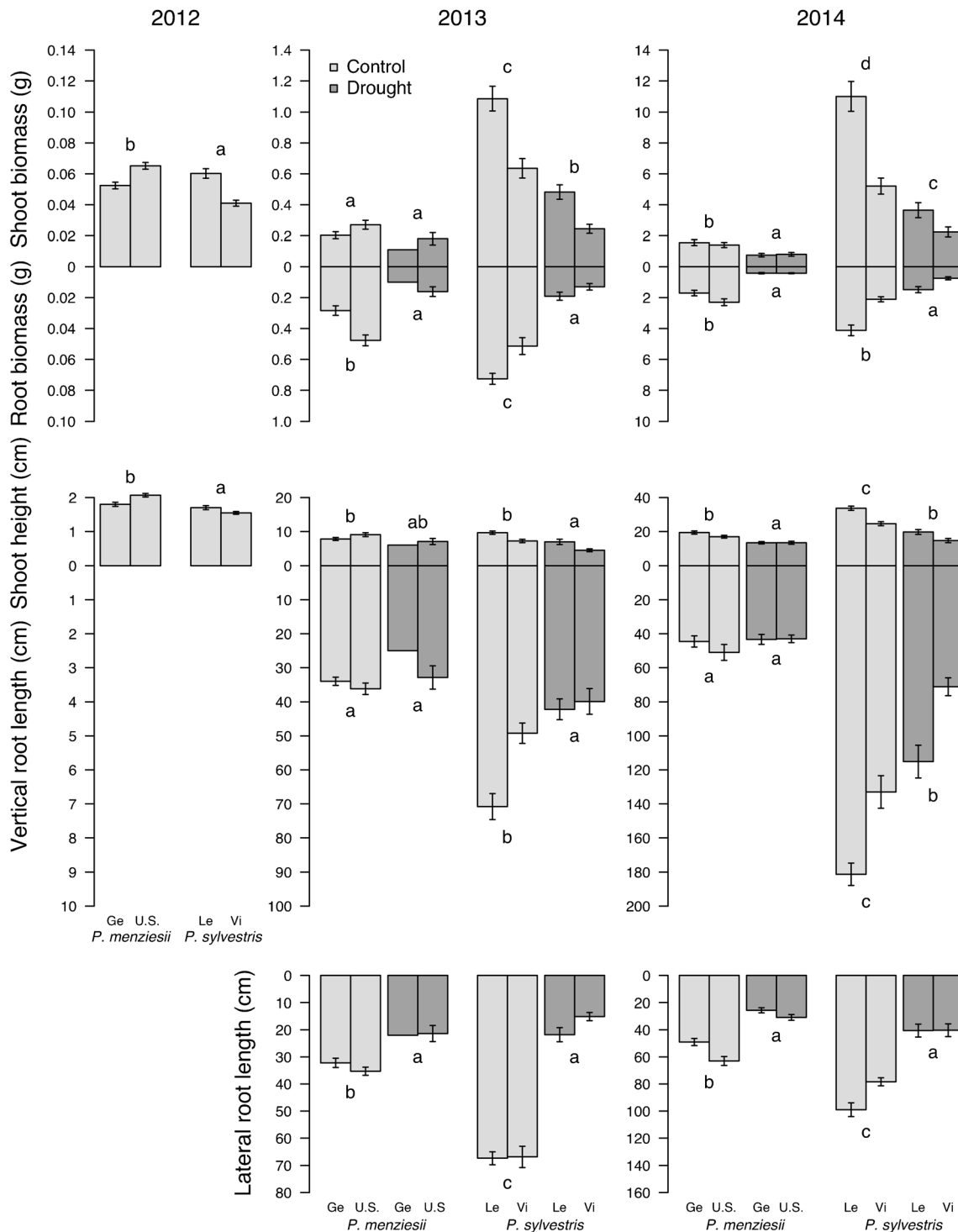
