

REVIEW OF INTRASPECIFIC RESPONSE FUNCTIONS OF MAJOR EUROPEAN FOREST TREE SPECIES

D.T1.3.1; A.T1.3

**Conservation and sustainable utilization of forest tree
diversity in Climate change (Project n° CE614)**

REVIEW OF INTRASPECIFIC RESPONSE FUNCTIONS OF MAJOR EUROPEAN FOREST TREE SPECIES

CITATION:

Chakraborty D¹, Gaviria J², Gömöry D³, Kowalczyk J⁴, Lackner M¹, Mátyás C⁵, Nagy L⁶, Rasztovits E⁶, Tomášková I⁷, Schüller S¹ (2017). Review Of Intraspecific Response Functions of major European Forest Tree Species. Conservation and sustainable utilization of forest tree diversity in Climate change (SUSTREE: Project n° CE614). Interreg, Central . Europe. Report on A.T1.3, D.T1.3.3.

¹ Department of Forest Genetics, Federal Research and Training Centre for Forest, Natural Hazards and Landscape, Vienna, Austria

² Bavarian Office for Forest Seeding and Planting, Bavaria, Germany

³ Faculty of Forestry Technical University in Zvolen, Slovakia

⁴ Forest Research Institute, Poland

⁵ Institute of Environmental and Earth Sciences, University of Sopron, Hungary

⁶ National Agricultural Research and Innovation Centre, Hungary

⁷ Czech University of Life Sciences, Prague, Czech Republic

Abstract

A process based or mechanistic understanding of the intraspecific variation in growth/fitness within tree species is crucial for identifying adapted planting materials under climate change. For this purpose empirical models, predicting performance in terms of fitness related traits are commonly used. Two types of empirical models; the site specific *Transfer functions* and the provenance specific *Response functions* are often used. Recent studies have attempted to combine the strengths of the two modeling approaches into integrated functions termed as *Universal Response Function* (URFs), aiming to overcome the site specific and provenance specific limitations of the traditional empirical models.

A systematic literature review was done on intraspecific variation in climate response of six widely occurring and economically important forest tree species of central Europe within the SUSTREE project. In total 190 published literatures were found which studied the intraspecific climate response based on traits such as growth, phenology, ecophysiological response etc. Common gardens or provenance trials were found to be the most common assessment method. Climatic drivers of fitness varied considerably both within and between the distribution range of the six species. In total 19 studies reported Transfer or Response functions for five out of the six examined species. No URFs were found to be reported. This review identified the applicability of the available *Transfer* and *Response* functions within Central Europe.

Contents

Introduction.....	1
Materials and methods.....	4
Results	
Available response functions in Central Europe	4
1. Norway spruce.....	8
2. Scots Pine.....	10
3. European larch	13
4. European Beech.....	13
5. Sessile and Pedunculate Oaks	15
Conclusions	16
Reference	18

Introduction

It has been increasingly realized that understanding intraspecific variation in growth/fitness is crucial for developing adaptive management strategies for forests under climate change. This has revived the value of forest provenance trials around the world. These trials are now seen as important sources of data to understand the adaptive variation within the species that might enable its success under climate change. Typically, provenance trials consist of experiments where different provenances of a species are grown under a common environment. When replicated over a range of planting sites these trials enable modeling the variation in phenotypic traits due to genetics, environment or a combination of both.

Two major conceptual approaches are traditionally employed to guide the identification of suitable populations for reforestation under particular climatic conditions: i) climate envelope approach, ii) empirical response function approach. Conceptually the climate envelope approach (i) is based on the over arching concept of local adaptation, which means a population is locally adapted to the environmental conditions in which it occurs. Following this approach, best performing and fit populations for a given planting location are selected from a geographic origin which has similar climate as the planting location (Hamann et al. 2010). Hence, for a given planting location, a climatically identical seed origin is identified by statistical approaches like regression trees, principal component analysis, canonical correlations, or minimum environmental distances etc (Lesser and Parker 2006; Isaac-Renton et al. 2014). The climate envelope approach has been criticized because the assumption of local being optimal may be invalid if climate of population origin and planting locations are not analogous, which may be frequently the case in the future (Williams et al. 2007; Williams and Jackson 2007). Thus, their use may be irrelevant under climate change (Marris 2008; McKenney et al. 2009, Chakraborty et al. 2015).

The response function approach (ii) is based on empirical relations between climate and functional traits (Wang et al. 2006; Kapeller et al. 2012) and requires measures of traits related

to fitness components, such as growth, mortality, reproduction, etc. Potentially it may include any population genetic processes e.g. selection, demography, drift or gene flow that may have shaped the expression of the respective trait or the phenotypic plasticity of this trait when tested within different environments. A limitation of the response function approach is the availability of extensive data from common garden/ provenance trials to develop such response functions.

Two types of response functions have been widely used to model the intraspecific variation of the climate - growth relationship. A transfer function is based on correlations between the growth performance of several populations and the climate of a particular planting location (Matyas 1994; Carter 1996; Andalo et al. 2005), but such a transfer function is applicable only to the site for which it was developed. A response function on the other hand is based on the correlation between the growth performance of a particular population and the climatic conditions across a range of planting sites (Wang et al. 2006; Kapeller et al. 2012) and is specific for the population for which it was developed. To address the limitations of these two models, Wang et al. (2010) proposed to combine the transfer and response functions into an integrated model they referred to as Universal Response Function (URF). The URFs are flexible tools and can be used to identify suitable planting locations for specific seed sources, suitable seed sources for specific planting locations and also to predict potential distribution areas of populations (Chakraborty et al. 2015; Chakraborty et al. 2016, Schueler et al. 2016 (unpublished manuscript).

The main objective of this study is to review the existing knowledge on intraspecific variation in climate response of six widely occurring, economically and ecologically important tree species of Europe (Table1, Fig1) with an emphasis on the empirical response functions.

Table 1. Tree species under investigation within the SUSTREE project framework

Common name	Scientific name	Geographic distribution
European beech	<i>Fagus sylvatica</i>	The natural range extends from southern Sweden to northern Sicily, west to France, southern England, northern Portugal, central Spain, and east to northwest Turkey, where it intergrades with the oriental beech (<i>Fagus orientalis</i>).
European larch	<i>Larix decidua</i>	Native to mountains of Central Europe, in the Alps and Carpathian Mountains, with disjunct lowland populations in northern Poland and southern Lithuania.
Norway Spruce	<i>Picea abies</i>	Native to Northern, Central and Eastern Europe . It is very closely related to the Siberian spruce (<i>Picea obovata</i>), which replaces it east of the Ural Mountains, where both the species hybridizes.
Scots Pine	<i>Pinus sylvestris</i>	Native to Eurasia, ranging from Western Europe to Eastern Siberia, south to the Caucasus Mountains and Anatolia, and Scandinavia in the north.
Pedunculate oak	<i>Quercus robur</i>	Native to most of Europe west of the Caucasus.
Sessile oak	<i>Quercus petraea</i>	Most of Europe and into Anatolia and Iran.

