



Limited influence of air temperature and precipitation on six-year survival and growth of non-native tree species in a Central European multi-site field trial

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ABSTRACT

The biggest challenge for forest management in the near future will be the silvicultural adaptation of forests on sites where climate change will increase the risk for drought induced tree mortality and for a decrease of the growth performance. One management option is the diversification by promoting climate change adapted non-native tree species. Currently, we have in depth experience with only a few non-native tree species in Central Europe. Other tree species that may complement the species pool in Central Europe need to be carefully selected by a range of criteria. Before establishing larger silvicultural experiments at stand-level, the suitability of species to grow well with a low risk of failure under expected future climatic conditions as well as a good performance already today should be tested, amongst other aspects. We present results of a multi-site common garden experiment where growth and survival of five non-native tree species (*Abies bornmuelleriana*, *Cedrus libani*, *Fagus orientalis*, *Tilia tomentosa*, and *Tsuga heterophylla*) and one climate adapted local native species per site are tested in five field trials in Austria, Germany and Switzerland along a temperature (7.9–10.4 °C mean annual Temperature) and precipitation (490–1147 mm annual precipitation) gradient. Each species was replicated on three plots per site using a block-wise design. Lower survival and growth of the non-native species as the native reference on most sites indicate that the studied non-native species are today not as well adapted to current climatic conditions as native species. However, the performance of the non-native species was sufficiently high to justify further trials. Survival and growth rates were mostly equally high on the two sites at the opposing ends of the temperature and humidity gradient and lower on all other sites. Height growth and survival were only marginally affected by the strong summer drought in 2018 in all except one site, presumably due to the low water storage capacity of the sandy soils on this site. This indicates that the tested non-native tree species grow well in the wide range of climatically changing weather conditions from our transnational study sites across Central Europe. So far, the tested tree species did not reach their climatic growth limitation. However, edaphic site conditions may have influenced the performance of the tested non-native species as well and must be considered when discussing the suitability of these tree species.

1. Introduction

The impacts of climate change on Central European forests are

expected to be strong. Average air temperatures are going to rise, precipitation is going to decline, and extreme drought events will occur more frequently and with higher intensity (Pfleiderer et al., 2019; IPCC,

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¹ In memory of our dear friend and colleague Peter Brang, who passed away during the ongoing drafting process of this article on July 7th, 2022.

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2022). Changing climatic conditions are likely to lead to widespread tree mortality and to major changes in tree species composition (Buras and Menzel, 2018). Current climate change scenarios predict in extreme cases more than 50% loss of native conifer species, which will lead to their regional disappearance (Hanewinkel et al., 2012; Neumann et al., 2017; Hinze et al., 2023). Climate change is also presumed to trigger the appearance of new pests and diseases and to enhance their ability to attack or infect trees. This may result in widespread tree mortality and reduced ecosystem services (Hanewinkel et al., 2012; Lindner et al., 2014; Trumbore et al., 2015). One important option to reduce these threats is to diversify the tree species composition and to facilitate climate change adapted tree species (e.g., Bolte et al., 2009; Brang et al., 2016; Frischbier et al., 2019). However, the assessment of tree species suitability for future climate conditions on specific sites is challenging, as it depends on the amount of global greenhouse gas emissions, site-specific climate projections, soil properties, phytosanitary risks. Moreover, the potential of tree species to provide ecosystem services and the costs involved in promoting the species must be considered. The future development of these factors is currently unknown, as predictions are usually associated with large uncertainties. In this context, the question arises whether it is appropriate to speed up natural adaptation processes on specific sites by use of assisted migration.

Assisted migration of trees is the purposeful movement of non-native species to facilitate or mimic natural range expansion as a direct management response to climate change (Camacho, 2010; Vitt et al., 2010; Ste-Marie et al., 2011; Williams and Dumroese, 2013). The merits and limitations of assisted migration are intensely debated. While conservationists tend to be critical due to the risks associated with assisted migration, for example because maladapted species or genotypes are introduced or because introduced species may become invasive in their new habitat (Aubin et al., 2011). Forest managers on the other hand tend to view assisted migration as a valuable management option. From a forestry perspective, additional tree species may help to secure ecosystem services, including climate change mitigation through carbon sequestration, timber production, water regulation, soil protection and biodiversity (Allen et al., 2010; Lindner et al., 2010; Kreyling et al., 2011).

The species selected for assisted migration usually originate from regions where current climatic conditions resemble future conditions of the target habitat (Williams and Dumroese, 2013; Brang et al., 2016). Moreover, the climate envelope of new tree species should cover as well current conditions as first stands will need to be established soon (Schmiedinger et al., 2009). The number of tree species which have been introduced to Central Europe and for which long-term experience with the impact of their introduction on ecosystem functioning exists is small. Some of these examples include: *Pseudotsuga menziesii* (Pötzelsberger et al., 2020), *Quercus rubra* (Wozniwoda et al., 2014) or *Robinia pseudoacacia* (Staska et al., 2014; Sibikova et al., 2019). Introduced species in some cases turned out to be invasive, which limits their future use in forest management (Krumm and Vítková, 2016; Fanal et al., 2021).

However, there is a set of non-native and presumably non-invasive tree species that were previously identified as candidates for introductions to Central Europe for commercial forestry in a warmer and dryer climate (Schmiedinger et al., 2009) and that have not been subject to field tests for extended periods. Therefore, more long-term trials with a wider range of untested, non-native tree species are urgently needed. One such transnational trial has been established in 2012 by forest administrations, research institutes and universities in Germany, Switzerland and Austria to study the performance of five so far untested non-native tree species, preselected by Schmiedinger et al. (2009), in comparison to one local climate adapted native reference species per site. The transnational trial includes five sites along a climatic gradient throughout Central Europe, thus covering a range of temperatures, precipitation, and edaphic conditions (Frischbier et al., 2019).

This study reports on tree survival and height growth during the initial phase of this trial six years after planting between 2012 and 2018.

A particular focus is on species-specific responses to the weather conditions in 2018 which were exceptionally dry in three of five of the study sites. A former analysis of the same trial (Frischbier et al., 2019) characterized survival during the establishment phase of first four years after planting (including planting shock) and reported reasonably well survival rates. In particular the native and non-native broadleaved species did well during the phase of stand establishment. In this study we now focus on the two traits survival rate and tree height increment. This allows us to quantify early plant fitness and performance (Violle et al., 2007) of the planted trees over a longer observation period after they recovered from planting shock between 2016 and 2018 in relationship to climatic conditions on the sites. Additionally, we analyze tree height and survival over the complete six-year duration of the experiment. Even though of limited value to judge physiological fitness, from the perspective of implementing assisted migration the full period of the six-year trial is relevant as well because at least the first generation of non-native trees will need to be established by planting. The effort that is necessary to successfully establish a plantation will be affected by the severity of the planting shock. With our selection of traits, we mainly cover aspects of young tree performance. For a complete evaluation, future assessments of the performance of mature trees will be relevant as well. An additional aspect of plant fitness that will be possible to consider as soon as mature stands are established, is the capacity of non-native trees to reproduce and regenerate naturally.

By using the performance of the native species as reference, we have an objective way to evaluate the performance of the non-native species. However, under current climatic conditions, we do not yet expect to see a higher performance of the non-native species compared to the native species as the native species are currently still better adapted to the local site conditions today. Moreover, as investment in drought tolerance is expensive, slow growth of non-native species today is tolerable, if growth is continuous and stands of the non-native species can be established successfully already today.

When referring to specific climatic conditions, we differentiate between ‘aridity’, which describes the absolute conditions in terms of water supply and evaporative demand at a specific point in time, and ‘drought’, which describes unusually dry time periods relative to a given climate (Speich, 2019). Our objective is a comprehensive assessment of the tree species and their adaptability to the local climate conditions, given the available information six years after planting.

We hypothesize that (1) tree performance of all tested species is lower on sites with higher aridity. Moreover, even though we expect the non-native tree species to perform better in the future, we assume that native species are still better adapted to current climatic and site conditions. Therefore, we hypothesize that (2) currently native reference species still have a better performance than non-native species at same edaphic site conditions. Lastly, we hypothesize that (3) a decrease of the performance in drought years is present in all species but less pronounced for the non-native species as their seed material originates from warmer or drier habitats.

The results of this study will contribute to a better understanding of early tree height and growth and survival rates of five to date unexplored non-native tree species with potential use for assisted migration in Central Europe. This will (i) help researchers in filling data gaps about non-native tree species early-stage performance, and (ii) help forest managers to select or exclude non-native tree species that may or may not be suitable to sustain forest functions in future climate conditions.

