Phenotypic variability of tracheids in hybrid Larch breeding populations

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Abstract

Xylem cell characteristics are largely genetically determined. However, depending on site conditions, plant age and location within the tree, the expression of individual characteristics can vary over a wide range. The knowledge about specific wood characteristics is not only important for timber processing, but it is also a basis for the assessment of various physiological processes related to hydraulic architecture of a tree and thus, its capacity to adapt to environmental impacts.

A detailed analysis of different larch progenies on different sites and of specific annual rings provides information about the growth performance of the trees on an anatomical level and helps to explore the phenotypic variability of xylem cell size. Our research focuses on the characterization of tracheid size of 6 different hybrid larch (*Larix x eurolepis* A. Henry) progenies and one standard European larch (*Larix decidua* Mill.) (age 19 and 39 years) planted on different sites of Southeast Germany. Beside cell length within annual year rings (late and earlywood), cells of different cambial age and different height positions within the trunk (breast height and 6.5 m) were investigated. The span between longest and shortest cell within an individual genotype was calculated as a measure for the progeny-specific growth potential that can be expected regarding the individual study site. The aim of the study was to determine the progeny specific variability of cell size, to describe differences between late and earlywood and to explore differences between hybrid larch and European larch.

A negative correlation of the tracheid lengths with the trunk height above ground was found, which confirms the hypothesis of different authors that a significant decrease in cell size with increasing trunk height can be assumed. For each progeny and study site cell length increased with cambial age for both late and earlywood cells. Site specific differences of 3.6 % in a minimum and 13.6 % in a maximum between late and earlywood tracheids could be observed. A mayor finding is that tracheid lengths between individual sample trees of the same progeny at the same test site varies significantly which highlights the phenotypic plasticity of this morphological trait. Nevertheless, the comparison of sample trees of one progeny but different sites produced significant differences only for the young trial plots. The comparison of hybrid larch progenies with the European larch 'Hasselburg' couldn't prove a superiority of hybrid larch.

Keywords: *cell size, hybrid larch, Larix, phenotypic variability, tracheid length*

Introduction

The hybrid larch (*Larix x eurolepis* A. Henry) was first described at the beginning of the 20th century by Henry and Flood (1919). It was the product of the natural fertilisation of one European larch (*Larix decidua* Mill.) with two individuals of Japanese larch (*Larix kaempferi* Lamb.), which grew close together in Dunkeld Park in Scotland. In its morphological characteristics, hybrid larch is difficult to distinguish from both parents due to the variations within the characteristic expressions.

European larch is widely cultivated outside its natural range. This is due not only to its rapid juvenile growth but also to its wood quality in terms of wood density, mechanical properties and durability (Pâques, 2013). As a typical mountain tree species, the European larch is increasingly coming under pressure from climate change due to its widespread cultivation. It cannot be ruled out that this will also affect the provenances from warmer regions (Falk et al., 2012). The Japanese larch originates from higher altitudes with high precipitation of the volcanic mountains on the island of Honshū in Japan (Schütt, 1992). As early as the 18th century, it was introduced to the coastal areas of Central Europe as a vigorous and relatively

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undemanding tree species (Langner and Schneck, 1998). In contrast to the European larch, it has a high resistance to larch canker, but has high demands on air and soil moisture. Therefore, the Japanese larch only thrives on deep and fresh soils in locations further from the coast. However, cultivation might be critical by prolonged drought (Schütt, 1992; Rieckman et al., 2020).

Due to origin-related adaptations, European and Japanese larches have different demands on soil and site, which limit the cultivation success of both species in many places (Langner and Schneck, 1998). Hybrid larch progenies are in contrast expected to have a much higher site tolerance and adaptability (Marchal et al., 2019; Rieckmann et al., 2020; Sasani et al., 2021).

In a series of recent studies by Wolf et al. (2021), a clear superiority in growth performance of most hybrid over European larch progenies was demonstrated. Among other traits, a significantly higher mean volume performance was found, which indicates the potential for an increased volume performance. Weiser (1992) describes an average superiority of hybrid larches in diameter as well as in height growth. Within one site, Wolf et al. (2021) were able to demonstrate a higher proportion of latewood in all the hybrid larch progenies investigated compared to the parent species. Weiß (2020) on the other hand does not find any fundamental differences in microscopic wood structure between the investigated larch progenies.

As the site conditions between the experimental plots sometimes vary considerably, Wolf et al. (2021) were able to observe site-dependent differences in radial growth within one progeny. Furthermore, an evaluation of time series showed that increasing water availability accompanies an increased growth performance of hybrid larches compared to the parent species (Marchal et al., 2019). Sasani et al. (2021) analyzed different physiological and anatomical reactions of the European and Japanese larches and their hybrids with the result that hybrid larches react most strongly to water availability in the soil and start to form denser wood much earlier than the two parent species.

