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DOUGLAS-FIR CULTIVATION IN CENTRAL EUROPE - SUITABILITY OF FOREST SITES AND REPRODUCTIVE MATERIAL

Dissertation
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Submitted by
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Preface and list of papers

This work is a cumulative dissertation of three peer-reviewed articles either published or in press provided in the Appendix 8.1 to 8.3. The formatting of the publications varies due to the specific requirements of the different journals.

Paper I: **Eckhart, T.**, Hintsteiner, W., Lair, G., van Loo, M., Hasenauer, H., 2014. The Impact of Soil Conditions on the Growth of Douglas-fir in Austria. Austrian Journal of Forest Science, 131(2), 107-128.

Paper II: **Eckhart, T.**, Walcher, S., Hasenauer, H., van Loo, M., 2017. Genetic diversity and adaptive traits of European versus American Douglas-fir seedlings. European Journal of Forest Research, 136(5-6), 811-825. http://doi.org/10.1007/s10342-017-1072-1

Paper III: **Eckhart, T.**, Pötzelsberger, E., Koeck, R., Thom, D., Lair, G. J., van Loo, M., Hasenauer, H., in press. Forest stand productivity derived from site conditions: An assessment of old Douglas-fir stands (*Pseudotsuga menziesii* (Mirb.) Franco *var. menziesii*) in Central Europe. Annals of Forest Science.

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Abstract

An active forest transformation and the integration of more drought adapted native or non-native tree species is an important strategy to improve adaptiveness and to assure future productivity of European forests to a more extreme climate. Douglas-fir, a non-native tree species from North-Western America, is such an alternative tree species and due to its excellent growth performance, wood quality and its drought-tolerance, the interest in planting has increased substantially in Europe. The past experience in cultivating Douglas-fir in Europe has shown that the wrong selection of cultivation sites as well as origin of forest reproductive material resulted in periodic setbacks. To avoid costly plantation failures in the future, the overall aim of this study was to examine suitable site conditions for coastal Douglas-fir growth, and to investigate the suitability of reproductive material for a successful cultivation of Douglas-fir in Central Europe. Hence, important climatic and soil sensitive key drivers for Douglas-fir productivity across different forest regions in Central Europe were identified with the machine learning method *Random Forests*. We investigated European seed lots for their native origin, and we assessed the adaptability, growth and survival potential of European versus American Douglas-fir seed lots. We found that suitable site conditions for Douglas-fir cultivation refer to the climate, the soil moisture regime and the soil nutrient status. Douglas-fir grows well on acidic to slightly alkaline soil conditions, reflecting its broad physiological amplitude. Forest stand productivity is similar on carbonate and siliceous bedrock; no significant differences were found. Douglas-fir is able to perform well on forest sites classified as “high” risk of drought-stress, until a critical level of available water storage capacity is reached. This reflects the drought tolerance of Douglas-fir, and hence importance compared to other main native tree species like Norway spruce (*Picea abies*). Nonetheless, we also conclude that climate change may induce water stress at the warmest sites, e.g. in Eastern Austria. Genetic assignment tests showed that the European seedlings originate from recommended provenances but represent both varieties and inter-varietal admixed individuals. European seedlings have a lower genetic diversity versus the American seedlings and native populations, hence a reduced adaptive capacity. We conclude that the European seed lots originate from small sized stands with assortative mating, bearing the risk of bottleneck effects and inbreeding in next generations. Therefore, we recommend the use of Douglas-fir seedlings from certified Native American seed stands or seed orchards and/or from European seed orchards to ensure high genetic variation and adaptive capacity in the regenerated stands. To be able to cover the demand with local European seedlings, we advise to revise the national requirements for European Douglas-fir seed stands.

Key words: *Douglas-fir, climate change adaptation, site conditions, regeneration, adaptive capacity*

Kurzfassung

Die Einbringung trockenresistenter einheimischer oder nicht heimischer Baumarten ist eine wichtige Strategie, um die Anpassungsfähigkeit an den Klimawandel und somit Produktivität Europäischer Wälder zu steuern bzw. zu gewährleisten. Die Douglasie ist eine nordwestamerikanische Baumart und gilt aufgrund ihrer hervorragenden Wuchsleistung, Holzqualität und Trockenresistenz als eine der aussichtsreisten Alternativbaumarten in Europa. Die waldbauliche Bedeutung und das Interesse am Douglasienanbau nehmen stark zu. Bisherige Erfahrungen in Europa haben gezeigt, dass es vor allem durch die Wahl ungeeigneter Standorte und Provenienzen zu Misserfolgen kam. Daher ist ein fundiertes Wissen über die Standortseignung außerhalb ihres natürlichen Ursprunggebietes, sowie die Verfügbarkeit und Verwendung von qualitativ hochwertigem Vermehrungsgut ein zentrales Thema. Das Ziel der vorliegenden Arbeit war es daher, geeignete Standortbedingungen für das Wachstum der Küstendouglasien in Mitteleuropa abzuleiten, und die Eignung von europäischem im Vergleich zum heimischen Vermehrungsgut qualitativ zu testen. Die wichtigsten klimatischen und bodensensitiven Standortsfaktoren für das Douglasienwachstum wurden mit dem Klassifikationsverfahren *Random Forests* ermittelt. Europäische Saatgutpartien wurden auf ihre Herkunft im Ursprungsgebiet genetisch getestet, und wichtige Qualitätskriterien wie Anpassungsfähigkeit, Wachstum und Überlebensfähigkeit wurden mit amerikanischen Saatgutpartien verglichen. Die Analysen zeigten, dass die Standortseignung der Douglasie durch das Klima, den Bodenwasserhaushalt und den Nährstoffstatus des Bodens bestimmt wird. Die Douglasie kommt sowohl mit sauren als auch mit leicht alkalischen Bodenbedingungen sehr gut zurecht, was die breite physiologische Wachstumsamplitude widerspiegelt. Die Standortsproduktivität ist auf karbonatischem und silikatischem Grundgestein ähnlich, es konnten keine signifikanten Unterschiede festgestellt werden. Die Douglasie kann auch auf Standorten mit hohem Trockenstressrisiko eine gute Wachstumsleistung erbringen, bis das für die Douglasie ermittelte kritische Niveau der verfügbaren Wasserspeicherkapazität erreicht wird. Die Toleranz der Douglasie gegenüber Trockenstress ist vor allem im Vergleich zu anderen einheimischen Baumarten wie der Fichte (*Picea abies*) von großer Bedeutung. Dennoch gehen wir davon aus, dass es durch den Klimawandel auch in trockenen Regionen, wie etwa im Sommerwarmen Osten Österreichs, zu Trockenstress kommen kann. Die genetischen Analysen zeigten, dass die europäischen Saatgutpartien aus empfohlenen Herkunftsregionen stammen, einzelne Individuen jedoch der reinen Inlandsvarietät sowie einer Mischung (Intervarietät) zugeordnet werden konnten. Europäisches Saatgut weist im Vergleich zum amerikanischen Saatgut sowie einheimischen Populationen eine geringere genetische Vielfalt auf, was auf ein geringeres Anpassungspotenzial schließen lässt. Daraus kann abgeleitet werden, dass die europäischen Saatgutpartien aus kleineren Beständen abstammen, was zu einem erhöhten Risiko von Flaschenhalseffekten und Inzucht in den Folgegenerationen führen kann. Um eine hohe genetische Variation und Anpassungsfähigkeit der regenerierten Bestände sicherzustellen, empfehlen wir die Verwendung von identitätsgesichertem Douglasiensaatgut aus zertifizierten nordamerikanischen Saatgutbeständen oder Samenplantagen und/oder aus europäischen Samenplantagen mit hoher genetischer Diversität. Um die Nachfrage nach europäischem Saatgut decken zu können, empfehlen wir eine Überarbeitung der nationalen Anforderungen für europäische Douglasiensaatguterntebestände.

Schlüsselwörter: *Douglasie, Klimawandelanpassung, Standortsbedingungen, Regeneration, Anpassungsfähigkeit*

Contents

1 Introduction

Climatic warming has a huge impact on the world's forests, and may result in an increased or decreased forest productivity in the future (Bolte et al., 2009). The impacts on European forest ecosystems have been discussed controversially (Kapeller et al., 2012). While an increased forest growth can be attributed to an increase in the growing season length, atmospheric CO_2 concentrations and nitrogen deposition; an associated increase of prolonged drought periods poses a major constraint for forest stability and productivity (IPCC, 2014; Lindner et al., 2010). During recent decades, a general increasing forest growth trend was observed in Europe (Spiecker et al., 1996). The observed increase in European forest growth during the 20th century could be attributed to increasing nitrogen supply levels as key driver. In the future, however, the importance of climate change and increased CO_2 concentrations in the atmosphere will increase (Kahle et al., 2008). In Europe, the mean annual temperature for the last decade (2008-2017) was already 1.7°C warmer compared to pre-industrial conditions and is projected to increase in the range of 1.0°C to 4.5°C under RCP 4.5 and 2.5°C to 5.5°C under RCP 8.5 until the 21st century (EEA, 2018). Also an increase in the frequency and intensity of heat extremes was observed since 1950, and is projected to become even more frequent and intense across Europe during this century (EEA, 2018).

As most European forests are intensively managed, recent and future changes in forest stability and productivity are also recognized to be to a large extent anthropogenic (IPCC, 2014). In this context, an active forest transformation of forests which are especially sensitive to climate change, and the integration of more drought adapted native or non-native tree species, is suggested as an important strategy to improve adaptiveness and to assure future productivity of European forests to a more extreme climate (Bolte et al., 2010).

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is such a non-native tree species, and is seen as a promising option for adapting Central European forests and maintaining forest productivity (Eilmann et al., 2013). Douglas-fir, native in North-Western America, extends from British Columbia (Canada) to Mexico (2,200 x 4,500 km) and grows from sea level up to 3.000 m on the slopes of the Rocky mountains over a wide range of environmental conditions (Eckenwalder, 2009; Plomion et al., 2011). The species has adapted to different ecological conditions which resulted in specific patterns of genetic diversity and a large genetic variation in adaptive traits (e.g. growth performance, bud phenology, frost hardiness) within its wide natural distribution area (Gould et al., 2012; St. Clair, 2006; St. Clair et al., 2005). Two distinct varieties are known: (i) the coastal variety (*P. menziesii var. menziesii*) and (ii) the interior or Rocky Mountain variety (*P. menziesii var. glauca*) (Eckenwalder, 2009).

Due to its superior growth performance over a wide ecological niche, drought tolerance, high timber quality and its resistance towards diseases and insects, Douglas-fir was introduced into many countries worldwide (Bastien et al., 2013; Lavender and Hermann, 2014; Plomion et al., 2011). Douglas-fir wood has excellent mechanical properties, and is increasingly used for exterior wood covering (heartwood only), construction wood and in joinery (Bastien et al., 2013). In Europe, the species was introduced in 1827 and used for forest plantations by the end of the 19th century (Plomion et al., 2011). In most European countries, the first Douglas-fir stands showed excellent growth and healthy conditions. At the beginning of the twentieth century, however, further seed imports to Germany were less successful. This initiated the first systematic provenance trial in 1910 (east Berlin), followed by further provenance trials across Europe (Bastien et al., 2013). Results revealed the best growth performance of the coastal variety from the Cascades in Washington and Oregon (Bastien et al., 2013; Kleinschmit and Bastien, 1992). In Central Europe, provenances from the middle elevation zone of this area are better adapted to withstand fall and winter frosts (Ruetz, 1981; Weißenbacher, 2008). The interior variety shows lower growth rates and is more susceptible to needle cast (*Rhabdocline pseudotsugae*), and is only recommended for European countries with continental environments, like Sweden or Finland (Kleinschmit and Bastien, 1992).

Today, Douglas-fir is the economically most important non-native tree species in Europe (Lavender and Hermann, 2014), and regarded as a promising option to increase productivity and to adapt European forests to climate change (Spiecker et al., 2019). Currently, this species occupies more than 800,000 hectares in Europe (Kownatzki et al., 2011), which covers the largest area outside its natural range (Bastien et al., 2013). Most of the cultivated area is in France (50 %), followed by Germany with 25 % and other European countries. With the increasing promotion of Douglas-fir, also concerns about potential negative ecological impacts are expressed from nature conservation side. Studies of ecological consequences of Douglas-fir cultivation in Europe revealed minor ecological impacts compared to other non-native tree species (e.g. *Robinia pseudoacacia* in Europe) (Schmid et al., 2014). Douglas-fir, however, often causes changes in the species composition, and regenerates naturally especially on poor sites (dry, acidic), where it can outcompete native tree species (Schmid et al., 2014).

Choosing a suitable site is a prerequisite to ensure forest stand productivity and stability. Although climate characteristics in the natural range, especially the distribution of precipitation, are different from European patterns, Douglas-fir shows excellent growth performance and superior wood quality in Europe (Lavender and Hermann, 2014). While in Central Europe most of the precipitation occurs in summer, the native Douglas-fir region in North-Western America is dominated by winter precipitation and a dry summer period (Lavender and Hermann, 2014). It is widely accepted that in Central Europe, Douglas-fir prefers well drained, aerated and carbonate free soils (Vor et al., 2015). A lot of attention has been given to the carbonate content, as Douglas-fir growing on calcareous soils often shows leaf yellowing (chlorosis) (Englisch, 2008). Symptoms of toxicity are reported on sites with high manganese content and low pH value (LWF, 2008). However, little information is available on the growth performance across different soil types in Europe. To avoid any costly cultivation failures, suitable site conditions of non-native tree species have to be investigated thoroughly. In case of Douglas-fir, European forestry has already gained a lot of experience since the first introduction in 1827, and mature Douglas-fir stands can be analysed in retrospect.

In addition to site conditions, the genetic composition is also a decisive factor for the adaptation potential of forest stands. A high genetic diversity is essential for the long-term survival of forests, as it provides the basis for adaption and resistance to stress and changing site conditions (Ivetić et al., 2016). In Europe, Douglas-fir stands are established by natural or artificial regeneration. For artificial regeneration, the selection of suitable forest reproductive material (seeds, parts of plants, planting stocks) is essential to ensure high productivity rates and a high adaptive capacity. Two legal frameworks, (1) the European Council Directive 1999/105/EC for Members of the European Union; and (2) the regulation of the Organization for Economic Co-operation and Development (OECD) open for all countries (Ackzell, 2002), provide a system of traceability and quality control of forest reproductive material (FRM).

With the increasing promotion of Douglas-fir, also the demand in forest reproductive material increases. Currently, seeds from both non-native European and native American seed stands are used for plantations in Europe. European seed sources are often favoured over American seeds. Although many of the European seed sources from older plantations (established prior to the 1980s) are of unknown origin (Bastien et al., 2013), they are recognized as valuable seeds not only due to their growth performance, it is also assumed that the local plantations are appropriate for the current ecological conditions in Europe due to undergone natural selection processes (Berney, 1972).

During the last decade, intense research on the genetic characteristics of Douglas-fir populations throughout its native range (van Loo et al., 2015) and in Central Europe (Hintsteiner et al., 2018) was carried out at the Institute of Silviculture (University of Natural Resources and Life Sciences, Vienna). The established tool enables to (i) assess the genetic diversity, (ii) trace back the origin of forest stands and reproductive material and (iii) identify admixed populations in Douglas-fir stands. Hintsteiner et al. (2018) analysed the genetic population structure of more than 60 mature European Douglas-fir stands, most of them certified as seed stands. Although the majority were assigned to recommended seed zones, up to 30 % of the European stands were qualified as admixed populations.

For silvicultural practices and measures, an assured knowledge about the origin and genetic admixture is needed, to avoid (i) the contribution of unsuitable provenances to the genepool of regenerated stands and (ii) disadvantageous population structures and mating patterns which limit gene flow (Hintsteiner et al., 2018). There are also concerns about the effective number of parents in European seed stands as they are often small in size (less than 1 ha) and show a patchy tree distribution with an unbalanced parental reproduction success. If only a portion of individuals contribute to the gametes pool, gene flow to the next generation is limited (Ivetić et al., 2016). By comparison, large Douglas-fir stands in the native distribution range ensure a widespread population with an extensive gene flow.

The past experience in cultivating Douglas-fir in Europe has shown that the wrong selection of cultivation sites as well as origin of forest reproductive material resulted in periodic setbacks (Berney, 1972; Konnert and Ruetz, 2006). Hence, costly plantation failures in the future can only be avoided by selecting (i) forest sites suitable for Douglas-fir growth, and (ii) forest reproductive material with knowledge about the native origin and genetic diversity. Thereby, site suitability guides the selection of tree species for reforestation and forest management decisions. This includes climatic factors as well as the soil moisture and soil nutrient regimes on a given forest site. The approved origin and genetic diversity determines the current and future adaptation potential of the forest tree populations to stress and changing climatic conditions. Hence, a high genetic diversity must be guaranteed in the regenerated stands, and even more importantly, maintained in the next generations. This can only be achieved by avoiding the contribution of unsuitable provenances and populations structures to the genepool of regenerated stands.

2 Objectives

With the increasing demand in cultivating Douglas-fir in Central Europe, profound knowledge about suitable site conditions and reproductive material is indispensable to avoid costly plantation failures in the future. Hence, the aim of this thesis was to derive suitable site conditions for coastal Douglas-fir growth, and to investigate the suitability of reproductive material from native seed sources in North America and local non-native seeds in Europe. Data on tree growth, climate, soil characteristics and geology were sampled across different forest regions in Austria and Germany. Two different statistical methods were applied to analyse the relationship between site conditions and growth potential. We tested European seedlings for their native origin (variety and potential geographic origin in America), and investigated the adaptation, survival and growth potential of European versus American Douglas-fir seed sources.

The objectives can be specified as follows:

- Pre-analysis of Douglas-fir growth based on an individual tree basal area increment model and a site index model with preliminary data to understand forest dynamics and stand productivity,
- comprehensive assessment of Douglas-fir stand productivity based on an enlarged data set to elucidate non-linear impacts of climatic- and physico-chemical growth drivers and derive most suitable site conditions,
- assessment of the native origin population structure of European seed sources to avoid the contribution of unsuitable provenances to the genepool of regenerated stands, and
- multiple comparisons of genetic diversity and adaptive traits of European versus American Douglas-fir seed sources to ensure high genetic variation and adaptive capacity in the regenerated stands.

These objectives are addressed in three papers which are referenced as Paper I, Paper II and Paper III in the text and illustrated in Figure 1.

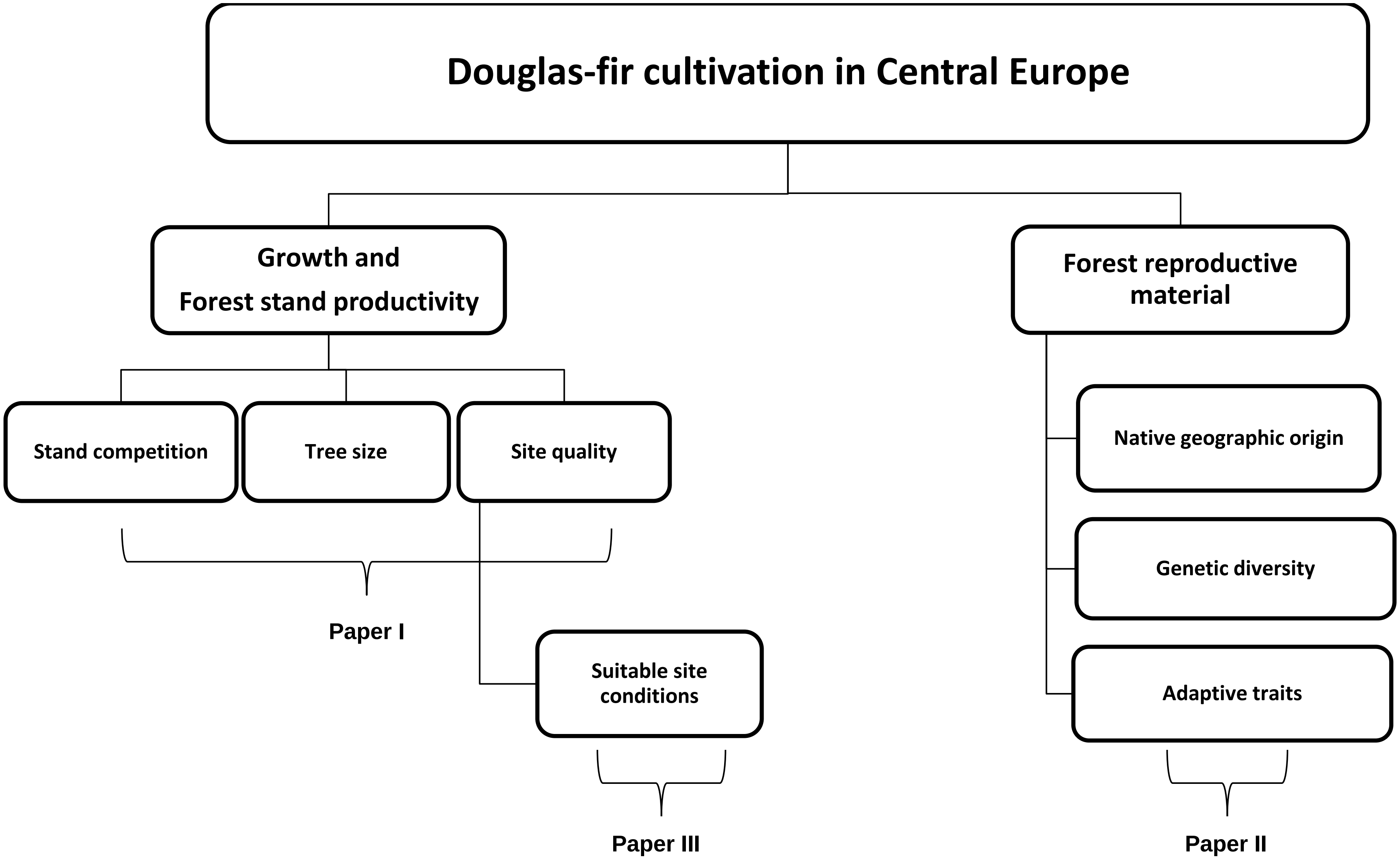

Figure 1: Schematic illustration of the contribution of the individual papers

3 Material and Methods

3.1 Study sites

In total, 28 mature Douglas-fir stands (D01-D28) were available to collect tree and physico-chemical soil data and to model climatic data. The forest stands are located in Eastern Austria in the provinces Burgenland, Lower Austria and Upper Austria, and in Southern Germany in Baden-Württemberg and Bavaria (Figure 2). The study sites represent a wide range of site, climatic, geological and topographic conditions. Mean annual temperature ranges from 570 mm to 2,100 mm and an annual temperature gradient between 7°C and 9.9°C is covered (see Paper III in Appendix 8.3 for details).

The 28 Douglas-fir stands originate from the western Cascades and the coastal region in Washington and Oregon (Hintsteiner et al., 2018). An important criteria was the assessment of productivity comprising only recommended Douglas-fir provenances (Chakraborty et al., 2016; Kleinschmit et al., 1979; Ruetz, 1981; Schultze and Raschka, 2002) to minimize any potential genetic differences in the growth performance.

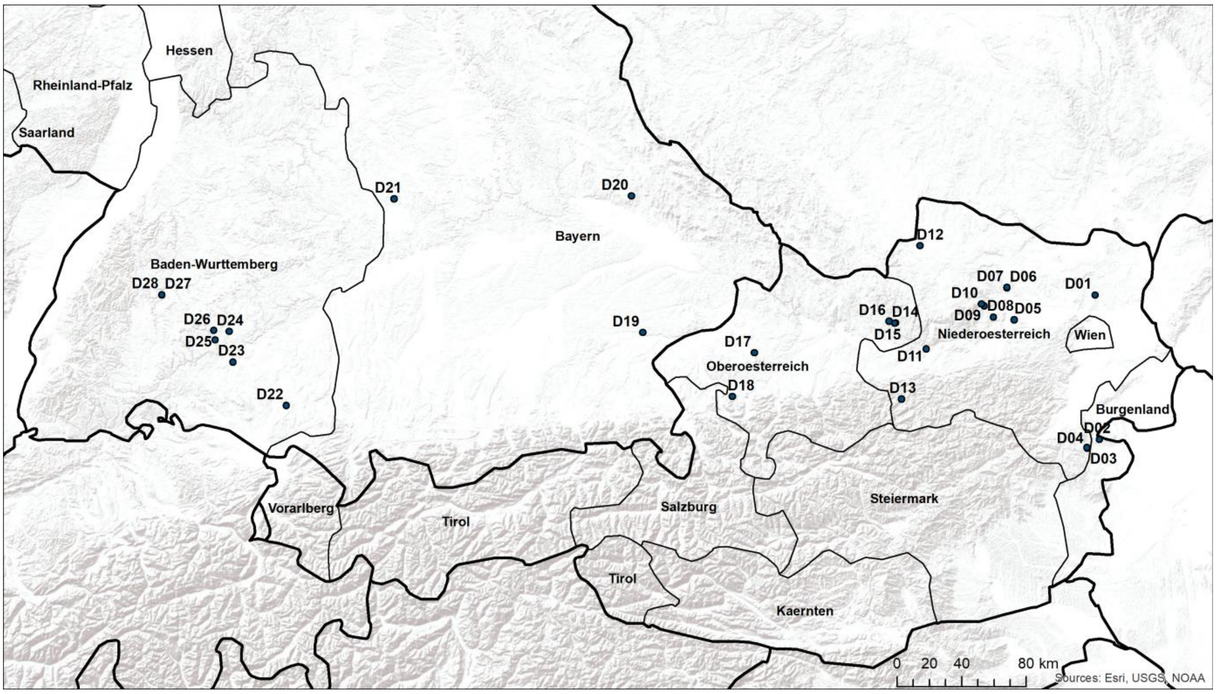

Figure 2: Location of all 28 Douglas-fir sites (D01-D28) in Austria and Germany.

3.2 Data collection

Individual tree and physico-chemical soil data were collected during three consecutive years from 2012 to 2014 in even-aged Douglas-fir stands with a minimum stand size of ≥ 1 ha and a proportion of Douglas-fir basal area of ≥ 80 %. For the years 2012 and 2013, a minimum age of 60 years of the forest stands was defined for data collection. For the year 2014, the minimum age was reduced to 40 years to be able to enlarge the site variation. Table 1 gives an overview of all collected/modelled data used for the forest growth and forest stand productivity assessment.

Table 1: Overview data collection.

Type of data and variables used for the assessment of forest growth and forest stand productivity. Sampling/modelling method describes the design or approach of data collection. Paper indicates in which publication the variables were used.