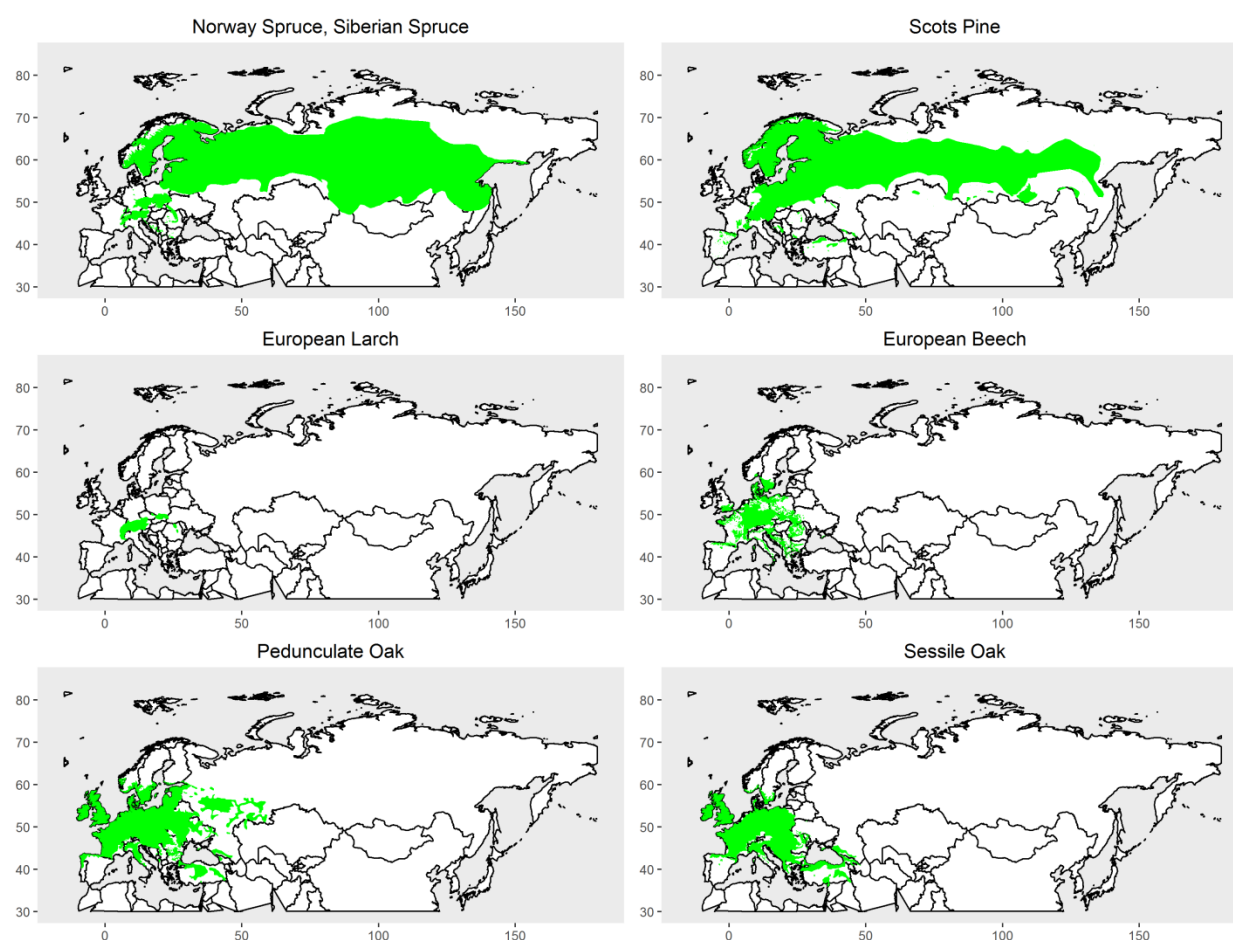


Fig. 1 Geographic distribution of the 6 tree species under investigation within the SUSTREE project framework according to EUFORGEN Species distribution maps (<http://www.euforgen.org/species>).

Materials and methods

We searched literature for studies on intraspecific genetic variation in response to climate for the six European tree species mentioned in Table 1. For this purpose, we used the search engine *Web of Science* with the following key words: “*botanical name*” or “*common name*” of the trees and “*provenance*” and “*climate*” and “*response*”. We focused on Europe and restricted our search with the cutoff date set to December 31, 2016. The entries returned by the search engine, which did not conform to the above key words, were eliminated from the review. For each study, we collected information on geographical location, assessment methodologies, studied traits, and information on common garden experiment if any. In addition to SCI listed literature, we also included publication published as reports and proceedings obtained from the national experts in forest genetics and ecology (i.e. mainly partners of the SUSTREE project) available in English and the various local languages.

Results

Available response functions in Central Europe

Central Europe is characterized by a wide range of climatic conditions ranging from oceanic, continental and a hybrid of the two. Under climate change, it would be crucial to identify climatic as well as genetic drivers of forests growth and development in order to adapt forests to maintain their ability to provide multiple ecosystem services. The SUSTREE project focuses on six tree species (Table 1) that occur across a wide range of site and environmental conditions in Europe.

In total we found 190 publications which investigate intraspecific variation in several traits (e.g. growth, phenology, fitness, productivity etc.) (Fig. 2) in response to climatic variables. Out of the 188 publications around 28% were from Germany (Fig.3). Most of the studies were regional in nature with only a few spanning across the whole of Europe. Scots pine, Norway spruce and European Beech were found to be the most studied species (Fig. 4) whereas studies pertaining to European larch and Oaks were relatively few. Assessment methods included common garden, in-situ ecophysiological experiment, geneecology model, ex-situ growth chamber

experiments, molecular-genetics and simulation models. The majority of the studies dealt with intra-specific variation in growth, utilizing data from common garden experiments (Table S1 in Appendix).