2. Material and methods

2.1. Study regions

The five study regions are located in Southern and Eastern Germany (Großostheim and Schmellenhof, both Bavaria, GRO and SCH, and Oldisleben, Thuringia, OLD), Eastern Austria (Bruckneudorf, Burgenland, BRU) and Western Switzerland (Muttrux, Canton of Vaud, MUT)

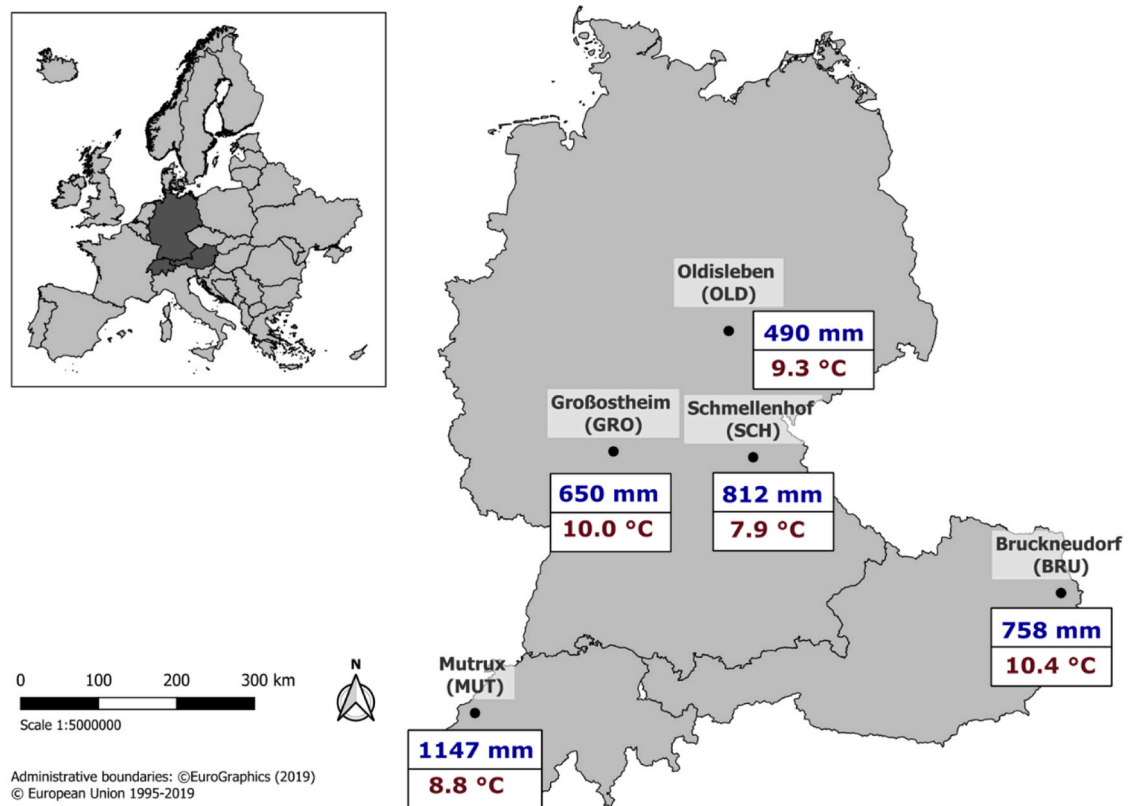


Fig. 1. Location of the study sites in Europe (inlay) and in Austria (Bruckneudorf, BRU), Germany (Großostheim, GRO, Oldisleben, OLD, Schmellenhof, SCH) and Switzerland (Muttrux, MUT). The numbers are the annual precipitation sum (blue) and the mean annual temperature (red) of the reference period (1981–2010) for each site.

(Fig. 1). The sites are situated between 127 m a.s.l. (GRO) and 658 m a.s.l. (MUT). The mean annual temperature in the period 1981–2010 ranged from 7.9 °C (SCH) to 10.4 °C (BRU), and the annual precipitation from 490 mm (OLD) to 1147 mm (MUT). The precipitation during the growing season ranges from 264 mm at OLD to 498 mm at MUT. Soil types are cambisols in four sites, but stagnosol in SCH. The forest communities are naturally dominated by *Fagus orientalis* (MUT, GRO, OLD), *Quercus robur* (SCH) or *Q. petraea* (BRU) Table 1.

In comparison to 2013–2016, average temperatures in the growing season 2017 were up to 0.7 °C warmer for the 5 sites, but precipitation sums differed by –72 to +110 mm (Table S1). The growing season 2018 was very warm and dry in the sites GRO, OLD and SCH (in comparison to 2013–2016: +1.7 to +2.2 °C, P – 195 to –180 mm), resulting in very low values of the de Martonne index (DMI) (3.1–7.8). In contrast, the growing season 2018 was quite warm, but not dry in the sites BRU und MUT (in comparison to 2013–2016: +1.4 to +1.5 °C, P – 19 to +156 mm, DMI 2018 11.1–13.1).

2.2. Non-native tree species and reference species

As the species selection process and the species themselves have been described in more detail in Schmiedinger et al. (2009) and Frischbier et al. (2019), we stay very brief here. Four of the non-native tree species were selected using a global screening of species found in regions that match the climate expected in Southern Germany in a +2 °C climate scenario (SRES-B1, Spekat et al., 2007). The screening filters included climate variables, economic and ecological benefits and the absence of known biotic and abiotic risks from a literature review.

This method led to the selection of Turkish fir (*Abies bornmuelleriana* Mattf., Pinaceae, called ‘*A. bornmuelleriana*’ in this paper), Oriental

beech (*Fagus orientalis* Lipsky, Fagaceae, ‘*F. orientalis*’), silver lime (*Tilia tomentosa* Moench, Tiliaceae, ‘*T. tomentosa*’), western hemlock (*Tsuga heterophylla* (Raf.) Sarg., Pinaceae, ‘*T. heterophylla*’) and Lebanon cedar (*Cedrus libani* A. Rich., Pinaceae, ‘*C. libani*’). The species were selected (1) for their low invasion potential, (2) because their natural distribution range suggested they would thrive in the projected warmer climate in Central Europe, (3) due to their timber quality and (4) after passing forest protection screening. Moreover, only species for which little knowledge on their performance was available were chosen (Schmiedinger et al., 2009). Even though *T. heterophylla* originates from a region with high precipitation in the Northwest of North America, it was included because it was one of the better ranking coniferous species according to Schmiedinger et al. (2009). The seed material of *T. heterophylla* was taken from a seed stand with relatively low precipitation. The evaluation of the potential for invasiveness was based on the knowledge at that time. In the meantime, for *T. heterophylla* additional studies documenting its dense natural regeneration potential in Central Europe with potential implications for the evaluation of its invasiveness were published (Frischbier et al., 2017; Fanal et al., 2021).

On each site, a native species supposed to grow well in a future warmer climate was planted as local reference for the five non-native species. The native reference species was not the same at all sites but was selected after consultation with the respective forest administration about which species would thrive best in a future warmer and drier climate. These species included *Quercus petraea* (Matt.) Liebl. (MUT, OLD) and *Q. robur* L. (GRO, SCH), and as locally recommended species *Pinus nigra* var. *austriaca* Badoux (BRU), the historical natural range of which starts about 40 km apart from the site BRU.

Table 1
Site and climatic characteristics of the study sites.