In general, the size of the tracheids, which compose the largest part of a conifers trunk, is limited due to the need to give the wood strength (Sperry et al., 2006). For European larch, a mean tracheid length of 3.40 mm is given (Wagenführ and Scheiber, 1989). Fabisiak et al. (2020) determined an average tracheid length of 3.10 mm. Furthermore, a linear correlation between tracheid length and wood density could be proven for European larch by Fabisiak and Molinski (2002). In individuals of *Picea sitchensis* and *P. abies*, Chalk (1930) and Herman et al. (1998) demonstrated a mostly regular increase in mean tracheid length from the pith to the bark. In the European Larch (*Larix decidua*), Japanese Larch (*Larix kaempferi*) and hybrid Larch (*Larix x eurolepis*) stems studied by Liang (1948) and Fabisiak et al. (2020), the length of the tracheids from pith to bark initially increased, but flattened out and was subject to slight fluctuations. A juvenile trend of wood characteristics has been reported for several tree species. Mature wood, which is located in the outer part of the stem, generally has longer tracheids and higher density (Cown, 1992; Gryc et al., 2011). Juvenile wood is found in the first 10 to 20 growth rings of trees (Moore and Cown, 2017). More precise information, especially for European larch, was provided by Boruszewski et al. (2017), who drew the boundary between the 12th and 15th growth ring under plantation conditions. For the dominant trees under plantation conditions Fabisiak et al. (2020) set the limit at the 29th growth ring for Norway spruce and European larch. For the Japanese larch, Zhu et al. (2000) considered a decrease in tracheid length at the tree age of 18 years. According to Wolf et al. (2021), the transition from the juvenile to the adult stage should be considered individually.

Furthermore, significant differences between early and latewood with regard to tracheid length can be observed. Thus, the latewood tracheids of investigated stems of Sitka and Norway spruce, Scots pine (*Pinus sylvestris*) and European larch are the longest in all cases (Chalk, 1930; Mäkinen et al., 2008; Fabisiak et al., 2014; Fabisiak et al., 2020). For European larch, Fabisiak et al. (2020) were able to demonstrate a difference of up to 14 % in this respect. An increasing tree ring width was accompanied by a decrease in tracheid length for trees of the genera *Picea* and *Pinus* (Fujiwara and Yang, 2000; Fabisiak and Fabisiak, 2021). Already Chalk (1930) found the longest tracheids usually in the narrowest part of the annual ring of Sitka spruce. Besides the horizontal variation within and between the annual rings, he also found a decrease in tracheid length with increasing stem height within an annual ring. Furthermore, a reduction in tracheid length is associated with the formation of compression wood. This is considered to be a consequence of the increased cell divisions in the reaction wood (Yoshizawa et al., 1987).

In the current study we describe the variability of the tracheid length within and between individual trees and provenances as well as differences of provenances on different test sites.

Materials and Methods

Plant Materials

A total of six hybrid larch progenies were examined. The progeny 'Graupa 68', 'Marienberg', 'Frauenstein I', 'Frauenstein II' and 'Cunnersdorf II' are directly related to each other, as they have either the same male or female parent. Progeny 'Fichtelberg' is an exception to this (Wolf *et al.* 2021). The European larch Seed Orchard 'Hasselburg' is an official recommended Standard (by gGA) for references and serves as reference for the investigation.

The material was sampled from a total of four test plots (Table1), which differ in soil qualities, climatic conditions and stand age. The test sites Leubnitz and Bad Liebenstein were established in spring 2001, while Frauenstein and Bärenstein were planted in spring 1982, both with 2 years old plants. Five trees per progeny and plot were harvested between June 2017 and May 2019. The trees from the younger trial plots were selected due to their superior growth. Due to a reduction of tree number over time on the older plots, 5 trees with

Table 1
Location and site conditions of the test sites (after Wolf et al., 2021)

Test Site	Leubnitz	Bad Liebenstein	Frauenstein	Bärenstein
State	Saxony	Thuringia	Saxony	Saxony
Forest District	Plauen	Bad Salzungen	Marienberg	Neudorf
Time of establishment	04-2001	04-2001	11-1982	11-1982
Age at harvest (years)	18.5	19	39	39
Height above sea level	310 m	310 m	645 m	860 m
Growth Area	Ore mountains foothill	South Thuringian Triassic Hills	Ore mountains	Ore mountains
Inclination	-	slight	slight	slight
Geology	Loess	Sandstone	Gneiss	Gneiss
Temperature	8,1 °C	7,0 °C	6,1 °C	5,5 °C
Annual Precipitation	680 mm	700 mm	918 mm	963 mm

comparable phenotype and vitality were selected for further investigation.