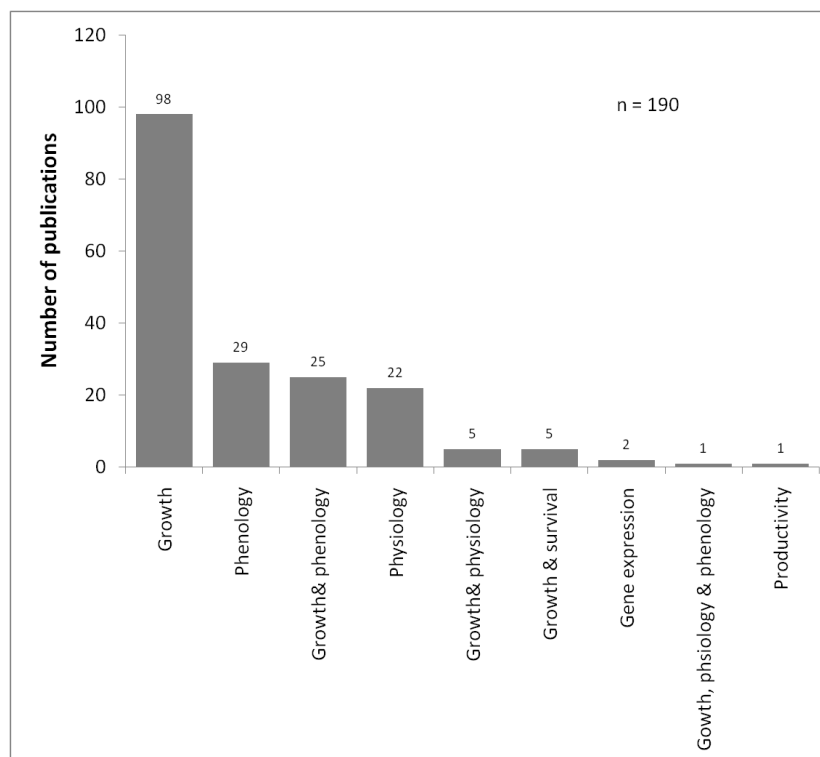


Fig. 2. Trait wise share of total number of publications used in this review

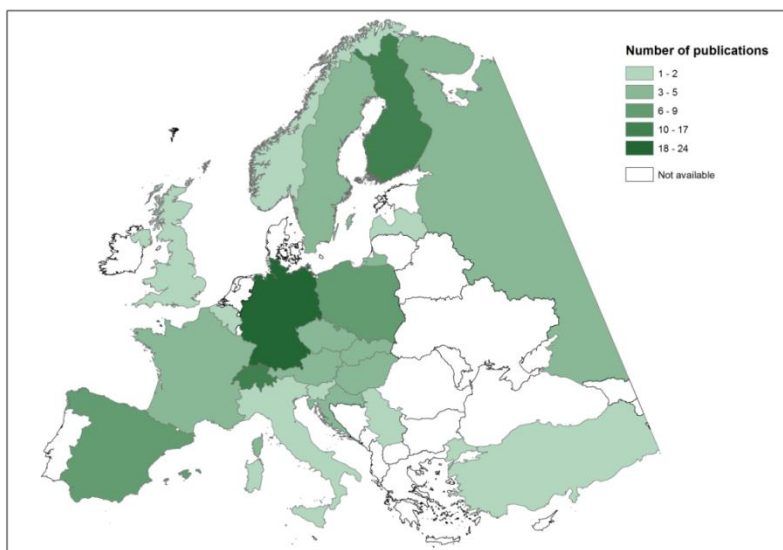


Fig. 3. Geographic share of the number of publications used in this review

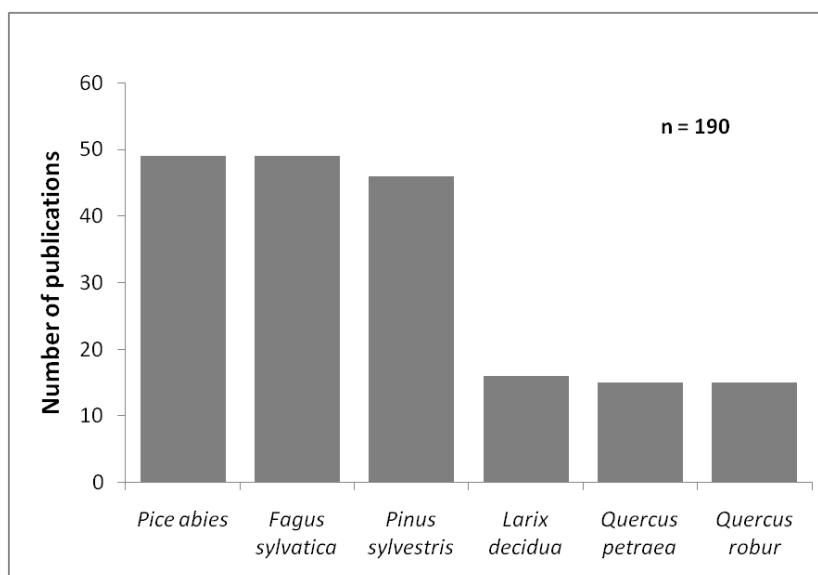


Fig. 4. Species wise share of the total number of publications used in this review

In total we found 19 published transfer or response functions for five out of the six tree species investigated within the SUSTREE framework (Table 2). In the following sections intraspecific variation in climatic response of the studied species are briefly discussed along with the transfer and response functions.

Table2. Available response functions for the tree species investigated under the SUSTREE framework

Species	Location	Trait type	Assessment Method	Response function type			Reference	Applicable to
				RF	TF	URF		
<i>P abies</i>	Austria	growth	common garden	✓			Kapeller et al.2012; Schueler et al.2013	Central Europe
	Slovakia	growth	common garden		✓		Gömöry et al.2012	Slovakia
	USA	growth	common garden	✓			Schmidtling 1994	N America
	Hungary	growth	common garden	✓			Ujvári 1969	Hungary& Central Europe
	Czech	growth	common garden	✓			Ulbrichová et al.2015	CzechR& Central Europe
	Finland	growth	common garden		✓		Beuker2008	Finland
<i>P sylvestris</i>	Europe	growth	common garden	✓			Reich et al.2008	Europe
	Russia	growth	common garden	✓			Rehfeldt et al.2002	Russia
	Sweden	growth	ecophysiological experiment	✓			Persson et al.1998	Sweden
	Poland	phenology	ecophysiological experiment	✓			Oleksyn et al.1998	Poland& Central Europe
	Finland	growth	common garden	✓			Beuker 2008	Finland& Central Europe
	Sweden	growth	common garden	✓			Prescher 1986	Sweden
<i>L decidua</i>	Germany, Slovakia	growth	common garden	✓			Foff et al.2014	Germany, Slovakia
	Canada	growth	common garden	✓			Rehfeldt et al.1999	Canada
<i>F sylvatica</i>	Europe	growth	common garden	✓			Gömöry 2010	Europe
	SE Europe	growth	common garden	✓			Mátyás et al.2009	SE Europe
	Europe	growth, survival	common garden				Alia et al. 2012	Europe
<i>Q petraea</i>	Europe	growth, survival	common garden	✓			Sáenz-Romero et al.2016	Europe
<i>Q robur</i>	-	-	-	-	-	-	-	-

RF= Response function, TF= Transfer function, URF= Universal Response Function. See Introduction for details

1. Norway spruce

Studies on fitness related traits such as dormancy and budburst found that Norway spruce seedlings are significantly affected by temperature during bud set, and these effects are modified by chilling and environmental conditions during forcing (Sogaard et al. 2008; Dalen et al. 2004; Spinnler et al. 2003; Leinonen & Hanninen 2002). In general the effect of provenance origin was weaker compared to environmental effects such as the temperature during bud set (Sogaard et al. 2008). However, the climate and photoperiod at the site, where fertilization and seed development occurs, largely determine timing of spring flushing, autumn growth cessation, height growth and frost hardiness (Johnsen et al. 2005). Consequently, phenological behavior can abruptly change between generations (Skrøppa et al. 2009). In addition to climatic drivers, increasing concentration of green house gases (GHGs) are also expected to play an important role on the future of forests under climate change (Thuiller et al. 2008; Engler et al. 2011). Dalen et al. (2004) studied the effect of cold and freezing temperatures response under a CO₂ enhanced environment and found clear difference between the provenances in terms of timing of bud set and freezing tolerance. Towards the end of cold acclimation, elevated CO₂ led to reduced freezing tolerance in the southern provenance (Dalen et al. 2004; Spinnler et al. 2003). In general, the frost risk was higher in the northern sites compared to the southern one, especially in genotypes with late bud burst (Leinonen & Hanninen 2002). Using computer simulations by applying a temperature sum model for predicting the timing of bud burst of different Norway spruce genotypes, Leinonen & Hanninen (2002) examined two contrasting theories of adaptedness; i) a fixed threshold for the risk of frost damage, or ii) a tradeoff between the risk of frost damage and the length of the growing season. They found that the tradeoff assumption resembles closely the empirical observations of provenance variation in bud burst in response to cold temperature. Beuker et al. (1998) also found that the northern provenances hardened earlier but they did not find provenance specific differences during the dehardening phase in spring.