Site (Abbreviation)	Bruckneudorf Austria (BRU)	Großostheim Germany/Bavaria (GRO)	Muttrux Switzerland (MUT)	Oldisleben Germany/Thuringia (OLD)	Schmellenhof Germany/Bavaria (SCH)
Geographical position (°)	47°58'18"N 16°41'20"E	49°95'32"N 9°05'58"E	46°52'44"N 6°44'21"E	51°29'05"N 11°19'99"E	49°82'46"N 11°56'87"E
Elevation (m a.s.l.)	330	127	658	195	495
Aspect	South-East	- no -	South-East	- no -	North-East
Slope (%)	0–10	0	10	0	5
Geology	Loess over pliocene gravel, schist and gneiss	Aeolian sand and aeolian sand over alluvial terrace gravel	Moraine	Loess over sandstone	Heavy clay over sandstone
Soil type ^{a)}	Dystric Cambisol	Arenic Dystric Cambisol	Cambisols (carbonate-free)	Cambisols (carbonate- free), partially Podzols	Haplic Stagnosol
Rooting depth (cm)	100	115	65	80	70
Natural plant association	<i>Carici pilosae-Carpinetum</i>	<i>Asperulo Fagetum</i> / <i>Luzulo Fagetum</i>	<i>Galio-odorati Fagetum typicum</i>	<i>Luzulo Fagetum</i> / <i>Galio Carpinetum</i>	<i>Stellario carpinetum caricetosum brizoides</i>
<i>Climate (1981–2010)</i>					
Meteorological stations used	Bruckneudorf	Schaaheim-Schlierbach	interpolated ^{b)}	Artern	interpolated ^{b)}
Mean annual temperature (°C)	10.4	10.0	8.8	9.3	7.9
Mean Min / Max annual temperature (°C)	6.5 / 15.0	5.5 / 14.6	5.0 / 13.3	5.2 / 13.7	3.5 / 12.8
Mean growing season ^{c)} temperature (°C)	18.2	16.2	15.5	16.2	14.6
Mean annual vegetation length ^{d)} (days year ⁻¹)	199	187	170	180	155
Annual precipitation sum (mm)	758	650	1147	490	812
Growing season precipitation sum (mm)	413	289	498	264	383
Annual de Martonne index ^{e)}	37.2	32.5	61.0	25.5	45.4
Growing season de Martonne index	14.6	11.0	19.6	10.1	15.6
Range of the annual extreme minimum temperature (°C)	-14.9 to - 12.3	-17.7 to - 15.0	-14.9 to - 12.3	-17.7 to - 15.0	-17.7 to - 15.0
Plant hardiness zone ^{f)}	7b	7a	8a	7a	7a

^{a)} Soil classification is according to [FAO \(2015\)](#).

^{b)} Daily means of temperature and precipitation were interpolated based on MeteoSwiss (for MUT) and DWD (for SCH) data recorded at meteorological stations closest to the sites.

^{c)} The growing season is defined as May 1 through September 30 ([Otto, 1994](#)).

^{d)} The mean annual vegetation length is calculated as the number of days per year with mean temperature ≥ 10 °C.

^{e)} The de Martonne index was calculated as $DMI = \frac{P}{T + 10}$, with P = precipitation sum (mm) and T = mean temperature (°C), for the corresponding period (year or growing season) ([de Martonne, 1926](#))

^{f)} Plant hardiness zone is according to [USDA \(2012\)](#).

2.3. Plant material

Seeds from all non-native tree species were collected in autochthonous stands. Seedlings were cultivated in nurseries in Southern Germany to provide similar environmental and soil conditions. Seedlings of the reference species were produced in local nurseries in Austria, Switzerland and Germany. Most seedlings were planted bare-rooted, but *A. borrmuelleriana* and *P. nigra* were grown in containers ([Table 2](#)).

2.4. Experimental design

The trial was established on clearcuts after removal of competing woody vegetation. The initial planting took place in fall 2012 and spring 2013 using similar common practice planting techniques as used by forest practitioners. Replacement plantings were conducted in spring 2014 and winter 2015/2016 to compensate for sapling mortality. This paper focuses exclusively on the performance of individuals from the initial planting. The sites were tended each summer, sometimes twice, to control ground vegetation. So far, no treatments to reduce intraspecific competition between planted trees were conducted. The experimental trees were protected from game browsing by a fence surrounding the individual sites. No treatments such as fertilization, soil liming or pesticide application were done.

The experimental setup at each site was a block design with three blocks (replicates) each containing one species and an embracing buffer of at least 15 m width for the whole site ([Fig. 2](#)). In each plot only one

individual species was planted. The buffer area was also clearcut to exclude impacts from adjacent stands. The five non-native and the reference species were randomly assigned to the six plots per block. In each plot 289 individuals of a single species were planted in a 17×17 grid with uniform quadratic spacing of 2.0 m. As *C. libani* was not planted at BRU, this resulted in an initial total number of 25143 seedlings. Each plot is subdivided in a core area with 169 individuals (13×13) and a buffer zone of two rows (120 individuals), to enable controlling for effects of interspecific competition at the edges of the plots. Only survival and growth of trees in the core zone were analysed in this study.

2.5. Climatic conditions

Mean annual air temperature and annual precipitation sum as well as mean growing season temperature and growing season precipitation sum were calculated for all study sites for all six growing seasons after the initial planting (i.e., 2013–2018). Growing season was defined as May 1 through September 30. Daily data of the meteorological stations closest to the sites were used. The data were obtained from ZAMG (<http://www.zamg.ac.at/>) for BRU (station: Bruckneudorf) and DWD (<https://opendata.dwd.de/>) for GRO (station: Schaaheim-Schlierbach), OLD (station: Artern) and SCH (station: Heinersreuth-Vollhof). Data for MUT were interpolated ([Thornton et al., 1997](#)) from climate station data provided by the Federal Office of Meteorology and Climatology (MeteoSwiss) by the Land Change Science Group at the Swiss Federal

Table 2Information about plant origin. Reference tree species are shown in bold letters, n.p. = not planted. Deviations from the originally planned design (3 blocks per site planted in Oct 2012) are shown in *italics*.

Tree species	Provenance	Stand of origin		Seedling characteristics before planting			Time of planting at study site (number of plots)				
	Regions/country of origin	National Identification number/seed material type	Latitude / longitude (elevation, m a.s.l.)	Height (cm)	Years in nursery Seed bed + transplant bed	Seedling type	Bruckneudorf Austria (BRU)	Großostheim Germany/Bavaria (GRO)	Mutrux Switzerland (MUT)	Oldisleben Germany/Thuringia (OLD)	Schmellenhof Germany/Bavaria (SCH)
<i>Abies bornmuelleriana</i>	Bolu-Kökeç / Turkey	225/selected seed stand	40°39'05"N / 31°36'56"E (1300)	10–15	2 + 2	container	Apr 2013 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Cedrus libani</i>	Mersin-Arslanköy / Turkey	233/ selected seed stand	37°00'20"N / 34°14'00"E (1800)	10–20	1 + 2	bare root	n.p.	<i>Mar 2013 (3)</i>	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (2) <i>Mar 2014 (1)</i>
<i>Fagus orientalis</i>	Devrek-Sarigöl / Turkey	357/selected seed stand		30–120	2 + 2	bare root	Apr 2013 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Tilia tomentosa</i>	Ludogorie / Bulgaria	1795102120111/ selected seed stand	43.4304°N / 26.0532°E (350)	80–120	2 + 2	bare root	Nov 2012 (2) Apr 2013 (1)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Tsuga heterophylla</i>	Washington / USA	Seed zone 011–05/ selected seed stand	not documented	50–100	3 + 1	bare root	Nov 2012 (1) Apr 2013 (2)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Pinus nigra ssp. nigra (var. austriaca)</i>	Baden, Lower Austria / Austria	Skie 16 (5.1)/ selected seed stand	47°58'26"N / 16°04'28"E (390–560)	15–20	1 + 1	container	Apr 2013 (3)				
<i>Quercus petraea</i>	Boudry / Switzerland	PSE 1236/selected seed stand	46.9603°N / 6.8184°E (540 – 560)	80–120	1 + 2	bare root			Oct 2012 (3)		
<i>Quercus robur</i>	Mitteldeutsches Tief- und Hügelland / Germany Westdeutsches Bergland; Süddeutsches Hügel- und Bergland sowie Alpen / Germany	818 05/approved seed stands within the zone 81,806 and 81,809/approved seed stands within the zone	not documented	30–50	3 + 0	bare root				Oct 2012 (3)	
			not documented	15–40	1 + 0	bare root		Oct 2012 (3)			Oct 2012 (3)

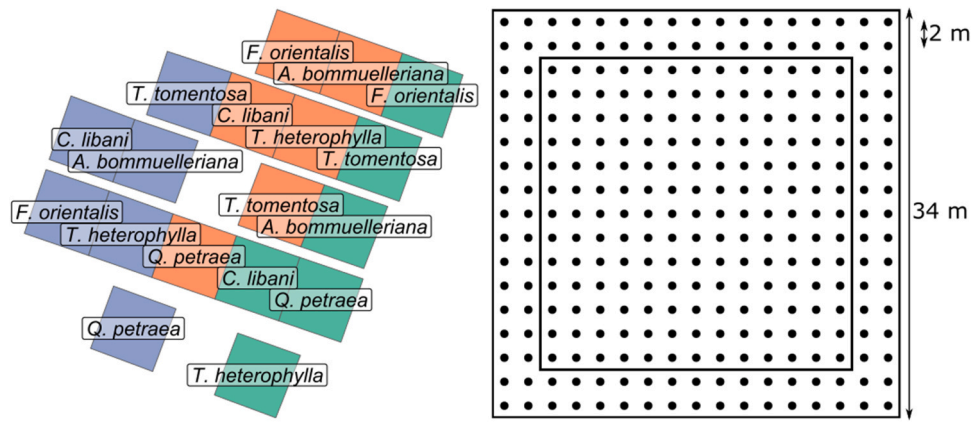


Fig. 2. Experimental layout. Left: block design (blue, red, green for block 1, 2, 3) of 5 non-native species and 1 native reference species by the example of Mutrux, Switzerland (MUT). Right: Planting layout of 17 by 17 trees per plot. The inner rectangle represents the core zone of the plot (13×13 trees).