The European larch 'Hasselburg' was used as reference and is represented on all the four test plots (Table 2).

Sample preparation and measurements

To be able to guarantee a year-ring-exact comparability of the samples, the investigation focused on the year rings 2009, 2012 and 2015 for all sample trees. For the older sample trees, the annual tree rings of 1990, 1993 and 1996 were additionally included in the investigation, to be able to track the development of the cells related to the cambial age. Thus, the sample trees of the experimental plots Frauenstein and Bärenstein in 1990 had the same cambial age as the trees of the plots Leubnitz and Bad Liebenstein in 2009.

5 cm thick stem slices were taken from each of the 70 sample trees at 1.3 m (DBH). Additionally, stem slices at a height of 6.5 m were also taken from the trees of the Leubnitz trial plot to enable a comparison of the tracheid lengths at different stem heights. Furthermore, the northern position of each slice was marked. 1 cm wide bars were taken from the disc diameter in each case and the southern part of them was processed further. First, the respective annual tree rings were extracted and dissected into early and latewood. Some early or latewood portions were too narrow to be analyzed reliably. They were therefore excluded from further measurements. In order to investigate the cellular structure of the samples, they were chemically macerated in chromic acid solution (1:1 ratio cromic acid : nitric acid, 10% each) for several hours. Afterwards the samples were rinsed carefully with distilled water and stained with safranin red solution. Tracheids with broken ends were excluded from the measurements. Cell length was determined by using a stereo microscope Stemi 2000-c (Zeiss, Jena, Germany) and the software Zen Blue (Zeiss, Jena, Germany). At least the length of 50 to 80 single cells per sample (sample means late resp. earlywood sample per year ring and tree) was measured.

Cell diameter was measured by determining the outer diameter in the center position of each intact tracheid.

Statistical analysis

The statistical analysis was carried out using the R Statistical Software (v4.1.1., R core Team, 2021). The data were checked graphically for normal assumption (QQ-Plot). To analyze whether the sample trees differ significantly from each other regarding tracheid lengths, a one-way analysis of variance (ANOVA) was performed. Furthermore, a multiple linear regression model was used to determine the individual effects and correlations of the cluster data using regression analysis.

$$length_i = a_{test\ site\ i} + b_{progeny,year\ i} + c_{progeny,earlywood/latewood\ i} + d_{test\ tree\ i} + \varepsilon_i$$

$i = 1, \dots n$ and independent $\varepsilon_i, \dots, \varepsilon_n \sim \mathrm{N}(0, \nu)$

The linear model assumes errors that are independently normally distributed. The basic requirement for the application is a linear relationship between at least one independent and one dependent variable (Georgii, 2009).

Thus, the change in tracheid size from early to latewood and from one year to the next can be quantified. To compare the tracheid lengths of larch progenies, the Tukey honestly significant difference (HSD) test was used. With this test, pairwise comparisons were made for all possible combinations of progenies within a site. In addition, we used the Tukey HSD test to examine differences in tracheid length of one progeny between the test sites.

Results

Tracheid length in general

The results show that the hybrid larches have on average longer tracheids than the reference progeny 'Hasselburg'. The hybrid larch progenies 'Cunnersdorf II', 'Marienberg' and 'Frauenstein' show the highest average value with a length of more than 3.0 mm. This corresponds to a plus of ca. 16 % compared to the cells of the European larch Hasselburg. Nevertheless, the absolutely longest wood cell with 7.66 mm is attributed to the

Table 2
Distribution of larch progenies across the test areas; age of the trees at harvest; x = marks distribution across specific test area; DBH = mean diameter at breast height (cm)

Progeny	Test sites							
	Leubnitz age 18.5 years		Bad Liebenstein age 19 years		Frauenstein age 39 years		Bärenstein age 39 years	
		DBH cm		DBH cm		DBH cm		DBH cm
Hasselburg	x	15.5	x	12.5	x	25.5	x	33.5
Graupa 68	x	16.0	x	18.0				
Marienberg			x	19.0	x	29.5		
Frauenstein I			x	19.5	x	38.0		
Frauenstein II					x	39.0	x	34.5
Cunnersdorf II			x	20.0				
Fichtelberg			x	20.0				

Table 3
Tracheid length pooled for all measured cells (early and latewood cells, cambial age between 11 and 17 years resp. 11 and 36 years) at stem height 1.3 m grouped by progeny and test site.