Type	Variable/Variable group	Description	Collected/Modelled	Paper
Forest data	Stand age	Borehole samples	fixed area plot/ 4 angel-count samples	I/III
	Stand basal area increment	Basal area increment 10yr	fixed area plot	I
	Stand density	Crown competition factor	fixed area plot	I
	Tree size effect	Mean DBH at the beginning of the growing period	fixed area plot	I
	Site index	Site index 100yr/60yr	fixed area plot/ 4 angel-count samples	I/III
Climate data	Annual precipitation	Period 1960-2010	DAYMENT Interpolation	I
	Summer precipitation [June, July, Aug]	Period 1960-2010/1981-2010	DAYMENT Interpolation	I/III
	Winter precipitation [Dec, Jan, Feb]	Period 1960-2010	DAYMENT Interpolation	I
	Mean annual temperature	Period 1960-2010	DAYMENT Interpolation	I
	Mean summer temperature [June, July, Aug]	Period 1960-2010/1981-2010	DAYMENT Interpolation	I/III
	Mean winter temperature [Dec, Jan, Feb]	Period 1960-2010	DAYMENT Interpolation	I
Physico-Chemical Soil parameters	pH value	Soil acidity	fixed area plot/ 3 angel-count samples	I, III
	N	Total nitrogen	fixed area plot/ 3 angel-count samples	I, III
	C	Carbon	fixed area plot/ 3 angel-count samples	I, III
	C/N	C/N ratio	fixed area plot/ 3 angel-count samples	I, III
	Cation soil nutrients	Calcium (Ca), Magnesium (Mg), Potassium (K), Iron (Fe), Aluminium (Al), Manganese (Mn)	fixed area plot/ 3 angel-count samples	I, III
	Anion soil nutrients	Nitrate ($NO3$), Nitrate ($NO2$), Phosphate ($PO4$), Sulfate ($SO4$)	fixed area plot/ 3 angel-count samples	I, III
	CEC eff.	Cation-Exchange Capacity	fixed area plot/ 3 angel-count samples	I, III
	BS	Base saturation	fixed area plot/ 3 angel-count samples	I, III
	Particle size distribution	Sand, silt, clay	fixed area plot/ 3 angel-count samples	I, III
	Skeleton	Soil Skeleton	fixed area plot/ 3 angel-count samples	I, III
	PV	Pore volume	fixed area plot/ 3 angel-count samples	I, III
	Soildepth	Effective soil depth	soil profile	III
	WHC	Water holding capacity	empirical pedo-transfer functions	III
Geology data	Bedrock material	Carbonate or siliceous bedrock	Geological maps of the Geological Survey of Austria and German Federal Institute for Geosciences and Natural Resources	III

3.2.1 Forest data

Data on tree diameter at breast height (dbh), height, wood cores, position and species were collected from one fixed area plot (radius 20 m) and three angle count samplings with a basal area factor of 4 (Bitterlich, 1948). The centre of the fixed area plot and the angle count samplings were randomly selected to represent relatively uniform forest stand and soil characteristics. Site index was used as a measure of forest stand productivity and calculated according to the dominant height growth function after Mitscherlich/Richard (1919) for "Douglas-fir northwestern Germany DoNwd" (Kindermann and Hasenauer, 2005) (details in Paper I and III).

For Paper I, forest data of the fixed area plot were used to determine stand age, stand basal area increment, stand density, tree size effect and the site index (SI) at the reference age of 100 years of eleven Douglas-fir stands (Table 1). Annual radial increments for the last 10 years were recorded and the values were converted to diameter increments (details in Paper I in Appendix 8.1).

For Paper III, forest data of 28 Douglas-fir stands were calculated based on four angel-count sampling plots to determine stand age and the site index (Table 1). Therefore, the fixed area plot was converted into the equivalent of an angle count sample based on tree distance to the centre and dbh for each stand (D01-D28). The limit maximum distance of a tree from the centre (D_{max}) based on the tree's dbh was calculated according to equation 1 with a basal area factor (*af*) of 4. Trees with a smaller distance to the centre than D_{max} were included in the derived angel-count sample.

Equation 1
$$Dmax = \frac{50 \times dbh}{\sqrt{af}}$$

Based on the stand age (40-120 years) of the sample plots, 60 years as reference age for the site index was used in Paper III.

3.2.2 Climate data

Site specific climate information for the years 1960 to 2010 and 1981 to 2010 (Table 1) were derived from the climate interpolation tool DAYMET using a network of national climate stations in Austria and Germany (Hasenauer et al., 2003; Petritsch, 2002; Thornton et al., 2000). The climate variables were calculated based on daily minimum and maximum temperature (Tmin, Tmax) and daily precipitation values and used as independent variables for the site index analysis (for details see Paper I and III).

3.2.3 Soil sampling and properties

At each sample plot (fixed area plot, 3 angel-count samplings) soil samples were collected to a depth of 35 cm with a gauge auger and separated into layer A (A horizon) and B (mineral soil). The bulk density for layer A and B was measured in undisturbed soil samples taken with metal cylinders (volume 100 cm³). Humus layers and mineral soil horizons were described according to the ‘‘Guidelines for Forest Site Mapping in Austria’’ (Englisch and Kilian, 1999) for each Douglas fir stand (see details in Paper III in Appendix 8.3).

The physico-chemical soil characteristics soil acidity (pH value), total nitrogen (N), carbon (C), C/N ratio, the cation nutrients calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^{+}), iron (Fe^{3+}), aluminum (Al^{3+}) and manganese (Mn^{2+}), the anion nutrients nitrate (NO^{3-}), nitrite (NO^{2-}), phosphate (PO_4^{3-}) and sulfate (SO_4^{2-}), cation exchange capacity (CEC_{eff}), base saturation (BS) and particle-size distribution (sand, silt, clay) were determined using standard laboratory methods (see Paper I and III).

For each soil parameter, the arithmetic mean of the four samples per layer, collected in one stand, was calculated. The physico-chemical soil variables were used as independent variables for the site index analysis (Table 1). To describe the soil water budget, the water holding capacity (WHC) at field capacity was calculated based on soil depth and sand, silt and clay percentages using empirical pedo-transfer functions (see details in Paper III).

3.2.4 Geology data

The exact geology for the Austrian stands was extracted from geological maps of the Geological Survey of Austria (GBA), if available 1:50,000 otherwise 1:200,000 maps for Upper Austria and Lower Austria. For the German stands, geological maps of the German Federal Institute for Geosciences and Natural Resources (BGR) were extracted from 1:200,000 geological maps (see details in Table 1 in Paper III). For the site index analysis, the bedrock material of the investigated Douglas-fir stands was separated into siliceous and carbonate bedrock (Table 1).

3.3 Seedlings and experimental design

For the assessment of Douglas-fir seedlings, 852 one-year-old seedlings from 10 different American and European seed lots and 5 provenance regions were available. Two seed stands are located in Austria, three in Germany and five in the US (Figure 3). The seed lots from the provenance regions Waldviertel (9.2) in Austria, Südostdeutsches Berg und Hügelland (853 06) in Germany, Darrington, Randle and Trout Lake in Washington were selected according to their high demand in Austria and Germany (Paper II in Appendix 8.2).

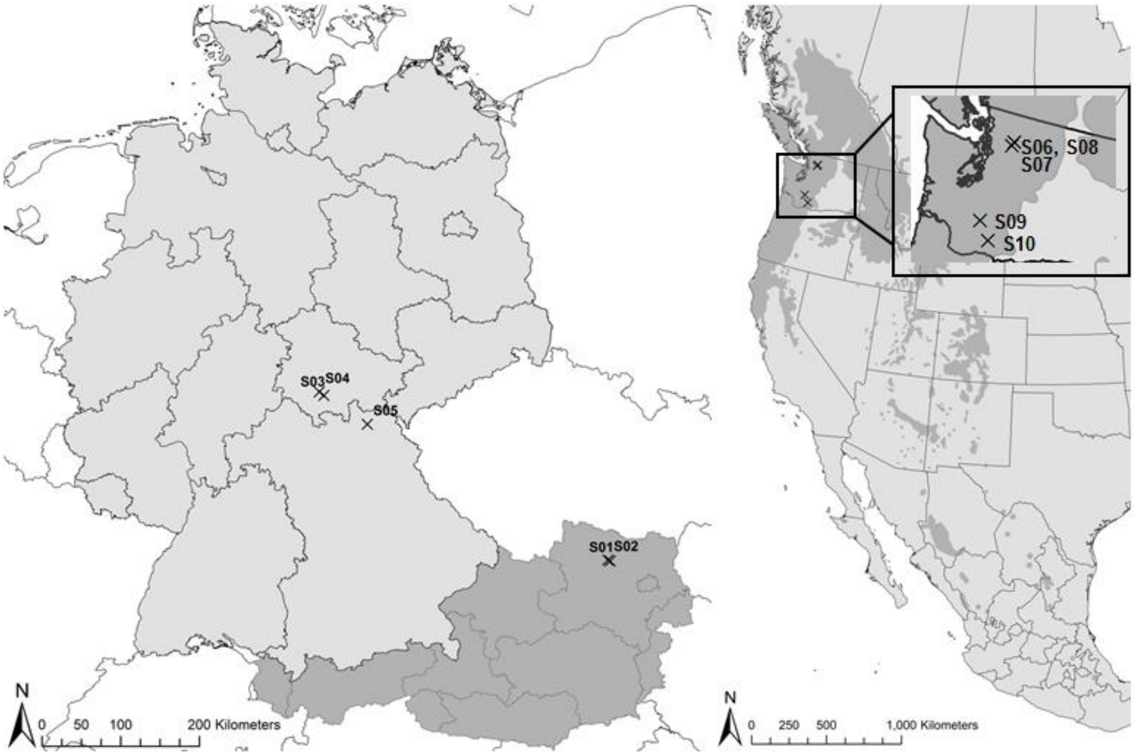

Figure 3: Map showing all seed source populations (S01-S10) in Europe and the US. The figure is taken from Paper II in Appendix 8.2.

In April 2012, the Douglas-fir seedlings were germinated in a commercial nursery in pots with a volume of 50 cm³ and a soil substrate of white peat (90 %) and horticultural pearlite (10 %). After germination, seedlings were separated and transported to the laboratory for DNA extraction and measurements. DNA was extracted from leaf samples of 30 seedlings per seed lot (in total 300 samples), amplified and genotyped with 13 nuclear SSRs to assess the geographic origin and genetic diversity of each seed lot. The morphological characteristics height and root collar diameter of each individual seedling was recorded. The seedlings were further cultivated in the experimental forest garden “Knödelhütte” in Vienna (Austria) to assess the bud burst development. Three different stages were recorded from February until April 2013: (1) dormant, (2) axillary bud burst completed and (3) terminal bud burst completed (Figure 4 of Paper II in Appendix 8.2).

3.4 Data analysis

3.4.1 Pre-analysis: Stand basal area increment and site index model

A basal area increment (BAI) model was developed for Douglas-fir based on a data set 11 mature Douglas-fir forest stands to predict basal area increment. As individual tree growth is potentially affected by the three factors (i) stand competition, (ii) tree size and (iii) site quality (Wykoff, 1990), these factors were tested for predicting the 10 year relative basal area increment per hectare (*rel.* BAI_{10}) of the Douglas-fir stands. Therefore, a nonlinear model was defined as follows:

Equation 2 $$rel.BAI_{10} = a \times x_{SD}^{b} \times x_{TSE}^{c} \times x_{SI}d$$

with the stand density x_{SD}, mean tree size x_{TSE} and the site index x_{SI}, and *a*, *b*, *c*, and *d* as model coefficients. The variation inflation factor (VIF) after Snee (1973, 1977) was calculated for each explanatory variable to test for multicollinearity (see details in Appendix 8.1). A sensitivity analysis was carried out to test the effects of the influencing factors on stand basal area increment (Paper I in Appendix 8.1).

In a next step, a site index model was defined based on the 11 mature Douglas-fir stands to assess significant growth drivers. Therefore, a multiple linear regression model was defined as follows:

Equation 3 $$SI = a + bx_t + cx_s + dx_c + \varepsilon$$

where *SI* is the site index at the reference age of 100 years, x_t, x_s, x_c are variables corresponding to the environmental factors topography, soil and climate, *a*, *b*, *c*, *d* represent model coefficients and ε is the additive error term. The simplified SI model assumed a linear relationship between the environmental factors and the site index. The variable selection process involved a series of steps beginning with an initial data exploration plotting the data and examining correlation statistics to identify those variables that may be useful in the SI model. The best predictor variables were selected according their significance level ($p < 0.05$) and tested for multicollinearity according to a variation inflation factor (VIF) < 5 (Paper I in Appendix 8.1).

3.4.2 Site Index model with *Random Forests*

The forest productivity assessment aimed to explore the dominant climatic and physico-chemical soil parameters and their effect size on the site index at age 60 years with the *Random Forests* regression approach (Breiman, 2001). The analysis comprised an enlarged data set of 28 mature Douglas-fir stands to increase the variation in forest site characteristics. *Random Forests* was used since it (i) is a non-parametric method, able to illustrate saturation levels as well as optimum ranges of key site factors driving Douglas-fir growth and (ii) has a high prediction accuracy even if predictor variables are moderately collinear (Dormann et al., 2013). In the *Random Forests* approach, multiple regression trees are constructed by randomizing the combinations and orders of the explanatory variables using the bootstrap approach. Thereby, 63 % of the data set is randomly selected for prediction, and the remaining 37 % are “out-of-bag” observations that determine the accuracy and error rates of the predictions (e.g. cross validation). Results are aggregated and form an ensemble, namely the random forest (Cutler et al., 2007).

The statistical analysis was carried out in two main steps:

I. Variable pre-selection:

   In a first step, relevant variables were selected using the Random Forests-based variable selection procedure of the VSURF package in R (Genuer et al., 2015)

II. Building final *Random Forests* model:

   The final *Random Forests* model was fitted using 2,000 regression trees. Results were illustrated in a variable importance plot and partial effect plots. The mean square error (MSE) was used as a measure of importance, indicating how much the prediction of the same model would get worse by omitting the variable. To show the effect of each explanatory variable on the site index variation, partial dependence plots were used (Cutler et al., 2007) (details in Paper III in Appendix 8.3).

3.4.3 Genetic population structure and adaptive traits of Douglas-fir seedlings

A number of factors that are important for successful regeneration of Douglas-fir in Central Europe were investigated. This included assignment tests to determine the variety and potential geographic origin of the European seedlings in North-western America, a comparison of the genetic diversity between the European and US seed source populations and multiple comparisons of adaptive traits among provenances.

3.4.3.1 Variety composition and potential native origin

The native origin of the European seed stands from where the seeds were harvested is unknown. Therefore, we were interested (i) which variety and native origin was represented, and (ii) whether there was an admixture of both varieties.

We used identical multilocus genotype data of the studied seedlings and the reference data set developed by van Loo et al. (2015). The reference data set represents genotypes of 746 individual Douglas-fir trees from 36 populations and covers the natural distribution range in North-western America.

For variety assessment, we performed a Bayesian cluster analysis of the individual seedlings and the 36 reference populations using the software STRUCTURE v.2.3.4 (Falush et al., 2007, 2003; Pritchard et al., 2000). Two clusters (K = 2), representing the coastal and the Rocky Mountain variety, were pre-defined based on the multilocus data of the reference data set, and individual seedlings were probabilistically assigned to clusters (K) that are genetically similar. For each independent model run, the program estimates a membership coefficient (Q), which corresponds to the probability of an individual belonging to each cluster. An individual was declared as coastal variety with $Q > 0.90$, as Rocky Mountain with $Q < 0.10$ and inter-varietal admixed with $0.90 > Q < 0.10$. Using the software CLUMPP v.1.1.2, we derived the optimal alignment of 20 independent runs in total, (Jakobsson and Rosenberg, 2007), and computed average values of *Q*. We plotted the average membership coefficients using DISTRUCT v.1.1 (Rosenberg, 2004) (see details of the analysis in Appendix 8.2).

In a next step, the potential geographic origin of the studied European seedlings (S01-S05) in North-western America was estimated and assigned to the reference populations using two genetic assignment tests of the software GeneClass2 (Piry et al., 2004), (i) the frequency-based method after Paetkau et al. (1995) and (ii) the distance-based method using Nei's (1972) standard genetic distance-based criteria (see details of the analysis in Paper II in Appendix 8.2).

3.4.3.2 Genetic diversity

Assessing potential differences in the genetic diversity of the European versus American seedlings, we used the software GenAlEx v. 6.5 (Peakall and Smouse, 2012, 2006) to calculate the following diversity parameters: (1) allelic diversity (*Na*), (2) effective number of alleles (*Ne*), (3) observed frequency of heterozygotes (*Ho*), (4) expected frequency of heterozygotes (*He*) and the (5) inbreeding coefficient (*Fis*). To be able to compare genetic diversity parameters of populations with different sample sizes, we further calculated the allelic diversity parameters (6) allelic richness (*As*) and (7) private allelic richness *As*(*p*), indicating the number of distinct alleles specific for a population, based on standardized populations size by rarefaction using ADZE v. 1.0 (Szpiech et al., 2008). We used a standardized population size of 8 individuals, which is the same as used in the reference data set by van Loo et al. (2015), allowing us to compare the allelic richness of the European seedlings (S01-S05) with their corresponding native reference populations.

Finally, an independent *t* test was performed to evaluate differences between the mean of the European versus American seedlings (see details of the analysis in Paper II in Appendix 8.2).

3.4.3.3 Statistical analysis of adaptive traits

PASW Statistics for Windows Version 18.0 was used for all data analyses. Mean values for the morphological characteristics height, root collar diameter, the ratio of height/diameter (h/d), and the timing of the terminal bud were calculated for each seed source population. For the timing of bud burst, a general linear model (GLM) was applied to estimate effects of the population, blocks and their interaction. Therefore, each population was treated as fixed, and blocks as random variable (Paper II in Appendix 8.2 for details).

All data were analysed with a one-way ANOVA using post hoc test Scheffé for multiple comparisons of equal variances at a significance level of $\alpha = 0.05$. For unequal variances, a one-way ANOVA with Welch’s F-test using the Games-Howell post hoc test was performed.

4 Results

4.1 Pre-analysis of Douglas-fir growth and productivity

The final basal area increment was modelled with the following nonlinear model, explaining 77 % of the variation in the 10 year BAI/ha (rel. BAI_{10}):

Equation 4 $$rel.BAI_{10} = a \times CCF^{b} \times \mu DBH_1^{c} \times SI \times d$$

Stand competition was described by the crown competition factor (*CCF*), μDBH_1 is the arithmetic mean diameter at breast height at the beginning of the growing period and corresponds to the factor tree size, and *SI* is the site index at the age of 100 years. Results were obtained by resampling the original data set to a random sample size of 100 with the bootstrapping method as recommend by Ader et al. (2008). With decreasing stand competition (*CCF*) and tree size (μDBH_1), and increasing site index (*SI*), the basal area increment increased (Table 2).

Table 2: Model coefficients of the final basal area increment model. The table is taken from Paper I in Appendix 8.1.

Regression coefficients related to equation 4, the bootstrapped standard error of the nonlinear model and the coefficient of determination (R^2) as a measure of the goodness of fit. All parameters have a VIF of < 5 to control multicollinearity and are significant at $\alpha = 0.05$.

	Coefficients	Estimates	Standard error*
Constant	a	8.587	13.284
CCF	b	-0.761	0.184
μDBH_1	c	-1.568	0.388
SI	d	8.591	13.281
R^2	0.77		

*Bootstrapped standard error based on a sample size of 100

Results of the sensitivity analysis indicated the strongest effect of *CCF* on basal area increment with a range between 11 to almost 40 %, followed by μDBH_1 and *SI* (Figure 4).

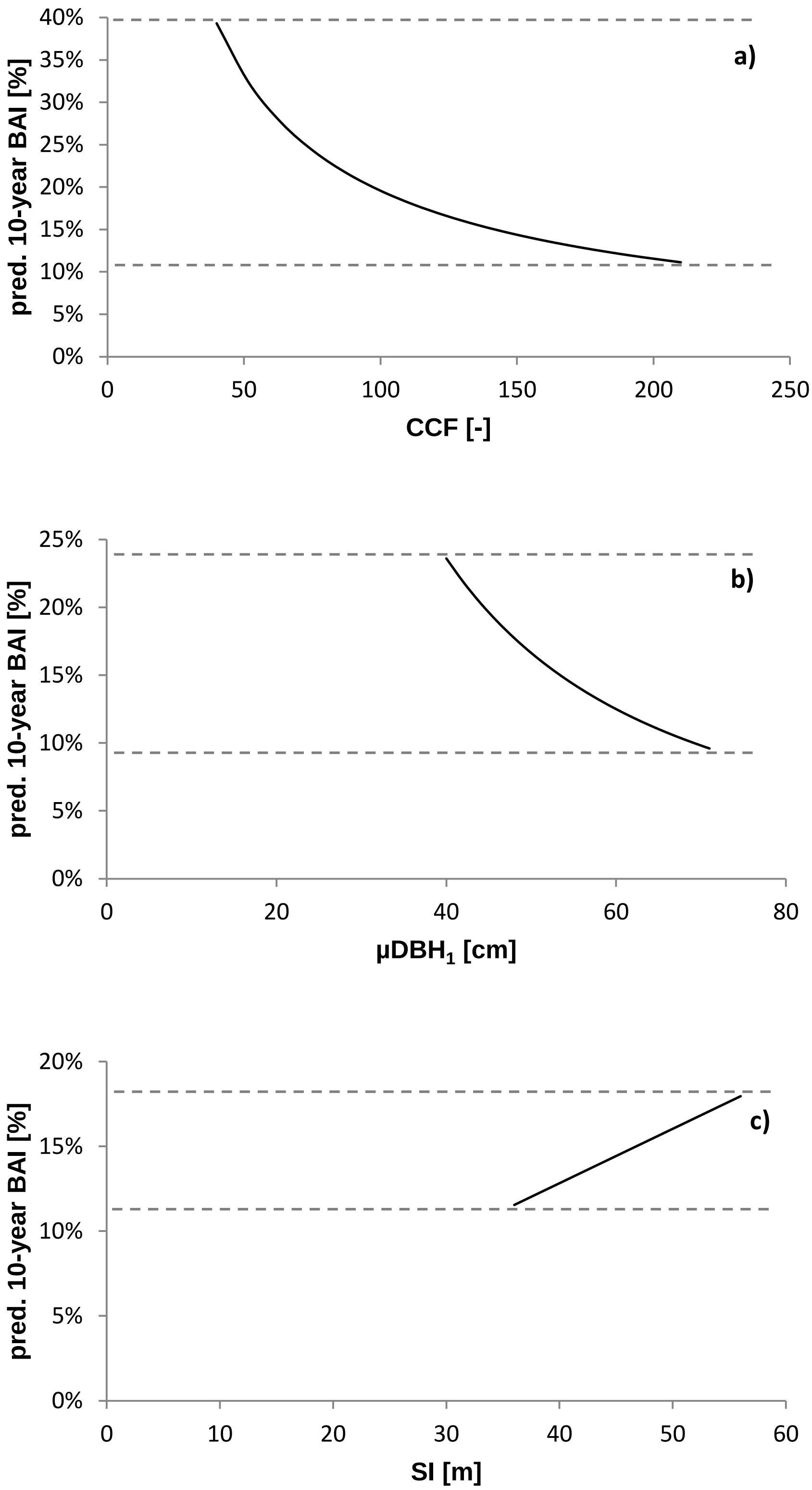

Figure 4: Sensitivity analysis of the predictor variables *CCF*, *µDBH$_1$* and *SI.* a) *CCF* within the range of min – max and the mean values of *µDBH$_1$* and *SI*, b) *µDBH$_1$* within the range of min – max and the mean values of *CCF* and *SI* and c) *SI* within the range of min – max and the mean values of *CCF* and *µDBH$_1$*. The figure is taken from Paper I in Appendix 8.1.

In addition, simple linear regression plots identified the following site variables which were significantly ($\alpha < 0.05$) correlated to the site index at the age of 100 years: nitrate, total nitrogen, manganese, pore volume, clay content, mean summer temperature and winter precipitation (see details in Paper I in Appendix 8.1). These variables were tested according to the procedure described in chapter 3.4.1.

The final site index model included the two site variables nitrate (NO_3^-) and manganese (Mn) and explained 73 % of the variation in site index:

Equation 5 $$SI = a + bNO_3^- + cMn$$

With increasing nitrate content and decreasing manganese content in the soil horizon B, site index increased (Table 3).

Table 3: Model coefficients of the final site index model. The table is modified from Paper I in Appendix 8.1.

Regression coefficients for the multiple regression model (equation 5). All parameters have a VIF of < 5 to control multicollinearity and are significant at $\alpha = 0.05$.

	Coefficients	Estimates	Standard error
Constant	a	45.502	2.270
NO_3^-	b	0.127	0.036
Mn	c	-0.028	0.010
R_{adj}^2	0.73		

The sensitivity analysis (Figure 5) showed a similar effect of NO_3^- and Mn on the development of the site index, with values ranging between 42 – 52 m and 40 – 49 m, respectively.

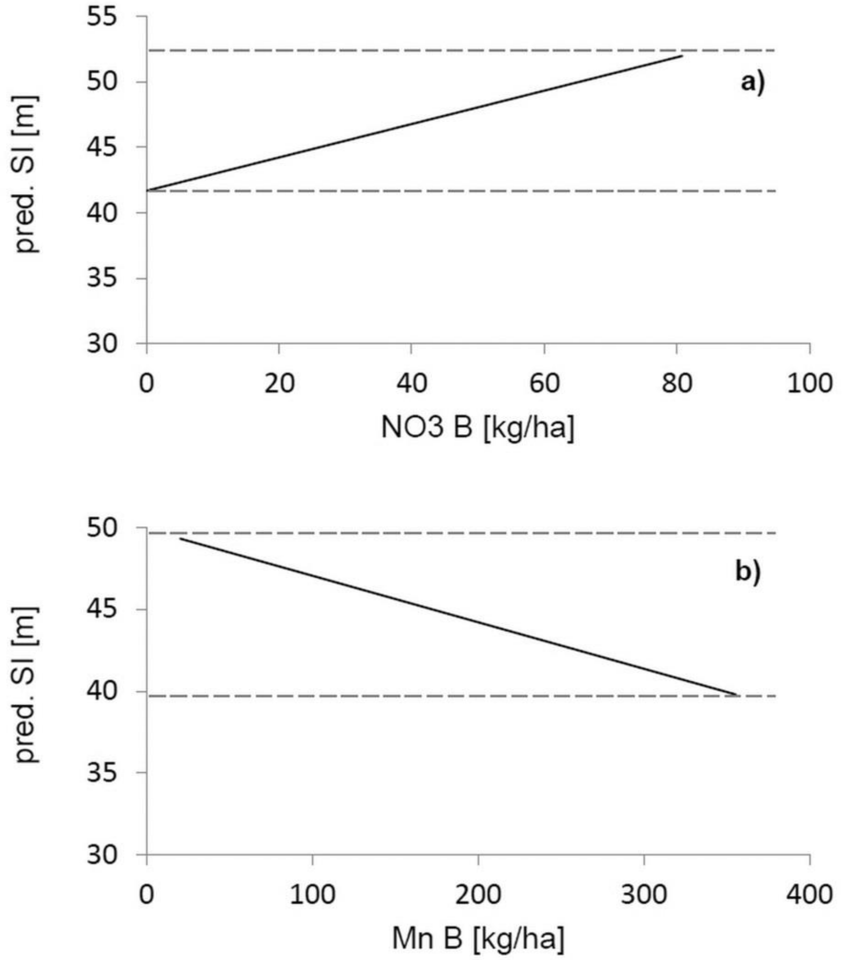

Figure 5: Sensitivity analysis of the main influencing soil parameters NO_3^- B and Mn B. (a) NO_3^- B within the range of min – max and the mean value of Mn B and (b) Mn B within the range of min – max and the mean value of NO_3^- B. The figure is taken from Paper I in Appendix 8.1.