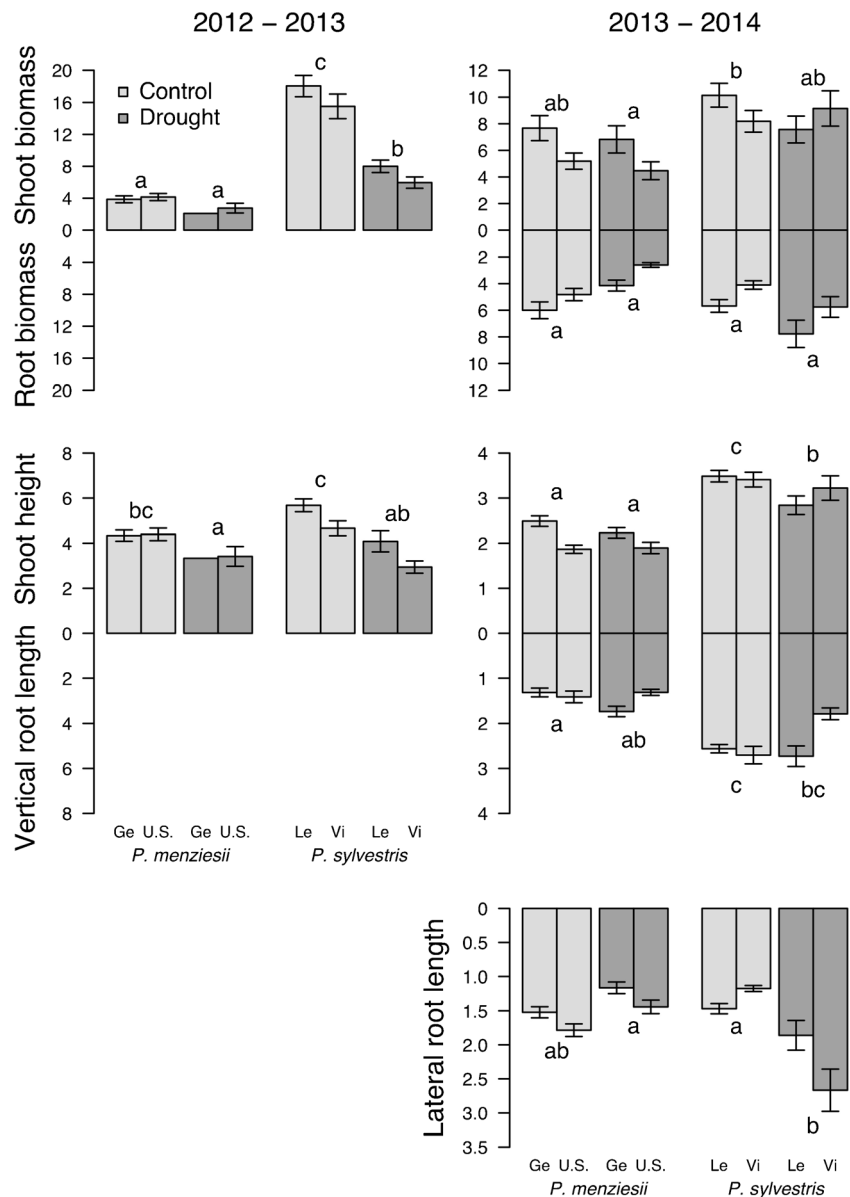