Progeny	Test site	Age at harvest (years)	Tracheid length (mm)					
			mean	min	max	±SD	Δ	N
Hasselburg	Leubnitz	18.5	2.251	0.508	4.854	0.825	4.346	1701
	Bad Liebenstein	19	2.692	0.712	5.192	0.665	4.479	1702
	Frauenstein	39	2.713	0.670	5.198	0.737	4.528	1935
	Bärenstein	39	2.857	0.052	7.665	0.824	7.612	2086
Fichtelberg	Bad Liebenstein	19	2.898	1.034	4.871	0.653	3.837	1521
Cunnersdorf II	Bad Liebenstein	19	3.036	1.086	5.441	0.655	4.355	1530
Marienberg	Bad Liebenstein	19	3.023	1.230	5.411	0.689	4.180	1520
	Frauenstein	39	3.099	0.080	7.093	0.804	7.013	2843
Graupa 68	Bad Liebenstein	19	2.840	1.061	5.085	0.596	4.023	1747
	Leubnitz	19	2.767	0.110	5.121	0.792	5.011	1697
Frauenstein I	Bad Liebenstein	19	2.604	0.738	4.676	0.632	3.937	1553
	Frauenstein	39	3.113	0.012	6.110	0.879	6.098	2604
Frauenstein II	Frauenstein	39	3.009	0.035	6.006	0.787	5.971	1913
	Bärenstein	39	2.788	0.100	5.465	0.704	5.364	2236

progeny 'Hasselburg', which also shows the largest span with 7.61 mm. The difference between largest and shortest cells (span) was calculated to give an impression of the possible variability of cell growth. The smallest span was observed for 'Fichtelberg' with 3.83 mm. The shortest wood cell with 0.01 mm was measured for a sample tree of the progeny 'Frauenstein I' (Table 3).

A comparison within the same progeny but between different test sites (data not shown) proved no significant differences with regard to the test site, except for progeny 'Marienberg', age 11, 14 and 17 years.

Tracheid length as a function of cambial age

The results indicate that in general for all larch progenies over all test sites a trend of significantly longer tracheids (early and late wood cells pooled) with increasing cambial age can be observed. This development trend is true for early as well as for late wood cells within one progeny. There are decreases for the year 2015 in several cases on test site Leubnitz.

The T-test for independent samples for the older test sites test determines a highly significant increase in cell length with age (cambial age 30 to 36 years) for each progeny established on test sites Frauenstein and Bärenstein.

Comparison late wood and earlywood cells

For all progenies, test plots and annual rings the latewood cells are significantly longer than earlywood cells (Figure 1). Table 4 shows the cell lengths of earlywood and latewood as well as the difference early to latewood tracheids (absolute and in relation to latewood cells). At cambial age 11 to 17 and 30 to 36 years progeny 'Frauenstein II' on trial plot Bärenstein realized the biggest difference of 0.36 mm and 0.45 mm, which