Research Institute WSL. The De Martonne Index (DMI, de Martonne, 1926) was used to characterize aridity during the growing season (1 May-30 September). This index is thus based on the average growing season temperature and the growing season precipitation sum.

2.6. Data collection and analysis

Repeated inventories took place in the fall and winter 2016/2017, 2017/2018 and 2018/2019, and tree state (alive/dead) and height were recorded for each planting site. Vertical tree height was measured on all living saplings of the initial planting in 2012/2013 in the core zone from the root collar to the highest living point. Two measuring instruments were used, depending on tree height: a customary 2 m folding rule or a 5 m or 10 m telescopic measuring rod. Annual height increment per individual tree was computed as difference of the heights measured in consecutive years.

Occasionally missing tree height measurements were interpolated from previous inventories before 2016, if existing. On few plots, tree state (dead/alive) of some trees was missing and survival rates were as

well adjusted by interpolation from previous inventories. See Table S2 for a complete list of observed and estimated tree states and heights.

Data processing and analysis was designed to answer the three hypotheses stated in the introduction. All statistical analyses were done using the statistical software R 4.3.0 (R Core Team, 2023). Generalised linear mixed models (GLMMs) were fitted using the glmmTMB package (Brooks et al., 2017). Model assumptions were checked using the DHARMA package (Hartig, 2017).

2.6.1. Tree performance of all tree species is lower on sites with higher aridity

In the years after planting, trees do suffer from planting shock with reduced growth and a lower survival rate. To gain insights in the ecological suitability of tree species to site conditions, initial years after planting need to be excluded from analysis to avoid that a potential response is confounded by the planting shock. However, from the perspective of forest management and assisted migration, at least until a sufficient number of seed stands are established in a region, new stands will originate from planting and the overall tree species response to

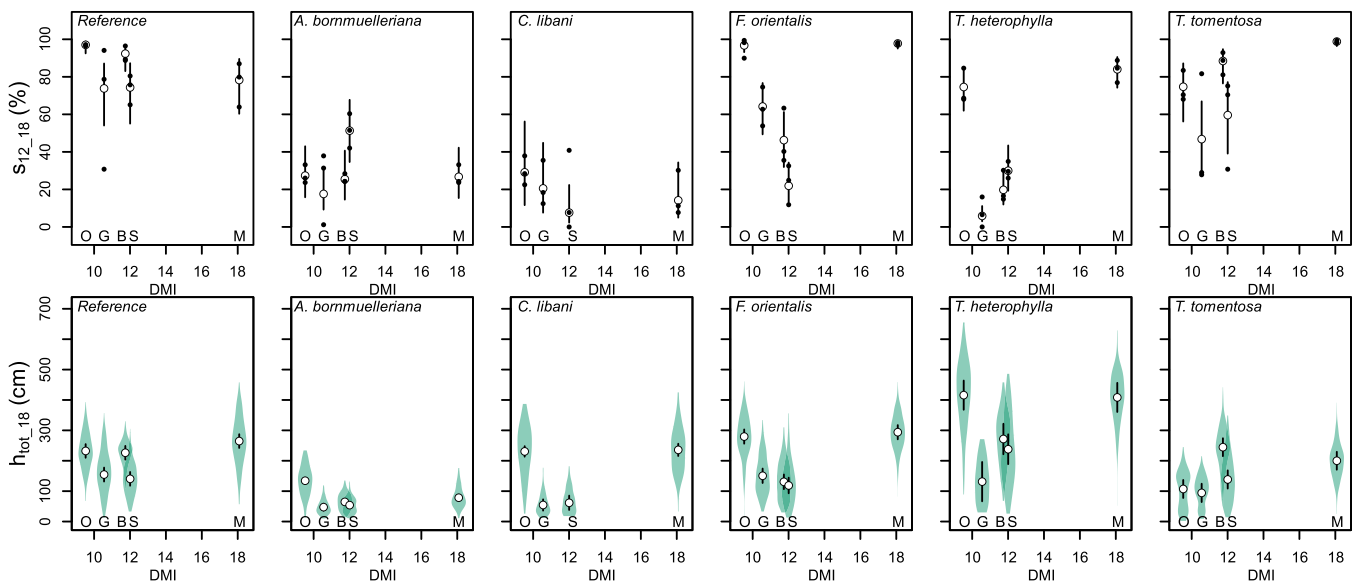


Fig. 3. Six-year survival rate between 2012 and 2018 and average height of surviving trees in 2018 in relation to average summer drought during the growing season. Sites are abbreviated with their first letter (OLD, GRO, BRU, SCH, MUT). Summer drought is quantified with the average DeMartonne Index during the growing seasons between 2013 and 2018 (DMI). Large white points with whiskers mark fitted values from linear mixed effect models and their 95% confidence intervals. Small black points (top) represent average survival rates per species and block. Green violin plots (bottom) depict the distribution of total heights of trees across all 3 blocks per species and site.

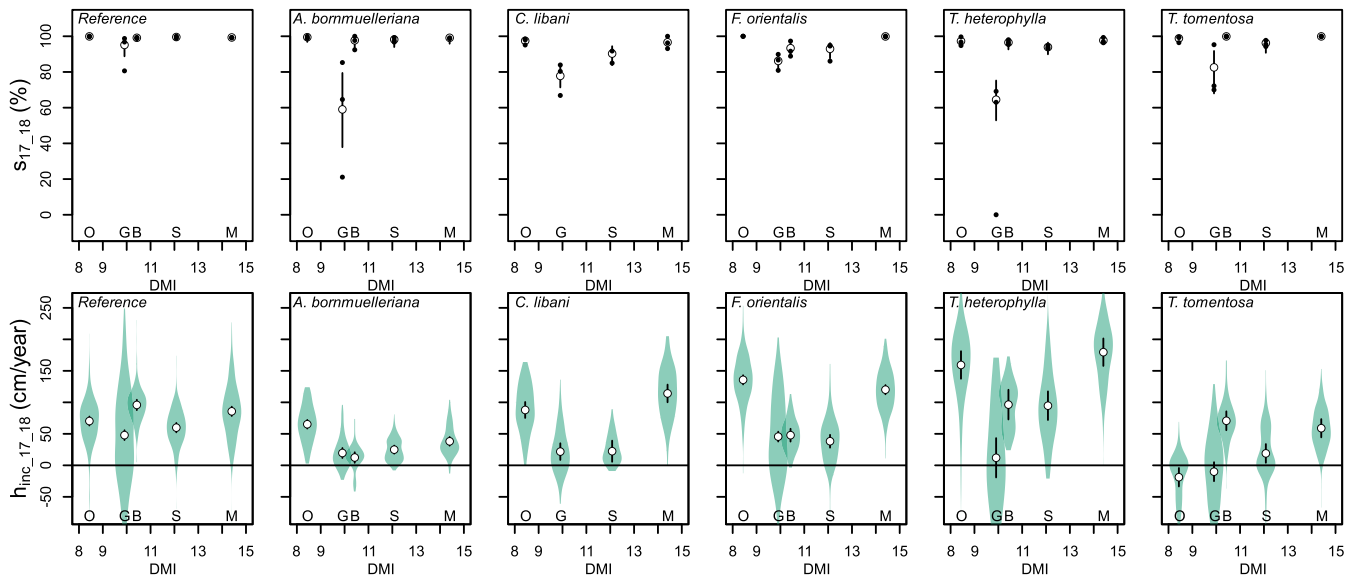


Fig. 4. Annual survival rate in 2017 and 2018 and average annual height increment in 2017 and 2018 in relation to average summer drought during the growing season. Sites are abbreviated with their first letter (OLD, GRO, BRU, SCH, MUT). Summer drought is quantified with the average DeMartonne Index in the growing seasons of 2017 and 2018 (DMI). Large white points with whiskers mark fitted values from linear mixed effect models and their 95% confidence intervals. Small black points (top) represent observed average survival rates per species and block. Green violin plots (bottom) depict the distribution of observed annual height increments of trees across all 3 blocks per species and site.