4.2 Forest stand productivity

The final *Random Forests* model contained 10 explanatory variables out of 25 climatic and physico-chemical soil parameters, and explained 30.3 % of the variance. Variables importance ranks revealed that summer precipitation (Psum) exhibited the larges impact, followed by phosphate (PO_4^{3-}), water holding capacity (WHC), sulfate (SO_4^{2-}), mean summer temperature (Tmean), iron (Fe^{3+}), sand content, nitrate (NO_3^-), clay content and pH value (see Figure 2 Appendix 8.3). Partial effect plots indicated a non-linear relationship between the ten explanatory variables and the site index, illustrating saturation levels as well as optimum ranges (Figure 6). Summer precipitation and water-holding capacity were positively correlated with the site index, and site index decreased if values dropped below 270 mm and 300 mm, respectively. Higher summer precipitation and water holding capacity values did not lead to a further improvement in site index and thus in productivity of Douglas fir stands. The partial dependence plots indicated that nutrient requirements of PO_4^{3-}, SO_4^{2-} and NO_3^- begin to saturate at stock rates of 0.2 kg/ha, 20 kg/ha and 10 kg/ha, respectively. Iron (Fe^{3+}) stocks above 18 kg/ha showed a negative relationship with SI. The impact of mean summer temperature on SI was optimal between 17°C and 18°C and decreased above 18°C. Site index dropped if the sand content exceeded 45 %. The clay content showed an optimal range between 18 – 26 %, and SI decreased with clay contents greater than 38 %. The pH value showed a broad optimum between 4.5 and 7.2.

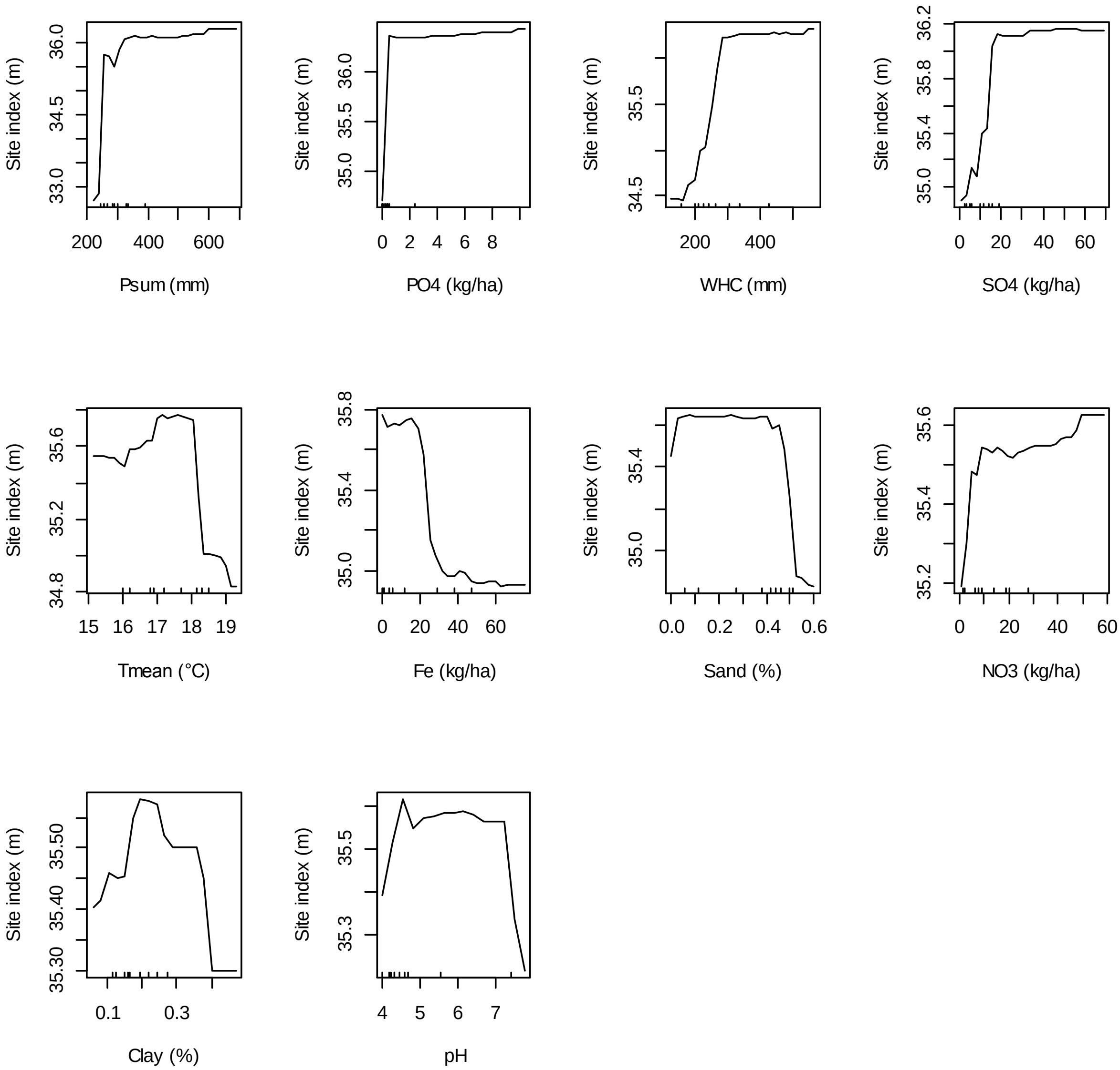

Figure 6: Partial effect plots based on results from the *Random Forests* analysis, showing the mean marginal influence of ten explanatory variables on site index variation. Each plot represents the effect of the explanatory variable while holding the other variables constant. The figure is taken from Paper III in Appendix 8.3.

4.3 European versus American Douglas-fir seedlings

4.3.1 Variety composition and native origin

The Bayesian cluster analysis resulted in an assignment of all individual seedlings from the seed source populations S03, S04, S05, S07, S08, S09 and S10 to the coastal variety. One inter-varietal admixed individual was detected in the Austrian stand S01 and in the US stand S06. Three of 30 individuals of the Austrian stand S02 were assigned to the Rocky Mountain variety and four individuals were allotted to be inter-varietal admixed seedlings. For the population assignments, S02 was analysed with 30 individuals to test if it was derived from the admixture zone in the natural distribution range (e.g. as represented by R18, see Figure S1 of Paper II in Appendix 8.2), and separated into the two varieties to investigate if it was established by two different seed sources.

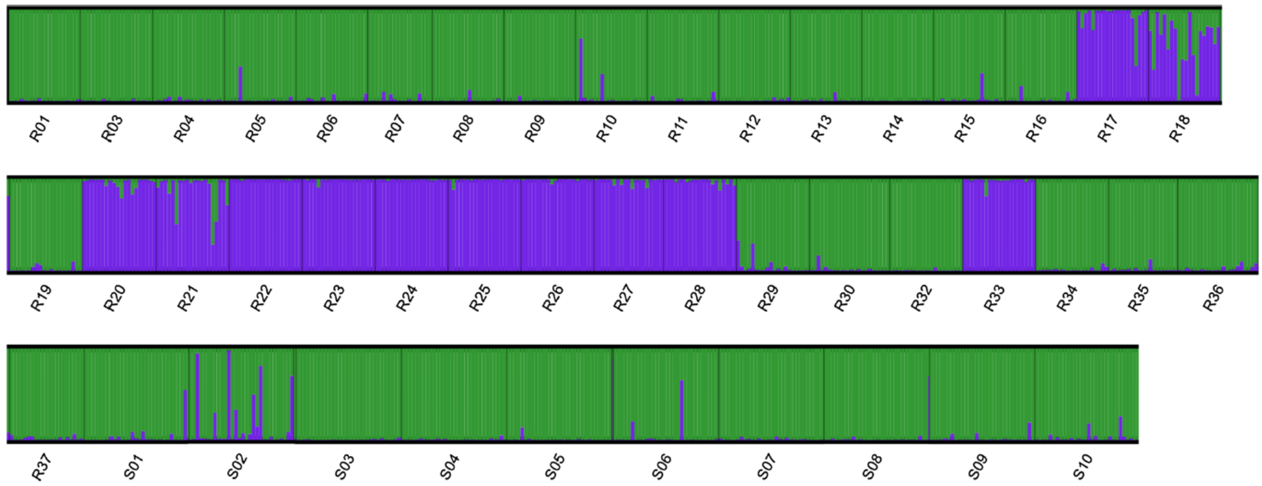

Figure 7: STRUCTURE results plotted using DISTRUCT v.1.1 for genetic structure (K = 2) representing 746 individuals of 36 reference populations (marked by R) and 300 individuals of the studied seed source populations (marked by S) of the coastal (green colour) and Rocky Mountain variety (blue colour). Individuals are grouped by populations. The figure is taken from Paper II in Appendix 8.2.

The potential geographic origin in America of the studied seed source populations S01-S10 according to the frequency-based method is illustrated in Figure 8. Score values of correctly assigned populations equal to 100 % were found in almost all studied populations (see details in Table 2 of Paper II in Appendix 8.2). Seedlings of the European stands (S01, S02, S03, S05) matched the reference populations of the coastal variety R11, R15, R16 and R11 in the Western Cascades in Washington, respectively. Seedlings of the German stand S04 were assigned to R32, a coastal variety from Vancouver Island in British Columbia. Seedlings of the variety mixed European stand S02 were assigned to the coastal variety R15, also when including only individuals of the coastal variety (27 individuals). Seedlings of the native US stands S06-S08 were assigned to R15, S09 to R11 and S10 to R05.

Based on Nei's distance approach for population assignments, the same reference populations for S01, S03 and S05-S10 were identified. The populations S02 and S04 were assigned to R30/R27 and R30, respectively (see details in Table 2 of Paper II in Appendix 8.2).

Figure 8: Illustration of the assignment results of the studied seed source populations S01-S10 (in parentheses beside the reference populations) according to the frequency-based approach after Paetkau et al. (1995). Geographic locations of the US populations (S06-S10) and the reference populations are marked with crosses and triangles, respectively. The figure is taken from Paper II in Appendix 8.2.

4.3.2 Genetic diversity

A high genetic diversity ensures a high adaptive capacity to withstand diverse environmental stress factors, especially under changing conditions. Results of the genetic diversity indices of the studied seedlings are given in Table 4. The *t* test revealed that *Na*, *Ne*, H_E and A_{S8} were significantly higher within the US populations versus the European populations. No significant differences could be found for the diversity indices *Ho*, F_{IS} and $As_8(p)$. The comparison of the European populations with the assigned native reference populations R11, R15, R16, R32 (see Paper II in Appendix 8.2, Table S1) showed that the allelic diversity parameter A_{S8} of the European seedlings was significantly lower.

Table 4: Genetic diversity indices. The table is modified from Paper II in Appendix 8.2.

Genetic diversity results for seedlings from seed source populations of Douglas-fir including the mean for the number of alleles (*Na*) and the effective number of alleles (*Ne*), the frequency of the observed heterozygosity (*Ho*) and the expected heterozygosity (*He*) after Hardy-Weinberg equilibrium, the inbreeding coefficient (F_{IS}), the number of alleles expressed as allelic richness (As_8) and unique alleles expressed as private allelic richness $As_8(p)$ at a standardized population level of 8.

Nr.	Country	N	*Na* (sd)	*Ne* (sd)	*Ho*	*He*	F_{IS}	As_8	$As_8(p)$
S01	Austria	30	18.00 (1.51)	10.45 (1.11)	0.66	0.88	0.26*	6.00	0.93
S02	Austria	30	18.15 (1.14)	10.57 (0.95)	0.68	0.89	0.24*	6.07	1.11
S02[1]	Austria	27/3	17.54 (1.12)	10.53 (0.90)	0.71	0.89	0.21*	6.10	1.02
S03	Germany	30	15.31 (1.30)	8.63 (1.04)	0.58	0.85	0.32*	5.58	0.98
S04	Germany	30	14.15 (1.15)	8.75 (0.74)	0.65	0.87	0.26*	5.68	0.98
S05	Germany	30	17.08 (1.24)	9.89 (0.70)	0.69	0.89	0.23*	5.96	0.92
S06	USA	30	18.46 (1.42)	11.39 (1.11)	0.63	0.90	0.30*	6.18	0.86
S07	USA	30	19.00 (1.90)	12.07 (1.34)	0.63	0.91	0.30*	6.21	0.94
S08	USA	30	18.00 (1.37)	11.36 (0.87)	0.60	0.90	0.33*	6.19	0.88
S09	USA	30	20.08 (1.62)	12.38 (1.27)	0.68	0.90	0.25*	6.29	1.02
S10	USA	30	19.54 (1.64)	12.54 (1.39)	0.65	0.90	0.28*	6.26	1.18

[1]Genetic diversity results refer to the coastal variety only

*Significant deviation from HWE (Hardy-Weinberg Equilibrium) p < 0.001

4.3.3 Morphological and phenological traits

Studying the variation of ecologically important adaptive traits in Douglas-fir seedlings allows the identification of appropriate source populations. Morphological characteristics are considered as an indicator of the growth and survival potential. Multiple comparisons of the height growth performance indicated significantly higher values of one European population (S02) compared to all other populations. Seedlings of the US population S10 exhibited the lowest growth rate. The remaining populations displayed similar growth rates (see Table 4, Fig. 5 from Paper II in Appendix 8.2). Comparisons of the growth trait root collar diameter showed the highest growth in diameter for population S01, which is significantly higher compared to all other populations except S01 and S09, and the lowest value for the US population S07 (see Table 4, Fig. 5 from Paper II in Appendix 8.2). The seedlings from the US population S09 displayed a significantly higher ratio in height to diameter compared to all other populations expect S02. The lowest mean value of the sturdiness quotient was evident in population S10 and S03. All other populations showed similar ratios in height to diameter (see Table 4, Fig. 5 in Paper II from Appendix 8.2).

Selecting the best seed source reduces the risk of frost damage due to the high heritability of bud burst traits by approximately 80 % (Janßen and Rau 2008). Multiple comparisons of the bud burst development showed that the European populations (S01, S04) exhibited a significantly earlier timing of bud burst as compared to the European population (S05) and the native US population (S08). Within the native range, population S09 exhibited a significantly earlier timing of bud burst as compared to S08. The remaining populations did not differ significantly from each other.

5 Discussion and conclusion

5.1 Douglas-fir growth and forest stand productivity

Knowledge about tree growth reflects the dynamics and productivity of forest stands, and may serve as basis for forest management decisions. With the assessment of Douglas-fir stands originating from recommended provenances, we were able to minimize any potential genetic differences in the growth performance. The growth analysis of eleven mature Douglas-fir stands showed that basal area increment at stand level was adequately modelled with a simple power function (R^2 0.77). Thereby, basal area increment relative to tree size was greatest in low density stands with a high forest stand quality. The main determinant of Douglas-fir growth was competitive stress, expressed by the crown competition factor (CCF), followed by tree size and the site index. Based on our sampling design, the basal area increment model is restricted to mature Douglas-fir stand (69 – 122 years) and a small range of site conditions. Hence, the relationship between increment and the three growth factors only reflects the later growth phase of Douglas-fir. As site suitability guides the selection of tree species for reforestation and forest management decisions, we further evaluated Douglas-fir stand productivity based on a linear regression analysis. We identified seven key site variables and the final site index model comprised the two soil variables nitrate and manganese, which are known to play an important role for Douglas-fir growth.

To overcome the methodological limits of the linear regression analysis and the restricted variation of site characteristics, 28 Douglas-fir stands, growing on siliceous as well as calcareous bedrock material, were analysed with the non-parametric method *Random Forests*. Here, we specifically aimed to elucidate non-linear impacts of climatic- and physico-chemical growth drivers. Compared to traditional statistical methods (e.g. linear regression in Paper I), the *Random Forests* approach ("black box" model) is able to identify structures in complex, often non-linear data sets (Olden et al., 2008). In our analysis, *Random Forests* identified ten of our 25 investigated climatic and physico-chemical soil parameters that drive Douglas-fir productivity in Central Europe, and showed a non-linear relationship between the predictors and the response (Figure 6). The effects of the predictors on the site index demonstrated comprehensible optimum ranges, critical levels as well as saturation levels and may serve forest owners as basis for the selection of suitable site conditions as an important pre-condition for a successful cultivation of Douglas-fir.

Suitable site conditions for Douglas-fir cultivation refer to the climate, the soil moisture regime and the soil nutrient status. Ideal growing conditions are related to an adequate level of soil moisture, well-drained soil conditions and adequate nutrient levels of phosphate, sulfate, nitrogen and iron. Douglas-fir grows well on acidic to slightly alkaline soil conditions, reflecting its broad physiological amplitude. Douglas-fir performs best until the critical level of available water storage capacity of 45 mm is reached. On such forest sites, the risk of drought-stress is already classified as high (Leitgeb et al., 2012). This reflects the drought tolerance of Douglas-fir, and hence importance compared to other main native tree species like Norway spruce (*Picea abies*). The detected moderate increase in Douglas-fir productivity with summer temperatures (Tmean) between 15°C and 18°C and the decrease at summer temperatures higher than 18°C, were important findings in context of the expected climate change. Since global mean annual temperatures are expected to increase between 1.1°C (RCP 4.5) and 4.8°C (RCP 8.5) by 2100 (IPCC, 2014), we conclude an increase in Douglas-fir stand productivity at higher elevations. At the warmest sites, e.g. in Eastern Austria, however, we also induce a decline in forest stand productivity for Douglas-fir. The growth performance of the 5 Douglas-fir sites on carbonate soils was comparable with those growing on siliceous soils (details see Table 3 in Paper III from Appendix 8.3). These results contradict current management recommendations to cultivate Douglas-fir on carbonate-free soils (e.g. Englisch, 2008). To consolidate our findings, further investigations of Douglas-fir sites as well as provenance trials on carbonate sites (e.g. Rendzina sites) are necessary.

5.2 Suitability of European versus American Douglas-fir seedlings

A prerequisite for a successful regeneration of Douglas-fir in Central Europe is the access to high-quality seedlings in terms of adaptability, growth performance and survival. Both, high genetic diversity and suitable origin are important factors for the future adaptive potential of regenerated Douglas-fir stands. Currently, the demand of Douglas-fir seedlings is covered by local non-native European and native American seed stands. Although we could show that the European seed stands originate from various recommended seed zones for Douglas-fir cultivation in Austria and Germany, they represent both varieties and inter-varietal admixed individuals. This is a crucial issue since (i) the interior variety is not recommended for planting due to its lower growth performance and higher susceptibility to fungi (*Rhabdocline pseudotsugae*), and (ii) admixed populations bear the risk of disadvantageous population structures and mating patterns which can limit gene flow. Moreover, the results indicated a reduced adaptation potential of the European seedlings; a significantly reduced genetic diversity of the European stands compared to the American and the assigned native reference populations was evident. We conclude that the European seed lots originate from small sized stands with assortative mating, with the risk of bottleneck effects and inbreeding in next generations. A recent study confirmed our results, showing a loss of genetic diversity of the offspring generations in comparison to the adults in small and isolated stands (Wojacki and Liesebach, 2018). To avoid inbreeding, seeds should only be collected in large stands and in years with a high density of flowering trees (White et al., 2007).

We found significant differences in adaptive traits such as morphological characteristics and bud burst development within and between the studied seed source populations. Overall, one European population showed the best growth performance but a higher risk of damages after planting due to the high ratio of height to diameter (*h/d* ratio µ 7.9). Two US populations showed the lowest growth performance in terms of height and root collar diameter, but a low susceptibility to wind, drought and frost damages due the balanced *h/d* ratio ranging between 5.5 and 7.5 (Bauer et al., 2009). The timing of bud burst is an indicator of the risk from spring frost damages. Bud burst of the European seedlings was similar to the native US seedlings; significant differences were found within and between the studied European and American populations.

To avoid costly plantation failures in the future, we recommend the selection of Douglas-fir reproductive material from certified North American seed stands or seed orchards and/or from European seed orchards (FRM category “qualified” or “tested”). Only these categories of reproductive material can preserve a high adaptive capacity in the regenerated stands. To be able to cover the demand with local European seedlings, we strongly advise to revise the national requirements for European Douglas-fir seed stands of the FRM category “source-identified” and “selected” by (i) enlarging the minimum area and minimum number of adult trees (different national requirements exist today) and (ii) testing seed stands of unknown origin for variety composition and potential native origin.

6 References

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7 List of figures

8 Appendix

8.1 Paper I

Eckhart, T., Hintsteiner, W., Lair, G., van Loo, M., Hasenauer, H., 2014. The Impact of Soil Conditions on the Growth of Douglas-fir in Austria. Austrian Journal of Forest Science, 131(2), 107-128.

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The Impact of Soil Conditons on the Growth of Douglas-fir in Austria

Der Einfluss des Bodens auf das Wachstum von Douglasie in Österreich

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Keywords: Douglas-fir, Climate change adaptation, Stand basal area increment model

Schlagwörter: Douglasie, Klimawandelanpassung, Bestandeskreisflächenzuwachs

Abstract

The Douglas-fir, native to western North America, is a drought-tolerant species and considered as one of the most promising key tree species in Western and Central Europe for forest adaption under changing climate conditions. The wide native distribution range of the Douglas-fir, covering a large latitudinal and elevation range, constitutes genetically differentiated populations. Thus, the selection of suitable proveniences and site conditions are of major importance in guaranteeing a successful cultivation outside its natural distribution range. In this study, we investigate how environmental conditions may influence the growth of Douglas-fir in Austria and Southern Bavaria-fir stands. We develop a basal area increment model based on stand density, tree size and site conditions. Furthermore, the environmental factors climate, topography and soil and their relationship versus site index

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are investigated. Eleven Douglas-fir stands from Austria and Bavaria are randomly selected. The genetic seed sources are from the Western Cascades in Washington and Oregon. The 10 year basal area increment per hectare (BAI10) was modeled with a nonlinear power function explaining 77 % of the existing variation.

Zusammenfassung

Die trockenresistente Douglasie ist eine nordwestamerikanische Baumart und gilt aufgrund der erwarteten Klimaerwärmung als eine der aussichtsreichsten Alternativbaumarten in West- und Mitteleuropa. Das große natürliche Verbreitungsgebiet umfasst unterschiedlichste Standorte und Klimabedingungen, an die sich die Douglasie regional angepasst hat. Aufgrund dieser hohen genetischen Differenzierung ist die Auswahl der geeigneten Herkunft sowie die richtige Standortswahl entscheidend für den Anbauerfolg der Douglasie außerhalb ihres Ursprungsgebietes. In dieser Studie wird der Einfluss des Standortes auf das Wachstum von Douglasienbeständen untersucht. Dazu wird ein Kreisflächenzuwachsmodell auf Bestandesebene mit den Eingangsparametern Bestandesdichte, Baumdimension und Standortsbedingungen entwickelt. Außerdem wird der Einfluss der Umweltfaktoren Klima, Topographie und Boden auf die Oberhöhenbonität untersucht. Die Studie basiert auf elf zufällig ausgewählten Douglasienbeständen in Österreich und Bayern mit bekannter Herkunft. Die untersuchten Douglasienbestände stammen aus dem Gebiet westlich der Kaskaden in Washington und Oregon. Der 10-jährige Kreisflächenzuwachs pro Hektar (BAI10) wurde mit einer nichtlinearen Potenzfunktion modelliert welche 77 % der Gesamtvariation erklärt.

1. Introduction

The range of European forests is mainly determined by climate, whereas climate extreme values limit the distribution of tree species rather than average values. Due to present and future changes of the major limiting factors temperature and precipitation, possible impacts of these changes are of interest. Climate change impacts on European forests vary regionally with diverse effects (Maracchi et al., 2005). While increasing temperature generally leads to higher photosynthesis activity, higher temperatures also trigger drought periods which are assumed to be limiting factors for tree growth in the future (Kapeller et al., 2012). In temperate forests, drought is a major constraint for forest stability and productivity. Due to the predicted increase in the frequency and duration of drought periods under a changing climate, this problem might become even more severe (Peters et al., 2013). Especially the Norway spruce, the most productive coniferous species, is more susceptible to dry periods and may (very likely) not survive under future conditions in some parts of Europe (Kapeller et al., 2012). Hence, adaption strategies have to be developed, and plantations of more tolerant species are highly discussed in Europe. The Douglas-fir (Pseudotsuga menziesii), native to western North America, is a drought-tolerant species and considered as one of the most promising key tree species in Western and Central Europe for forest adaption under changing climate conditions. Moreover, high productivity rates, high wood quality, as well as suitable ecological characteristics like high stability constitute great expectations from Douglas-fir cultivations in Austria and elsewhere (Englisch, 2008, Kleinschmit and Bastien, 1992).

The wide native distribution range of the Douglas-fir (Little, 1971) (Fig. 2), covering a large latitudinal and elevation range, constitutes genetically differentiated populations (Kleinschmit and Bastien, 1992). Accordingly, the selection of suitable proveniences and site conditions are of major importance to guarantee a successful cultivation outside its natural distribution range (Englisch, 2008). The purpose of this work is to understand the growth of the non-native tree species, explained by these three factors: (i) stand competition, (ii) tree size and (iii) site quality. Furthermore, the influence of environmental factors on the site quality is investigated. A common indicator for site quality is the site index, defined as the mean dominant tree height at a given reference age (Kindermann and Hasenauer, 2005).

The objectives of this study are (i) to model basal area increment per hectare by a nonlinear power function, (ii) to investigate the environmental factors affecting Douglas-fir growth, and based on these environmental factors, (ii) to assess soil, topographic and climate factors deriving from the site index.

2. Material and methods

2.1. Study area

In the present study, eleven old Douglas-fir stands were randomly selected in Eastern Austria and Lower Bavaria (Fig. 1) to investigate soil, climatic and topographic factors affecting Douglas-fir growth. The study area represents a variety of climatic environments, with mean annual precipitation ranging from 583 to 1608 mm and an annual temperature gradient between 6.5 and 10.3 °C. The elevation of the study center plots vary from 202 to 786 m above sea level and a slope inclination between 3 and 19 degrees (Table 1). The parent material was determined based on the soil map of Austria (Weber, 1997) and Germany (BGR, 2006) with various granites, gneiss and one limestone bedrock material.