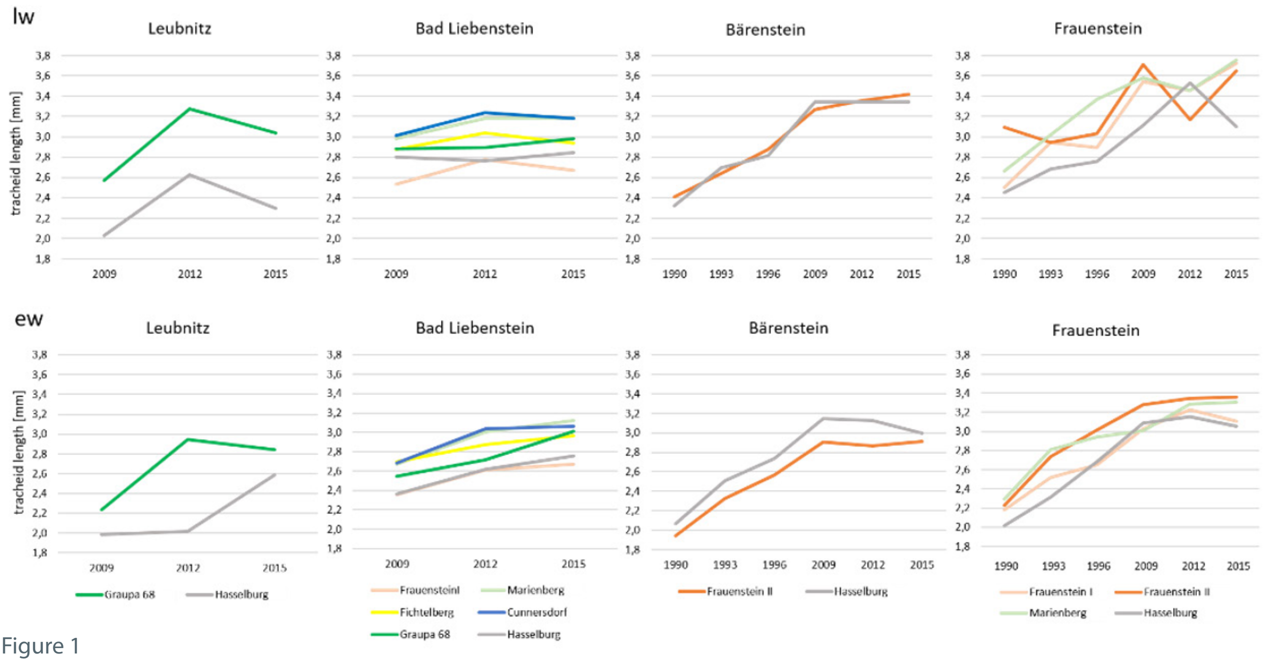

Figure 1
Course of tracheid length development [mm] for late and earlywood (top and bottom, lw and ew) of the respective progenies (colors) on different trial plots; years 1993-1996 of the older trials as cambial age correspond to 2009-2015 of the younger; x-axis indicates investigated year ring.

corresponds a length difference early to latewood of nearly 14% in both age groups. The smallest difference between late and earlywood cells was measured for the progeny 'Fichtelberg', test site Bad Liebenstein, with only 3.6% difference (Table 4). When all progenies per plot are combined, the difference between the cell length of the earlywood and the latewood is smallest in the Bad Liebenstein plot and largest in the Bärenstein plot.

Table 4
Tracheid length of early and latewood cells ; range means year rings, which were pooled.

Progeny	Test site	Range cambial age (years)	Tracheid length [mm]			Δ%
			ew	lw	Δ lw-ew	
Hasselburg	Leubnitz	11 - 17	2.194	2.315	0.121	5.2
	Bad Liebenstein	11 - 17	2.580	2.783	0.203	7.3
	Frauenstein	11 - 17	2.362	2.635	0.273	10.4
	Frauenstein	30 - 36	3.098	3.246	0.148	4.6
	Bärenstein	11 - 17	2.432	2.616	0.184	7.0
	Bärenstein	30 - 36	3.090	3.344	0.254	7.6
Graupa 68	Leubnitz	11 - 17	2.608	2.935	0.327	11.1
	Bad Liebenstein	11 - 17	2.756	2.920	0.164	5.6
Marienberg	Bad Liebenstein	11 - 17	2.931	3.115	0.184	5.9
	Frauenstein	11 - 17	2.683	2.960	0.277	9.4
	Frauenstein	30 - 36	3.202	3.595	0.393	10.9
Frauenstein I	Bad Liebenstein	11 - 17	2.549	2.660	0.111	4.2
	Frauenstein	11 - 17	2.673	3.019	0.346	11.5
	Frauenstein	30 - 36	3.325	3.508	0.183	5.2
Frauenstein II	Frauenstein	11 - 17	2.465	2.794	0.329	11.8
	Frauenstein	30 - 36	3.121	3.574	0.453	12.7
	Bärenstein	11 - 17	2.272	2.640	0.368	13.9
	Bärenstein	30 - 36	2.895	3.348	0.453	13.5
Cunnersdorf II	Bad Liebenstein	11 - 17	2.929	3.143	0.214	6.8
Fichtelberg	Bad Liebenstein	11 - 17	2.845	2.951	0.106	3.6

ew = earlywood, lw = latewood, Δ = length difference between early and latewood cells

Table 5
Tracheid length at stem height 1.3m and 6.5m of 'Hasselburg' and 'Graupa 68', test site Leubnitz

Progeny	Stem height	min	max	mean	N	±SD
Hasselburg	1.3 m	0.509	4.854	4.345	1724	0.827
	6.5 m	0.595	4.148	4.148	1831	0.581
Graupa 68	1.3 m	0.111	5.122	2.767	1692	0.792
	6.5 m	0.552	5.274	1.952	1783	0.725

Tracheid length as a function of position within the stem

In order to compare the cell length at different stem heights the tracheids of the European larch 'Hasselburg' and hybrid larch 'Graupa 68' at the Leubnitz test plot were investigated. In addition to the cells at trunk height 1.3 m, we also investigated cells at 6.5 m above ground. It turns out that the mean values of both larch progenies are lower at 6.5 m than at 1.3 m stem position (Tab. 5).