Tree ring data revealed winter and spring temperatures to be dominant drivers of intraspecific variation in growth of Norway spruce in the Boreal zone (Suvanto et al. 2016). Unlike northern

provenances, warm winters led to faster growth in the southern provenances (Suvanto et al. 2016). Altitude was also found to be an important indirect driver of intraspecific variation in growth and phenology of Norway spruce (Worrall & Mergen 1967). Oleksyn et al. (1998) investigated the adaptive features of tree populations originating from cold, high-altitude environments and found that in the common garden, the Norway spruce populations from colder, high-altitude habitats had higher N concentration and chlorophyll in needles than those from low altitudes. However in spite of having higher photosynthetic rates in high-altitude populations, seedling height and dry mass in the common garden declined with altitude of seed origin. The high respiration rates and high allocation to roots are probably responsible for the low growth rate potential of high-altitude populations, more than offsetting their higher photosynthetic rates.

Response functions with dominant height as a function of annual heat moisture index revealed that the most productive provenances for future climates originate from the warm and dry areas of the Norway spruce distribution in Austria (Kapeller et al. 2012; Schueler et al. 2013) or certain provenances, mostly from Southeastern Europe (Ujvári 1969). Kapeller et al. (2012) further showed that the most productive provenances of Norway spruce in Austria originate from regions, which are phylogenetically distinct from the Alpine distribution area of Norway spruce, suggesting the role of population history in their climatic growth response.

Geographic transfer functions developed by Gömöry et al. (2012) found height and productivity of Norway spruce provenances responding positively to transfer into lower altitudes, i.e., warmer conditions with less precipitations. Gömöry et al. (2012) also revealed that climatic growth responses of provenances from higher altitudes, colder and wetter climates tend to be more stable, whereas provenances from lower altitudes, drier and warmer sites are more responsive to site quality. Schmidtling (1994) developed transfer function of Norway spruce populations that relate growth expressed as a percent deviation from the "local" source in response to difference in temperature of planting and source location. However these transfer functions are based on trials located in the USA and therefore their applicability to Europe is questionable. The transfer functions predicted a loss of about 5 to 10% in height growth below

that expected for a genetically adapted seed source, if the average yearly temperature increases by 4°C (Schmidtling 1994).

2. Scots Pine

Growth chamber and field experiments revealed that the northern populations ceased height growth earlier than southern populations (Oleksyn et al. 1998). Stephan et al. (1996) analyzed the IUFRO 1982 Scots pine provenance experiment in Southwestern Germany with respect to height growth after several vegetation periods, diameter at breast height, branching, stem form, and mortality and found a clear tradeoff between height growth performance and stem form. The fast growing provenances from Poland, Germany, France and Hungary also had a high percentage of trees with unsuitable stem form (Stephan et al. 1996). Hertel & Schneck (1999) found that the growth performance of provenances from higher altitudes and Eastern Europe was poor under the conditions of the test locations. In addition, significant differences exist between the two test sites for all three traits. Alía et al. (2001) analyzed growth and phenological traits of several Spanish and German Scots Pine provenances and found that the rate of height growth of the Spanish is lower than that of the German provenances, whereas for the other traits such as phenology the best Spanish compare favorably with the Germans. Alía et al. (2001) also found indications of local optimality whereby provenances closest to each trial site seemed to be better adapted than more distant ones. Barzdajn et al. (2016) analyzed variation in growth and survival among European provenances of *Pinus sylvestris* in a 30-years-old experiment and found that populations originating from the latitudinal band between 49° N and 54° N showing the best growth performance. Populations originating from both north and south of this band showed lower productivity, and survival rates reflecting the lack of adaptation to the environment of the research site. Aris et al. (2013) found sensitivity to temperature in May and precipitation in previous July and September; however, fast growing trees showed higher correlation coefficients and additional sensitivity to summer and seasonal amounts of precipitation. Palomar et al. (2016) modeled tree height allometry as a combination of climate at the growing site and geographic characteristics at the origin site of the population. They found the climate allometry relation in Scots pine is weaker than other Pine species such

as the *Pinus halepensis*, *P.pinaster* and *P.nigra*. In general, Palomar et al. (2016) found that provenances originating from warmer climate perform better on account of both growth and survival. Irrespective of the assessment method intraspecific responses of Scots pine were found to be sensitive towards thermal variables like growing degree days, summer temperature and moisture related variables, such as annual precipitation and mean summer precipitation (Rehfeldt et al. 2002, 2008, Aris et al. 2013, Seidel et al. 2016 a, Seidel et al. 2016 b, Richter et al. 2012).

Phenological and growth response (Taeger et al. 2013, Taeger et al. 2015) of *P. sylvestris* to drought was found to have strongest phenotypic plasticity of root growth for southwestern provenances, indicating a specific drought adaptation at the cost of overall low growth of aboveground structures even under non-drought conditions. Taeger et al. (2015) additionally found that warming had a minor effect on growth, but advanced phenological development depending on water availability. Drought stress responses based on thermal indices (crop water stress index and stomata' conductance index) (Seidel et al. 2016 a) and drought-induced mortality experiments (Seidle et al. 2016 b) with Scots pine seedlings from six provenances (Bulgaria, France, Germany, Italy, Poland, and Spain) revealed that the stress magnitude and response to soil water deficit depended on provenance. Under moderate drought conditions, pines from western and eastern Mediterranean provenances (Bulgaria, France, and Spain) expressed lower stress levels than those from both continental provenances (Germany and Poland) (Seidel et al. 2016a, Seidel et al. 2016b). However, under extreme drought, all provenances were equally stressed with almost no significant differences in their thermal indices. Provenance-specific differences in drought resistance were found to be associated to summer precipitation at the origin of Scots pine seedlings (Seidel et al. 2016a, Seidel et al. 2016b, Richter et al. 2012). Provenances from the warm and dry origins in Mediterranean Europe were found to have higher drought resistance under semiarid conditions such as in Turkey (Kulac et al. 2015).