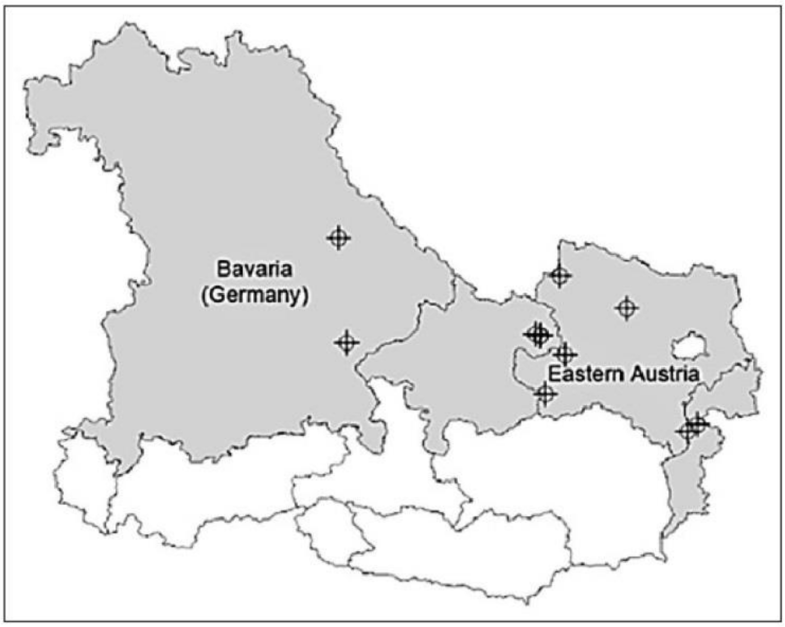


Fig. 1: Location of the study area and plots across Eastern Austria and Bavaria

2.2. Sampling design

All sample plots are located in pure even-aged Douglas-fir stands, with the following constraints:

(i) all stands belong to the coastal variety of the Western Cascades in Washington and Oregon, (ii) stand size ≥ 1 ha, (iii) proportion of Douglas-fir basal area ≥ 80 % and (iiii) a minimum age of 60 years.

The previously unknown origin of the selected Douglas-fir stands, which are recommended for seed harvesting and breeding, was assessed by genetic provenance analyses and could be assigned to the coastal variety of the Western Cascades in Washington and Oregon (Hintsteiner et al., 2014) (Fig. 2).

Fixed area plot

In each forest stand, a fixed area plot with a radius of 20 m (0.02 ha) was randomly selected to represent relatively uniform stand and soil characteristics. Forest stand, soil, and climatic characteristics were assessed on each plot through different variables, which are summarized in table 1.

Fig. 2: Natural origin area of the coastal (dark grey) and inland (light grey) Douglas-fir in North America and assigned provenances of the Western Cascades in Washington and Oregon, (adapted after Little, 1971)

Within a radius of 20 m, the diameter at breast height (DBH), the horizontal distance and the azimuth to the plot center of each tree with a DBH ≥ 10 cm was measured. In order to calculate the stand age and the basal area increment, wood core samples at breast height were taken from five trees closest to the central point of the fixed area plot. Tree height and height to the living crown base were measured with a vertex.

Table 1: Variables and analytical procedures concerning forest stand, topography, soil and climate

	Variable		Unit	Mean (min-max)	Method
Stand parameters	DBH	Diameter at breast height	cm	62 (41 - 82)	Tree tape
	H	Height	m	40 (23 - 50)	Vertex
	ELEV	Elevation	m a.s.l	538 (202 - 786)	GPS
	SLO	Slope inclination	Degrees	12 (3 - 19)	Inclinometer
	Aspect	Aspect	Degrees	139 (6 - 337)	Wyssen compass
	rel. BAI10	Basal area increment 10yr	%	15 (7-21)	Tree ring analysis
	CCF	Crown competition factor	[-]	145 (40 – 210)	Krajicek et al. (1961), Hasenauer (1997)
	μDBH_1	Mean DBH at the beginning of the growing period	cm	54 (39 – 71)	Equation 6
	SI	Site index 100yr	m	46 (36 - 56)	Mitscherlich and Richards (1919), Kindermann and Hasenauer (2005)
Soil parameters	pH H2O*	Actual pH	[-]	4.5 (4.0 - 5.9)	ÖNORM L 1083
	pH CaCl2*	Potential pH	[-]	4.0 (3.7 - 5.4)	ÖNORM L 1083
	C*	Carbon	%	2.8 (1.4 - 5.4)	ÖNORM L 1080
	N*	Nitrogen	%	0.2 (0.1 - 0.3)	ÖNORM L 1082
	C/N*	C/N ratio	[-]	16.7 (12.6 - 21.0)	ÖNORM L 1082
	AVP*	Available phospor	kg/ha	32 (1 - 139)	Bray and Kurtz 1945
	Ca*	Calcium	kg/ha	4680 (249 - 25589)	ÖNORM L 1086-1
	Mg*	Magnesium	kg/ha	257 (19 - 1058)	ÖNORM L 1086-1
	K*	Potassium	kg/ha	110 (54 - 221)	ÖNORM L 1086-1
	Na*	Natrium	kg/ha	35 (9 - 122)	ÖNORM L 1086-1
	Al*	Aluminum	kg/ha	663 (263 - 1257)	ÖNORM L 1086-1
	Fe*	Iron	kg/ha	17 (0.7 - 52)	ÖNORM L 1086-1
	Mn*	Manganese	kg/ha	120 (18 - 305)	ÖNORM L 1086-1
	H+*	Hydron	mmol/kg	2.4 (0.5 - 4.3)	ÖNORM L 1086-1
	CEC eff.*	Cation-Exchange Capacity	mmol/kg	164 (61 - 654)	ÖNORM L 1086-1
	Bsat*	Base saturation	%	43 (13 - 91)	ÖNORM L 1086-1
	PO43-*	Phosphate	kg/ha	1 (0 - 4)	ÖNORM L 1092
	NO3-*	Nitrate	kg/ha	33 (1 - 77)	ÖNORM L 1092
	NO2-*	Nitrite	kg/ha	1 (0 - 13)	ÖNORM L 1092
	SO42-*	Sulfate	kg/ha	101 (41 - 248)	ÖNORM L 1092
	Clay*	Clay	%	17 (13 - 24)	ÖNORM L 1061
	Silt*	Silt	%	42 (30 - 64)	ÖNORM L 1061
	Sand*	Sand	%	40 (13 - 50)	ÖNORM L 1061
	Skeleton*	Skeleton	%	17 (1 - 34)	ÖNORM L 1061
	PV*	Pore volume	%	67 (55 - 78)	ÖNORM L 1068
Climatic parameters	A-PPT	Mean annual precipitation	mm	886 (583 - 1608)	DAYMET
	S-PPT	Mean summer precipitation [June, July, Aug]	mm	324 (234 - 551)	DAYMET
	W-PPT	Mean winter precipitation [Dec, Jan, Feb]	mm	160 (83 - 340)	DAYMET
	A-TEMP	Mean annual temperature	°C	8.2 (6.5 - 10.3)	DAYMET
	S-TEMP	Mean summer temperature [June, July, Aug]	°C	19.4 (15.4 - 17.1)	DAYMET
	W-TEMP	Mean winter temperature [Dec, Jan, Feb]	°C	-3.2 (-6.3 - 2.1)	DAYMET

*Separately assessed in A and B horizon (0-35 cm)

2.3. Stand parameters

Topography

On each sample plot topographic characteristics were assessed through different variables as listed in table 1. Elevation, slope inclination, aspect and coordinates of each forest stand were taken at the fixed area plot center and measured by a GPS device, inclinometer and Wyssen-compass, respectively.

Stand basal area increment

The basal area increment per hectare over past 10 years in percent was calculated as follows:

$$rel.BAI10 = \frac{rmsBAI10 * N * BUF}{BA} \quad [1]$$

$$BUF = \frac{10000}{A} \quad [2]$$

rel.BAI10 is the 10 year basal area increment in percent, rmsBAI10 is the quadratic mean of the 10 year basal increment of the sample trees, N is the number of Douglas-fir trees, BUF is the blow up factor, BA is the actual basal area per hectare. To get values per hectare, the blow up factor was calculated by dividing 10000 (1 ha) through the area of the plot (A, m²).

Index of stand density

Stand density of forests is commonly assessed with the crown competition factor (CCF) or the stand density index (SDI) (see Hasenauer et al., 2012). For this study, the CCF was applied (Monserud and Sterba, 1995). According to Krajicek et al. (1961), the CCF is the sum of the species-specific potential crown area (PCAi) divided by the plot area (A).

$$CCF = \frac{\sum PCA_i}{A} \quad [3]$$

The potential crown area was calculated with the open grown crown widths (CW, in m) given by Hasenauer et al. (1997), which defines the crown area of a tree at a given diameter at breast height (DBH, in cm) assuming open grown conditions.

$$PCA = \frac{\pi * CW^2}{4} \tag{4}$$

$$\ln(CW) = a + b * \ln(dbh) \tag{5}$$

a and b are species specific coefficients (table 2)

Table 2: Species specific coefficients for the crown width function after Hasenauer (1997).

Tree species	a	b
Norway spruce and other coniferous trees	-0.323	0.6441
Larch	-0.339	0.6823
Black pine	-0.157	0.631
Beech and other broad-leafed trees	0.2662	0.6072

Tree size effect

To describe the mean diameter increment relative to the tree size, the mean diameter at breast height at the beginning of the growing period (µDBH1) was calculated as follows:

$$\mu DBH_1 = \mu DBH_2 - \mu id_{10} \tag{6}$$

μDBH_2 is the arithmetic mean diameter at breast height of the sample trees at the end of growing period and μid_{10} is the mean 10 year diameter increment.

Index of site quality

The site index, as the most common indicator of site quality, is defined as the mean dominant tree height at a given reference age (Kindermann and

Hasenauer, 2005). In this study, SI was defined as the mean height of the 100 tallest trees per hectare (2 tallest trees on 0.02 ha plot) at the base age of 100 years. To calculate the site index at reference age, tree growth functions available for different tree species can be used by applying the dominant height growth function after Mitscherlich/Richard (1919) for the "Douglas-fir northwestern Germany", the SI_{100} was iteratively calculated:

$$OH = a(1 - e^{-b*t})^{c} \qquad [7]$$

$$a = a_0 + a_1 * OH_{100} + a_2 * OH^2{}_{100}$$

$$a = a_0 + a_1 * OH_{100} + a_2 * OH^2{}_{100}$$

$$c = c_0 + c_1 * OH_{100} + c_2 * OH^2{}_{100}$$

OH = dominant tree height

OH_{100} = dominant tree height at the age of 100 (directly correlated to SI)

t = stand age at DBH + 10 years

a, b, c = coefficients for „Douglas-fir northwestern Germany" based on the yield table after Bergel (1985) from table 3

Table 3: Coefficients for the dominant tree height function after Mitscherlich/Richard (1919) for "Douglas-fir northwestern Germany (DoNwd)" (Kindermann and Hasenauer, 2005)

	a0	a1	a2	b0	b1	b2	c0	c1	c2
DoNwd	-5.92E+00	1.26E+00	0	9.90E-02	-2.79E-03	2.54E-05	9.43E+00	-3.15E-01	3.03E-03

2.4. Soil parameters

The soil characteristics were assessed through borehole samples and separated into A and B horizon (0-35 cm). In total, 44 borehole samples of four transects distributed across each forest stand were taken in order to overcome the expected heterogeneity of forest soils. The chemical and physical soil properties were analyzed for each transect by standard laboratory methods. Four density core samples per forest stand were taken at the center of each transect to determine the pore volume of A and B horizon. The analytical results were expressed as soil stocks on a mass per unit area basis using bulk density, coarse fragment content, and depth of A and B horizon (0-35 cm). The soil variables listed in table 1 are the weighted mean values of A and B horizon.

2.5. Climatic parameters

The Austrian version of the climate interpolation model DAYMET was applied to calculate daily climatic data (minimum and maximum temperature and precipitation as well as solar radiation) for each study plot from 1960 to 2010 (Thornton et al., 1997, 2000, Hasenauer et al., 2003).

3. Statistical analysis

3.1. Stand basal area increment model

Stand basal area increment per hectare is determined by the three factors: (i) stand competition, (ii) tree size and (iii) site index parameters (Wykoff, 1990). Thus, a nonlinear power function including these three factors was defined:

$$rel.BAI_{10} = a * x_{SD}^{b} * x_{TSE}^{c} * x_{SI}\ d \qquad [8]$$

rel. BAI is the 10 year relative basal area increment per hectare of the Douglas-fir stands, x_{SD}, x_{TSE}, x_{SI} are variables corresponding to the three factors stand density, mean tree size and site index, and a, b, c, d represent model coefficients. The coefficients b and d describe the curvature of the power function. The parameterization of the nonlinear model function rel. BAI_{10} was carried out with the statistical program PASW 18. In order to test for multicollinearity, the variation inflation factor (VIF) after Snee (1973, 1977) was calculated for each explanatory variable.

$$VIF = \frac{1}{1-R^2} \qquad [9]$$

A large VIF (e.g. > 5) would indicate a strong correlation between certain predictor variables which can produce misleading results due to inadequate independent information (Hasenauer, 1997).

3.2. Site index versus site variables

Linear regression plots of Site Index (SI) versus site variables did not indicate any non-linear relation. Thus the following multiple linear equation was used to study the variation of site index in relation to site variables:

$$SI = a + bx_t + cx_s + dx_c + \varepsilon \quad [10]$$

SI is the site index, x_t, x_s, x_c are variables corresponding to topographic, soil and climatic factors, a, b, c, d represent model coefficients and ε is the additive error term. For statistical calculations, the program R was applied.

The analysis of the data followed four steps:

I. The selection of environmental factors that are significantly related to the variation in the SI and ecologically sound
II. The entering of significant variables sequentially according to their coefficient of determination R^2, starting with the most significant variable
III. Testing for multicollinearity according to a variation inflation factor (VIF) < 5 for each predictor variable after Snee (1973, 1977)
IV. The selection of the best model to explain and predict the SI of environmental variables according to the adjusted coefficient of determination $Radj^2$

4. Results

4.1. Prediction model for stand basal area increment

A basal area increment model at stand level was developed for the 11 Douglas-fir sites. The following nonlinear model was determined to predict the relative 10 year basal area increment projection per hectare for the Douglas-fir (rel.BAI_{10}):

$$rel.BAI_{10} = a * CCF^b * \mu DBH_1^c * SI * d \quad [11]$$

CCF is the crown competition factor, μDBH_1 corresponds to the mean diameter at breast height at the beginning of the growing period and SI is the site index.

Due to the rather small sample size of only eleven Doulgas-fir stands, a re-sampling of the data was necessary to increase the accuracy of the model, defined by the standard error. The bootstrapping method was applied, as recommended by Adèr et al. (2008), to resample the original data set to a random sample size of 100 and to calculate the bootstrapped standard error. The resulting model explains 77 % of the variation in the 10 year basal area increment per hectare. All parameters entered the model significant at a 5 % probability level and multicolinearity was controlled to be a required variation inflation factor (VIF) < 5.

Table 4: Regression coefficients related to equation 11, the bootstrapped standard error of the nonlinear model and the coefficient of determination (R^2) as a measure of the goodness of fit.

	Coefficients	Estimates	Standard error*
Constant	a	8.587	13.284
CCF	b	-0.761	0.184
μDBH_1	c	-1.568	0.388
SI	d	8.591	13.281
R^2	0.77		
*Bootstrapped standard error based on a sample size of 100			

The predictor variables CCF and μDBH_1 correlate negatively and the SI positively, versus the predicted 10 year stand basal area increment per hectare.

Sensitivity analysis

The theoretical effects of the independent variables CCF, μDBH_1 and SI versus the stand basal area increment was tested by modeling the rel. BAI_{10} variation and carrying one variable within its measured range (minimum – maximum value) while the other independent drivers were kept constant at the corresponding mean values. Figure 3 provides the results for the competition factor CCF, which indicates the strongest effect, followed by the tree size factor μDBH_1 and the site index SI.

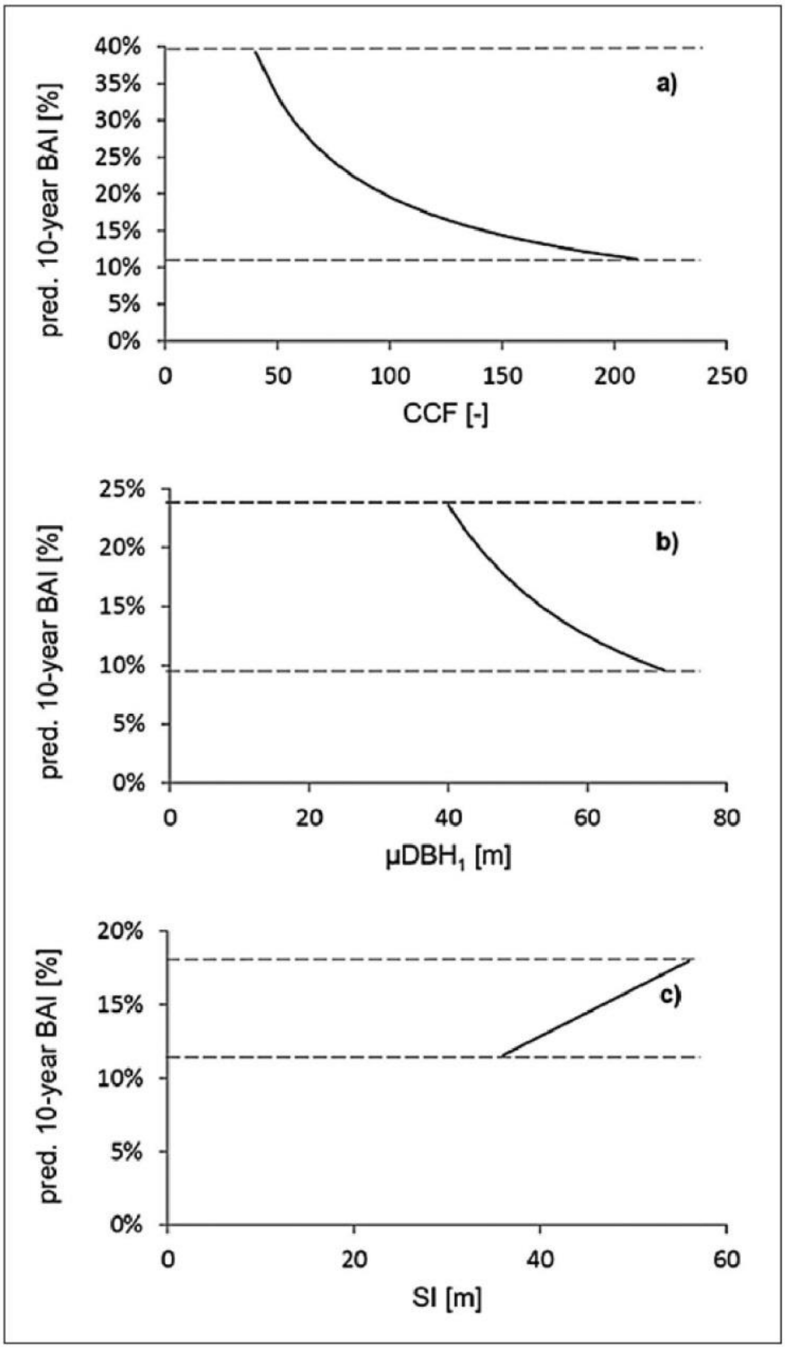
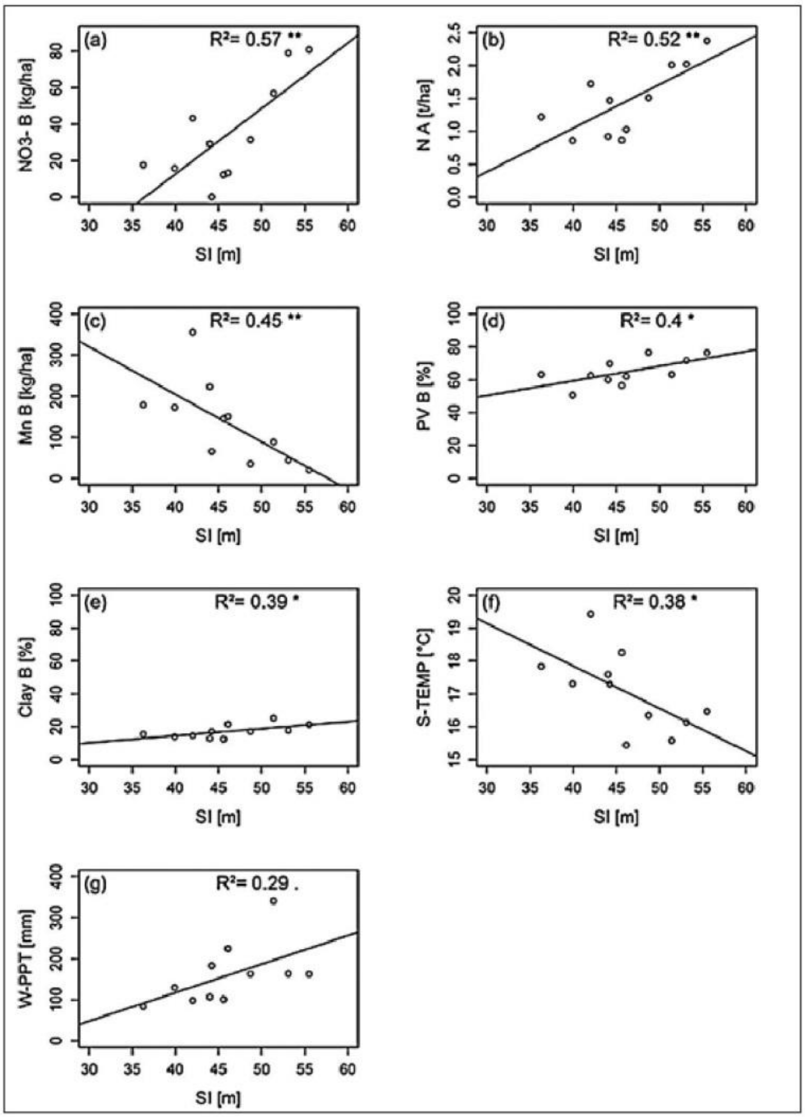


Fig. 3: Sensitivity analysis of the main influencing parameters CCF, μDBH_1 and SI
(a) CCF within the range of min – max and the mean values of SI and μDBH_1, (b) DBH_1 within the range of min – max and the mean values of CCF and SI (c) SI within the range of min – max and the mean values of CCF and μDBH_1

4.2. Site index versus site variables

The site index, defined as the dominant stand height attained at a particular age, may be considered as a surrogate of the environmental and/or site conditions for a forest stand. Thus, we next relate the site index to a number of soil parameters available for our forest sites to identify and explore the key drivers in the site index variation. Figure 4 provides the results including the correlation coefficients.



Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Fig. 4: Environmental factors (a-g) significantly related to the variation in Douglas-fir site index

According to Fig. 4, nitrogen in the form of nitrate (NO_3^-) in horizon B indicates the highest positive correlation and accounts for 57 % of the variation in SI. Manganese stock in horizon B (Mn B) is negatively correlated (R^2 0.45) to the SI. Pore volume PV and clay content in horizon B show positive correlations to the SI and account for 40 % and 39% of the variation, respectively. Mean summer temperature indicates a negative correlation to SI (R^2 0.38) and winter precipitation shows a weak positive correlation (R^2 0.29). In a next step, those variables with the greatest influence were sequentially combined into a multiple regression equation.

Best model output

Multiple linear regression method was used to calibrate a model for predicting the site index as it may depend on quantitative environmental drivers.

$$SI = a + bNO_3^- \mathrm{B} + cMn\,B \qquad [12]$$

The linear model includes the two soil variables NO_3^- B and Mn B, which are statistically highly significant at the 95 percent level, and explains 73 % percent of the variation in the site index (table 5). Multicolinarity was controlled by a requested inflation factor (VIF) of ≤ 5. The remaining standard error of the model estimate is 2.98 m.

Table 5: Estimates, standard error and p-values for the multiple regression model (equ. 12)

	Estimates	Standard error	p-value	VIF
Constant	45.501767	2.269763	< 0.001	
NO3- B	0.127458	0.036029	< 0.01	1.10
Mn B	-0.02842	0.009963	< 0.05	1.10
Radj²	0.73			

Sensitivity analysis

Again, the theoretical behavior of the predictor variables NO_3^- B and Mn B versus the resulting SI (Site index) was tested by modeling the SI development for different levels by varying one parameter within the measured range (minimum to maximum value), while keeping the other parameters constant at its mean value (see Fig. 5). The effect of NO3- B and Mn B on the SI development ranges between 42 – 52 m and 40 – 49 m, respectively. According to Fig. 5, the predictor variables NO3- B and Mn B have a similar effect on the development of the site index.

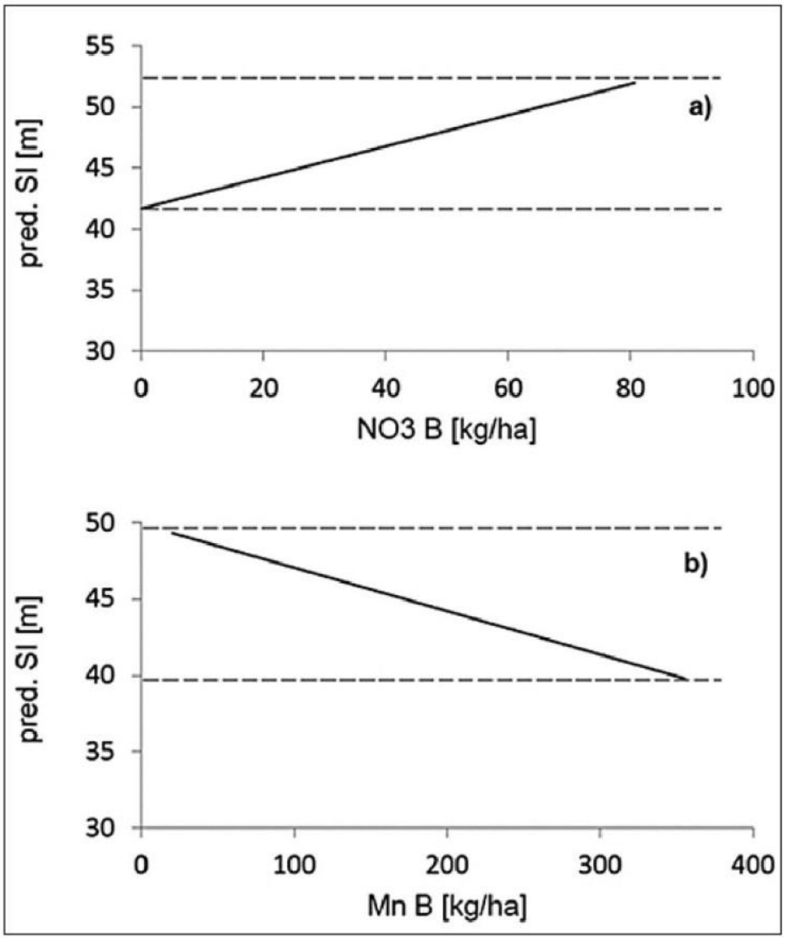


Fig. 5: Sensitivity analysis of the main influencing parameters NO3- B and Mn B (a) NO3- B within the range of min – max and the mean value of Mn B and (b) Mn B within the range of min – max and the mean value of NO_3^- B

5. Discussion

The stand level of the Douglas-fir model predicts the relative 10 year basal area increment per hectare as a nonlinear power function with the predictor variables crown competition factor, mean diameter at breast height at the beginning of the growing period and site index (equ. 11). The basal area increment relative to tree size is greatest in low density stands with a high site quality. Theoretically, the accurate relationship between increment and tree size would have a positively skewed unimodal form as increment increases to a maximum in early life and then gradually decreases (Wykoff, 1990).