Furthermore, the results show that the cells of the hybrid larch progenies are nevertheless longer than those of the European Larch. In particular, there is a difference of more than 0.80 mm for the hybrid larch 'Graupa 68' and only 0.28 mm for the standard. 'Graupa 68' forms longer tracheids in the lower stem part than the standard by more than 0.50 mm. In the upper stem position, we observed no difference between the two progenys. The length differences (positon 1.3 m to 6.5 m, Hasselburg: -0343 - -0,254 mm ; Graupa 68: -0.906 - -0.816 mm) with regard to stem position refer to the 95% confidence interval and are considered statistically significant determined by a multiple linear regression.

Figure 2 illustrates the differences in tracheid lengths at the two stem heights for 'Hasselburg' and 'Graupa 68' using boxplots.

Variability of individual trees

The five sample trees of each larch progeny on the experimental plots have a similar genetic background and are of the same age. This means that they were exposed to the same environmental conditions during the growth phase. To find out whether the sample trees differ significantly from each other in terms of cell lengths, a one-factor analysis of variance is performed and normal assumption was tested by QQ Plots. Here, the mean length values of the individual trees belonging to the same progeny are compared with each other. The differences are considered significant if the p-value assumes values smaller than 0.05. For all trial plots and progenies p-values between 5.71e-03 for 'Hasselburg' (plot Frauenstein) and <2.0e-16 for Marienberg (test site Frauenstein) are obtained. These results confirm that the sample trees within one progeny differ significantly from each other with respect to tracheid lengths. The differences in the tracheid lengths of the sample trees are shown for the hybrid larch 'Marienberg' and European larch 'Hasselburg', trial plot Frauenstein (Figure 3).

Tracheid diameter

Taking the progenies 'Frauenstein I' and 'Marienberg' at test plot Frauenstein as an example we observed an age trend regarding the outer cell diameter (Figure 4). With increasing cambial age the cell diameter increases slightly. This applies to both early and latewood.

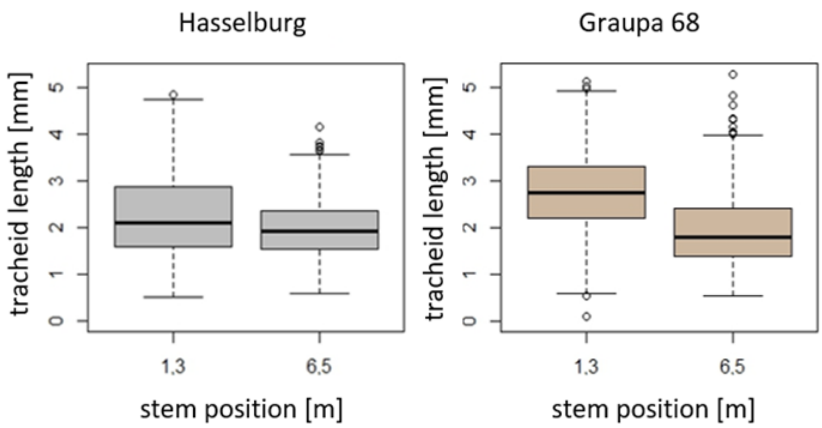

Figure 2
Tracheid length at stem height 1.3 and 6.5 m of the 'Hasselburg' ($N_{1.3}$=1,724, $N_{6.5}$=1,831) and 'Graupa 68° ($N_{1.3}$=1,692, $N_{6.5}$=1,783) at test site Leubnitz, cambial age 11, 14 and 17 years pooled, boxplots with central tendency, variability outside the upper and lower quartile and outliers.