Provenance specific response functions for Scots pine were developed across specific parts of the natural distribution of Scots pine such as Russia, Sweden, Poland etc. (Reich et al. 2008,

Rehfeldt et al. 2002, Persson et al. 1998, Oleksyn et al. 1998 and Beuker 2008). Till date none of the response function studies cover the entire natural range of Scots pine. Reich et al. (2008) developed climate transfer distance for *P. sylvestris* in Europe in terms of mean annual temperature. Rehfeldt et al. (2002, 2008) also developed population-specific response functions of *P. sylvestris* growing at 47 planting sites in Eurasia and North America and found that warm-degree-days > 5 degrees C; mean annual temperature; cold-degree-days < 0 degrees C; summer-winter temperature differential; a moisture index, and the ratio of warm-degree-days > 5 degrees C to mean annual precipitation are all important climatic predictors of height growth. Rehfeldt et al. (2002) generally concluded that populations tend to inhabit climates colder than their optima, with the disparity between the optimal and inhabited climates becoming greater as the climate becomes more severe. Persson & Bengt (1998) developed response function of Scots pine in Sweden with climatic variables, such as temperature sum of the site and geographic variables, such as latitudinal origin of the provenance. The effects of latitudinal transfer were influenced by temperature sum at the growing site (Persson 1998, Persson & Beuker 1997). Persson (1998) found that at the harshest situated sites southward transfer longer than 3 degree was optimal for survival and yield, whereas transfer effects in a mild climate were weak.

Reich et al. (2008) found that climate transfers equivalent to warming by MAT of 1-4 °C markedly increased the survival of populations in northern Europe and modestly increased height growth, but decreased survival and height growth at sites lower than 54 °N latitude in Europe. Beuker (2000) also developed transfer functions of Scots pine in Norway and found that the northernmost provenances showed an increase in wood production when transferred southwards into a climate with an annual mean effective temperature sum close to that which is expected in northern areas as a result of the projected climatic change. Fresher (1986) developed transfer functions for Scots pine provenances in Sweden and found that for southern Sweden a transfer of $\pm 1^\circ$ MAT combined with an altitudinal downward transfer of 100-200 meters is optimum for enhancing and maintaining adaptive potential of the populations.

3. European larch

Intraspecific variation in ecophysiological response of Austrian provenances of European larch was studied by Tranquillini et al. (1986). Below 15°C daily mean temperature the photosynthetic rate of cold-acclimated plants was found to be higher than that of warm-acclimated plants, but above 15°C an opposite response was observed (Tranquillini et al. 1986). Studies on transfer functions of European larch both in Central Europe and North America found climatic variables such as mean annual temperature, degree-days < 0 degree C, mean temperature in the coldest month, ratio of the mean annual temperature to mean annual precipitation, and the summer-winter temperature range driving growth and survival of European larch (Rehfeldt et al. 1999; Foff 2014). Foff et al. (2014) developed transfer functions for European larch in Germany and Slovakia and found that Sudetic provenances were the best performing provenances for Central Europe. Rehfeldt et al. (1999) examined the long distance transfer of European Larch into Canada. Both, Rehfeldt et al. (1999) and Foff et al. (2014) found indication of local adaptation in European larch, whereby provenances originating from climatically and geographically similar regions are the optimum for a given planting site. Müller-Starck et al. (2010) developed transfer functions based on genetic diversity and genetic multiplicity in response to altitude and found that genetic diversity and genetic multiplicity in European larch does not seem to respond to transfers across altitudinal gradient. We did not find any study with provenance specific response function in European Larch.

Both, observed (Giertych 1979; Laffers 1988) and modeled (Foff 2014; Rehfeldt, 1999) growth performance of European larch indicated the superiority of Sudetan and West Carpathian provenances across its distribution range.

4. European Beech

Intraspecific variation in European beech was widely studied in relation to drought sensitivity and tolerance (Garcia-Plazaola & Becerril 2000; Arend et al. 2016; Dziedek et al. 2016; Baudis et al. 2015; Knutzen et al. 2015; Psidova et al. 2015). Studies on photosynthetic and phenological response of beech provenances, in response to artificially simulated severe drought, reveals high drought sensitivity of Cantabrian beech populations, when planted in southern European

sites (Arend et al. 2016; Dzedek et al. 2016). In climatic conditions of southern Europe a high degree of phenotypic plasticity in growth performance and drought resistance was found within provenances originating from Central/Eastern Europe and on mesic sites, indicating that beech provenances from warmer sites in Southern Europe may not necessarily be the only source of drought-resistant ecotypes (Stojnic et al. 2015; Stojnic et al. 2013; Harter et al. 2015). Knutzen et al. (2015) found that intraspecific drought sensitivity of beech shows variable response on different traits, for example physiological traits were more strongly influenced by water availability while structural traits were not. Phenotypic plasticity indices were the highest in regards of stomatal density, potential conductance index and relative stomatal pore surface, indicating that these traits would be good candidates for improvement in breeding programs aimed at selection of drought resistant (Stojnic et al. 2015). Thiel et al. (2014) tested the drought tolerance and growth performance of provenances belonging to the marginal and central region of the distribution of European Beech and found drought resistance of the marginal provenances were significantly superior compared to the central provenances. A slightly opposite trend was observed in case of the growth performance, indicating a trade-off between drought tolerance and growth. Phenological response to drought in its southernmost distribution limit in Europe was studied by Robson et al. (2013).

Provenances from continental southeast and Central Europe flush earlier and grow faster compared to provenances originating from maritime Europe (Robson et al. 2013; Chmura & Rozkowski 2002; Wolf 2011). However provenances from south of Europe, the Balkans and western Alps were found to have comparatively better growth as well as drought resistance over a wide range of planting conditions in Central Europe, which deserves some conservation efforts in order to sustain planting material under climate change (Alía et al. 2010; Robson et al. 2012; Robson et al. 2013; Robson et al. 2010; Vitasse et al. 2013). Kreyling et al. (2012) studied intraspecific variation in frost sensitivity between Central European and Southern European provenances when planted in Central Europe and found that Central European provenances have superior frost resistance indicating local adaptation. Jazbec et al. (2007) found Carpathian provenances to have higher frost resistance compared to any other provenance when planted

in Mediterranean conditions of Europe. In spite of this, delayed flushing seems to be the main mechanism of local adaptation to late frost in European beech (Gömöry & Paule 2001, von Wühlisch et al. 1995), and beech provenances show a considerable phenotypic plasticity in this trait (Kramer et al. 2017).

Modelled transferred functions for European beech were developed for different parts of the natural distribution range of European Beech such as Central, eastern and south eastern Europe (Gömöry 2010; Mátyás et al. 2009; Sułkowska & Matras 2003). Both geographic (latitude, longitude and altitude) and climate variables of both planting location and provenance origin were utilized to develop the transfer functions. Mátyás et al. (2009) estimated juvenile height growth response of beech provenances in test sites located in southeastern Europe with respect to ecological transfer distance based on Ellenberg's climate quotient. Ellenberg's climate quotient is defined as the mean temperature of the warmest month divided by the annual precipitation. In general, the transfer functions suggest that maritime provenances show improving performance with warming and dryer conditions, while continental populations display an opposite trend (Mátyás et al. 2009). Gömory (2010) also developed transfer functions for beech provenances at the southeastern limit of beech. These transfer functions were based on geographical coordinates (longitude, latitude, altitude) and (mean annual temperature, total annual precipitation) of the provenance origin. In general the geographical distribution of the optimum transfer rates was found to be spatially continuous; and both growth and survival improve with the transfer towards the center of the range indicating local adaptation (Gömöry 2010; Mátyás et al. 2009). Provenance specific response functions were, however, not developed for European beech so far.