As our sampling design was restricted to forest stands with a minimum age of 60 years, no modification of the power function was necessary. The sensitivity analysis (Figure 3) indicated a substantial effect of the competition parameter CCF on the basal area increment. Note that in our data we had covered a wide range of CCF values (40-120) (see Table 1). For the tree size parameters, the sampling design restricted a broader range in our data due to the fact that we only recorded stands older than 60 years. This is also evident for the site conditions which would have required a broader range in the sampled forest stands.

The genetic material of our Douglas-fir stands comes from the coastal variety of the Western Cascades in Washington and Oregon (Hintsteiner et al., 2014). Furthermore we selected only pure even aged Douglas-fir forests by ensuring a relative Douglas-fir proportion in a total stand basal area of ≥ 80%. This suggests that any difference in the growth rates of our Douglas-fir stands are only driven by stand density as well as soil and/or site conditions. As shown in Table 4, crown competition factor CCF, a measure for stand density, mean diameter at breast height and the site index entered the model significantly.

A correlational study determining the key driver for the site index (see Figure 4 a-g) revealed that the large number of environmental parameters (Table 1) can be reduced to only seven where the two soil parameters NO_3^- B and Mn B explain about 73 % of the site index variation (see Table 5). While nitrogen is the most limiting macronutrient in forests all over the world (Littke Hanft, 2012), manganese as a micronutrient intervenes in photosynthesis (Millaleo et al., 2010). Previous studies that examined the correlations between nitrogen fertilization and growth response in the Pacific Northwest illustrated positive responses of Douglas-fir growth (e.g. Gardner, 1990; Miller et al., 1986). Moreover, nutrient deficiencies in Douglas-fir stands were consistently demonstrated only for nitrogen (Weetman et al., 1992), which is consistent with our results.

Compared to the positive effect of nitrogen, manganese was negatively correlated to the site index (Fig. 4c). Manganese is an essential micronutrient for plants but may turn toxic in excessive concentrations. The amount of available manganese is influenced by soil pH, excess of water, poor drainage or applications of organic material (Millaleo et al., 2010). According to our study, the negative impact of manganese could be an indication of waterlogged soil conditions, as Mn B is positively correlated to the pore volume in horizon B ($R^2 = 0.40^*$). No correlation between Mn B and soil pH B was found. The sensitivity analysis (Figure 5) showed an equal effect of both soil parameters on the Douglas-fir site index.

Pore volume PV, indicating the air- and water holding capacity of soils, and clay content, alluding the water- and nutrient holding capacity of soils, in horizon B showed positive correlations to the SI (Fig. 4 d-e). The positive effect of the soil parameter clay content in B horizon is in agreement with the results of the soil-site study after Steinbrenner (1979) on sedimentary and volcanic soils in western Oregon. Other studies also revealed negative correlations of clay content and site index (e.g. Corona et al., 1998). Soil nutrients and soil texture were varied highly within all assigned bedrock materials (gneiss, granite, limestone). Accordingly, the use of soil parent material differentiated site indices would not be meaningful.

Correlations between climatic parameters and the SI are evident, with a negative correlation of mean annual summer temperature (Fig. 4f) and a positive correlation of mean winter precipitation (Fig. 4g) versus the SI. Under a changing climate with projected increases of mean summer temperatures and mean winter precipitation in Austria (Loibl et al., 2011), the climate sensitivity of the Douglas-fir is of particular interest to enable a successful incorporation in adaptive forest management considerations.

No significant correlations were found between the SI and the remaining environmental parameters (see Table 1), possibly due to the limited range of the selected Douglas-fir sites. To enlarge the gradient of the environmental parameters, Douglas-fir stands developed under extreme conditions should be sampled. This includes Douglas-fir sites under dry conditions as well as calcareous sites. Current recommendations for Douglas-fir cultivation in Austria and Germany are basically restricted to non-calcareous soils (e.g. Englisch, 2008), which could not be confirmed in our study.

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8.2 Paper II

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ORIGINAL PAPER

Genetic diversity and adaptive traits of European versus American Douglas-fir seedlings

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Abstract Due to its productivity and potential to adapt to the expected climate change, the Douglas-fir is one of the most important commercial non-native forest tree species in Europe. Currently, seeds from both non-native European and native American seed stands are used for plantations. In this study, we investigate European seed lots for their native origin (variety and potential geographic origin in America) and assess the adaptability, growth and survival potential of European versus American Douglas-fir seed lots. We compare the genetic diversity, morphological characteristics such as height (*h*), root collar diameter (rcd) and the ratio of *h*/rcd, and the timing of bud burst. We investigate 852 1-year-old seedlings from 10 different US and European seed lots representing 5 provenance regions which are sold in Germany and Austria. Seedlings are genotyped for 13 nuclear SSRs and analysed together with reference data set and standard genetic structuring and assignment methods. Adaptive traits of morphological characteristics and timing of bud burst of the seedlings are recorded and statistically analysed. The results show that the investigated European seedlings originate from recommended American native seed sources and represent both varieties and inter-varietal admixed individuals. European seedlings have a lower genetic diversity versus the American seedlings and native populations. They show significant differences in the adaptive traits such as morphological characteristics and timing of bud burst. According to the genetic diversity indices, certified North American Douglas-fir seed sources should be preferred for planting in Central Europe.

Keywords Douglas-fir · Genetic diversity · Forest management · Climate change adaptation

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Introduction

The Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the second most cultivated non-native conifer tree species in Europe after the Sitka spruce (Köble and Seufert 2001), which grows in more than 35 European countries. Within its native distribution range, in western North America, two distinct varieties of the Douglas-fir are known: the coastal variety (*P. menziesii* var. *menziesii*) and the interior variety (*P. menziesii* var. *glauca*). The coastal variety grows along the Pacific coast and the west facing slopes of the Rocky Mountain range from British Columbia, Canada to California, USA. The interior variety (also called Rocky Mountain variety) grows further east of British Columbia, across the Rocky Mountains to New Mexico (USA) (Eckenwalder 2009). In the contact zone of the two varieties, hybridization is evident (Gugger et al. 2010; van Loo et al. 2015; Wei et al. 2011).

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different ecological conditions led to specific patterns of genetic diversity and a large genetic variation in adaptive traits (e.g. bud burst, bud set, growth performance, fall and spring frost hardiness) within the native distribution range (Gould et al. 2012; St. Clair 2006; St. Clair et al. 2005).

In Europe, the current distribution of the Douglas-fir is the result of a long introduction history, which started in 1826 (Köble and Seufert 2001). In most European countries, the first Douglas-fir stands were characterized by excellent growth and health conditions. At the beginning of the twentieth century, further imports of Douglas-fir seeds to Germany were less successful. This initiated the first provenance tests in Europe, which confirmed the importance of seed origin for cultivation (Bastien et al. 2013), since it affects the growth, frost sensitivity and tolerance to diseases. As a result, the recommended provenances for Western and Central Europe are the coastal variety from the Western Cascades and the coastal region in Washington as well as Oregon (Barner 1973; Kleinschmit and Bastien 1992). The interior variety is not as productive as the coastal Douglas-fir and has a higher susceptibility to needle cast (*Rhabdocline pseudotsugae*) (Eilmann et al. 2013). Hence, the interior variety is generally not recommended for cultivation in Europe (Boyle 1999). Only in continental environments (e.g. Sweden, Finland and former Czechoslovakia) does the interior variety from British Columbia perform better than the coastal variety (Kleinschmit and Bastien 1992).

Although European Douglas-fir stands planted prior to the 1980s are of unknown geographic seed origin (Bastien et al. 2013), several of these stands were selected and certified for harvesting and trading forest reproductive material of the Douglas-fir (seeds, parts of plants, planting stocks). The underlying assumption was that Douglas-fir is appropriate for the ecological conditions in Europe. Since these stands have largely not been tested for their genetic origin, an artificial mixture of both varieties and different native origins cannot be excluded (Bastien et al. 2013; Klumpp 1999; Konnert and Ruetz 2006). Such mixtures can influence the genetic diversity in natural regeneration and in seeds, which may decrease due to inbreeding and assortative mating (Fussi et al. 2013; Konnert and Ruetz 2006). Furthermore, the European seed stands are rather small in size (less than 1 ha) and often show a patchy tree distribution, which negatively influences the population structure and mating patterns (Ratnam et al. 2014). In the native distribution range, large Douglas-fir stands ensure a widespread population with an extensive pollen gene flow. Today, Douglas-fir seedlings from European stands as well as from native forest stands in North America are planted.

In Europe, two legal frameworks for the trading of forest reproductive material (seeds, parts of plants, planting stocks) are in place: (1) the European Council Directive 1999/105/EC for Members of the European Union; and (2) the regulation of the Organization for Economic Co-operation and Development (OECD) open for all countries who wish to participate (Ackzell 2002). The EU directive differentiates between four categories (1) "source identified", (2) "selected", (3) "qualified" and (4) "tested" according to the basic material, e.g. seed sources, seed stands and seed orchards. Each European member state can enforce its own more rigorous rules for the approval of basic material and production of FRM (forest reproductive material) (Konnert et al. 2015). At an international level, the OECD scheme defines the same four categories (OECD 2007).

With the increasing interest in cultivating Douglas-fir as an adaptation option to climate change in Europe, planting suitable FRM is of increasing importance. Thus, assessing the differences in the characteristics between American versus European FRM is important. Commonly, the genetic diversity is seen as a measure of the adaptive potential (Adams et al. 1998; Konnert and Fussi 2012) of the tree population to changing growing conditions. Demographic processes (e.g. bottlenecks, founder events) caused by forest management practices such as selective thinning followed by natural or artificial regeneration may shape the genetic composition of the European seedlings leading to a reduced genetic variation (Ratnam et al. 2014). Adaptive traits are reflected in the morphology and phenology of a plant. The morphological characteristics (1) shoot height and (2) root collar diameter of seedlings are considered as an indicator for the growth and survival potential (Haase 2007; Landis et al. 2010). The timing of bud burst is an important adaptive parameter, as young shoots of the Douglas-fir are highly susceptible to late-frost damages caused by late-spring frost temperatures (Steiner 1979).

In this study, we test European seed sources for their native origin (variety and potential geographic origin in America) and investigate the adaptation, survival and growth potential of European versus American Douglas-fir seed sources. We use cultivated one-year-old seedlings from 10 different American and European seed lots to assess (1) the native origin and genetic diversity of seedlings of a given seed lot, (2) morphological characteristics, such as height, diameter as well as sturdiness (height/diameter) as an indicator for seedling quality and (3) the timing of bud burst, which is an adaptive trait and reflects susceptibility to late frost. Here, we combine two different approaches: firstly population genetics to determine the native origin and genetic diversity and secondly the assessment of adaptive traits to elucidate the growing and survival potential.

Materials and methods

Seedlings

The seedlings for our study are provided by an Austrian company producing containerized forest seedlings. The commercial available seed lots come from 10 different seed stands (S01–S10) (Table 1) and represent 5 provenance regions: two seed stands are located in Austria, three in Germany and five in the US (Fig. 1). Each seedling population consists of 65–98 plants (Table 1). The seed lots are selected according to the demand in Austria and Germany. Since Darrington is currently the most demanded provenance, three seed sources are selected (B. Igler, personal communication, 31 May 2015). The European seed stands grow in the Waldviertel (Austria) and in the Südostdeutsches Berg- und Hügelland (Germany) and belong to the FRM (forest reproductive material) category "selected". According to national legislation, the minimum number of harvested trees for this category requires 10 individuals within a given seed stand in Austria (Müller and Strohschneider 2004) and 20 in Germany (Behm et al. 2007).

The American seed stands are Darrington, Trout Lake and Randle and belong to the category either "selected" or "source identified" (Table 1). In the native range, the seed stands are harvested with the help of Douglas squirrels (*Tamiasciurus douglasi*), which collect and store Douglas-fir cones in holes. These cones are collected within the harvesting area which can encompass several hundred hectares (Konnert and Ruetz 2011).

The category "source identified" defines FRM as material from a seed stand located within a single region of provenance, where little or no phenotypic selection has taken place. The FRM category "selected" defines material from a phenotypically selected stand (Council Directive 1999/105/EC). In Austria, both categories are common; in Germany, only the category "selected" (see § 13 FoVG) (Forstvermehrungsgutgesetz (FoVG) 2002) is permitted.

Experimental set-up

In April 2012, the commercial seeds were germinated in pots with a volume of 50 cm^3 and the components of the soil substrate were white peat with fraction 0–5 mm (90%) and horticultural pearlite with fraction 0–3 mm (10%). After germination, the seedlings were separated and in December 2012 transported to the laboratory of the Institute of Silviculture in Vienna, Austria. Leaf samples of 30 (10 small, 10 medium and 10 large) seedlings per seed lot (in total 300 samples) were collected, dried and stored in silica gel prior to the DNA extraction. The morphological characteristics height and root collar diameter of each individual seedling were recorded.

The seedlings were further cultivated in the same pots with a distance of 3 cm to each other as a randomized block design and placed at the experimental forest garden "Knödelhütte". The garden is located in the western part of Vienna at an elevation of 290 m above sea level (N 48°13′ E 16°14′) with a mean annual temperature of 10.3 °C and a mean annual precipitation rate of 603 mm. Three different stages (1) dormant, (2) axillary (lateral) bud burst completed and (3) terminal bud burst completed (when green needles were first visible) were recorded to assess the bud burst development (Fig. 2). The bud stages were recorded every second week from 20 February to 15 April 2013, until the first bud was flushing. From 15 April, the stages were recorded on a daily basis at 9 am until terminal bud burst of each seedling was completed.

Table 1 Description of 10 Douglas-fir seed stands (S01–S10), of which seeds were used in this study

Nr.	Country	State	Provenance region (number)	FRM category	Latitude [DD]	Longitude [DD]	Elevation [m]	*N*	Crop year
S01	Austria	Lower Austria	Waldviertel (9.2)	Selected	48.5131	15.7618	300–500	81	2008
S02	Austria	Lower Austria	Waldviertel (9.2)	Selected	48.5253	15.7244	300–500	81	2006
S03	Germany	Thuringia	Südostd. Berg u. Hügelland (853 06)	Selected	50.581	10.8141	670–680	65	2009
S04	Germany	Thuringia	Südostd. Berg u. Hügelland (853 06)	Selected	50.6222	10.7300	480–580	98	2006
S05	Germany	Bavaria	Südostd. Berg u. Hügelland 853 06	Selected	50.2385	11.5919	420–610	69	2011
S06	USA	Washington	Darrington (403/13)	Selected	48.3699	−121.582	250–500	88	2009
S07	USA	Washington	Darrington (403)	Source identified	48.2781	−121.628	200–300	93	2007
S08	USA	Washington	Darrington (403/13)	Selected	48.3697	−121.580	250–500	85	2009
S09	USA	Washington	Randle (652)	Source identified	46.4219	−121.975	300–500	95	2009
S10	USA	Washington	Trout Lake (430/31)	Selected	46.0261	−121.536	700–800	97	2007

Location of populations is defined by country, state, provenance region and number, geographic location (latitude, longitude in decimal degrees (WGS 84 projection) and elevation in m above sea level). *N* provides the number of seedlings used for analyses of height, root collar and bud burst. Crop year refers to the year when seeds were collected in populations

Fig. 1 Distribution map of seed source populations (S01–S10) in the USA and Europe

DNA extraction and nuSSR genotyping

Total DNA from 25 g of powdered leaf samples per individual was extracted applying the commercial OMEGA E. Z.N.A Plant DNA Kit (OMEGA Bio-Tek, Inc., Norcross, Georgia, USA) according to the manufacturer´s instructions. The extracted DNA samples were amplified and genotyped with 13 nuSSRs. The 13 nuSSRs are identical to those used by van Loo et al. (2015). Details on the PCR procedure are given in van Loo et al. (2015).

Analyses and results

Variety composition and potential native origin

We started our analysis by assessing the variety (coastal or interior) and the potential geographic origin of the seed lots in Northwest America. Both the variety composition and the potential native origin were assessed using multilocus genotype data of the studied seedlings and the reference data set developed by van Loo et al. (2015). Genotypes

Fig. 2 Investigated stages of bud burst development: (1) dormant, (2) axillary bud completed (3) terminal bud completed

were not corrected for null alleles. The reference data set represents genotypes of 746 individual Douglas-fir trees from 36 reference populations and covers the natural distribution range in Northwestern America (Figure S1 in the supplementary materials). The reference populations were genotyped with identical nuSSRs to those used in our study.

The variety composition was assessed by applying the software STRUCTURE v.2.3.4, which uses a Bayesian clustering approach by applying the Markov chain Monte Carlo (MCMC) algorithm to allocate individuals to clusters (K) that are genetically similar (Falush et al. 2003, 2007; Pritchard et al. 2000). We used the multilocus data of the reference data set to pre-define 2 clusters ($K = 2$), representing the two varieties, and probabilistically assigned all individual seedlings to these clusters. Twenty independent runs were applied, one for each cluster (K) with a burn-in period of 50,000, followed by a run length of 100,000 iterations. As recommended by Falush et al. (2003), we used an admixture model that allows the seedlings to have admixed ancestries, permitting it to detect inter-varietal admixed individuals. In addition, we used correlated allele frequencies, as we expected similar frequencies due to the common ancestors of the two varieties. For each independent run, the software STRUCTURE estimates a membership coefficient (Q), which corresponds to the probability of an individual belonging to each cluster. An individual was declared as coastal with $Q > 0.90$, as Rocky Mountain with $Q < 0.10$ and inter-varietal admixed with $0.90 > Q > 0.10$. To find the optimal alignment of the 20 independent runs, the software CLUMPP v.1.1.2. was used. The estimated individual membership coefficients (Q) were averaged using the greedy algorithm in CLUMPP to correct for discrepancies between runs (Jakobsson and Rosenberg 2007). Then, the average Q values were plotted using DISTRUCT v.1.1 (Rosenberg 2004).

The potential geographic origin of the studied European seedlings in Northwestern America was estimated using genetic assignments of the software GeneClass2 (Piry et al. 2004). Although we knew the origin of the American seedlings, we also applied the analyses of these seedlings to test the accuracy of the applied assignment methodology. Seedlings of all seed stands (here S01-S10) were assigned to the reference populations of the reference data set. Three types of methods for likelihood estimation are available in GeneClass2. In our study, we applied two of them: (1) the frequency-based method after Paetkau et al. (1995) and (2) the distance-based method using Nei's (1972) standard genetic distance-based criteria according to Takezaki and Nei (1996). The frequency method after Paetkau et al. (1995) assigns an individual or group of individuals to the reference population with the highest likelihood (score) according to its multilocus genotypes and the allele frequencies (Hauser et al. 2006). We applied a threshold likelihood value for assignment of $p < 0.05$. The distance-based method (Nei 1972; Takezaki and Nei 1996) assigns an individual or group of individuals to the reference population according to the smallest genetic distance (Piry et al. 2004). We use Nei's (1972) standard genetic distance D_S to calculate a rank with the corresponding scores (%) to all reference populations. Commonly, frequency-based methods are more powerful than distance-based methods (Hauser et al. 2006). The distance-based methods tend to be less sensitive to violations of the Hardy–Weinberg Equilibrium (HWE) (Hauser et al. 2006), which could be the case in European populations as they might originate from small, fragmented but also cultivated variety mixed stands. This suggests using both methods.

All seedlings of the stands S03, S04, S05, S07, S08, S09 and S10 were assigned to the coastal variety (Fig. 3). For the Austrian stand S02, three of 30 individuals were assigned to the interior variety and four individuals were allotted to be inter-varietal admixed seedlings. The remaining 23 seedlings were assigned to the coastal variety. For population assignments, S02 was analysed with 30 individuals to test if it is derived from the admixture zone in the natural distribution range. Furthermore, S02 was separated into the 2 varieties (coastal and interior Douglas-fir) to investigate if it was established by two different seed sources. One inter-varietal admixed individual was detected in the US stand S06 and the Austrian stand S01 (Fig. 3).

The assignment results for the potential native origin are given in Table 2 and Fig. 4. The frequency-based assignment method of Paetkau et al. (1995) showed score values of correctly assigned populations of 100% in almost all studied populations. Accordingly, seedlings of the European stands (S01, S02, S03, S05) matched the reference populations (R) of the coastal variety R11, R15, R16 and R11 in the Western Cascades in Washington, respectively. The seedlings of S04 were allocated to R32, a coastal variety from Vancouver Island in British Columbia, Canada. Three seedlings of the Rocky Mountain variety of S02 referred to R18 in British Columbia. Results of S02 showed that the population with 30 variety mixed and admixed individuals, and if separated by variety (27 coastal individuals), was allotted to the same reference populations (Table 2). Hence, we conclude that S02 includes two different seed sources and does not originate from the admixture zone. The seedlings of the native US populations were assigned to reference populations in the Western Cascades in Washington and Oregon with the following results: S06–S08 (Darrington) to R15, the seedlings of S09 (Randle) to R11 and those from S10 (Trout Lake) to R05.

When using the second method based on Nei's distance approach, the same reference populations for S01, S03 and S05-S10 were identified. However, the populations S02 and S04 were assigned to R30/R27 and R30, respectively. The likelihood score values, a measure for the probability of a studied population belonging to the reference population, ranged between 5.2 and 11.1%. We built 10 small subsamples with 3 randomly selected individuals of the reference population R18 and R27 to analyse the reliability of group assignments with 3 interior individuals for S02, (Table 3). The subsamples were assigned to reference populations following identical steps as for the other assignments. The randomly selected individuals were left out in the corresponding reference population. Results showed that the subsamples (1–10) were correctly assigned to R27 and R18 (Table 3).

Genetic diversity

Using the software GenAlEx v. 6.5 (Peakall and Smouse 2006, 2012), we assessed the genetic diversity of the seedlings using the following diversity parameters: (1) allelic diversity (*Na*), (2) effective number of alleles (*Ne*), (3) observed frequency of heterozygotes (*Ho*), (4) expected frequency of heterozygotes (*He*) and the (5) inbreeding coefficient (*Fis*). *Fis* values were tested for significance (*p* 0.05) of their deviation from the HWE (Hardy–Weinberg Equilibrium), also using the software GENEPOP v.4.1.4 (Raymond and Rousset 1995; Rousset 2008). We further calculated the allelic diversity parameters (6) allelic richness (*As*) and (7) private allelic richness *As*(*p*) (the number of distinct alleles private (specific) to a population based on a standardized population size by rarefaction using ADZE v. 1.0) to allow a comparison of populations

Fig. 4 Illustration of the assignment results according to the ▶ frequency-based approach after Paetkau et al. (1995). Geographic locations of the US populations (S06–S10) and the reference populations are marked with *crosses* and *circles*, respectively

with different sample sizes (Szpiech et al. 2008). We applied a standardized population size of 8 individuals, which is the same as used in the reference data set (van Loo et al. 2015).

The procedure allowed us to compare the allelic richness of the European seedlings with their corresponding native reference population since it accounts for differences in the sample size. If a population consists of a mixture of both varieties (as was the case with the Austrian S02), the genetic diversity indices by variety were calculated as well.

An independent *t* test was applied (with PASW Statistics for Windows Version 18.0) to evaluate the differences between the mean of the two independent groups. We compared the genetic diversity parameters between seedlings from the US and the European stands and the allelic richness parameter (As_8) of the seedlings from European stands with the reference populations from van Loo et al. (2015).

The results for the calculated genetic diversity indices (*Na, Ne, Ho, He, Fis*, As_8 and $As_8(p)$) of the European and American seedlings are given in Table 2. For S02, these indices were additionally calculated for the coastal Douglas-fir variety. The *t* test revealed that *Na* ($p = 0.021$), *Ne* ($p = 0.001$), H_E ($p = 0.023$) and As_8 ($p = 0.015$) were significantly higher within the US populations versus the European populations. Other diversity parameters (*Ho*, *Fis* and $As_8(p)$) of the European seedlings were within the range of the American seedlings. The *Fis* were significantly positive, indicating deviations from HWE. This could confirm previously published data on the Douglas-fir. The

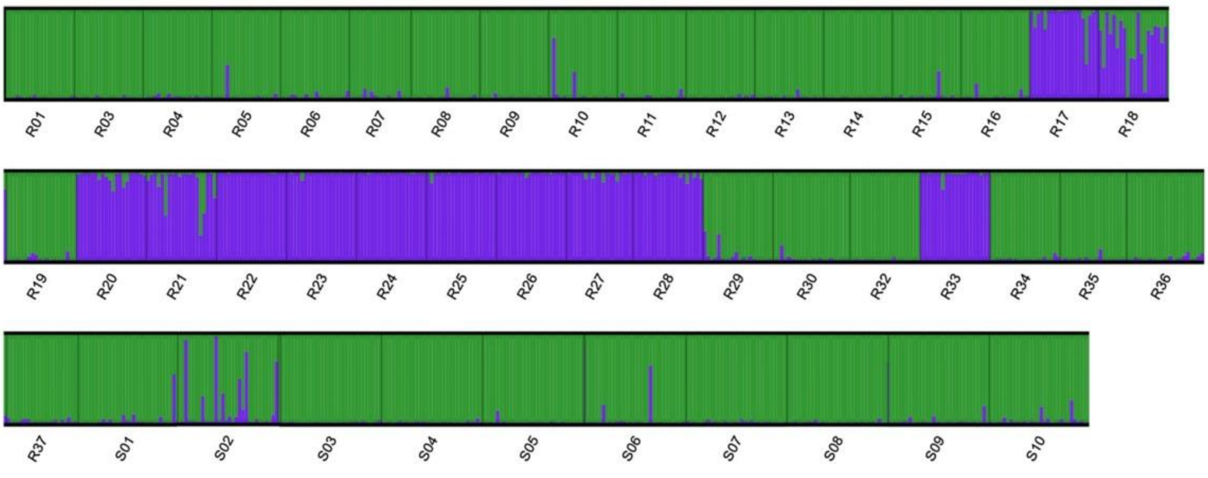

Fig. 3 STRUCTURE results plotted using DISTRUCT v.1.1 for genetic structure ($K = 2$) representing 746 individuals of the 36 reference populations (marked by *R*) and 300 individuals of the 10 seed source populations (marked by *S*) of the coastal (*green colour*) and Rocky Mountain variety (*blue colour*). Individuals are grouped by populations. (Color figure online)


R38
R18 (S02)
R17
R32 (S04)
R19
R14
R20
R12
S08
S07
S06
R15 (S02, S06, S07, S08)
R08
R11 (S01, S04, S09)
R16 (S03)
S09
R07
R10
S10
R09
R03
R06
R05 (S10)
R28
R30
R01
R04
N
0 30 60 120 Kilometers
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comparison with the assigned native reference populations R11, R15, R16, R32 (Table S1 in the supplementary materials) of the frequency-based approach, revealed that the allelic diversity parameter As_8 of the European seedlings was significantly lower ($p = 0.008$).

Morphological characteristics

For the statistical analyses of the morphological characteristics, the PASW Statistics for Windows Version 18.0 was used. The Levene test was applied to verify the assumptions of equal variances. For equal variances, an analysis of variance (one-way ANOVA) using the post hoc test Scheffé for multiple comparisons was used at a significance level of $\alpha = 0.05$. If the assumption of homogeneity of variances was violated, a one-way ANOVA with Welch's F-test using the post hoc test Games-Howell for multiple comparisons of unequal variances was performed at a significance level of $\alpha = 0.05$.