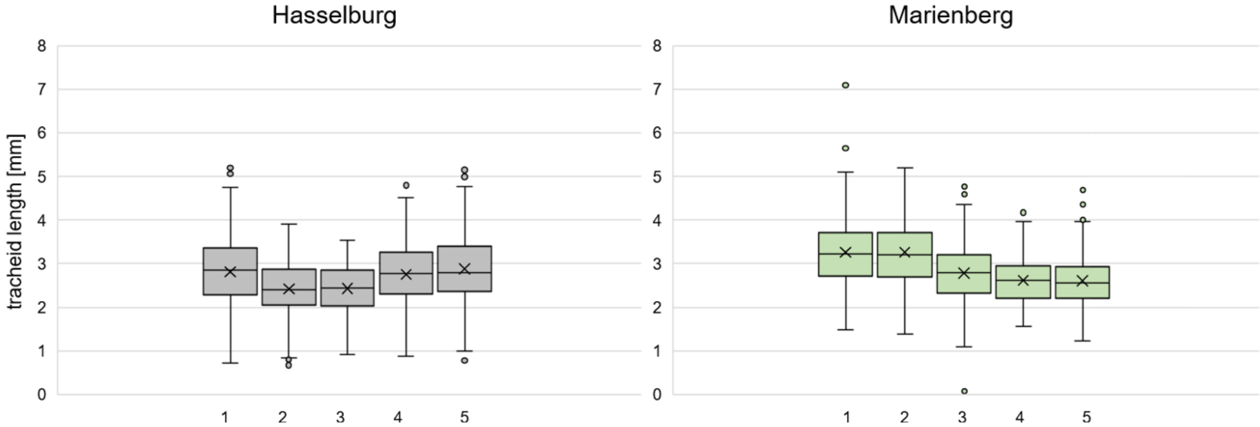

Figure 3
Cell length of individual trees (1-5), trial plot Frauenstein, 'Hasselburg' and 'Marienberg', cambial age 11, 14, 17, 30, 33 and 36 years pooled. Boxplots represent central tendency, mean, distribution and outliers.

The progeny 'Marienberg' shows its maximum in the earlywood at cambial age 33, while 'Frauenstein I' has its maxima (early and latewood) at age 30. Both progenies remain above the minimum value after they reached the maximum value despite a slight drop. The latewood shows less variation between young and older growth rings than the earlywood.

The individual tree comparison shows, as already determined for the tracheid lengths, that the values of the individual trees are quite variable and significant differences can be observed between the individual trees within a progeny on the same test site (data not shown).

To check a possible correlation between tracheid outer diameter and length, the data of the Bad Liebenstein and Leubnitz test plots were pooled. We found a slight positive trend for the latewood, which might indicate that the larger the cell diameter, the longer the cells seem to be. For earlywood an opposite trend is indicated, which could mean the larger the diameter, the shorter the cells (Figure 5).

Discussion

The investigations of the tracheid lengths on the experimental plots Leubnitz, Bad Liebenstein, Frauenstein and Bärenstein allow a comparison of the hybrid larches (*Larix x eurolepis*) under different site conditions as well as a comparison of the growth performance of hybrid larch progenies and the European larch reference. This is important insofar as the prevailing environmental conditions have a significant influence on the phenotype of wood cells (Wricke, 1972; Hering, 1994).

Fabisiak et al. (2020) determined an average tracheid length of 3.10 mm in the 29th annual ring of the European larch. This information agrees with our results from test sites Frauenstein and Bärenstein. An average length of 3.40 mm, which Wagenführ and Scheiber (1989) indicated for the European larch, was at least observed for the hybrid larches 'Marienberg' and 'Frauenstein I' at the age of 30 to 36 years. In agreement with the results of Liang (1948) and Fabisiak et al. (2020)

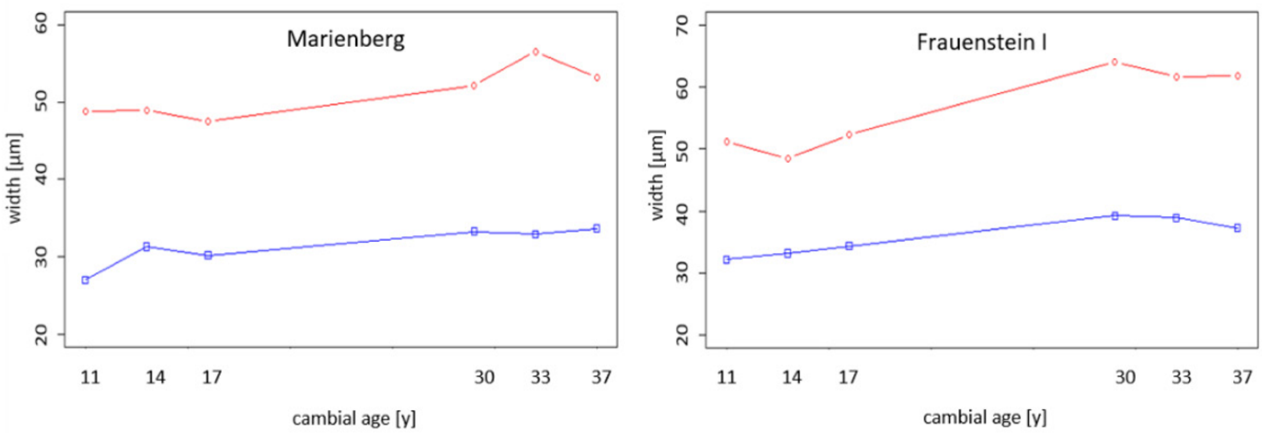

Figure 4
Course of tracheid outer cell diameter development over time. Test site Frauenstein - progeny 'Marienberg' (N=2974 cells) left and progeny 'Frauenstein I' (N=2736 cells) right; latewood (blue), earlywood (red).