5. Sessile and Pedunculate Oaks

Both oak species were intensively studied with respect to intraspecific variation in drought response. Vander Mijnsbrugge (2016) and Vitasse et al. (2009a, 2009b) studied the response of *Quercus petraea* seedlings to water deficit conditions in maritime and Mediterranean European test sites and found indications of local optimality in provenances. Here, the local provenances displayed the earliest leaf senescence and the latest flushing, suggesting an adaptation to local

maritime climate. Local provenances also displayed adaptation to variable and unpredictable weather conditions, where smaller plants are favoured in drought-prone summers and taller plants in more normal growing seasons (Vander Mijnsbrugge et al. 2016). Arend et al. (2011) and Bruschi (2010) however found that growth was more sensitive to drought in provenances from northern latitudes than in provenances from southern latitudes, suggesting absence of local adaptation in sites located in central and Mediterranean Europe.

Kuster et al. (2013) found expected drought tolerance behaviors in *both Quercus petraea* and *Quercus robur* where the provenances originating from drier sites produced more root biomass than those from more humid sites under drought conditions. With respect to responses of leaf nitrogen and mobile carbohydrates, Li et al. (2013) did not find any intraspecific variations at the sites located in Switzerland. However nitrogen partitioning in both oak species was found to exhibit provenance specific variation, whereby provenances originating from drier climate had higher allocation of leaf nitrogen, a drought adaptation feature (Hu et al. 2013)

Transfer functions models were developed for *Quercus petraea* across Europe by Sáenz-Romero et al. (2016) using mixed modelling approach. They also found local adaptation within *Quercus petraea* population in general. However, there was also significant clinal population differentiation for height growth with winter temperature at the site of origin (Sáenz-Romero et al. 2016). To our knowledge there is no published response function for *Quercus robur* and *Quercus petraea* in Central Europe.

Conclusions

As discussed earlier the concept of transfer function is limited to the sites where they were developed and response function to the provenances. In our review we found mostly transfer functions and only a few response functions (Table 2). However, we did not find any study that integrates the Response and Transfer functions to an Universal response function. For *Quercus* species the available transfer function may not be applicable for a wide range of sites in Central Europe. For Norway Spruce, Scots Pine and European beech on the other hand, substantial

information with respect to both response and transfer functions are available and can be readily utilized in the project.

Reference

Alía R, Moro-Serrano J, Notivol E (2001) Genetic Variability of Scots Pine (*Pinus sylvestris*) Provenances in Spain: Growth Traits and Survival. *Silva Fennica* 35(1): 27–38.

Andalo C, Beaulieu J, Bousquet J (2005) The impact of climate change on growth of local white spruce populations in Québec, Canada. *Forest Ecology and Management* 205:169–182.

Arend M, Kuster T, Guenthardt G, Madeleine S, Dobbertin M (2011) Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*) *Tree Physiology* 3: 287–297

Arend M, Sever K, Pflug E, Gessler A, Schaub M (2016) Seasonal photosynthetic response of European beech to severe summer drought: Limitation, recovery and post-drought stimulation. *Agricultural and forest meteorology* 220: 83–89

Arend M, Gessler A, Schaub M (2016) The influence of the soil on spring and autumn phenology in European beech. *Tree Physiology* 36:1 78–85

Baudis M, Ellerbrock R H, Felsmann K et al (2014) Intraspecific differences in responses to rainshelter-induced drought and competition of *Fagus sylvatica* L. across Germany. *Forest Ecology and Management* 330 283–293

Baudis M, Premper T, Welk Erik B (2015) The response of three *Fagus sylvatica* L. provenances to water availability at different soil depths. *Ecological Research* 35: 853–865

Beuker E, Valtonen E, Repo T (1998) Seasonal variation in the frost hardiness of Scots pine and Norway spruce in old provenance experiments in Finland. *Forest Ecology and Management* 107: 42372, 87–98

Bruschi P (2010) Geographical variation in morphology of *Quercus petraea* (Matt.) Liebl. as related to drought stress. *Plant Biosystems* 2: 298–307

Barzdajn W, Kowalkowski W, Chmura DJ (2016) Variation in growth and survival among European provenances of *Pinus sylvestris* in a 30-year-old experiment. *Sylvan*. Vol. 75, 67–77

Carter KK (1996) Provenance tests as Indicators of growth response to climate change in 10 north temperate tree species. *Canadian Journal of Forest Research* 26:1089–1095.

Chakraborty D, Wang T, Andre K, et al. (2016) Adapting Douglas-fir forestry in Central Europe: evaluation, application, and uncertainty analysis of a genetically based model. *European Journal of Forest Research*. 1–18.

Chakraborty D, Wang T, Andre K, et al. (2015) Selecting Populations for Non-Analogous Climate Conditions Using Universal Response Functions: The Case of Douglas-Fir in Central Europe. PLoS One 10:e0136357.

Dalen LS, Johnsen O (2004) CO₂ enrichment, nitrogen fertilization and development of freezing tolerance in Norway spruce. Trees-structure and function 18:1 10-18

Dziedek, C, von Oheimb G, Calvo, Leonor F, Andreas K et al. (2016) Does excess nitrogen supply increase the drought sensitivity of European beech (*Fagus sylvatica* L.) seedlings? Plant Ecology 217:4 393-405

Egbert B (2008) Long-term effects of temperature on the wood production of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. In old provenance experiments. Scandinavian Journal of Forest Research 9:1-4, 34-45

Engler R, Randin CF, Thuiller W, et al. (2011) 21st century climate change threatens mountain flora unequally across Europe. Global Change Biology 17:2330–2341.

Foff V, Weiser F, Foffová E, Gömöry D (2014) Growth response of European larch (*Larix decidua* Mill.) populations to climatic transfer. Silvae Genetica 63, 1–2 (2014)

Garcia-Plazaola, JI, Becerril, JM (2000) Effects of drought on photoprotective mechanisms in European beech (*Fagus sylvatica* L.) seedlings from different provenances. Trees-Structure and Function 14: 8 485- 490

Giertych M (1979) Summary of results on European larch (*Larix decidua* Mill.) height growth in the IUFRO 1944 provenance experiment. Silvae Genetica 28, 5-6 244-256

Gömöry D (2010) Geographic patterns in the reactions of beech provenances to transfer Proceedings of the Workshop and MC Meeting of the COST Action E52. Evaluation of Beech Genetic Resources for Sustainable Forestry. Thessaloniki, May 5-7, 2009 90- 97

Gömöry D, Longauer R, Hlasny T et al. (2012) Adaptation to common optimum in different populations of Norway spruce (*Picea abies* Karst.). European Journal of Forest Research 131:2 401-411

Hamann A, Gylander T, Chen P yu (2010) Developing seed zones and transfer guidelines with multivariate regression trees. Tree Genet Genomes 7:399–408.