Height

The adjusted Welch ANOVA determined a statistically significant difference between seedlings of the 10 seed populations ($p < 0.001$). Multiple comparisons (see Table 4; Fig. 5) of the studied populations indicated a significantly higher growth performance of the Austrian seedlings from S02 (μ 16.9 cm) when compared to seedlings from all other studied seed populations, followed by the seedlings of the US population S09 (μ 15.7 cm). The seedlings from the US population S10 (Fig. 6) showed the lowest growth performance with a mean value of 11.5 cm (highly significant). The seedlings from the remaining populations from Europe (S01, S03–S05) and the USA (S06–S08) indicated similar height growth rates ranging from 13.1 to 14.1 cm.

Root collar diameter

The one-way ANOVA determined a statistically significant difference between seedlings of the 10 seed populations ($p < 0.001$) of the morphological feature root collar diameter (range 1.8 to 2.2 mm) (Table 4; Fig. 5). Again the seedlings of the Austrian population S02 showed the highest growth in diameter (μ 2.2 mm) compared to seedlings from all other populations (significantly, except S01 and S09). The seedlings of the US population S07 revealed the lowest mean diameter at 1.8 mm. The German population S03 (μ 2.1 mm) indicated a significantly better growth performance in diameter compared to the US populations S06, S07 and S10.

Height/diameter

The adjusted Welch ANOVA determined a statistically significant difference between the seedlings of the 10 stands ($p < 0.001$). Multiple comparisons (see Table 4; Fig. 5) indicated the highest ratio in height to diameter in seedlings from the US population S09 (μ 8.4), which is significantly higher compared to seedlings of all other populations, except S02 (μ 7.9). The seedlings of the US population S10 showed the lowest mean value of the sturdiness quotient at 6.3, followed by S03 at 6.6. In all other populations, similar values ranging between 7.0 and 7.4 were found.

Timing of bud burst

The investigated bud burst development stages showed that within 15 days (15.04.2013 to 29.04.2013), all seedlings completed stage number 3, when the first green needles of the terminal bud were visible. The separate examination of lateral and terminal bud burst indicated that 70% of the auxiliary buds flushed earlier than the terminal buds. Following this, the timing of the terminal buds was evaluated. The same statistical analysis, as described in "Morphological characteristics" section, was applied to compare the timing of bud burst. For estimating the effect of the population, blocks and their interaction, a general linear model (GLM) was applied. Therefore, each population was treated as fixed, and blocks as a random variable. Results of the GLM analysis showed that the main effect of population is significant (p 0.015) (see Table 5). Random block effects and population times block interactions were not significant (p 0.167 and 0.234, respectively) (Table 5). The timing of the terminal buds was further evaluated according to Welch's one-way ANOVA and the statistically significant difference between seedlings of the 10 seed populations was determined ($p < 0.001$). The post hoc test Games-Howell for multiple comparisons was used to determine which specific seed lots differ. Results of the multiple comparisons showed the earliest bud burst of seedlings from the European stands S01 and S04 with a mean of 8.3 days, which is significantly earlier compared to seedlings from the German population S05 (μ 9.8 days) and the US population S08 (μ 10.1 days) (Table 6; Fig. 7). Bud flushing within the native US populations (S06–S10) ranged between 8.6 and 10.1 days (Table 6). Multiple comparisons showed a significantly earlier timing of bud burst of S09 (μ 8.6 days) as compared to S08 (μ 10.1 days) (Table 6; Fig. 7). In all other populations, no significant differences were found with mean values ranging between 8.9 and 9.6 days.

Table 2 Genetic diversity and assignment results for seedlings from seed source populations of Douglas-fir including the mean for the number of alleles (*Na*) and the effective number of alleles (*Ne*), the frequency of the observed heterozygosity (*Ho*) and the expected heterozygosity (*He*) after Hardy–Weinberg equilibrium, the inbreeding coefficient (F_{IS}), the number of alleles expressed as allelic richness (As_8) and unique alleles expressed as private allelic richness $As_8(p)$ at a standardized population level of 8 as well as AR (assignment to reference populations with 18–22 individuals) according to Nei's standard distance (D_S) and the frequency-based approach (*F*) after Paetkau et al. (1995) including score (in %) of GeneClass2

Nr.	Country	*N*	*Na* (sd)	*Ne* (sd)	*Ho*	*He*	F_{IS}	As_8	As_8 (*p*)	AR (score)	
										D_S	*F*
S01	Austria	30	18.00 (1.51)	10.45 (1.11)	0.66	0.88	0.26*	6.00	0.93	R11 (6.8)	R11 (100)
S02	Austria	30	18.15 (1.14)	10.57 (0.95)	0.68	0.89	0.24*	6.07	1.11	R30 (4.5)	R15 (100)
S02[a]	Austria	27/3	17.54 (1.12)	10.53 (0.90)	0.71	0.89	0.21*	6.10	1.02	R30 (5.9), R27 (11.1)	R15 (100), R18 (96)
S03	Germany	30	15.31 (1.30)	8.63 (1.04)	0.58	0.85	0.32*	5.58	0.98	R16 (5.2)	R16 (100)
S04	Germany	30	14.15 (1.15)	8.75 (0.74)	0.65	0.87	0.26*	5.68	0.98	R30 (5.5)	R32 (93.4)
S05	Germany	30	17.08 (1.24)	9.89 (0.70)	0.69	0.89	0.23*	5.96	0.92	R11 (6.3)	R11 (100)
S06	USA	30	18.46 (1.42)	11.39 (1.11)	0.63	0.90	0.30*	6.18	0.86	R15 (6.9)	R15 (98.9)
S07	USA	30	19.00 (1.90)	12.07 (1.34)	0.63	0.91	0.30*	6.21	0.94	R15 (6.6)	R15 (100)
S08	USA	30	18.00 (1.37)	11.36 (0.87)	0.60	0.90	0.33*	6.19	0.88	R15 (6.4)	R15 (100)
S09	USA	30	20.08 (1.62)	12.38 (1.27)	0.68	0.90	0.25*	6.29	1.02	R11 (5.9)	R11 (100)
S10	USA	30	19.54 (1.64)	12.54 (1.39)	0.65	0.90	0.28*	6.26	1.18	R05 (6.3)	R05 (100)

N provides the number of investigated seedlings per seed source population

[a] Genetic diversity results refer to the coastal variety only, and assignment results refer to coastal and interior individuals

* Significant deviation from HWE (Hardy–Weinberg equilibrium) $p < 0.001$

Table 3 Assignment tests with 10 small subsamples of reference populations R27 and R18

Subsample	Reference population		*N*	AR (score)	
				D_S	*F*
1	R18	R27	3	R18 (11.4), R27 (14.0)	R18 (99.9), R27 (100)
2	R18	R27	3	R18 (10.9), R27 (12.3)	R18 (100), R27 (100)
3	R18	R27	3	R18 (13.6), R27 (14.4)	R18 (100), R27 (100)
4	R18	R27	3	R18 (11.3), R27 (15.4)	R18 (100), R27 (100)
5	R18	R27	3	R18 (11.1), R27 (14.0)	R18 (100), R27 (100)
6	R18	R27	3	R18 (12.6), R27 (13.8)	R18 (91.1), R27 (58.1)
7	R18	R27	3	R18 (10.3), R27 (14.9)	R18 (100), R27 (100)
8	R18	R27	3	R18 (12.2), R27 (14.3)	R18 (100), R27 (100)
9	R18	R27	3	R18 (11.5), R27 (15.1)	R18 (100), R27 (100)
10	R18	R27	3	R18 (10.5), R27 (13.0)	R18 (100), R27 (100)

Subsamples were built by using 3 randomly selected individuals from R27 and R18. AR (assignment to reference populations) according to Nei's standard distance (D_S) and the frequency-based approach (*F*) after Paetkau et al. (1995) including score (in %) of GeneClass2

Discussion

The assignment tests of the European stands (see Table 2; Fig. 4) showed that they come from the recommended seed zones for Douglas-fir cultivation in Austria and Germany (Kleinschmit et al. 1979; Weißenbacher 2008). However, the assignment results also show that forest stands from the European provenances "Waldviertel" (S01, S02) and "Südostdeutsches Berg und Hügelland" (S03, S04, S05) come from various native provenances (Table 2; Fig. 4). We also found that the Austrian stand (S02) contained a mixture of coastal, interior and inter-varietal admixed seedlings (Fig. 3). This is crucial since the interior variety is not recommended for planting due to its lower growth performance and higher susceptibility to fungi. In Bavaria (Germany), this problem has been recognized and certified seed stands must be genetically tested to ensure that no seed collections come from mixed variety stands (Konnert

Table 4 Multiple comparisons of the morphological characteristics height, diameter and height:diameter. Post hoc comparisons for height (Games-Howell), diameter (Scheffé) and height:diameter (Games-Howell) were used to determine which pairs of the 10 populations means differ

Mean differences										
Nr.	S01	S02	S03	S04	S05	S06	S07	S08	S09	S10
Height (cm)										
Mean	14.1	16.9	13.6	14.1	14.0	13.1	12.7	13.3	15.7	11.5
S01	–									
S02	−2.72*	–								
S03	0.52	3.24*	–							
S04	0.07	2.79*	−0.45	–						
S05	0.16	2.88*	−0.36	0.09	–					
S06	1.08*	3.80*	0.56	1.01	0.92	–				
S07	1.47*	4.19*	0.95	1.40*	1.31*	0.39	–			
S08	0.82	3.54*	0.30	0.75	0.66	−0.26	−0.65	–		
S09	1.58*	−1.14*	2.10*	1.65*	1.74*	2.66*	3.05*	2.40*	–	
S10	−2.66*	−5.37*	−2.14*	−2.59*	−2.50*	−1.57*	−1.19*	−1.84*	−4.24*	–
Diameter (mm)										
Mean	2.0	2.2	2.1	1.9	1.9	1.9	1.8	1.9	1.9	1.9
S01	–									
S02	−0.17	–								
S03	−0.08	0.09	–							
S04	0.07	0.25*	0.15	–						
S05	0.05	0.22*	0.13	−0.03	–					
S06	0.12	0.29*	0.20*	0.04	0.07	–				
S07	0.18*	0.40*	0.26*	0.10	0.13	0.06	–			
S08	0.10	0.27*	0.18	0.02	0.05	−0.02	−0.08	–		
S09	0.07	0.24*	0.15	−0.00	0.02	−0.05	−0.11	−0.03	–	
S10	0.13	0.31*	0.21*	0.06	0.09	0.02	−0.05	0.04	0.06	–
Height:diameter (−)										
Mean	7.2	7.9	6.6	7.4	7.3	7.0	7.1	7.1	8.4	6.3
S01	–									
S02	−0.66	–								
S03	0.60*	1.26*	–							
S04	−0.15	0.51	−0.75*	–						
S05	−0.05	0.61	−0.66*	0.10	–					
S06	0.23	0.89*	−0.38	0.37	0.28	–				
S07	0.12	0.78*	−0.48	0.27	0.18	−0.10	–			
S08	0.11	0.77*	−0.49	0.26	0.16	−0.12	−0.01	–		
S09	−1.13*	−0.47	−1.73*	−0.98*	−1.07*	−1.35*	−1.25*	−1.24*	–	
S10	0.96*	1.62*	0.36	1.11*	1.01*	0.74*	−0.84*	0.85*	2.09*	–

[a] Results of the univariate analysis (ANOVA) using the post hoc test Games-Howell and Scheffé

* $p < 0.05$

Table 5 General linear model analysis of bud burst timing

Source	Type III sum of squares	Degree of freedom	Mean square	*F*	Sig.
Population	368.755	9	40.973	4.758	0.015*
Block	19.268	1	19.268	2.249	0.167
Population × block	77.503	9	8.611	8.611	0.234

Population was considered as fixed and block as random effect

* $p < 0.05$

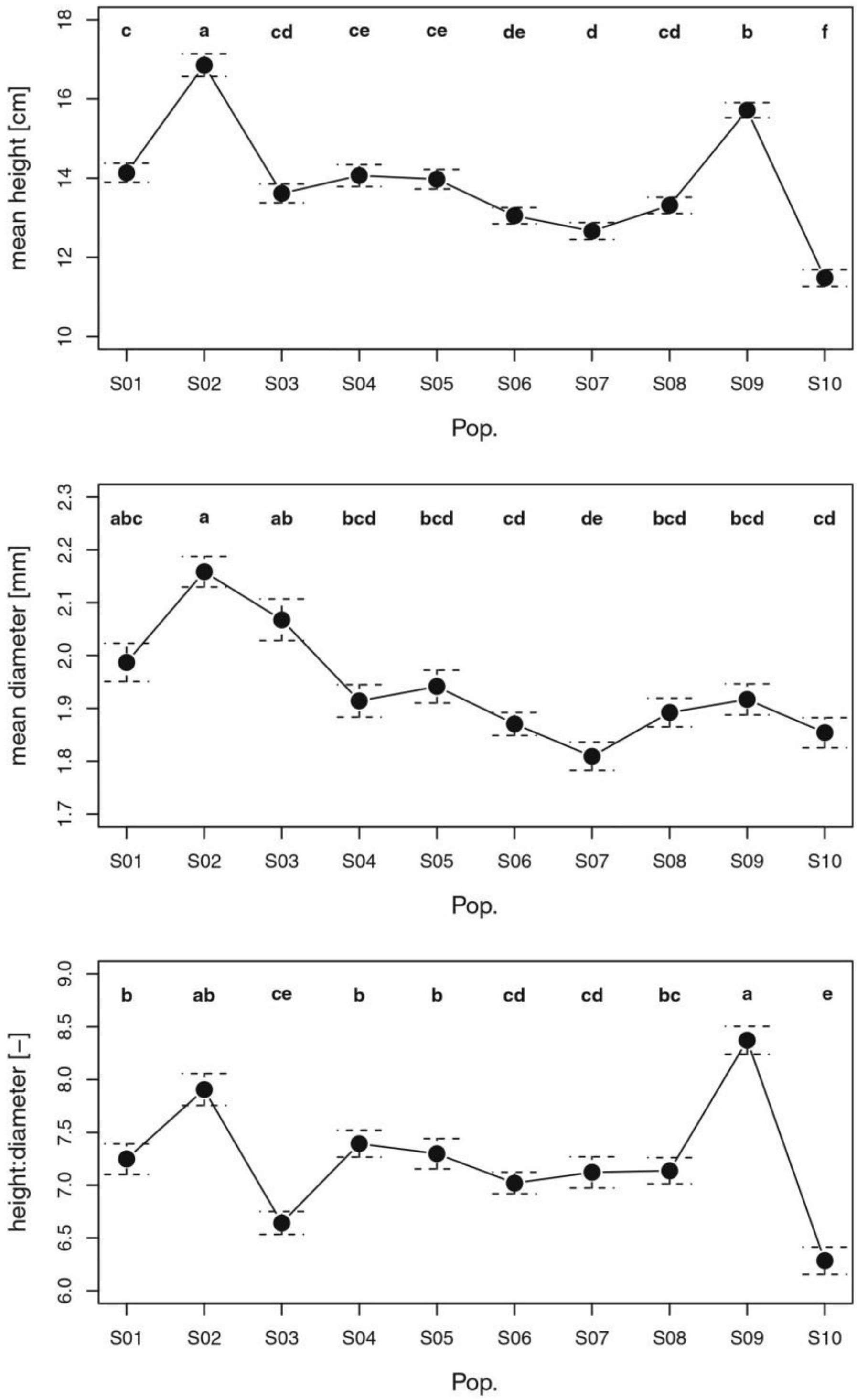

Fig. 5 Mean differences of the assessed morphological characteristics. Different letters indicate significant differences between populations ($p < 0.05$)

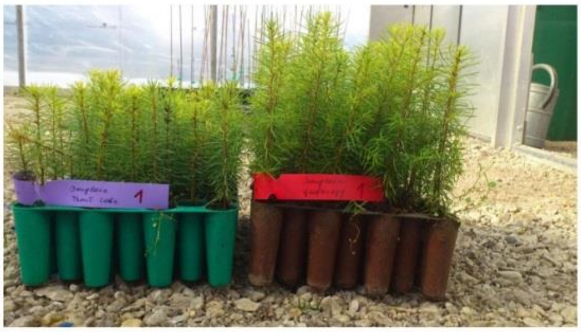

Fig. 6 Height performance of the US population S10 (Trout Lake) versus Austrian population S02 (Waldviertel)

and Fussi 2012). These genetic tests are planned for other German states (BLE 2016) and should be extended on an European level to ensure the best growing potential.

By assigning the native US seed lots to the reference populations, the performance of the applied assignment methods revealed the validity of the procedure since seed lots were correctly referenced to populations of similar geographic locations in the USA (Fig. 4). Nevertheless, further testing of the European planting material is suggested because (1) our analyses addressed the population level only and not the individual level and (2) all genetic analyses were restricted to 30 individuals. Analyses of larger sets might also reveal a larger number of interior variety and intervarietal admixed individuals, and (3) European FRM might

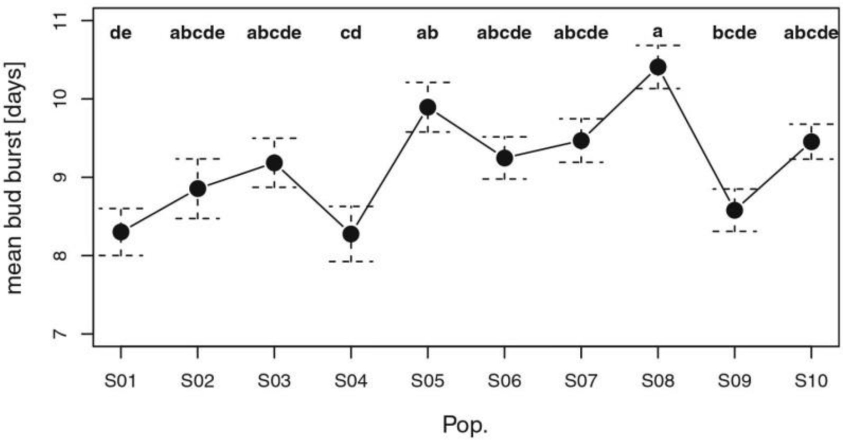

Fig. 7 Mean differences in bud burst timing. Different letters indicate significant differences between populations ($p < 0.05$)

Table 6 Multiple comparisons of bud burst timing

Mean differences										
Nr.	S01	S02	S03	S04	S05	S06	S07	S08	S09	S10
Bud burst (days)										
Mean	8.3	8.9	9.2	8.3	9.8	9.3	9.6	10.1	8.6	9.5
S01	–									
S02	−0.55	–								
S03	−0.88	−0.33	–							
S04	−0.04	0.59	0.92	–						
S05	−1.47*	−0.97	−0.59	−1.51*	–					
S06	−1.02	−0.47	−0.14	−1.10	0.45	–				
S07	−1.32	−0.77	−−0.44	−1.36	0.15	−0.30	–			
S08	−1.79*	−1.24	−0.91	−1.83*	−0.32	−0.77	−0.47	–		
S09	−0.32	0.23	0.56	−0.36	1.15	0.70	1.00	1.47*	–	
S10	−1.18	−0.63	−0.30	−1.22	0.29	−0.16	0.14	0.61	−0.86	–

Post hoc comparisons using Games-Howell procedures were used to determine which pairs of the 10 populations means differ

Results of the univariate analysis (ANOVA) using the post hoc test Games-Howell

* $p < 0.05$

originate from variety mixed stands or be influenced by gene flow from neighbouring Douglas-fir stands.

The genetic diversity indices of *Na* ($p = 0.021$), *Ne* ($p = 0.001$), H_E ($p = 0.023$) and As_8 ($p = 0.015$) were significantly higher within the US populations versus the European populations (Table 2). The private allelic richness ($As(p)$) of the European seed lots revealed overlapping values compared to American seed lots indicating distinct alleles specific to each population. In the European population S02, the highest $As(p)$ value was found (Table 2), most probable as a result of the detected interior and intervarietal admixed individuals which account for the distinct alleles. The comparison of the assigned native reference populations R11, R15, R16, R32 (Table S1 in the supplementary materials) with the European seed lots showed significantly higher values of allelic richness (As_8) ($p = 0.008$). The allelic richness is an estimator for the genetic diversity within populations and may decline for smaller populations (bottleneck or founder effect) (El Mousadik and Petit 1996). This indicates that the European seed lots come from stands with assortative mating, where the small sized, and sometimes patchily distributed seed stands can limit gene flow or have been collected from a small number of trees.

The seedling height can be related to the photosynthetic capacity and the transpiration, leading to a competitive advantage of taller seedlings within the shrub layer, but decreasing the survival rate due to drought stress and/or wind damage (Haase 2007). A larger root collar diameter suggests a larger root system, which is important for tree growth (Haase 2007). Blake et al. (1989) reported increased survival rates of Douglas-fir seedlings and a correlation with increased stem diameter. According to Rose and Ketchum (2003), a difference of 2 mm leads to an increase in stem volume of 35–43% after 4 years.

Although we could only obtain data from one growing season, the height and root collar diameter suggest that the best growing potential was evident for the Austrian population S02 (Table 4; Fig. 5), while the seedlings from the US population S10 (Fig. 6) showed the lowest height growth performance of all the investigated populations ($p < 0.05$). The ratio of height to diameter suggests that seedlings with high ratios are more susceptible to wind, drought and frost damages (Haase 2007). Thus, to reduce the risk, the h/d ratio should range between 5.5 and 7.5 for planted Douglas-fir plants (1.5–2 years old) (Bauer et al. 2009). The highest *h*/*d* ratio was evident for the US population S09 (μ 8.4) and was significantly higher versus all other populations except S02 ($p < 0.05$) (Table 4; Fig. 5). According to Bauer et al. (2009), the US population S09 (μ 8.4) and the European population S02 (μ 7.9), have a higher susceptibility to damages after planting.

Summing up, the European population S02 showed the best growth performance (see Table 4; Fig. 5), but the *h*/*d* ratio of 7.9 indicates a higher risk of damages after planting. The US populations S10 and S07 showed the lowest growth performance in terms of height and root collar diameter, respectively. The highest risk for damages after planting is evident for the US population S09.

Selecting the best seed source reduces the risk of frost damage due to the high heritability of bud burst traits by approximately 80% (Janßen and Rau 2008). Multiple comparisons showed that the European populations (S01, S04) exhibited a significantly earlier timing of bud burst (Table 6) as compared to the European population (S05) and the native US population (S08). Within the native range, population S09 exhibited a significantly earlier timing of bud burst as compared to S08 (Table 6). Hence, the European seed sources S01 and S04 and the US seed source S09 might be more susceptible to frost damages. The high range of bud burst within the native populations (μ 8.6 and 10.1 days) confirms the results of a previous study by St. Clair et al. (2015), which also showed a high variation in bud burst and early bud flushing related to latitude and summer drought of coastal Douglas-fir.

Conclusion

European provenance regions consist of different native origins and represent both varieties of Douglas-fir. The genetic diversity of the European seed lots was lower in comparison with seed lots from America and native populations. According to these results, we recommend native FRM from certified North American Douglas-fir seed sources. Provenances from coastal British Columbia, the Western Cascade Mountains and Oregon with a mean annual temperature ranging from 6 to 9.5 °C are predicted to be the most productive for Central Europe under both current and future climate conditions (Chakraborty et al. 2016). They are also characterized by the highest genetic diversity for the Douglas-fir (Table S1, Figure S1 in the supplementary materials), with a peak in Northern Oregon and Southern Washington west of the Cascades and decreasing trends towards south and north of the distribution range (Li and Adams 1989; Neophytou et al. 2016; van Loo et al. 2015).

When using European FRM, only FRM of known variety and native origin should be planted. Hence, we strongly advise to continue testing European seed stands of unknown origin for variety composition and potential native origin. This would be a valuable improvement in FRM certificates provided by/for seed and forest managers and forest owners in Europe.

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Supplementary materials: Figure

Genetic diversity and Adaptive traits of European versus American Douglas-Fir seedlings

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Figure S1: Distribution map of reference populations (R01, R03-R39) within its natural range in Northwest America (adapted after van Loo et al. 2015)

Supplementary materials: Table

Genetic diversity and Adaptive traits of European versus American Douglas-Fir seedlings

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Table S1: Geographical location and genetic diversity indices of the Douglas-fir reference data set (R01, R03-R39) within its natural range in Northwest America provided by van Loo et al. (2015). Latitude and Longitude refer to the location in decimal degrees (WGS 84 projection). N provides the number of investigated individual trees per seed source population. The number of alleles expressed as allelic richness (*As_8*) at a standardized population level of 8 was calculated for 13 nuclear microsatellite.

Nr.	Country	Latitude [DD]	Longitude [DD]	N	*As_8*
R01	US-OR	44.41	-122.47	20	6.4
R03	US-OR	45.77	-123.22	20	6.3
R04	US-OR	44.50	-122.00	20	6.5
R05	US-OR	45.40	-121.38	20	6.4
R06	US-OR	45.38	-122.30	20	6.2
R07	US-WA	46.37	-123.73	18	6.1
R08	US-WA	47.25	-123.42	20	6.2
R09	US-WA	45.97	-121.53	20	6.3
R10	US-WA	46.04	-121.44	20	6.2
R11	US-WA	46.75	-122.13	20	6.5
R12	US-WA	48.30	-121.60	20	6.1
R13	US-WA	48.26	-121.56	20	6.3
R14	US-WA	48.65	-121.72	20	6.0
R15	US-WA	47.54	-121.55	20	6.4
R16	US-WA	46.50	-121.89	20	6.3
R19	CA-BC	49.00	-121.75	20	6.2
R29	US-CA	40.85	-123.43	20	6.5
R30	US-OR	44.38	-123.88	22	6.5
R32	CA-BC	49.10	-124.03	20	6.0
R34	US-CA	37.92	-120.05	20	5.4
R35	US-CA	39.87	-122.67	20	5.7
R36	US-CA	40.36	-121.83	22	6.1
R37	US-CA	40.14	-124.05	22	6.3
R38	CA-BC	52.35	-126.03	22	5.4
R17	CA-BC	49.50	-117.27	20	5.8
R18	CA-BC	51.17	-119.54	20	6.4
R20	US-WA	48.60	-118.73	20	5.9
R21	CA-BC	52.69	-122.43	20	6.1
R22	US-AZ	34.93	-111.35	20	5.7
R23	US-NM	33.43	-108.60	20	5.7
R24	US-NM	32.83	-105.55	20	5.7
R25	US-NM	35.75	-105.83	20	6.0
R26	US-CO	37.95	-105.07	20	6.0
R27	US-ID	46.47	-115.35	20	6.3
R28	US-OR	44.95	-118.15	20	5.9
R33	US-MT	46.99	-110.70	20	6.1
R39	CA-BC	54.04	-125.34	20	5.4

8.3 Paper III

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Forest stand productivity derived from site conditions: An assessment of old Douglas-fir stands (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) in Central Europe.