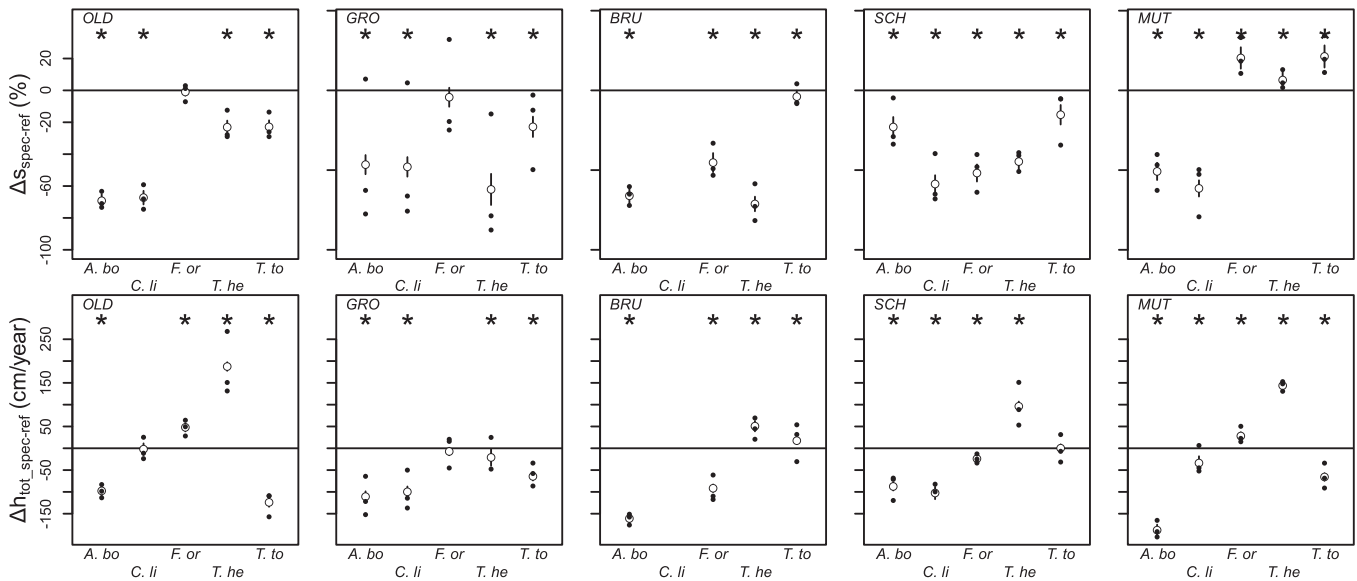


Fig. 5. Contrast of six-year survival rates between 2012 and 2018 and average height in 2018 between non-native species and native reference species ($\Delta h_{tot_18_spec-ref} = h_{tot_18_spec} - h_{tot_18_ref}$ and $\Delta S_{13_18_spec-ref} = S_{13_18_spec} - S_{13_18_ref}$). Tree species are abbreviated with their first letters (*A. bornmuelleriana*, *C. libani*, *F. orientalis*, *T. heterophylla*, *T. tomentosa*). Large white points with whiskers mark contrasts estimated from linear mixed effect models and their 95% confidence intervals. Small black points represent observed average differences between non-native species and a native reference species of survival rates and average annual height increments per species and block. Stars mark significant differences between non-native and the native reference species (p-values in Table S5).

transplanting to a specific site is highly relevant to better account for possible failures. To be able to discuss performance from both perspectives, we conducted (i) one analysis that addresses mortality during the complete six-year period from planting and overall tree height in 2018 and (ii) a second analysis about the last two vegetation periods between the fourth and sixth year after planting.

The survival rate was assessed (i) as the proportion of surviving trees of 2018 in relation to the initial number of 169 trees ($S_{13,18}$) and (ii) the proportion of trees that survived the vegetation periods of 2017 and 2018 (average annual survival rate $S_{17,18}$ [%]). Overall tree height until 2018 ($h_{tot,18}$ [cm]; i.e., the combined tree height at the point in time of

planting and height increment until 2018) and height increment of the trees during the vegetation periods of 2017 and 2018 ($h_{inc,17,18}$ [cm/year]) were assessed at individual tree level. For each target variable and species two GLMMs were fitted. The first model accounted for site differences with a categorical covariable that specified the five growing regions. The second model quantified aridity during the vegetation period using the average de Martonne aridity index (DMI, ratio between precipitation and temperature plus 10, de Martonne, 1926) for the respective growing seasons (1 May-30 September) as covariable. The first model was used to report mean values for each study site. The second model is used to analyse potential continuous aridity effects

during the study period by comparing its fit (using the Akaike Information Criterion AIC) with the first model. Only if the fit of the DMI-specific model is better than the site-specific model and if the relationship between DMI and performance is significant, we interpret this as indication for a potential climate effect.

2.6.2. Native reference species have a better performance than non-native species

For this analysis, the survival rate and total height six years after planting ($s_{13,18}$ and $h_{tot,18}$, with planting shock) and for the vegetation periods of 2017 and 2018 ($s_{17,18}$ and $h_{inc,17,18}$, after planting shock) were used as target variables. For each study site, one GLMM was fitted per target variable using the tree species as categorical covariables. Contrasts between non-native and reference species ($\Delta s_{13,18,spec-ref}$, $\Delta h_{tot,spec-ref}$, $\Delta s_{17,18,spec-ref}$ and $\Delta h_{inc,17,18,spec-ref}$) were estimated post-hoc from the models using the emmeans package (Russell, 2023).

2.6.3. Decrease of plant performance in drought years

To estimate the effect of drought years on plant performance, the performances in the vegetation periods of 2017 (moist year) and 2018 (drought year) were compared with each other. The intensity of the summer drought in 2018 was estimated using the difference of the DMI between 2017 and 2018 (ΔDMI). Again, two different models were fitted for each target variable. The first model was fitted using the growing region and year as covariable. The second model used ΔDMI instead of region as covariables. Relationships between the contrasts in mortality between 2017 and 2018 (Δs_{18-17}) were related to differences in ΔDMI using the emmeans package. The models about height increment differed slightly from the mortality models because the difference between height increment in 2017 and 2018 ($\Delta h_{inc,18-17}$) could be calculated directly for each individual tree. The response variable $\Delta h_{inc,18-17}$ was then again analysed using two different models with either the region or ΔDMI as covariables (see analysis regarding hypothesis 1).

All models included block as a random factor. The height increment model was fitted using a gaussian distribution, for the model of the survival rate a binomial distribution was applied. Variance inhomogeneity was accounted for at site- (hypotheses 1 and 3) or species-level (hypothesis 2).

3. Results

3.1. Tree performance and aridity

The average six-year survival rates of non-native species found in our study were species- and site-specific, varying from 16% (*C. libani*) to 83% (*T. tomentosa*) for the species and from 34% (GRO) to 80% (MUT) for the sites. In particular due to high mortality during the first years, there was a low overall survival rate and growth until 2018 ($s_{13,18}$, $h_{tot,18}$) of some non-native species on some sites (Fig. 3). However, the overall response of the performance to the climate was similar as the one of height increment and survival rates in 2017 and 2018 ($h_{inc,17,18}$ and $s_{17,18}$), after the trees had recovered from planting shock (Fig. 4). The response variables differed greatly between species and sites but there was no clear pattern in relation to DMI. *C. libani*, *F. orientalis* and *T. heterophylla* showed even clearly highest height increment and survival rates in the regions with the most extreme DMI-values OLD and MUT. As expected, climate adapted native tree species had a high performance on all sites. *A. bornmuelleriana* was doing best in OLD, whereas *T. tomentosa* had a higher performance in BRU and MUT, in comparison with the other sites. *T. tomentosa* was the only species with a significant relationship between one of the performance variables ($s_{13,18}$) and the DMI (Table S3 and S4). However, in no case the DMI-specific GLMMs had a better model fit (in terms of AIC) than the site-specific models (Table S3 and S4). Therefore, we did not find support for the hypothesis of a strong relationship between aridity and tree performance of the studied tree species.

3.2. Comparison of native and non-native species

There was a strong species identity effect on tree performance. Nearly all non-native species had a significantly different performance than the native species, irrespective of the respective response variable (Fig. 5, Fig. 6 and Table S5, Table S6 for the respective quantitative estimates).