Fig. 1 Aboveground and belowground biomass, shoot height and vertical and lateral root length of 1- (2012), 2- (2013) and 3-year old (2014) *Pseudotsuga menziesii* and *Pinus sylvestris* seedlings growing under current precipitation (control) and recurrent, prolonged drought

(2013 and 2014), respectively. Bars represent means ± SE. Identical letters above/below two bars indicate no statistical differences between means in the same year. Note the different scales on the y-axis in different years

Fig. 2 Relative growth rates of *Pseudotsuga menziesii* and *Pinus sylvestris* seedlings growing under current precipitation (control) and recurrent, prolonged drought (2013 and 2014), respectively: shoot biomass, shoot height, root biomass, vertical root length and lateral root length



The phenotypic plasticity of individual species-population combinations was quantified using the relative distance plasticity index (RDPI) proposed by Valladares et al. (2006), which is based on phenotypic distances among individuals of a given species-population combination exposed to different environments. In our study, RDPI was defined as the average of partial RDPIs for shoot biomass, root biomass, vertical root length and lateral root length.

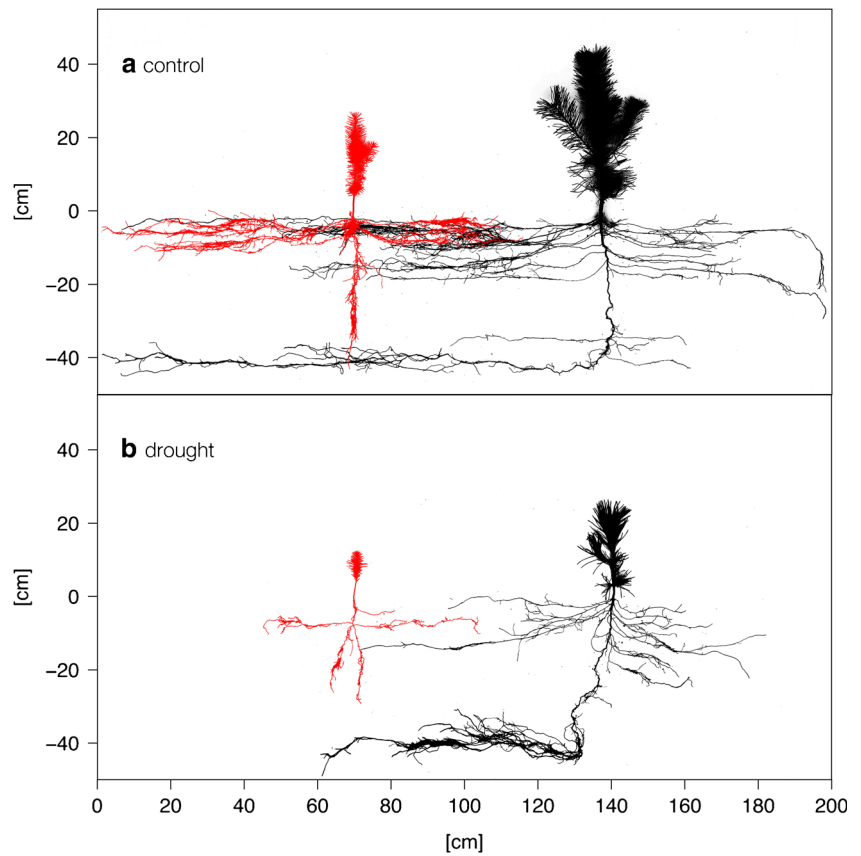
3 Results

3.1 Aboveground biomass and shoot height

Pseudotsuga menziesii and *Pinus sylvestris* differed considerably in their temporal pattern of biomass allocation. While

Pseudotsuga menziesii seedlings had slightly more biomass and were slightly taller than *Pinus sylvestris* seedlings at the end of the first growing season (Fig. 1, Table 2), the growth rate of the aboveground biomass was considerably higher in *Pinus sylvestris* between 2012 and 2013 (Fig. 2, Table 3). Consequently, *Pinus sylvestris* seedlings were equally tall but heavier than the *Pseudotsuga menziesii* seedlings by the end of the second growing season (Fig. 1). Between 2013 and 2014, both species grew at similar rates in terms of aboveground biomass, but *Pinus sylvestris* had a more pronounced shoot height growth than did *Pseudotsuga menziesii* (Fig. 2). The higher relative growth rates of *Pinus sylvestris* in terms of aboveground biomass 2012–2013 and in terms of shoot height 2013–2014 resulted in up to eight (control) and five (drought) times more aboveground biomass and two (control) and 1.5

Fig. 3 *Pseudotsuga menziesii* (red) and *Pinus sylvestris* (black) seedlings grown under contrasting water conditions in a common garden in the Rhone valley, Switzerland. The seedlings were excavated from mesocosms (200 cm × 80 cm × 50 cm) at the end of the third growing season. Original photograph in Online Resource 5



(drought) times taller seedlings by the end of the experiment (Fig. 1). Both species reduced shoot height growth in response to the drought between 2012 and 2013. Droughted *Pinus sylvestris* seedlings simultaneously diminished aboveground biomass growth and further reduced shoot height growth between 2013 and 2014 (Fig. 2, Table 3). As a result, droughted *Pinus sylvestris* seedlings reduced aboveground biomass to a larger extent than did

Pseudotsuga menziesii seedlings, but overall, they were still heavier and taller than *Pseudotsuga menziesii* after the third growing season (Fig. 1, Table 2). Populations differed in both species and all years with respect to both shoot biomass and shoot height. Population effects, however, were smaller than species (shoot biomass) or treatment (shoot height) effects, as indicated by the lower F-values (Table 2).