Heike H & Volker S (1999) genetic and phenotypical variation of scots pine (*Pinus sylvestris* L.) Populations due to seed origin and environmental conditions at experimental sites. Forest Genetics 6(2) 65-72

Isaac-Renton MG, Roberts DR, Hamann A, Spiecker H (2014) Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change. *Global Change Biology* 20:2607–17

Jansons, A, Matisons R, Baumanis , Purina L (2013) Effect of climatic factors on height increment of Scots pine in experimental plantation in Kalsnava, Latvia *Forest Ecology and Management* 306:185-191

Jazbec A, Segoti K, Ivankovic M, Marjanovic H, Peric,S (2007) Ranking of European beech provenances in Croatia using statistical analysis and analytical hierarchy process. *Forestry* 80: 2151-162

Kapeller S, Lexer MJ, Geburek T, et al. (2012) Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: Selecting appropriate provenances for future climate. *Forest Ecology and Management* 271:46–57.

Knutzen F, Meie I, Christin L (2015) Does reduced precipitation trigger physiological and morphological drought adaptations in European beech (*Fagus sylvatica* L.)? Comparing provenances across a precipitation gradient *Tree Physiology* 35: 9 949-963

Kreyling J, Thiel D, Nagy L, Jentsch A, Huber G et al. (2012) Late frost sensitivity of juvenile *Fagus sylvatica* L. differs between southern Germany and Bulgaria and depends on preceding air temperature. *European Journal Of Forest Research* 131:3, 717- 725

Kulac S, Turna I, Cicek E, Saglam A, Tasdemir U (2015) early field performance of drought-stressed scots pine (*Pinus sylvestris* L.) Seedlings. *Pakistan journal of botany* 47:4 1317-1324

Kuster TM , Arend M, Guenthardt-Goerg, M et al. (2013) Root growth of different oak provenances in two soils under drought stress and air warming conditions. *Plant and Soil* 2:01 61-71

Li, MH, Cherubini P, Dobbertin M, Arend M. Xiao W F, Rigling A (2013) Responses of leaf nitrogen and mobile carbohydrates in different *Quercus* species/provenances to moderate climate changes. *Plant Biology* 177- 184

Laffers, A (1988) valuation of provenance tests on Larch aged 40 years on the first international provenance experimental plot in Podbanské *Acta Instituti Forestalis Zvolensis* 1988: 24-48

Lesser MR, Parker WH (2006) Comparison of canonical correlation and regression based focal point seed zones of white spruce. *Canadian Journal of Forest Research* 36:1572–1586.

Leinonen I, Hanninen H (2002) Adaptation of the timing of bud burst of Norway spruce to temperate and boreal climates. *Silva Fennica* 36: 3 695-701

Mátyás C, Bozic G, Gömöry D, Ivankovic M, Rasztoivits E (2009) Juvenile growth response of European beech (*Fagus sylvatica* L.) to sudden change of climatic environment in SE European trials. *iForest* 2: 213-220

Mátyás Cs, Bozic G, Gömöry D, Ivankovic M, Rasztoivits E (2009) Transfer analysis reveals macroclimatic adaptation of European beech (*Fagus sylvatica* L.). *Acta Silvatica Et Lignaria Hungarica* 5

Marris E (2008) Moving on assisted migration. *Nat Reports Climate Change* 2:112–113.

Matyas C (1994) Modeling climate change effects with provenance test data. *Tree Physiology* 14:797–804.

Mátyás Cs, Božič G, Gömöry D, Ivanković M, Rasztoivits (2009) Response of European Beech (*Fagussylvatica* L.) to Sudden Change of Climatic Environment in SE European Provenance trials. In: Wühlisch G, Alia R (szerk.): Genetic resources of European beech for sustainable forestry. *iForest* 2: 213- 220 127-140.

McKenney D, Pedlar J, O'Neill G (2009) Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *Forest Chronology* 85:258–266.

Müller-Starck, G, Haas, J, ZieheM (2010) Genetic response of juvenile plants to translocation along an altitudinal gradient: a case study with *Larix europaea* and *Pinus mugo*. *Forstarchiv* 81: 4 142-145

Oleksyn J, Modrzynski J, Tjoelker MG, Zytkowski R, Reich PB, Karolewski P (1998) Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology* 12:4 573-590

Oleksyn J, Tjoelker, M G., Reich P (1998) Adaptation to changing environment in Scots pine populations across a latitudinal gradient. *Silva Fennica* 32: 2129-21140

Persson B, Beuker E (1997) Distinguishing between the effects of changes in temperature and light climate using provenance trials with *Pinus sylvestris* in Sweden. *Canadian Journal of Forest Research* 27: 4 572- 579

Persson, Bengt (1998) Will climate change affect the optimal choice of *Pinus sylvestris* provenances? *Silva Fennica* 32: 2 121-128

Psidova E, Ditmarova L, Jamnicka G, Kurja D, Majerova J, Czajkowski T, Bolte A (2015) Photosynthetic response of beech seedlings of different origin to water deficit. *Photosynthetica* 53: 2 187-194

Reich, P. B., Oleksyn, J.(2008) Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters* 11: 6 588- 597

Rehfeldt, GE, Tchebakova, NM, Parfenova, YI, Wykoff, WR, Kuzmina, NA, Milyutin, LI (2009) Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology* 8: 9 912- 929

Rehfeldt, G.E, Tchebakova, NM, Milyutin LI, Parfenova EI, Wykoff WR, Kuzmina NA (2008) Assessing population responses to climate in *Pinus sylvestris* and *Larix* spp. of Eurasia with climate transfer models. *Eurasian Journal of Forest Research* 6: 283-98

Rehfeldt, GE, Tchebakova, NM, Barnhardt, LK (1999) Efficacy of climate transfer functions: introduction of Eurasian populations of *Larix* into Alberta. *Canadian Journal Of Forest Research* 29: 11 1660-1668

Ricardo A, Javier MS, Eduardo N (2001) Genetic Variability of Scots Pine (*Pinus sylvestris*) Provenances in Spain: Growth Traits and Survival. *Silva Fennica* 35(1): 27–38

Richter S , Kipfer T, Wohlgemuth T, Calderon G et al (2012) Phenotypic plasticity facilitates resistance to climate change in a highly variable environment *Oecologia* 169:1 269-279

Robson M T, Rasztovits E, Aphalo PJ, Alia, R Aranda I et al. (2013) Flushing phenology and fitness of European beech (*Fagus sylvatica* L.) provenances from a trial in La Rioja, Spain, segregate according to their climate of origin. *Agricultural and Forest Meteorology* 180:76- 85

Robson T M, Sanchez-Gomez, D, Javier CF, Aranda I (2012) Variation in functional leaf traits among beech provenances during a Spanish summer reflects the differences in their origin Tree. *Genetics & Genomes* 8: 5 1111-1121