The direction and strength of the results depended to a large degree on species and site. In particular in GRO but as well in BRU and SCH we observed substantially lower survival and growth rates for nearly all non-native species (Fig. 5, Fig. 6) with occasional exceptions (e.g., *F. orientalis* in GRO and *T. heterophylla* in BRU and SCH grew at least as fast as the reference species). In OLD and MUT patterns depended more on the phase of the trial. During the first years, mortality of *A. bornmuelleriana* and *C. libani* was rather high in comparison to the local reference. However, mortality decreased in OLD and MUT after 2016, resulting in differences of the survival rates between 2017 and 2018 between non-native species and the local reference of 5% points or lower (Fig. 6). Height growth of *F. orientalis* and *T. heterophylla* in MUT were greater than the reference, whereas *A. bornmuelleriana* in MUT and *T. tomentosa* was lower than the reference (Fig. 5, Fig. 6). Despite initially low growth rates of *C. libani* in OLD and MUT, height increment recovered after 2016, resulting in slightly higher growth rates in 2017 and 2018 than the reference (Fig. 6).

3.3. Decline of survival rate and growth rates during drought events

There is a significant relationship between ΔDMI and the survival rate of all tree species (Table S7). However, this was probably largely driven by one site (GRO) with exceptionally low survival rates. Only GRO did have substantially lower survival rates in 2018 for all tree species compared to 2017 (Fig. 7). Apart from GRO, only *T. heterophylla* did have a lower survival rate in 2018 (between 91% and 96%) than in 2017 (100%). In all other regions the survival rates were approximately equal in 2017 and 2018, even in OLD and SCH, where drought during the vegetation period in 2018 was a lot stronger as in 2017 (ΔDMI between -8 and -12). Apart from the non-native species in GRO, only *T. heterophylla* in BRU had a slightly lower survival rate in 2018 than in 2017 (even though the DMI did not differ much in BRU between 2017 and 2018). As the site-specific GLMMs that use the study site as categorical covariable have a consistently higher fit (in terms of AIC) than the climate-specific models (Table S7), the relationship between survival rate and site is more likely due to differences of the site characteristics than due to climatic differences.

Differences in height growth between 2018 and 2017 were highly variable. At individual tree level, we observed both, trees with larger and with lower height growth in 2018 compared to 2017 for all tree species and on all sites (Fig. 7, Table S7). On average, height growth of *A. bornmuelleriana*, *T. heterophylla* and *T. tomentosa* was not significantly related to ΔDMI (Table S7). At regional level, *F. orientalis* and *T. tomentosa* in OLD did have a substantially lower height increment in 2018 than in 2017. According to the model, across all sites only the average growth rates of the native reference species, *C. libani* and *F. orientalis* responded with a significant but moderately higher growth decrease of around -10 to -20 cm from 2017 to 2018 in regions where the DMI during the growing season differed by approximately 10 units (Fig. 7, Table S7).

4. Discussion

Our study shows that five non-native tree species, selected for being potentially suitable in future Central European climate and for which no rigorous tests had been conducted so far, have performed not as well as the native reference species during the first six years in a multi-site trial. Nevertheless, survival and growth rates were sufficiently high to successfully establish the test plantations. It remains to be seen how

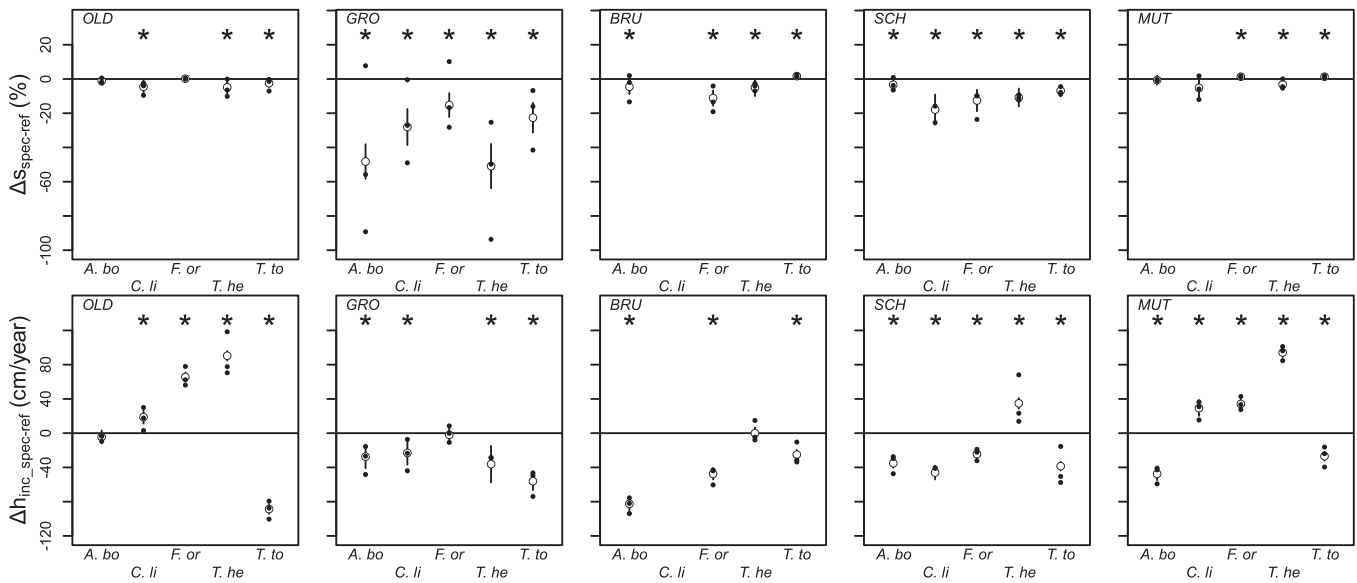


Fig. 6. Contrast of annual survival rates in 2017 and 2018 and annual height increments in 2017 and 2018 between non-native species and native reference species ($\Delta h_{\text{inc, 17, 18, spec-ref}} = h_{\text{inc, 17, 18, spec}} - h_{\text{inc, 17, 18, ref}}$ and $\Delta S_{17, 18, \text{spec-ref}} = S_{17, 18, \text{spec}} - S_{17, 18, \text{ref}}$). Tree species are abbreviated with their first letters (*A. bornmuelleriana*, *C. libani*, *F. orientalis*, *T. heterophylla*, *T. tomentosa*). Large white points with whiskers mark contrasts estimated from linear mixed effect models and their 95% confidence intervals. Small black points represent observed average differences between non-native species and a native reference species of survival rates and average annual height increments per species and block. Stars mark significant differences between non-native and the native reference species (p-values in Table S6).