Table 2 Shoot and root biomass, shoot height and vertical and lateral root length of *Pseudotsuga menziesii* and *Pinus sylvestris* seedlings: ANOVA results for the effects of drought treatment (whole-plot factor), species (split-plot factor) and population (nested within species)

Year	Source of variation	Shoot biomass			Shoot height			Root biomass			Vertical root length			Lateral root length			
		d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	
2012	Species	1,85	14.5	<0.001	1,84	33.5	<0.001										
	Population in species	2,85	22.9	<0.001	2,84	7.8	<0.001										
2013	Treatment	1,47	29.9	<0.001	1,100	20.4	<0.001	1,62	71.5	<0.001	1,52	15.8	<0.001	1,61	111.5	<0.001	
	Species	1,132	88.3	<0.001	1,132	0.6	0.435	1,62	7.5	0.008	1,3	20.7	0.026	1,61	18.9	<0.001	
	Treatment x species	1,131	1.9	0.171	1,132	0.5	0.469	1,62	0.8	0.376	1,52	5.7	0.020	1,61	27.1	<0.001	
	Population in species	2,132	15.8	<0.001	2,132	11.4	<0.001	2,62	6.9	<0.001				2,61	1.2	0.316	
2014	Treatment	1,178	80.5	<0.001	1,178	105.4	<0.001	1,60	99.1	<0.001	1,60	18.4	<0.001	1,59	88.7	<0.001	
	Species	1,178	192.9	<0.001	1,178	69.4	<0.001	1,5	2.0	0.215	1,2	70.1	0.014	1,4	5.2	0.083	
	Treatment x species	1,178	7.0	0.009	1,178	14.2	<0.001	1,60	0.4	0.515	1,60	13.6	<0.001	1,59	3.5	0.067	
	Population in species	2,178	7.8	<0.001	2,178	17.4	<0.001	2,6	1.4	0.322				2,4	0.6	0.574	

Bold font indicates *P* values <0.05

Table 3 Relative growth rates of *Pseudotsuga menziesii* and *Pinus sylvestris* seedlings: ANOVA results for the effects of drought treatment (whole-plot factor), species (split-plot factor) and population (nested within species)

Period	Source of variation	Shoot biomass			Shoot height			Root biomass			Vertical root length			Lateral root length			
		d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	
2012–2013	Treatment	1,47	29.9	<0.001	1,97	20.1	<0.001										
	Species	1,132	115.7	<0.001	1,132	1.8	0.179										
	Treatment x species	1,131	1.9	0.171	1,132	0.9	0.344										
	Population in species	2,132	2.0	0.140	2,132	5.4	0.006										
2013–2014	Treatment	1,178	4.7	0.032	1,178	6.2	0.013	1,60	0.5	0.465	1,67	0.0	0.957	1,60	1.7	0.193	
	Species	1,178	11.0	0.001	1,178	84.1	<0.001	1,5	0.5	0.503	1,67	22.2	<0.001	1,4	0.6	0.491	
	Treatment x species	1,178	0.7	0.420	1,178	2.1	0.148	1,60	6.3	0.015	1,67	3.3	0.075	1,60	14.3	<0.001	
	Population in species	2,178	4.0	0.019	2,178	5.6	0.005	2,5	0.6	0.590	2,67	0.6	0.545	2,4	0.3	0.754	

Bold font indicates P values <0.05

3.2 Belowground biomass and root architecture

The proportion of biomass allocated to roots was two to three times higher in *Pseudotsuga menziesii* than in *Pinus sylvestris*, irrespective of the treatment (2013 and 2014: $P < 0.001$; Online Resource 6). In absolute terms, *Pinus sylvestris* seedlings had higher root biomass than did *Pseudotsuga menziesii* in the control treatment in 2013, but this difference disappeared in 2014 (Fig. 1, Table 2). Under dry conditions, both species drastically reduced root biomass and lateral root length, while vertical root length was only affected in *Pinus sylvestris* seedlings. Nevertheless, the vertical roots of *Pinus sylvestris* were distinctly longer than those of *Pseudotsuga menziesii* at the end of the third growing season, both under dry and control conditions. Relative growth rates of root biomass and vertical root length were unaffected by drought in both species, but *Pinus sylvestris* seedlings clearly expanded their lateral roots under dry conditions (Fig. 2, Table 3). Lateral root length of *Pseudotsuga menziesii* and *Pinus sylvestris* seedlings were similar under dry conditions (Fig. 1). In the controls, by contrast, *Pinus sylvestris* had longer lateral and vertical roots than did *Pseudotsuga menziesii* (Fig. 3).