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Douglas-fir productivity in Central Europe

Keywords

Non-native tree species, climate change adaptation, site conditions, site index

Contributions of the co-authors

TE collected and analysed the data and led the writing of the manuscript. EP helped in designing the study, contributed to the data collection, analysis and writing, and verified the whole manuscript. RK collected the data, helped with the interpretation and verified parts of the manuscript. DT analysed the data and contributed to the writing. GJL provided advice for the soil laboratory analysis and verified parts of the manuscript. MVL helped in designing the study. HH designed the study and verified the whole manuscript.

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Forest stand productivity derived from site conditions: An assessment of old Douglas-fir stands (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) in Central Europe.

Key message

Douglas-fir growth correlates with the climate, the soil moisture regime and the soil nutrient status, reflecting a broad physiological amplitude. Even though planting this non-native tree species is suggested as an viable strategy to improve adaptiveness of European forests to a more extreme climate and to assure future productivity, the expected temperature increase may induce a decline in forest stand productivity for Douglas-fir in already warm and dry regions.

Abstract

Context:

Tree species selection is one of the most important forest management decisions to enhance forest productivity and stand stability on a given site. Douglas-fir **(***Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), a non-native species from north-western America, is seen as an important additional species option for adapting Central European forests to a changing climate.

Aims:

This study assesses Douglas-fir forest productivity derived from site conditions. We investigate climatic and physico-chemical soil characteristics and productivity of 28 mature Douglas-fir stands growing on siliceous, as well as carbonate bedrock material in southern Germany and north-eastern Austria.

Methods:

The importance of climatic and physico-chemical soil characteristics was analysed with the machine learning method *Random Forests*.

Results:

The results show that Douglas-fir growth correlates with climate, soil moisture and soil nutrient availability derived from 10 climatic and physico-chemical soil parameters.

Conclusion

The broad pH optimum between 4.5 and 7.2 reflects the broad physiological amplitude of Douglas-fir and no significant differences were detectable between carbonate and siliceous bedrock. We also conclude that climate change may induce a forest stand productivity decline, because lower productivity with the highest mean summer temperature across our study range was observed at the warmest sites in Eastern Austria.

Keywords:

Non-native tree species; climate change adaptation; site conditions; site index

1. Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a native tree species in western North America, which was introduced to Europe about 150 years ago (Plomion et al. 2011). Currently, Douglas-fir covers more than 800,000 hectares of which 50 % are in France, 25 % in Germany, and the remaining 25 % are distributed across other European countries. In Germany and Austria, 2 % and 0.2 %, respectively, of the total forest area within the country are covered with Douglas-fir (Englisch 2008; Kownatzki et al. 2011). In its native range, Douglas-fir covers an area from British Columbia (Canada) to Mexico (2,200 x 4,500 km). The species has adapted to different ecological conditions, resulting in different growth patterns and varying phenological traits (Gould et al. 2012; Lavender and Hermann 2014). Two distinct varieties of Douglas-fir are known: (i) the coastal variety (*P. menziesii var. menziesii*) and (ii) the interior variety (*P. menziesii var. glauca*) (Eckenwalder 2009). Its excellent growth performance across a wide range of site conditions, the high wood quality, and its resistance towards diseases and insects have made the species one of the most important commercial tree species in the world (Bastien et al. 2013). Based on the growth performance, provenances recommended for Central Europe come from the Cascades in Washington and Oregon (Kleinschmit and Bastien 1992; Weißenbacher 2008; Bastien et al. 2013). The interior variety is generally not recommended for Central Europe due to lower growth rates and a higher susceptibility to Swiss needle cast (Boyle 1999; Bastien et al. 2013), and therefore is not very common in this region (Hintsteiner et al. 2018). *Pseudotsuga menziesii var. menziesii* is however widely regarded as an especially promising option to increase productivity and to adapt European forests to climate change (Spiecker et al. 2019). With the increasing promotion of Douglas-fir, also concerns about potential negative ecological impacts are expressed from nature conservation side. Studies of ecological consequences of Douglas-fir cultivation in Europe were reviewed by Schmid et al. (2014). This review concludes that in Europe, Douglas-fir regenerates naturally especially on poor sites (dry, acidic), where it is not outcompeted by native tree species, but the ecological impacts of Douglas-fir seem to be minor compared to other non-native trees (e.g. *Robinia pseudoacacia* in Europe). Nevertheless Douglas-fir can cause changes in species composition.

Within its natural distribution range, Douglas-fir grows on a wide range of soils and different parent materials, including marine sandstones, shales in the coastal region of northern California, Oregon and Washington as well as soils of glacial origin in southwestern British Columbia. The soils of the northern range of the Cascades are derived from metamorphosed sedimentary material, while igneous rocks and formations of volcanic origin are important in the southern Cascades. The highest growth rates are reported on well aerated soils with a pH value ranging from 5 to 6. Poorly drained or compacted soils inhibit Douglas-fir growth (Lavender and Hermann, 2014). Climatic variation in the natural range is large. The coastal variety in the Pacific Northwest experiences a maritime climate with mean annual precipitation rates of 760 – 3,000 mm, and a more continental climate towards the east of the Cascades (annual precipitation 600 – 3,000 mm) (Lavender and Hermann, 2014). Compared to the climate in Central Europe, most of the precipitation occurs in winter (Englisch, 2008) and the summer period is relatively dry.

In Central Europe, Douglas-fir has mainly been introduced on well drained, aerated and carbonate free soils. Since the beginning of Douglas-fir management in Europe, a lot of attention has been given to the carbonate content, as Douglas-fir growing on calcareous soils often shows leaf yellowing (chlorosis) (Englisch, 2008). Furthermore, on sites with high manganese concentration, symptoms of toxicity have been reported (LWF 2008). However, little information is available on the growth performance across different soil types in Europe. This lack of knowledge is problematic, as for an active forest transformation, where tree species sensitive to climate change are replaced by better adapted native or non-native trees (Bolte et al. 2010), Douglas-fir is seen as one of the most promising options and is therefore more and more planted by forest owners. Consequently, with the increasing interest in planting Douglas-fir, there is also higher interest of forest owners in better understanding the site-suitability of Douglas-fir to avoid costly cultivation failures. In case of this non-native tree species, which has been first introduced to Europe in 1827, a limited number of mature stands still exist. These stands can be analyzed in retrospect to determine the site impact on the productivity potential. In this paper, we investigate a wide range of physico-chemical soil and climatic characteristics to assess the productivity of 28 mature Douglas-fir stands growing on soils developed on siliceous and carbonate bedrock in southern Germany and north-eastern Austria. We are interested in deriving the forest stand productivity across different site conditions by assessing the importance of specific climatic and physico-chemical soil characteristics for the recorded growth performance of even-aged mature Douglas-fir stands. As a proxy of forest stand productivity, the site index at the age of 60 years was used. Because of the strong interdependency of impacts of climate and soil on forest growth, the aim was to derive the effect sizes and independent effects of climate and soil parameters on the site index with an advanced statistical method, the *Random Forests* regression approach. The objectives of this study were to (i) determine the dominant climatic and physico-chemical soil parameters and (ii) to show their effect size and correlation with the forest stand productivity of Douglas-fir in Central Europe.

2. Material and methods

2.1. Study sites

In 28 even-aged Douglas-fir stands with (i) stand age 40-120 years, (ii) stand size ≥ 1 ha and (iii) proportion of Douglas-fir basal area ≥ 80 %, tree data, physico-chemical soil data and climatic data were collected. The forest stands are located over a 600 km long and 150 km wide band north-east of the Alps, stretching across three Austrian provinces (Burgenland, Lower Austria, Upper Austria) and two German provinces (Baden-Württemberg, Bavaria) (see Fig. 1). With these forest stands, we cover a wide range of site, climatic, geological and topographic variation in Central Europe (Table 1).

In the drier areas of Eastern Austria (Burgenland, parts of Lower Austria), annual precipitation ranges from 570 mm to 790 mm and the mean annual temperature ranges between 8.9°C and 9.9°C. In Southern Germany and along the northern border of the Austrian Alps, the conditions are more humid with an annual precipitation between 810 mm and 2100 mm and a mean annual temperature between 7.0°C and 9.1°C.

All selected forest stands originate from the coastal and western Cascade region of Oregon and Washington. The native origin of the Douglas-fir stands was analyzed in a recent study by Hintsteiner et al. (2018), and/or was confirmed by the forest owners. Hintsteiner et al. (2018) assigned 26 out of 28 study sites to only one genetic cluster, cluster I, and two sites to the directly adjacent genetic cluster II (Fig. S1). These genetic clusters (cluster I and cluster II) comprise the most important Douglas-fir provenances, which are recommended for the study area in Germany and Austria and for which a similar growth performance in provenance trials have been determined (Kleinschmit et al. 1979; Ruetz 1981; Schultze and Raschka 2002; Chakraborty et al. 2016). Hence, we were able to minimize any potential genetic differences in the growth performances, and the bias genetic differences may have induced in assessing the forest stand productivity.

2.2. Forest data

In each of the 28 Douglas-fir stands, individual tree data were collected based on four angle-count sampling plots with a basal area factor of 4 (see Bitterlich, 1948). For each tree, we recorded the diameter at breast height (dbh), height, age, position and tree species. The dominant tree height by species of the angle-count sample plots was calculated as the mean height of the three trees with the largest dbh (Pollanschütz 1971). Stand age was determined by coring and counting the year-rings of the mean diameter tree of the angle-count sample.

The site index (SI) for all 28 Douglas-fir stands was defined as the mean dominant tree height at age 60 years (Kindermann and Hasenauer 2005). This site index at 60 years (SI60) was iteratively calculated according to the dominant height growth function after Mitscherlich/Richard (1919) for "Douglas-fir north-western Germany DoNwd" (Kindermann and Hasenauer 2005):

$$SI = a(1 - e^{-b*t})^{\,c} \quad (1)$$
$$a = a_0 + a_1 * SI_{60} + a_2 * SI^2{}_{60} \quad (2)$$
$$b = b_0 + b_1 * SI_{60} + b_2 * SI^2{}_{60} \quad (3)$$
$$c = c_0 + c_1 * SI_{60} + c_2 * SI^2{}_{60} \quad (4)$$

where, SI is the mean dominant tree height, SI60 is the dominant tree height at the age of 60 years, t the stand age and a, b, c the coefficients for „Douglas-fir northwestern Germany (DoNwd)" based on the yield table from Bergel (1985) (see Table S1).

2.3. Climate data

Site specific climate information for the years 1981 to 2010 was derived with the climate interpolation tool DAYMET, which had been validated and adapted for Austria, using the national climate station network (several hundreds of stations) from Austria and Germany (Thornton et al. 2000; Petritsch 2002; Hasenauer et al. 2003). With DAYMET, daily minimum and maximum temperature (Tmin, Tmax) and precipitation (Prcp) were interpolated to each site from surrounding, 25 (temperature) and 15 (precipitation) climate stations, respectively, and daily mean temperature (Tmean) was calculated as the mean of Tmin and Tmax (Table 1). For more details on the interpolation routine see Petritsch and Hasenauer (2014).

2.4. Soil sampling and properties

Humus layers and mineral soil horizons were determined according to the ''Guidelines for Forest Site Mapping in Austria'' (Englisch and Kilian 1999) for each of our 28 Douglas-fir stands. Mineral soil samples were extracted with a Pürckhauer type gauge auger. Diagnostic soil horizons were separated and described according to depth, horizon boundaries, texture, rock content, color, concretions, carbonate presence, structure, rooting intensity and earthworm activity.

At each plot, eleven sub-samples in 1 m distance along a diagonal transect were collected to a depth of 35 cm with a gauge auger. The eleven soil samples were separated into layer A (A horizon) and B (mineral soil), mixed and homogenized in a bucket before further use. At each stand four separate soil profiles, each derived from 11 subsamples, were analyzed. The bulk density for layer A and B was measured in undisturbed soil samples taken with metal cylinders (volume 100 cm³). The composite (mixed) samples were air-dried and sieved to 2 mm. We used the weight of the macroscopic organic material (including roots) and rocks to calculate the coarse fragment content in the air-dried soil sample.

Soil acidity (pH value) was determined in a H_2O saturation extract with a soil-to-solution ratio of 1:2.5 as described in the Austrian standard ÖNORM L 1083 (1989). Total carbon of the bulk soils was measured after dry combustion as described in ÖNORM L 1080 (1999). The carbonate content of the soil samples was measured by the Scheibler method (see ÖNORM L 1084, 1989) to calculate the content of inorganic C. Organic carbon was then calculated as the difference of total and carbonate carbon. The determination of total nitrogen (N) was carried out with the method after Kjieldahl as described in the Austrian standard ÖNORM L 1082 (2009), and the carbon to nitrogen ratio (C/N) is the organic carbon content divided by the total nitrogen content. The exchangeable cations (Ca, Mg, K, Na, Al, Fe, Mn, H) were measured according to the Austrian standard ÖNORM L 1086 (2001), extracting 5 g of soil with 100 ml 0.1 M $BaCl_2$ solution. Effective cation-exchange capacity (CEC eff.) and base saturation (BS) were calculated as the sum of the exchangeable cations and the percentage of the CEC occupied by the basic cations K, Na, Ca and Mg. The anion nutrients nitrate (NO_3^-), nitrite (NO_2^-), phosphate (PO_4^{3-}) and sulfate (SO_4^{2-}) were determined in a H_2O saturation extract as described in ÖNORM L 1092 (2005), extracting 5 g of soil with 50 ml H_2O solution. The water extraction determines the anion nutrients in the soil solution, thus dissolved of readily soluble forms. The soil particle size distribution was determined by use of wet-sieving and sedimentation with the pipette analysis (Köhn pipette) after adding H_2O_2 to remove organic matter and dispersing with 50 ml sodium pyrophosphate (ÖNORM L 1061, 2002). For each soil parameter, we calculated the arithmetic mean of the four samples per layer, collected in one stand. The cation and anion nutrients, total nitrogen and carbon were expressed as soil stocks on a mass per unit area basis using bulk density, coarse fragment content and depth of layer A and B (0-35 cm). Pore volume (PV) was calculated using bulk density and a particle density following Osman (2013). The water holding capacity at field capacity, defined as -0.015 MPa, was calculated based on soil depth and sand, silt and clay percentages using empirical pedo-transfer functions of Clapp and Hornberger (1978) and Cosby et al. (1984) (Table S2, Equations 1-5).

2.5. Geology data

The investigated Douglas-fir stands grow on soils developed on siliceous (D01-D23) and carbonate bedrock (D24-D28) (see Table 1). The exact geology for the Austrian stands was extracted from geological maps of the Geological Survey of Austria (GBA), if available 1:50,000 otherwise 1:200,000 maps for Upper Austria (Oberösterreich) and Lower Austria (Niederösterreich). The geology for the German stands was extracted from 1:200,000 geological maps of the German Federal Institute for Geosciences and Natural Resources (BGR).

2.6. Statistical analysis of Douglas-fir productivity versus site parameters

The site index defined as the mean dominant tree height at age 60 is used as a measure for forest stand productivity. Thus, we correlate the site index (Table 2) to a set of 25 climatic and physico-chemical soil parameters determined for each of the 28 Douglas-fir stands (D01-D28 – see Table 2). We used the statistical method *Random Forests* (Breiman 2001) to select the number of predictors and derive their effect size on the site index. *Random Forests* fits decision trees according to hierarchical levels. Subsequently, all individual trees (weak learners) are aggregated to a random forest (strong learner) using the bootstrap approach, where about 63 % of the original observations are used for the prediction and the remaining 37 % are "out-of-bag" observations that determine the accuracy and error rates of the predictions (e.g. cross-validation). In contrast to many other statistical methods (e.g. AIC and BIC), *Random Forests* measures the importance of a variable directly using the misclassification rate of the out-of-bag observations (Cutler et al. 2007).

Random Forests was used since it (i) is a non-parametric method, which is able to illustrate saturation levels as well as optimum ranges of key site factors driving Douglas-fir growth, (ii) has a high prediction accuracy even if predictor variables are moderately collinear (Dormann et al., 2013) and (iii) can deal with different variable types. The statistical analysis was carried out in two main steps.

I. Variable pre-selection:

First, we eliminated irrelevant predictors using the *Random Forests*-based variable selection procedure of the VSURF package in R (Genuer et al. 2015) and optimized the number of variables randomly sampled as candidates for each tree using the tuneRF function of the *Random Forests* package (Liaw and Wiener 2015). This function uses different numbers of candidate variables to fit the regression trees. The model with the lowest out-of-bag-error indicates the best estimate.

II. Building the final *Random Forests* model:

We fitted the *Random Forests* model using 2,000 regression trees. We used the mean square error (MSE) as a measure of variable importance, which indicates the decrease in model accuracy by randomly permuting the observations of a variable. Partial dependence plots illustrate the marginal effect of each explanatory variable on site index variation while averaging other variable effects (Cutler et al. 2007).

3. Results

Site index as the dominant height at age 60 years (Table 1) ranged between 25.3 m (D07) and 42.1 m (D23). For the analysis with *Random Forests* we used 25 potential explanatory variables (Table 2) from 28 observations to explain the variation in site index. From the 25 candidate variables forward selection procedure resulted in 10 variables which were further analyzed with *Random Forests*. These 10 variables contained soil and climatic parameters and explained 30.3 % of the variance (pseudo R^2=0.303). Variable importance rankings revealed that summer precipitation exhibited the largest impact in explaining site index variation (Fig. 2). Next, phosphate (PO_4^{3-}) and water holding capacity (WHC) were found to be important, followed by sulfate (SO_4^{2-}), summer mean temperature, iron (Fe^{3+}), sand content, nitrate (NO_3^-), clay content and pH value. Partial effect plots indicated a non-linear relationship between site index and the 10 explanatory variables (see Fig. 3).

Summer precipitation and water holding capacity were positively correlated with the site index. Both impacted distinctively Douglas-fir growth if values dropped below 270 mm and 300 mm, respectively. Higher summer precipitation and water holding capacity values did not lead to a further improvement in site index and thus in productivity of Douglas-fir stands. The partial dependence plots also indicated that nutrient requirements of phosphate (PO_4^{3-}), sulfate (SO_4^{2-}) and nitrate (NO_3^-) begin to saturate at stock rates of 0.2 kg/ha, 20 kg/ha and 10 kg/ha, respectively. Iron (Fe^{3+}) stocks above 18 kg/ha showed a negative sigmoidal relationship with the site index. The impact of mean summer temperature on the site index was optimal between 17°C and 18°C and decreased above 18°C.

Site index dropped if the sand content exceeded 45 %. The clay content showed an optimal range between 18 – 26 %, whereas the site index decreased with clay contents greater than 38 %. The pH value showed a broad optimum between 4.5 and 7.2. The 3-d plot (Fig. 4) illustrates the joint impact of climate variables, summer precipitation and mean summer temperature. The temperature optimum is independent from the amount of precipitation (Fig. 4). High summer precipitation does not avoid a drop in the site index if mean summer temperatures exceed 18°C. A decline in site index by 3-4 classes is evident, if the summer precipitation drops below 300 mm.

4. Discussion

Studying the relationship between forest stand productivity and site characteristics has a long tradition in forest science (Aertsen et al. 2010). Many of the early studies used basic statistical methods like linear regression for the analysis (e.g. Carter and Klinka 1990, Curt et al. 2001, Fontes et al. 2003), which do not account for potential non-linearities in ecological relations and show problems with collinearity (Aertsen et al. 2010). The *Random Forests* approach, compared to traditional statistical methods can be classified as less transparent ("black box" model). It is able to identify structures in complex, often non-linear data sets (Olden et al. 2008) and is resilient to collinearity (Dormann et al. 2013). In our analysis, *Random Forests* identified ten of our 25 investigated climatic and physico-chemical soil parameters that drive Douglas-fir productivity (see Fig. 2) in Central Europe, and assessed a non-linear relationship between the predictors and the response (Fig. 3). The summer precipitation (Psum) and water holding capacity (WHC) (Fig. 2) are two of the three most important site characteristics and directly refer to the water budget. The third of the three important variables is phosphate (PO_4^{3-}), a common cause for forest productivity limitation, which is often neglected in site-growth studies (Bontemps and Bouriaud 2014).

Our results suggest that a low summer precipitation (< 270 mm) and a low water holding capacity (< 300 mm) reduce productivity (see Fig. 3). This confirms the findings by Carter and Klinka (1990) as well as Curt et al. (2001), who showed a significant correlation between Douglas-fir site index versus soil water-deficit and available soil water storage, respectively. The optimal soil water conditions for Douglas-fir can be expressed by the available water storage capacity (AWSC). The AWSC describes the portion of soil water which is accessible to plant roots, i.e. water in medium sized pores. It can be estimated from the water holding capacity (WHC) and the soil type (Blume et al. 2010). On silty soils, a proportion of 15 % for medium pores (Blume et al. 2010) can be assumed. According to the detected optimal WHC of > 300 mm, the estimated AWSC is about 45 mm and can be classified as "low" for Douglas-fir (Leitgeb et al. 2012).

Douglas-fir productivity declines if the mean summer temperature (Tmean) exceeds 18°C (Fig. 3). This temperature sensitivity at high temperatures might be related to an increase in vapor pressure deficit, which was shown by Restaino et al. (2016) to be strongly correlated with decreased Douglas-fir growth across forests in the western United States. The detected moderate increase in productivity with mean summer temperatures between 15°C and 17°C (Fig. 3) supports the findings of Jansen et al. (2013), who found higher growth rates at lower elevations. These findings are important in the context of expected climate change, since global mean annual temperatures are projected to increase between 1.1°C (RCP 4.5) and 4.8°C (RCP 8.5) by 2100 (IPCC 2014). Accordingly, water stress may become an important limitation for productivity due to a combined effect of changes in summer temperature and summer precipitation (Fig. 4) on the warmest sites in Eastern Austria (D01-D11, mean summer temperature > 18°C) (Fig. 1, Table S3). Higher soil phosphate (PO_4^{3-}), sulfate (SO_4^{2-}) and nitrogen (NO_3^-) contents show an increase in Douglas-fir productivity (Fig. 3). Phosphorus and nitrogen are often the main limiting nutrients for plant growth (Lambers et al. 1998). Crop production studies show a link between sulfur and nitrogen, which are often co-limiting (Hawkesford and De Kok 2006; Fageria 2014). If the iron (Fe^{3+}) concentration exceeds 18 kg/ha, site productivity dropped (see Fig. 3). This confirms that iron plays a crucial role in metabolic processes, but may turn toxic if critical accumulation levels are exceeded (Rout and Sahoo 2015).

The physical soil properties sand and clay content lead to varying soil fertility and productivity. While on sandy soils (sand content > 45 %) and clayey soils (clay content > 38 %), a decline in Douglas-fir growth is evident, a moderate clay content improved productivity (see Fig. 3). Sandy soils drain more water and are poor in fertility as well as water supply (Osman 2013). Soils with clay content above 40 %, which are classified as clayey soils (Blume et al. 2010), retain large amounts of water but drain very slowly. Thus they are often waterlogged (Osman 2013), which induces damages of the fine root system of Douglas-fir (Englisch 2008; Lavender and Hermann 2014). Rout and Sahoo (2015) found that under waterlogged and acidic soil conditions, iron may be taken up excessively leading to damages of vital cellular constituents in plants.

Our study included five Douglas-fir stands growing on carbonate soils (see Table 1). Although current management recommendations in Austria and Germany suggest planting Douglas-fir on carbonate-free soils (e.g. Englisch, 2008), no significant decline in productivity (e.g. site index) between our old Douglas-fir stands on carbonate soils (SI: μ = 34.2 m) versus siliceous soils (SI: μ = 35.7 m) was detectable (see Table 3). This finding was also supported by our analysis with *Random Forests*, where the dummy variable “carbonate” or “siliceous bedrock” (1/0) did not enter the final model (Fig. 2, Table 2). Within this context it has to be highlighted that the forest soils of all 5 Douglas-fir stands on carbonate sites show high loam contents and the results cannot be extrapolated e.g. to Rendzina sites. The carbonate sites showed phosphorus below the detection limit (Table 3), which is typical for soils with pH values above 7 as phosphorus is fixed as calcium phosphate (Rowell 1994). Phosphorus is a rather immobile element in the soil compared to other nutrients and its availability is pH dependent (Rowell 1994). However, plants are able to change the pH value in the rhizosphere by root exudation to mobilize P of calcium phosphates (George et al. 2012). Moreover, mycorrhizal associations to enhance plant P uptake (Lambers et al. 2006) may supply the trees especially in cases of very low readily available phosphate content. Considering these mechanisms for increasing P-availability and the potentially different relative importance of the other site parameters on carbonate sites, the measured zero value of PO_4^{3-} on carbonate sites does not contradict our finding of the overall high importance of phosphate. Essentially, with the selection of our studied forest stands we did not intend to explore the very limits of Douglas-fir growth for any specific site parameter. Our study design of investigating old Douglas-fir stands, however, revealed ecologically meaningful non-linear relations over a wide range of site qualities where Douglas-fir has been planted during the last century.

5. Conclusion

Douglas-fir growth correlates with the climate, the soil moisture regime and the soil nutrient status. The observed pH optimum between 4.5 and 7.2 corresponds to the broad physiological amplitude of Douglas-fir. Even though the non-native tree species Douglas-fir is more drought resistant than our main native species, the expected temperature increase (e.g. higher summer temperatures) will also induce a decline in forest stand productivity for Douglas-fir. A lower productivity due to mean summer temperatures above 18°C was observed at the warmest sites in Eastern Austria. Important macronutrients for Douglas-fir growth are phosphate, sulfate and nitrogen; whereas high contents of the micronutrient iron reduce growth. The negative impact of clayey soils (clay content > 38 %) on Douglas-fir growth could be confirmed in our study, as they are often waterlogged.

Despite the current recommendations in avoiding Douglas-fir plantation on calcareous soils, our study showed no significant differences in growth performance on carbonate and siliceous bedrock. However, it is important to note that our study covered only 5 out of 28 forest sites on rather loamy carbonate soils. We suggest that further Douglas-fir sites on carbonate soils need to be investigated.

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Tables

Table 1 Investigated Douglas-fir stands (D01-D28): Site index (SI, height at the age of 60 years), annual precipitation (Annual Precip.), mean annual temperature (Annual Temp.), elevation in m above sea level and geology.