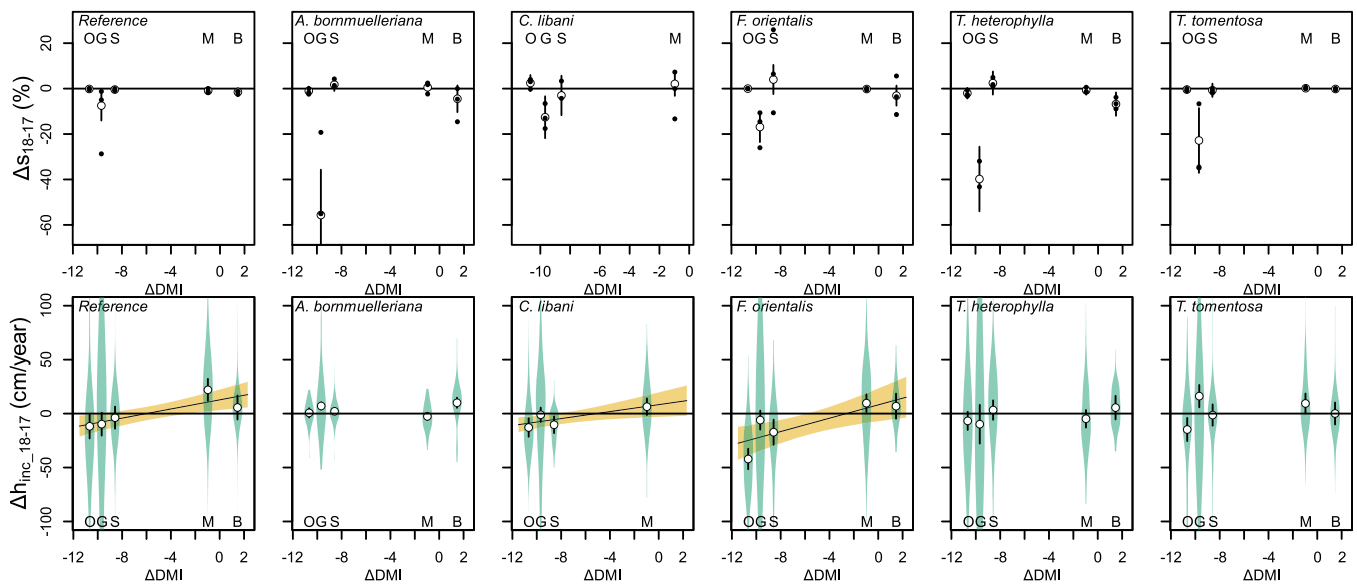


Fig. 7. Contrast of annual survival rates and annual height increments between the drought year 2018 and the non-drought year 2017 ($\Delta h_{\text{inc, 18-17}} = h_{\text{inc, 18}} - h_{\text{inc, 17}}$ and $\Delta S_{18-17} = S_{18} - S_{17}$) in relation to drought intensity during the vegetation period. Drought intensity is quantified via the site-specific difference of the DeMartonne Index of the growing seasons of 2017 and 2018 ($\Delta \text{DMI} = \text{DMI}_{18} - \text{DMI}_{17}$). Large white points with whiskers mark contrasts estimated from linear mixed effect models and their 95% confidence intervals. Small black points (top) represent observed average differences of survival rates per species and block. Green violin plots (bottom) depict the distribution of the observed differences of total annual height increments between 2018 and 2017 of individual trees across all 3 blocks per species and site. If model fit was improved by use of ΔDMI as covariable and the regression coefficient of ΔDMI was significant, regression lines with 95% confidence bands (yellow) are included in the panels (only occurred for height increment models, survival rate models were never improved by use of ΔDMI as covariable).

performance of non-native and native species compares under future climatic conditions.

The establishment of plantings of non-native species was rather difficult due to high mortality after planting, leading to high replanting efforts and partially low growth rates of the non-native species on most sites during the first years. As this was largely driven by the suffered planting shock, this is not indicative for the general physiological capacity of the species on these sites. This shows anyways that more

research about how to reduce the planting shock of particular non-native species is necessary in the context of assisted migration. For example, optimal planting times, seedling size and age, use of bare-rooted vs. container seedlings and planting may lead to improved planting success (Grossnickle and El-Kassaby, 2015; Preece et al., 2023).

The physiological performance of planted trees in the context of assisted migration can be high after the stands recovered from planting shock. If the requirements of the species regarding the climatic and

edaphic niche are met, and if limiting or even lethal abiotic and biotic influences, such as frost, drought, pathogens and browsing are absent and competition through natural regeneration is kept at a low level, survival and growth rates are sufficiently high. Negative impacts often strongly fluctuate, i.e., climatic extremes or pest outbreaks may not occur for long time periods (decades), but may have strong negative impacts in single years (Barbeito et al., 2012). During the first six years of our trial, we have encountered unusual drought in 2018 on several sites, but no other extreme influences, suggesting that the test conditions were therefore not very selective. Regarding the performance indicators used in this study – six-year survival and height, two-year survival and height increment between 2017 and 2018 after recovery from potential planting shocks – the image is highly variable. Our assessment of an overall performance of all species should not hide that differences in performance between species and sites were considerable. Future analyses of the trial will need to show if replacement plantings were sufficient to compensate early losses and if height growth and survival rate will develop in a way that may secure successful stand establishment of species on sites with low survival rate or height growth.

In plantings, a sizeable proportion of the trees does often not survive the first few years (e.g., Waters et al., 1991). The survival rates of this trial are similar to the ones observed by other studies with native and non-native tree species on clear-cut areas. One example is the REINFFORCE project with 33 species planted on 38 sites along a much larger environmental gradient than in our study, where the median four-year survival of each species ranged from 0.20 to 0.98 (Correia et al., 2018). Planted trees initially often fail to meet their transpirative demand for water due to damage to the root system caused by lifting and planting, insufficient contact of the roots to the soil, and insufficient hydraulic conductivity of the roots (Grossnickle, 2005). While we did not investigate in detail the causes for the partially poor six-year survival in our trial, the marked differences between species and sites suggest that both species-specific traits and site factors have contributed to early mortality. In contrast, we did not observe major biotic or abiotic damage so far. The mostly higher survival rates during the first six years after planting of the native species may be due to the better adaptation of the native trees to the specific site conditions and current climatic conditions.

The total height differences between tree species after six growing seasons were large, exceeding a factor of four. The general performance four years after planting during the vegetation periods of 2017 and 2018 show as well great differences. However, the variability of survival and growth rates of the tree species is reduced compared with the six-year period, indicating that some tree species were affected more by planting shock than others. Sapling mortality decreased over time, but early after planting, it differed between species (Frischbier et al., 2019). After recovery, tree species may at least partially catch up in height growth.

4.1. Early tree performance is unrelated to aridity

In contrast to our first hypothesis, the DMI during the vegetation period cannot explain the observed differences in survival and height growth between sites. *T. heterophylla*, *C. libani*, and *F. orientalis* grew taller and faster in MUT and OLD, which are at opposing ends of the covered DMI-range, than on the other sites (Fig. 3 and Fig. 4). *A. bornmuelleriana* grew taller and faster in OLD than in all other sites, even though OLD is the driest of all sites. *T. tomentosa* was growing extraordinary well in BRU compared with the other sites, even though all other non-native species have an intermediate performance in BRU. A part of the variation within species is probably due to differences in site quality and soil type. These findings are in contrast to other studies that observed a relationship between seedling survival and drought (Padilla and Pugnaire, 2007; Matías et al., 2016). One potential reason is that currently for the planted species precipitation and air temperature are no limiting factors for survival and growth of the studied species on

these sites. These results indicate that stand establishment of the studied species is possible under current climatic conditions as the physiological niche of the planted species seems to be wider than the range of environmental conditions covered by the sites. In the regions that today still have a moderate climate with a DMI during the growing season of 12 and higher, stand establishment of non-native tree species will probably be possible as well in the future, when the climate will be dryer. According to the current annual DMI in OLD (Table S1), this site can still be classified as “semi-humid”. We cannot estimate a threshold below which early performance of tree species will be decreasing in this study, as most species had a surprisingly high performance even in OLD during the exceptional drought in 2018. There was no species that had outstanding performance everywhere. However, even if performance of some non-native species was rather low on some sites, all of the non-native species did have a growth rate of at least 50 cm/year and survival rates of 95% or higher on at least one of the study sites. *T. tomentosa* for example did do best in BRU and MUT and had a low performance on all other sites and in particular in OLD, where all the other tree species were performing well. These large species-specific site differences irrespective of temperature and precipitation emphasize the outstanding importance of site conditions for the successful establishment of plantings with non-native species.

Apart from the observed site effect, we argue that the species-specific differences in height growth largely reflect the known characteristics of the life history of the tested species. Some species, in particular pioneer species, show fast early growth, while the juvenile growth of others is slow. The slowest growing species in our trial was *A. bornmuelleriana*, and it remained small after six growing seasons on all five sites. However, growth of *A. bornmuelleriana* was very stable during the summer drought of 2018, which indicates a high growth stability even in extreme conditions. The fastest growing non-native species in our trial on all sites – *T. heterophylla* – is known to grow slowly at the very beginning (the stage passed in the nursery in our trial), but later annual height growth rates of 60 cm and more have been reported in its original distribution range (Kayahara et al., 1995), also in open environments. Therefore, long-term results need to be awaited for species that currently still have a slow height growth such as *A. bornmuelleriana* and *T. tomentosa* before judging their suitability.

4.2. Native reference species may have a better early performance than non-native species

Our initial second hypothesis that the tested non-native species have a lower performance than native species could not be confirmed in general. On the sites with favourable growing conditions OLD and MUT (indicated by the high growth rates of the native species), all species had as high survival rates during 2017 and 2018 as the reference species. Only *T. tomentosa* and *A. bornmuelleriana* had lower growth rates than the local reference species there, the other species had growth rates of up to 1 m per year greater than the reference in OLD and MUT, indicating that on suitable sites at least *C. libani*, *F. orientalis* and *T. heterophylla* may have an outstanding performance and are prime candidates for testing on larger scales. However, the initially high mortality of *C. libani* during the first years must be considered as well, as this indicates a rather difficult stand establishment (Frischbier et al., 2019). On sites with a lower site quality, in particular GRO and SCH, performance of nearly all non-native species was lower than the native reference. The exception is *T. heterophylla*, which has higher growth rates than the native species on all sites except in GRO. This experiment was not designed to test other site factors than aridity. The observational finding of this study that site quality seems to affect the performance of non-native species more intensely than the performance of native species was not part of our hypothesis and needs to be confirmed by other experiments first. For forest management this may have implications for the selection of sites to establish stands with non-native tree species. In case this observation is confirmed in the future, the first generation of new non-native tree

species should rather be planted on sites with favourable growing conditions to prevent expensive replacement plantings and tending costs.