3.3 Phenotypic plasticity

The contrasting responses of *Pseudotsuga menziesii* and *Pinus sylvestris* to the drought treatment with respect to shoot biomass and vertical root length are also reflected in the relative distance plasticity index (RDPI). While the *Pinus sylvestris* populations were moderately plastic in both years, the RDPI of the *Pseudotsuga menziesii* populations was considerably lower after the first summer drought (i.e. the second growing season; $P < 0.001$, Fig. 4). The plasticity of *Pseudotsuga menziesii* increased during the third growing

season and reached similar levels as *Pinus sylvestris* in 2014 ($P = 0.905$).

3.4 Seedling mortality

We were not able to record the mortality of the individual trees, but the proportion of squares that contains living seedlings at a given point in time indicates that in the German *Pseudotsuga menziesii* population, mortality occurred already in April/May 2013, i.e. before the onset of the summer drought treatment (Fig. 5). Lower germination under lab conditions and lower emergence in the common garden compared to *Pseudotsuga menziesii* from USA (Online Resource 2) suggest that the seed quality of the German *Pseudotsuga menziesii* population was poor, which might be the cause of

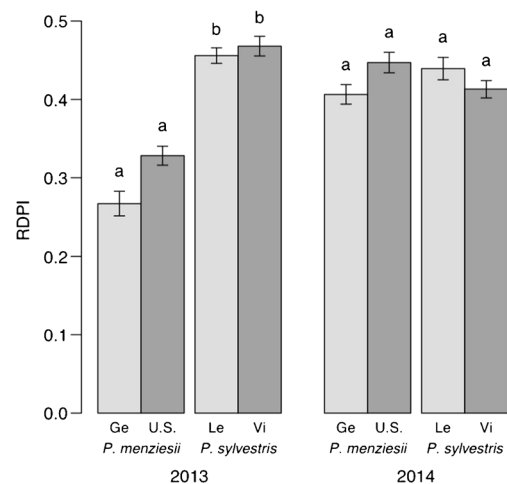


Fig. 4 Phenotypic plasticity of *Pseudotsuga menziesii* and *Pinus sylvestris* populations in terms of the relative distance plasticity index (RDPI), which was calculated based on shoot biomass, root biomass, maximum vertical root length and maximum lateral root length. Identical letters above two bars indicate no statistical differences between means in the same year

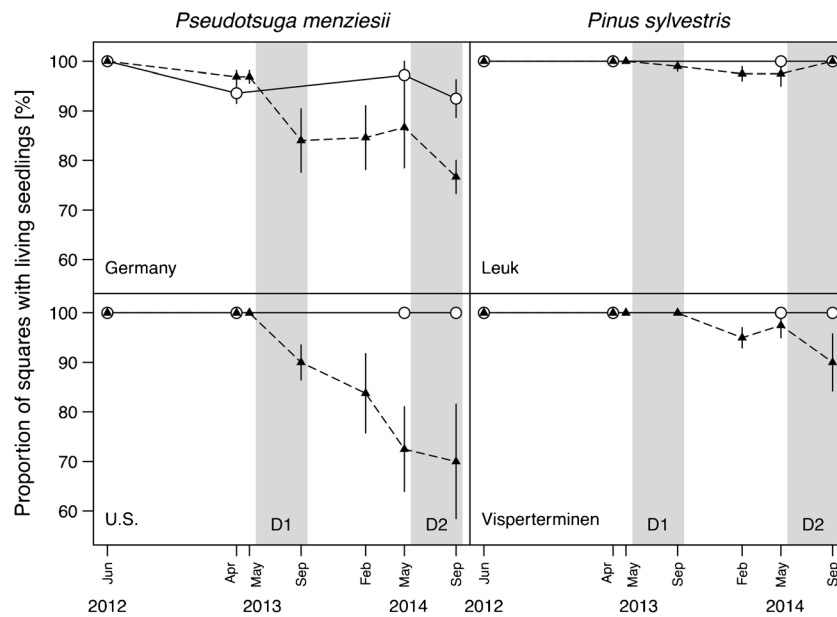


Fig. 5 Survival of *Pseudotsuga menziesii* and *Pinus sylvestris* seedlings of different origin in the course of the experiment measured in terms of the proportion of squares containing at least one living seedling. *Black line and open circles* denote the control treatment, *dashed line and triangles* the drought treatment and *vertical bars* represent standard