Robson T. M, Alía R, Bozic G, et al. (2011) The timing of leaf flush in European beech (*Fagus sylvatica* L.) saplings.Proceedings of the COST E52. Evaluation of beech genetic resources for sustainable forestry. Final Meeting. 4-6 May 2010. Burgos. Spain 61- 79

Seidel H, Schunk C, Matiu M, Menzel A (2016a) Diverging Drought Resistance of Scots Pine Provenances Revealed by Infrared Thermography. *Frontiers In Plant Science* 7: 1247-1247

Seidel H, Schunk C, Matiu M, Menzel A (2016b) Above-Ground Dimensions and Acclimation Explain Variation in Drought Mortality of Scots Pine Seedlings from Various Provenances. *Frontiers In Plant Science* 7: 1014

Spinnler D, Egli P, Korner C (2003) Provenance effects and allometry in beech and spruce under elevated CO₂ and nitrogen on two different forest soils. *Basic and Applied Ecology* 4: 467-478

Stephan B.R. and Liesebach M (1996) Results of the IUFRO 1982 Scots Pine (*Pinus sylvestris* L.) Provenance Experiment in Southwestern Germany. *Silvae Genetica* 45, 5-6, 342-349

Schueler S, Kapeller S, Konrad H, Geburek T, Mengl, et al. (2013) Adaptive genetic diversity of trees for forest conservation in a future climate: a case study on Norway spruce in Austria. *Biodiversity and Conservation* 22: 5 1151- 1166

Schueler S, Chakraborty D, Lexer MJL, Tongli Wang T (unpublished)There and back again: genetic trials enable the transfer of Douglas-fir distribution models across continents

Schmidtling R. C (1994) Use of provenance tests to predict response to climatic change: Loblolly pine and Norway spruce *Tree Physiology* 14:42560 805-817

Stojnic S, Orlovic S, Trudic B et al. (2015) Phenotypic plasticity of European beech (*Fagus sylvatica* L.) stomatal features under water deficit assessed in provenance trial. *Dendrobiology* 73: 163 -173

Sogaard G, Johnsen O; Nilsen J, Junttila O (2008) Climatic control of bud burst in young seedlings of nine provenances of Norway spruce. *Tree Physiology* 28: 2 311- 320

Suvanto S, Nojd P, Henttonen H et al. (2016) Geographical patterns in the radial growth response of Norway spruce provenances to climatic variation. *Agricultural and Forest Meteorology* 222:10 -20

Sułkowska, M, Matras, J (2003) Diversity of European beech (*Fagus sylvatica* L.) ecotypes in Poland. *Proceedings of Conference – “Monitoring and estimation of vegetative cover”*. Minsk Oct. 28 – 31, 2003

Stojnic S, Orlovic, Sasa M, Danijela, Galic Z, Kebert M, von Wuehlisch, G (2015) Provenance plasticity of European beech leaf traits under differing environmental conditions at two Serbian common garden sites. *European Journal of Forest Research* 134: 6 1109-1125

Stojnic S, Sass-Klaassen, Ute, Orlovic, Sasa, Matovic, Bratislav, Eilmann, Britta (2013) Plastic Growth Response Of European Beech Provenances To Dry Site Conditions. *Iawa Journal* 34:4 475-484

Sáenz-R C, Lamy JB, Ducousso A, Musch B, Ehrenmann F, Delzon S, Cavers S, Chałupka W, Dağdaş S, Hansen JK, Lee SJ, Liesebach M, Rau HM, Psomas A, Schneck V, Steiner W, Zimmermann NE, Kremer A.(2016) Adaptive and plastic responses of *Quercus petraea*

populations to climate across Europe. Global change biology. 2016. Online doi: 10.1111/gcb.13576

Taeger S, Sparks T. H , Menzel A (2015) Effects of temperature and drought manipulations on seedlings of Scots pine provenances. Plant Biology 17:2 361-372

Taeger S , Zang C, Liesebach M, Schneck Volker, Menzel A (2013) Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenance. Forest Ecology And Management 307: 30-42

Thuiller W, Albert C, Araújo MB, et al. (2008) Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology Evolution and Systematics 9:137–152. doi: 10.1016/j.ppees.2007.09.004

Tranquillini W, Havranek W M, Ecker P (1986) Effects Of Atmospheric Humidity And Acclimation Temperature On The Temperature Response Of Photosynthesis In Young Larix-Decidua Mill. Tree Physiology 1: 1 37- 46

Thiel D, Kreyling J, Backhaus Sabrina et al. (2014) Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. European Journal Of Forest Research 133: 247-260

Ujvári-Jármay E & Ujvari F (2006) Adaption of Progenies of a Norway Spruce Provenance Test (IUFRO 1964/68) to Local Environment. Acta Silvatica & Lignaria Hungarica 2: 47-56

Ujvári-Jármay E (1969) Results of a 10-year old IUFRO international provenance trial Norway Spruce(IPTNS1964/68) and their introduction in breeding and in practice. IUFRO Norway Spruce meeting Bucharest 1969 475-481

Ujvári-Jármay,É.L.Nagy, C Mátyás (2016) The IUFRO 1964/68 Inventory Provenance Trial of Norway Spruce in Nyírjes, Hungary – results and conclusions of five decades. Acta Silvatica & Lignaria Hungarica 12, special issue, 178

Vander Mijnsbrugge, K, Turcsán, A, Maes, J, Duchêne, N, Meeus,S, Steppe, K, Steenackers, M(2016) Repeated Summer Drought and Re-watering during the First Growing Year of Oak (*Quercus petraea*) Delay Autumn Senescence and Bud Burst in the Following Spring. Frontiers In Plant Science 7, Art. No 419

Vizcaino-P, N, Ibanez I, Gonzalez-Martinez SC et al. (2016) Adaptation and plasticity in aboveground allometry variation of four pine species along environmental gradients. Ecology and Evolution 6: 21 7561-7573

Vitasse, Y, Delzon S, Dufrene E, Pontailier J Y et al (2009 a) Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology* 149: 5 735-744

Vitasse,Y, Delzon S, Bresson C, Michalet R, Kremer A (2009) Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal Of Forest Research* 7:1259-1269

Wang T, Hamann A, Yanchuk A et al. (2006) Use of response functions in selecting lodgepole pine populations for future climates. *Glob Chang Biology* 12:2404–2416. doi: 10.1111/j.1365-2486.2006.01271.x

Wang T, O'Neill GA, Aitken SN (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Application* 20:153–163. doi: 10.1890/08-2257.1

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. *Front Ecol Environ* 5:475–482. doi: 10.1890/070037

Williams JW, Jackson ST, Kutzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. *PNAS. USA* 104:5738–42. doi: 10.1073/pnas.0606292104

Worrall J, Mergen F (1967) Environmental and genetic control of dormancy in *Picea abies*. *Plant Physiology* 20:3 733-745

Wolf H (2011) Austrieb und Trockentoleranz von Rotbuchen-Herkünften (*Fagus sylvatica* L.) unter sich ändernden Klimabedingungen Mitteilungen aus der Forschungsanstalt für Waldökologie und Forstwirtschaft Rheinland-Pfalz. Germany 2011