Site	**SI (m)**	**Annual Precip. (mm)**	**Annual Temp. (°C)**	**Elevation [m]**	**Geology**
D01	28.2	600	9.9	290	Loess
D02	36	720	9.6	460	Boulders in a sand-loam matrix
D03	36.9	790	9.1	560	Mica schist, quartz phyllonite
D04	31.1	770	9.3	520	Muscovite gneiss
D05	34.4	650	9.5	360	Sand and argillaceous marl
D06	29.6	570	9.1	370	Granulite
D07	25.3	580	9	400	Granulite
D08	34	640	9.1	430	Granulite
D09	39	620	8.9	440	Migmatised granite-gneiss
D10	36.6	610	9	410	Paragneiss, locally mica schist (partly migmatised)
D11	36	960	9.4	330	Rubble
D12	30.3	710	7.9	530	Granite
D13	41.7	2100	7.1	820	Carbonate-free, fine sand-stone, arkose, slate, stone coal
D14	39.7	900	8	640	Granite
D15	41.6	910	7.9	660	Granite
D16	39.9	890	8.3	590	Granite
D17	34.8	1111	8.1	660	Gravel in sand matrix, fluvial
D18	34.6	1450	7.7	810	Sandstone, calcareous marl
D19	38.9	960	8.8	480	Silt, clayey-sandy, often gravelly
D20	34	900	7.3	680	Biotite-granite
D21	37.5	780	8.6	480	Impact breccia
D22	38.5	1120	8.2	670	Glacial till, silt, sand, gravel and stones
D23	42.1	870	7.9	660	Gravel, silt, clay, often stones, rubble
D24	30.7	900	7.7	700	Limestone, dolomite
D25	31.1	890	7.8	700	Sponge-stromatolite-corallian limestone
D26	36.7	1050	7	890	Limestone, dolomite
D27	37.3	970	9.1	450	Limestone, dolomite
D28	35.4	1010	8.8	520	Dolomite

Table 2 Summary of the dependent variable and the 25 candidate variables of the 28 Douglas-fir stands for statistical analysis with Random Forests. Climate variables refer to the summer months July, June and August. Soil variables are the depth-weighted mean values of layer A and B. Geology relate to calcareous site or silicate site.

Variable group	**Acronym**	**Description**	**Unit**	**Mean**	**Min**	**Max**
Site index	SI	Mean dominant tree height at age 60 years	m	35.4	25.3	42.1
Climate	Tmean	Mean summer temperature [JJA]	°C	17.4	15.8	19.3
	Psum	Summer precipitation [JJA]	mm	313	219	690
Soil	pH H_2O	Actual pH	[-]	5.0	4.0	7.8
	C	Carbon	t/ha	43	14	119
	N	Nitrogen	t/ha	3	0.5	9
	C/N	C/N ratio	[-]	18	11	30
	Ca	Calcium	kg/ha	3,929	23	25,298
	Mg	Magnesium	kg/ha	312	3	2,508
	K	Potassium	kg/ha	108	22	250
	Fe	Iron	kg/ha	18	0	76
	Al	Aluminum	kg/ha	592	0	1,859
	Mn	Manganese	kg/ha	72	0.1	275
	CEC eff.	Cation-exchange capacity	mmol/kg	157	40	657
	Bsat	Base saturation	%	47	10	100
	NO_3^-	Nitrate	kg/ha	13	0.4	58
	NO_2^-	Nitrite	kg/ha	1	0	6
	PO_4^{3-}	Phosphate	kg/ha	1	0	10
	SO_4^{2-}	Sulfate	kg/ha	13	1	69
	Clay	Clay	%	19	6	47
	Sand	Sand	%	36	0	60
	Skeleton	Soil skeleton	%	14	1	40
	PV	Pore volume	%	69	50	84
	Soildepth	Effective soil depth	cm	82	33	149
	WHC	Water holding capacity	mm	275	128	565
Discrete variable group	**Description**		**Unit**	**Allocation**		
Geology	Carbonate or siliceous bedrock		dummy (1/0)	5 sites (1), 23 sites (0)		

Table 3 Mean value and standard deviation (sd) of site index (SI) and the ten influencing site variables grouped by geology: Calc. group refer to calcareous sites (n 5) and silic. group to silicate sites (n 23).

	Calc. Group		**Silic. Group**	
Variables	mean	sd	mean	sd
Site index (SI)	34.2	3.1	35.7	4.5
Summer precipitation (Psum)	287.8	26.1	319.7	103.8
Phosphate (PO_4^{3-})	0.0	0.0	1.3	2.8
Water holding capacity (WHC)	255.2	92.2	280.7	114.2
Sulfate (SO_4^{2-})	2.9	1.3	14.9	14.7
Mean summer temperature (Tmean)	16.3	0.9	17.5	1.0
Iron (Fe)	0.0	0.0	20.9	21.9
Sand content	4%	3%	41%	12%
Nitrate (NO_3^-)	17.6	6.5	12.8	14.5
Clay content	31%	9%	17%	5%
pH value	7.5	0.2	4.4	0.4

Figure captions

Fig.1 Location of all 28 Douglas-fir sites, climatic region (mean annual temperature and mean annual precipitation) and selected climate diagrams which are representative for the different regions for the years 1981-2010.

Fig.2 Variable importance plot (all other variables were not meaningful), where the variable importance is expressed as the percentage increase in mean square error (%IncMSE). The mean square error (MSE) indicates the loss of predictive power of the same model by omitting a variable. Variable elimination using VSURF (Step 1: Preliminary elimination and ranking). The variables summer precipitation (Psum, mm), phosphate (PO4, kg/ha), water holding capacity (WHC, mm), sulfate (SO4, kg/ha), mean summer temperature (Tmean, °C), iron (Fe, kg/ha), sand content, %, nitrate (NO3, kg/ha), clay content (%) and pH value explain 30.3 percent of the variance (pseudo R^2=0.303).

Fig.3 Partial effect plots based on results from the *Random Forests* analysis, showing the mean marginal influence of ten explanatory variables summer precipitation (Psum), phosphate (PO4), water holding capacity (WHC), sulfate (SO4), mean summer temperature (Tmean), iron (Fe), nitrate (NO3), sand content, nitrate (NO3), clay content and pH value on site index variation. Each plot represents the effect of the explanatory variable while holding the other variables constant.

Fig.4 3d plot for the climate variables summer precipitation and mean summer temperature. For the prediction of the site index, all other predictors were kept constant at their mean values.

Figures

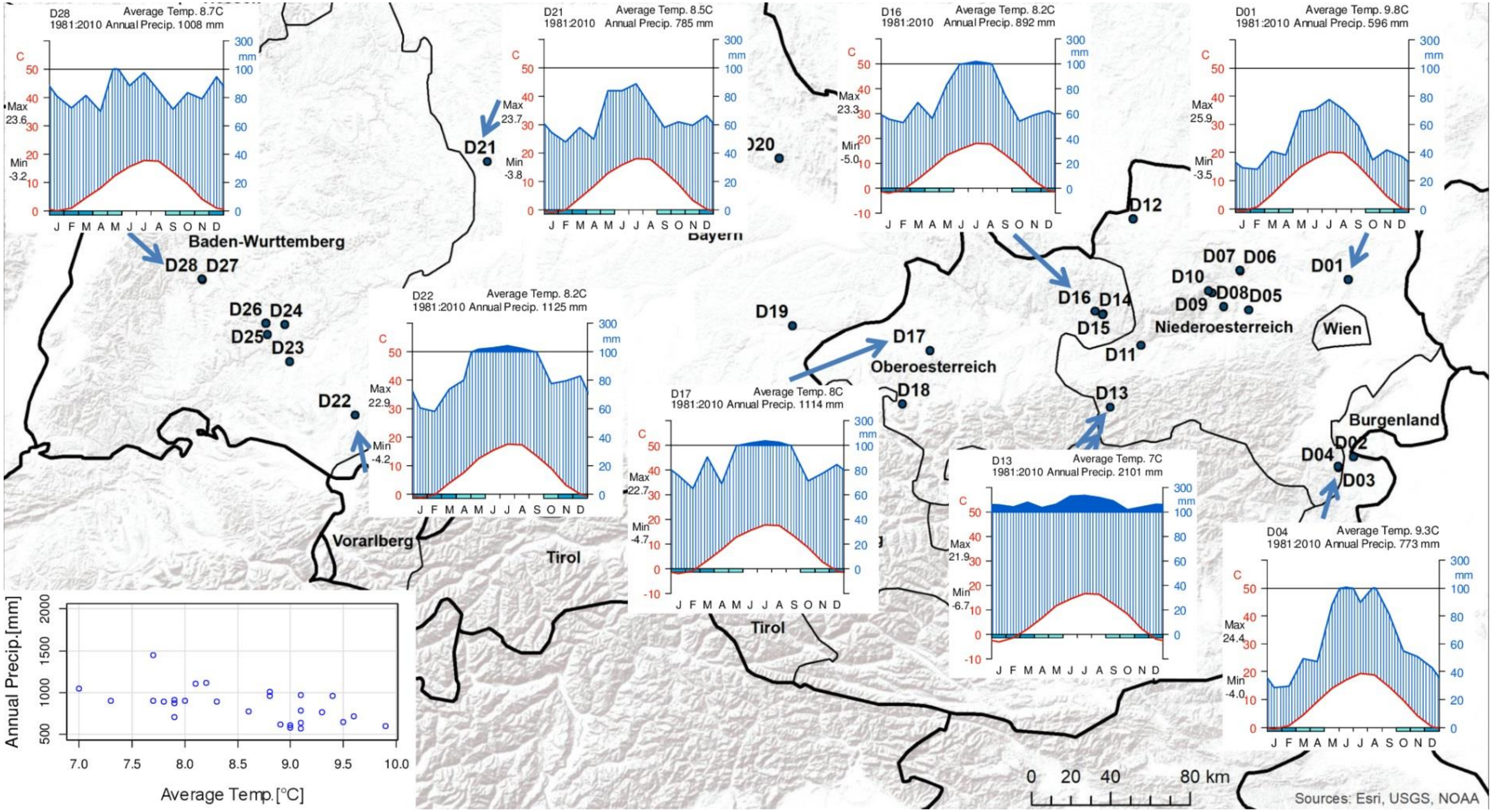


Fig.1

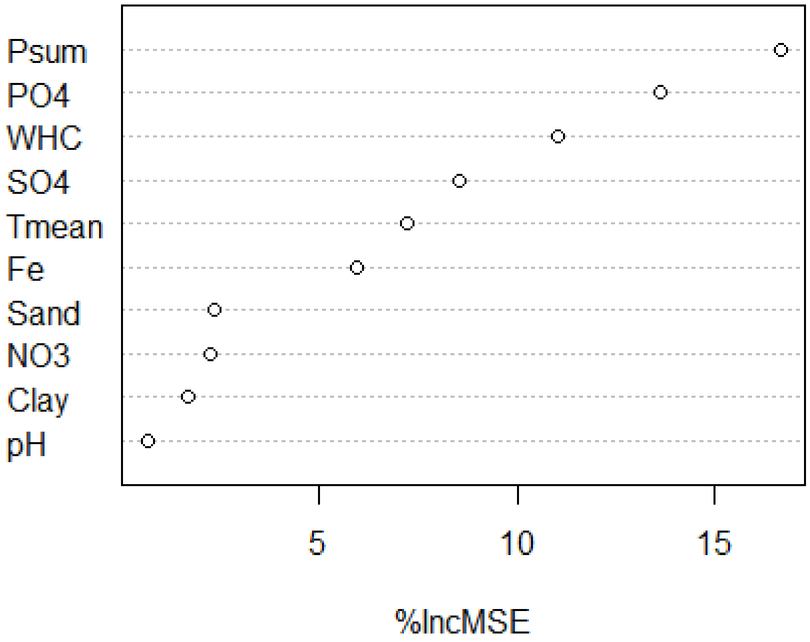
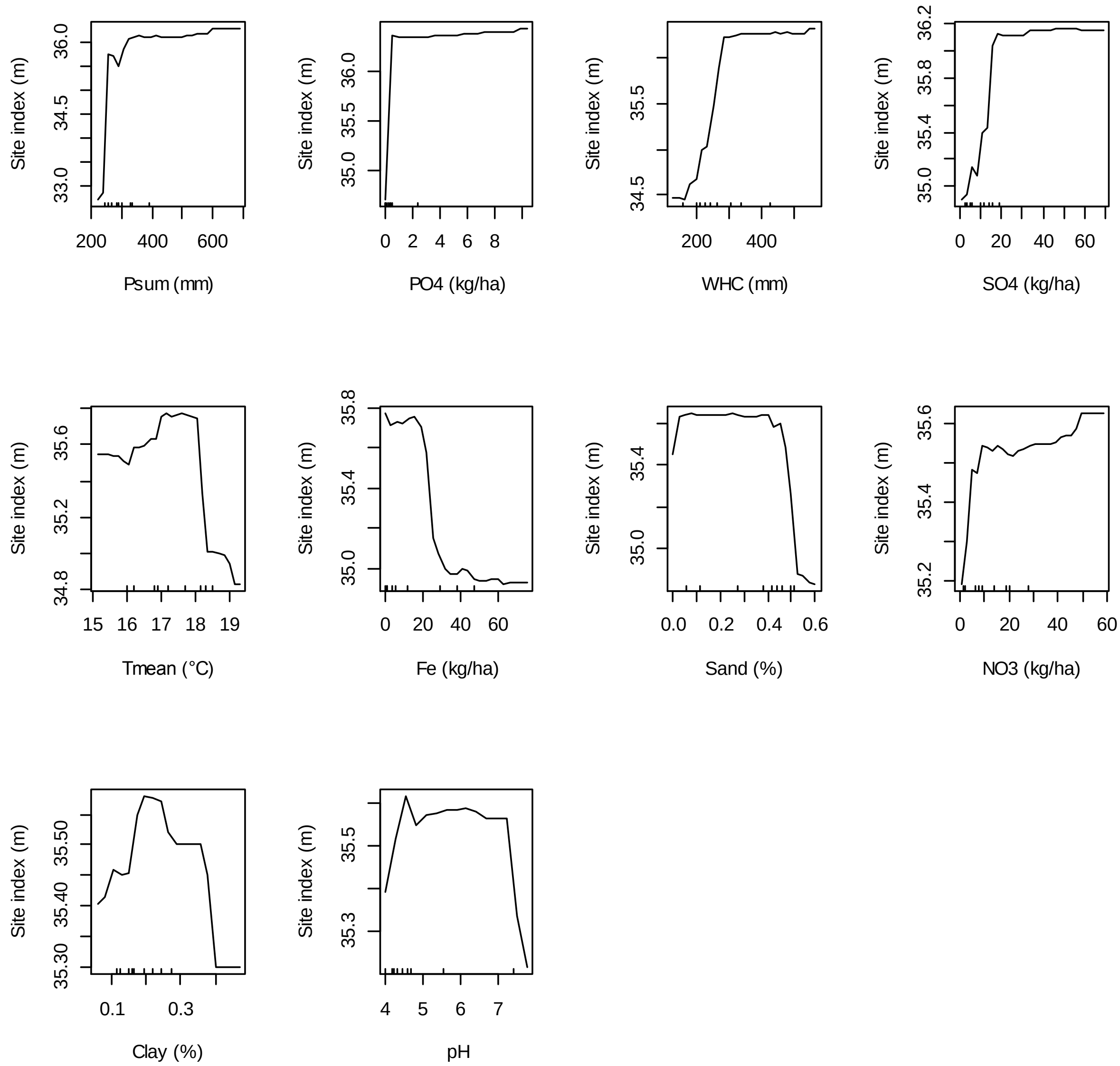
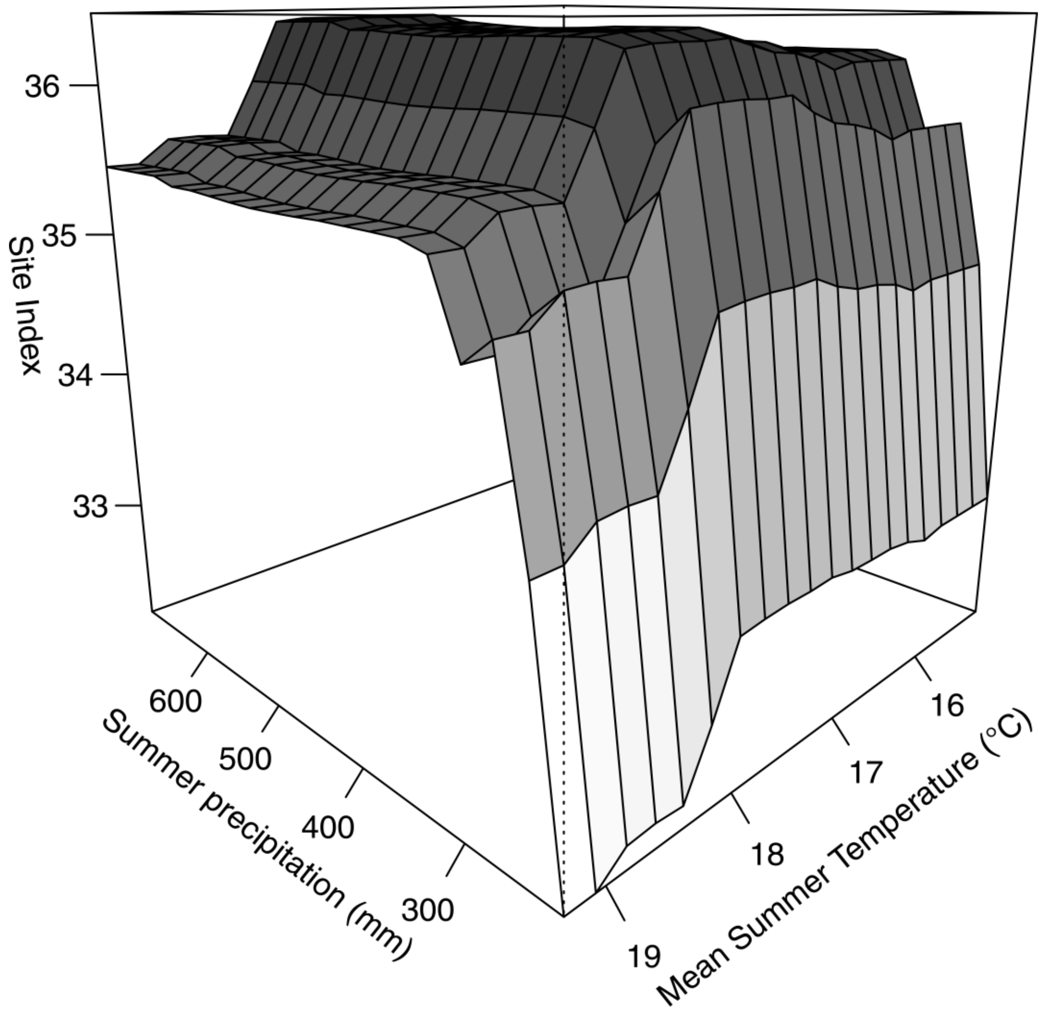


Fig.2



Site index (m)
Psum (mm)
PO4 (kg/ha)
WHC (mm)
SO4 (kg/ha)
Tmean (°C)
Fe (kg/ha)
Sand (%)
NO3 (kg/ha)
Clay (%)
pH

Fig.3



36
35
34
33
Site Index
600
500
400
300
Summer precipitation (mm)
16
17
18
19
Mean Summer Temperature (°C)

Fig.4

Supplementary material

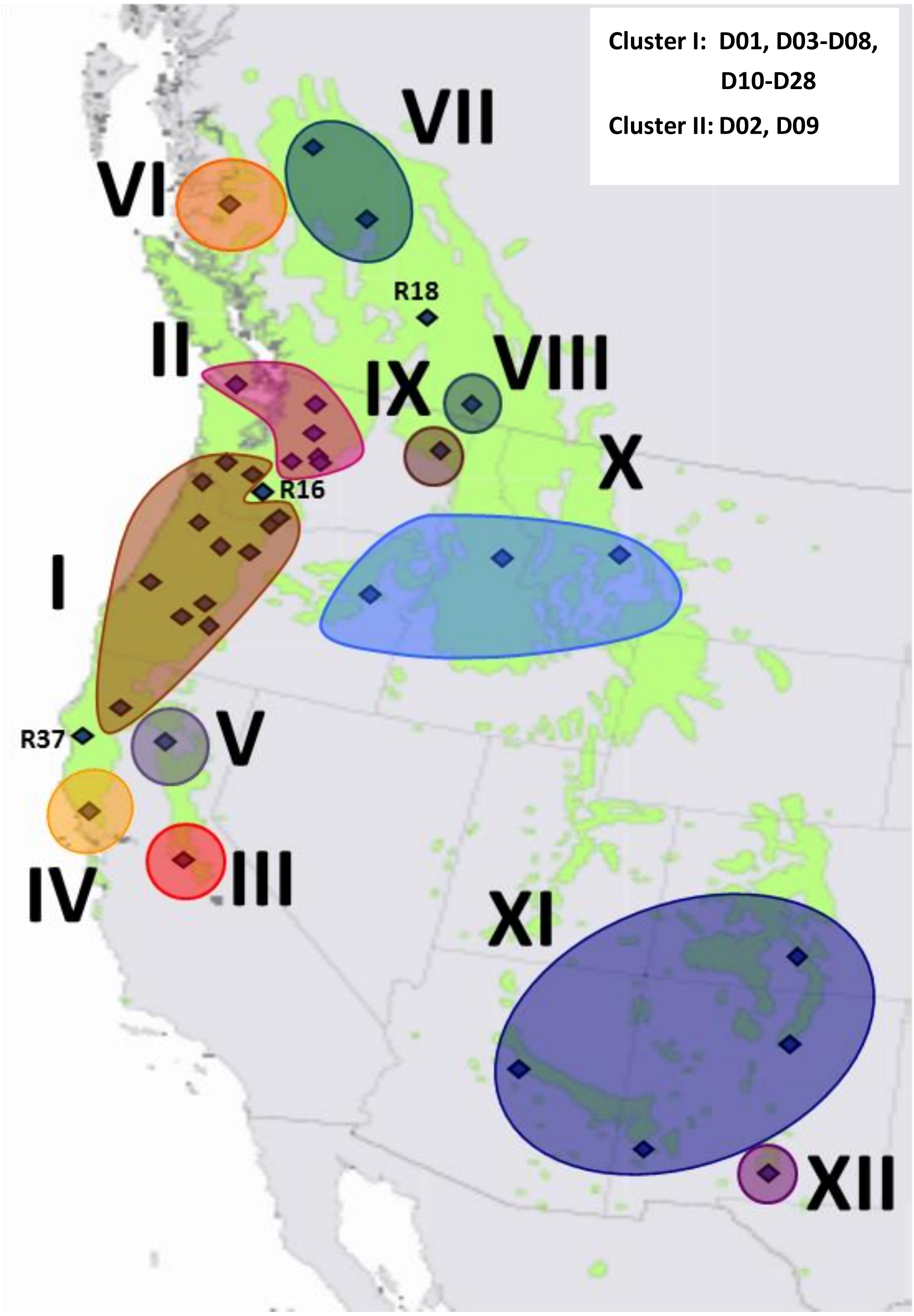


Fig. S1 Distribution map of the hierarchical cluster level 3 (HL3) for 38 Douglas-fir populations within its natural range in Northwest America. HL3 contains 12 differentiated genetic clusters (I-XII). Cluster I-VI refer to the coastal variety, Cluster VII-XII to the interior variety. Three reference populations (R16, R18, R37) are cluster-admixed populations. Study populations (D01-D28) were assigned to the coastal and western Cascade region in Oregon and Washington (Cluster I-II) (Hintsteiner et al., 2018).

Table S1 Coefficients for the dominant tree height function after Mitscherlich/Richard (1919) for “Douglas-fir northwestern Germany (DoNwd)” (Kindermann and Hasenauer, 2005).

	a0	**a1**	**a2**	**b0**	**b1**	**b2**	**c0**	**c1**	**c2**
DoNwd	-5.92E+00	1.26E+00	0	9.90E-02	-2.79E-03	2.54E-05	9.43E+00	-3.15E-01	3.03E-03

Table S2 Equations for the soil water content at field capacity.

Equations	**Parameters**	
$\Psi_{sat} = -e^{\left[(1.54 - 0.0095 \cdot P_{sand} + 0.0063 \cdot P_{silt}) \cdot \log(10)\right]} \cdot 9.8e-5$	Ψ_{sat} (MPa)	Soil water potential at field capacity
$\theta_{sat} = \frac{(50.5 - 0.142 \cdot P_{sand} - 0.037 \cdot P_{clay})}{100}$	Θ_{sat}, Θ_{fc}	Volumetric water content at saturation and at field capacity
$b = -3.10 - 0.157 \cdot P_{clay} + 0.003 \cdot P_{sand}$	b	Empirical shape parameter
$\theta_{fc} = \theta_{sat} \left(\frac{-0.015}{\Psi_{sat}} \right)^{\frac{1}{b}}$	P_{sand}, P_{silt}, P_{clay} (%)	Percentage of sand, silt and clay (Σ=100)
$W_{fc} = 1000 \cdot d_{soil} \cdot \theta_{fc}$	W_{fc} (mm)	Soil water content at field capacity
	d_{soil} (m)	Soil depth

Table S3 SI (Site index) and the 10 influencing site variables Psum (Summer precipitation), PO4 (Phosphate), WHC (Water holding capacity), SO4 (Sulfate), Tmean (Mean summer temperature), Fe (Iron), Sand, NO3 (Nitrate), Clay, pH value.

Site	SI (m)	Psum (mm)	PO4 (kg/ha)	WHC (mm)	SO4 (kg/ha)	Tmean (°C)	Fe (kg/ha)	Sand (%)	NO3 (kg/ha)	Clay (%)	pH (-)
D01	28.2	219	0.3	259	6	19.3	32	43	9.1	12	4.3
D02	36	274	0.1	229	13	18.7	11	44	6.1	13	4.5
D03	36.9	307	0.5	212	10	18.1	1	42	8.0	14	4.4
D04	31.1	301	0.5	194	2	18.4	44	60	0.4	6	4.2
D05	34.4	259	0.0	337	6	18.7	1	12	17.9	28	4.7
D06	29.6	237	0.4	206	10	18.4	52	42	0.9	12	4.2
D07	25.3	239	1.0	158	8	18.2	4	52	6.2	16	4.9
D08	34	258	0.0	154	4	18.2	40	51	1.3	10	4.2
D09	39	252	0.4	245	5	18.0	5	41	8.8	11	4.6
D10	36.6	249	0.1	226	5	18.1	6	36	1.7	12	4.6
D11	36	338	0.0	260	4	18.5	2	27	1.8	16	4.1
D12	30.3	281	0.1	244	14	16.8	37	50	3.1	15	4
D13	41.7	690	0.4	337	11	15.8	1	11	15.6	24	5.9
D14	39.7	330	0.4	300	18	16.9	17	46	25.7	16	4.4
D15	41.6	332	0.6	279	15	16.8	17	49	7.8	19	4.3
D16	39.9	325	0.4	305	18	17.2	47	45	18.7	22	4
D17	34.8	388	0.3	128	22	16.9	48	55	33.9	16	4
D18	34.6	510	0.0	518	12	16.1	76	33	13.5	22	4.3
D19	38.9	345	0.1	565	15	17.6	4	26	5.7	22	5
D20	34	293	0.0	413	16	16.0	31	48	1.3	18	4
D21	37.5	245	5.5	188	69	17.2	5	50	40.1	23	4.2
D22	38.5	396	8.5	238	14	16.7	1	39	9.2	17	4.6
D23	42.1	285	10.4	462	46	16.3	0	46	58.3	16	4.5
D24	30.7	288	0.0	229	3	16.0	0	0	20.0	47	7.5
D25	31.1	286	0.0	145	3	16.1	0	9	19.5	25	7.8
D26	36.7	331	0.0	311	4	15.1	0	2	22.5	29	7.4
D27	37.3	265	0.0	382	1	17.3	0	6	6.1	27	7.4
D28	35.4	269	0.0	210	3	17.0	0	4	19.9	27	7.6