errors at the block level. Surveys in different treatments took place at different times and did not always include the same replicates (Online Resource 4); thus, the proportion of squares with living seedlings can increase from one time step to the next. *D1* summer drought June–September 2013; *D2* summer drought June–September 2014

some of the observed mortality. Apart from German *Pseudotsuga menziesii*, seedling survival was so high in the control treatment that living seedlings were recorded in all squares at the end of the experiment in September 2014. At the same time, more than 90 % of the droughted *Pinus sylvestris* squares contained living seedlings but only 76.6 % of German *Pseudotsuga menziesii* and 70 % of *Pseudotsuga menziesii* from the USA. The mortality of the latter two concurs with lower plasticity and limited vertical root proliferation in *Pseudotsuga menziesii* populations.

4 Discussion

Pseudotsuga menziesii is discussed as a non-native alternative to *Picea abies* for wood production in Central Europe given the projections of a drier future climate (Vor et al. 2015). As a result, its use in plantations has increased in recent years (Forest Europe 2015). Nature conservationists, on the other hand, point to its potential to spread outside plantations (Essl 2005) as well as to the risk of co-introducing exotic organisms, which may potentially jump from their original host to native species (Roques et al. 2006; Schmid et al. 2014). The wide field of uncertainties that lies between the propagation of *Pseudotsuga menziesii* for wood production and the risks of its natural spread might be reduced by assessing the species’ potential to naturally regenerate under current and future climatic conditions. The successful establishment of any (tree)

species is primarily driven by its ability to efficiently capture resources such as light, water and nutrients (Rewald and Leuschner 2009; Schulte et al. 2013) and is consequently related to its ability to quickly extend roots and occupy a large soil volume (Mommer et al. 2011; Rajaniemi 2007; Zhang et al. 2012). Root architecture and soil exploitation strategy are thus important components of a species’ competitive ability (Messier et al. 2009). The relative competitive ability of individual species growing in mixtures under specific environmental conditions can be estimated in terms of their relative growth rates (Rewald and Leuschner 2009). By the end of the first growing season, *Pseudotsuga menziesii* seedlings had accumulated slightly more aboveground biomass and were slightly taller than the *Pinus sylvestris* seedlings, which is likely to be a consequence of a 1.5-fold higher seed mass. During the following years, however, *Pinus sylvestris* grew faster both under moist and dry conditions, first in terms of shoot biomass (2012–2013) and then in terms of shoot height (2013–2014; Fig. 2). The growth rate of root biomass was similar in both species and treatments, but *Pinus sylvestris* exhibited a larger increment of vertical roots under moist conditions as opposed to a higher increment of lateral roots under dry conditions (2013–2014). We confer that, relative to *Pinus sylvestris*, *Pseudotsuga menziesii* is less competitive during early establishment both under current levels of summer precipitation as well as under prolonged summer drought. This is corroborated by the fact that seedling survival was lower in *Pseudotsuga menziesii* (Fig. 5), even though the seedlings