4.3. Early growth but not mortality of some species is moderately affected by drought years

Our third hypothesis that tree performance is lower during drought years was only partially confirmed. The only site where all trees except the native reference species responded with a substantially lower survival rate to the exceptionally dry growing season in 2018 compared to 2017 was GRO. In particular, *A. bornmuelleriana* and *T. heterophylla* had survival rates of up to 50% points lower in 2018 than in 2017. However, even though the drought probably contributed to the high mortality in GRO, the low mortality on the sites OLD and SCH, that experienced an equally intense drought period in 2018 as GRO, indicates that there must have been other interacting factors that contributed to the massive dieback of non-native trees in GRO. We assume that the high mortality in 2018 in GRO is due to the poor water-holding capacity of the soil composed of sand together with the high temperature, frost damage, lower precipitation in 2018 (arenic dystric cambisol, Table 1). Other factors such as a higher water holding capacity, may have mitigated drought effects in OLD and SCH. The slight increase of the mortality in *T. heterophylla* on the site BRU (Fig. 7) cannot be explained by summer drought since there was none.

Even though some species (native reference, *C. libani*, *F. orientalis*) had a moderately lower growth rate in 2018 compared to 2017 on sites with drought (OLD, GRO, SCH), this relationship was with on average approximately 10 cm reduced growth (range between -1 cm and -42 cm) surprisingly small. Even the trees that survived during 2018 in GRO had only slightly lower growth rates in 2018 than in 2017. However, as tree height growth culminates early on during the year, height increment may have been completed before the soil water was depleted by the drought event. Moreover, the drought in 2018 may have had a legacy effect on growth during the next vegetation period, which we did not analyse. The nearly unaffected survival rates on most sites and the moderate growth response to the drought of 2018 during the growing season anyways indicates that at least in the early phase of plantings of native and non-native species right after plants recovered from the planting shock, the current climatic conditions are no immediate threat for the performance of the trees. However, on sandy sites with a low water holding capacity such as GRO, an increase of the mortality in drought years is likely.

4.4. Methodological aspects and contribution of the trial to the assisted migration debate

A critical evaluation of over 150 years of assisted migration in Central Europe reveals that very few non-native species can be considered successful introductions (e.g., *Pseudotsuga menziesii*, *Quercus rubra*; Brang et al., 2016; Nyssen et al., 2016). Based on a literature review, it has been estimated that > 150 species have been tested, mostly in a management context (Brang et al., 2016). It is important to note that, even after apparent success for several decades, non-native species may later fail, often due to diseases (e.g., *Pinus strobus* due to white pine blister rust, Butin and Zycha, 1973, and *Pinus nigra*, due to several pathogens, Enescu et al., 2016). This means late failures must be expected, which could also happen to the species tested in this, with six years duration, still very short study. However, this should not hinder us to subject additional non-native tree species to scientific testing.

When conducting such tests, we see a shift from single-site tests with few species, which started already in the 19th century, to single-site tests with many species (e.g., Buffi, 1987), and recently to multi-site tests with several to many species across environmental gradients, sometimes even in different mixtures (Scherer-Lorenzen et al., 2005). A particular strength of multi-site trials is that they are more likely to capture extreme climatic or biotic impacts that may occur only locally. Such

extreme events are expected to increase with ongoing climate change (Lindner et al., 2010). The strength of our trial in this respect is the temperature and precipitation gradient, which allowed for a more differentiated interpretation. Future studies should pay additional attention on replicating plantings in regions with similar climatic conditions but different soil types and edaphic conditions to provide more insights in interactions between climate and other site conditions. Even though the necessary size of study sites increases by taking multiple site conditions into account, the additional effort is well justified as forest practitioners need to know which sites are best suited for each species.

Additionally, it must be carefully evaluated which inference from trials in a continuously changing climate can be made. Depending on the selection of the species tested and of the trial sites, the changing climate entails either an increasing match of the requirements of the species with the site-specific climate, or an increasing mismatch. An increasing match is expected if species that are pre-adapted to future climate are tested, and they should therefore perform increasingly better. Conversely, an increasing mismatch is expected if species adapted to current or even past climatic conditions are tested and if the climate develops faster than expected, in particular since the climatically most sensitive juvenile development is tested under comparably suitable conditions. For inference on climatic suitability, it is therefore important to relate the performance observed to the climate during the observation period. In our trial, we argue that the assumption when selecting the non-native species, i.e., a warming of 1.5–2.2 K for Central Europe in comparison to the period 1950–2000 (Schmiedinger et al., 2009), was optimistic, and that now a stronger warming must be anticipated. This means that the long-term inference from the trial may rather be applicable for cooler, and possibly wetter, parts of our site gradient.

The choices made when establishing such trials are hard, for example with respect to reference species, provenances and plot size. In our trial, we decided to use a site-specific reference species, ending up with three different species (and overall four provenances, Frischbier et al., 2019). In retrospect, this makes it difficult to relate the performance of the non-native species to an additional common reference. It would have been preferable to include a common native reference species of the same provenance to all sites. For example in BRU, the selection of the rather fast growing and drought resistant *P. nigra* as reference species may have resulted in comparatively high reference values for the performance of the non-native species. Therefore, the assessment of the performance of the non-native species in BRU in relation to the native reference (hypothesis 2) may be more rigid than on the other sites.

Even though high growth rates are commonly associated with vitality and high plant performance (Violle et al., 2007), reduced growth may actually be as well an indication for adaptation to drought. Morphological and physiological adaptation strategies to drought such as stomatal closure or altered wood properties (Chen et al., 2022) or an increased belowground growth (Zang et al., 2014) may come at the expense of reduced aboveground growth (Nikolova et al., 2011). Therefore, low aboveground growth may be an indication as well for adaptation to drought that may lead to more stable growth and reduced drought induced mortality in the future. There is little knowledge about the relationship between the short-term growth response of trees to drought and long-term growth stability and survival rates. Our long-term trial offers the potential for addressing many more questions regarding assisted migration, for example how local organismic community (fauna, invertebrates, fungi, lichens) is using the habitat created by the different non-native species, and how these species influence soil properties including the soil microbiome. Additionally, we suggest addressing the ability of non-native trees to regenerate in a new environment as an additional performance trait in future studies as soon as the trees start to produce seeds in sufficient numbers.

Regarding management implications, we caution against drawing premature conclusions, for the reasons stated above. We have, however, no indication that the species tested are unsuitable. For a more robust evaluation, we advocate tests of the species in additional trials, covering

a broader range of marginal site and climatic conditions or integrating the lessons from existing studies at climatically analogue site conditions (Mette et al., 2021). High initial mortality rates of non-native species like *C. libani* and *A. bornmuelleriana* in the year after planting may result in stands with rather low stem density. As forest managers typically aim for higher plant densities, it may be an option to use greater planting numbers than this study (2500 trees per hectare) to successfully establish plantings without replanting efforts in the years after.

5. Conclusion

There was partially poor growth and survival of the non-native species during the first years after planting. Nevertheless, in 2017 and 2018 after recovering from planting shock, all species established across the range of studied climatic conditions, showing their potential aptitude under climate change conditions. At edaphically hampered sites, reaching from nutrient poor and extremely dry soils at GRO to water-logged soils at SCH, the native reference species had better survival and growth than the tested non-native species. Nonetheless, all non-native species established here as well, showing, besides a climatic tolerance, suitability to cope with the prevailing site-specific conditions. Also, at least the performance in an early development stage of the non-native trees seems to be less influenced by the climatic conditions than by the respective site-specific, possibly edaphic factors. As the response of the performance to the climate may depend as well on the age of the trees, the results of this study will need to be complemented by future studies about mature stands. By combining the study of tree species performance using a multi-site experiment with a species distribution approach along a climatic gradient this study contributes to the assessment of the conditions under which non-native tree species are potentially suitable for the establishment of forest stands to mitigate climate change effects.

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Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Author contributions

PB, NF, RK, PSN and GA designed the experiment and collected the data before 2018, BM collected the 2018 data, JG conducted the analysis, BM, PB and JG drafted the manuscript. All authors substantially contributed to revision. PB passed away before the manuscript was

completed. The team of authors finalized this piece of research in his memory and as he would have wished.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121645.

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