allocated a considerably larger proportion of biomass to roots than did *Pinus sylvestris*. Padilla and Pugnaire (2007) demonstrated, however, that the drought resistance of several Mediterranean shrubs is related to rooting depth rather than to root/shoot ratio. Regarding our experiment, all seedlings had lower shoot and root biomass as well as shorter lateral roots after two consecutive summer droughts than did the control seedlings. But, the two species contrasted in terms of absolute vertical root length and how this was affected by drought: after three growing seasons, the vertical roots of *Pinus sylvestris* extended up to 400 % (control) and 250 % (drought) farther than those of *Pseudotsuga menziesii*. We are aware that these results might be a consequence of the specific soil conditions in our experiment. But, they are in accordance with greenhouse studies showing that *Pseudotsuga menziesii* seedlings enhance resource use efficiency under dry conditions rather than altering root architecture (Conlin and van den Driessche 2006), which might be attained by increasing fine root biomass (Tingey et al. 2005). The fact that the root architecture of *Pseudotsuga menziesii* is unresponsive to abrupt changes in environmental conditions is also known from adult trees (Briggs et al. 2012). Longer roots enable *Pinus sylvestris* seedlings to reach deeper water pools already during early establishment. Deep water pools are depleted more slowly (Ryel et al. 2008) and enable plants with an extensive root system to outlast transient drought periods (Niinemets 2010). By contrast, 40–50-year-old *Pseudotsuga menziesii* have been shown to concentrate their root biomass in the top 10–40 cm of the forest soil (Curt et al. 2001; Eis 1987), which, according to our results, seems to hold for seedlings as well (Fig. 3). The accumulation of fine roots in the upper soil layers seems to allow the species to efficiently exploit soil nutrients (Mauer and Palatova 2012) and might be the reason why *Pseudotsuga menziesii*, once established, is able to maintain high radial growth rates also under drier conditions (Eilmann and Rigling 2012; Lévesque et al. 2014). Plant available water in the upper soil layers is, on the other hand, strongly tied to single precipitation events (Rennenberg et al. 2006), which may put seedlings at risk of desiccation during long dry periods. Higher drought resistance of old (>400 years) compared to young (0–15 years) *Pseudotsuga menziesii* stands (Wharton et al. 2009) indicates that drought tolerance changes during the species' life cycle, and there is evidence that these changes are related to root properties. Old, but not young, *Pseudotsuga menziesii* trees are able to hydraulically redistribute water from deeper soil layers, thus increasing the soil water potential of the top soil and reducing the loss of shallow root function during drought (Domec et al. 2004). The absence of hydraulic redistribution in young *Pseudotsuga menziesii* might be the consequence of slow root proliferation to deeper soil layers during early life stages, as supported by the short vertical root lengths observed in our study. The susceptibility of *Pseudotsuga menziesii* to drought during establishment is further aggravated in deep

shade, as e.g. in dense stands (Marshall 1986), and on less fertile sites (Sergent et al. 2014). There may also be a genetic component to the drought resistance of individual populations (Eilmann et al. 2013). We found some differences between populations in both species, but they were far outweighed by species or treatment effects. In summary, root architecture seems to hamper the establishment of *Pseudotsuga menziesii* from seed under very dry conditions due to slow vertical root development, while the dense system of fine roots in the topsoil enables established saplings and mature trees to resist extended drought spells.

5 Conclusion

In contrast to *Pinus sylvestris*, *Pseudotsuga menziesii* seedlings have a shallow rooting behaviour and lower phenotypic plasticity, which concurs with lower survival rates under dry conditions. On the one hand, this implies that *Pseudotsuga menziesii* has only a low potential to spontaneously spread from plantations in drier regions of Central Europe, especially since climate change models project longer dry spells in the future (Lindner et al. 2014). On the other hand, extending plantations of *Pseudotsuga menziesii* from the current suitable range of *Picea abies* to that of *Pinus sylvestris*, as suggested by recent reports of higher radial growth rates of adult *Pseudotsuga menziesii* compared to *Pinus sylvestris* under dry conditions (Eilmann and Rigling 2012; Lévesque et al. 2014), has to be evaluated carefully. Since the early life stages of *Pseudotsuga menziesii* rely almost exclusively on the water available in the top soil, costly irrigation would be necessary to establish the species in dryer regions, such as lower elevations in Central Alpine valleys (Eilmann and Rigling 2012). The rooting behaviour of *Pinus sylvestris*, by contrast, with a distinct taproot that develops early during the seedling stage (Fig. 3), enables the species to quickly reach deeper soil layers (Lyr and Hoffmann 1967; Moser et al. 2015). Likewise, high phenotypic plasticity facilitates the establishment of *Pinus sylvestris* in disturbed environments despite their heterogeneity and low predictability (Chevin and Lande 2011). On shallow soils and under conditions of limiting water resources, as for instance in dry Central Alpine valleys, it is currently able to colonise and dominate drier locations than *Picea abies* (Brändli 2010).

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Compliance with ethical standards

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