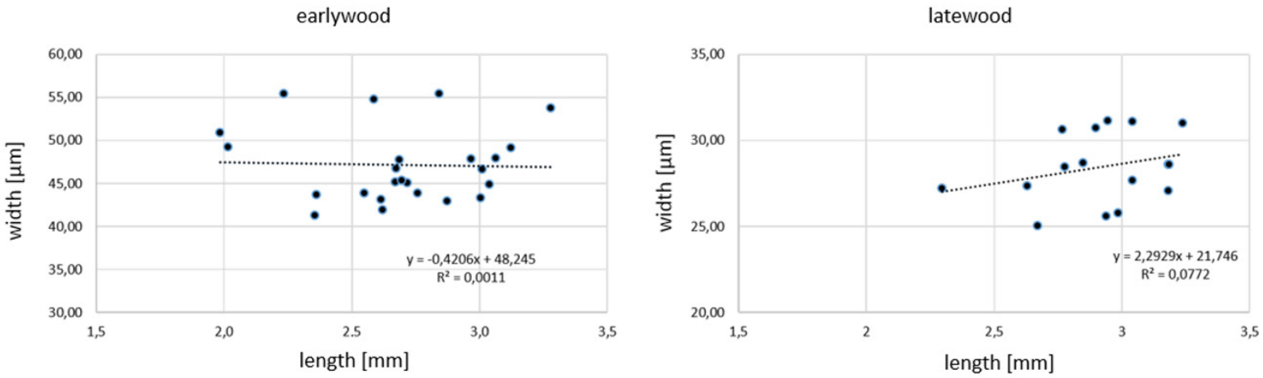

Figure 5
Relationship between cell diameter and cell length of earlywood (left) and latewood (right) for progenies summarized for test site Bad Liebenstein and Leubnitz. The dots represent mean values of the cell diameter and assigned lengths of growth rings of the individual provenances. For latewood, it was not possible to assign a width and length to each growth ring.

the tracheid length increased at the age of 11 to 14 with some differentiation at age 17 years. Maybe some alternating effects driven by climate conditions are disturbing in the warmer-than-average year 2015.This asymptotic like increase of tracheid length growth flattened out at 30 and 36 years and was subject to fluctuations (earlywood, latatewood). Due to the observation of only six year rings, no statements can be made as to whether the maximum tracheid length of the progenies has already been reached. However, in view of the smaller increase in length at the age of 30 to 36 years, a culmination point in this age period can be assumed. Mencuccini et al. (1997) approved a maximum of tracheid length at the age of 15 to 35 years of *Pinus sylvestris*.

Tracheid width is thought to reflect the diameter of the cells. Keith and Chauret (1988) found that the tracheids of European larches increase in width with increasing cambial age and they may vary with climatic and other environmental variations, even within a single tree. This finding can be approved by our investigation, which show an age trend for the two progenies under investigation. This trend is obvious for both tissues early and latewood. The question of a relationship between tracheid diameter and cell wall thickness was investigated in Latvia on common spruce trees. The results show that there is no clear correspondence between the diameter of earlywood tracheids and its cell wall thicknesses. While widths increased with age, no significant increase in cell wall thickness was found. The situation is different for latewood. Here, an increase in cell wall thickness with an increase in tracheid width with age was evident (Irbe et al. 2015). Regarding the change in tracheid width, Abe and Nakai (1999) studied three-year-old *Cryptomeria japonica* (D. Don.) under controlled conditions and found that wider and more tracheids were formed with increased water supply.

A significant length difference between the early and latewood cells within a tree ring could be demonstrated, analogous to the results of Chalk (1930), Mäkinen et al. (2008) and Fabisiak et al. (2020). According to this, the latewood tracheids of all investigated larch progenies are significantly longer than the earlywood tracheids. According to the results of Fabisiak et al. (2020), a difference of up to 14 % could be determined. The largest difference in length between the early and latewood tracheids is found in the hybrid larch ‘Frauenstein II’ on the Bärenstein plot. Nevertheless, this progeny has the lowest average tracheid length among the hybrid larches for all observation periods. Furthermore, a higher variability of the tracheid lengths within the latewood could be proven for the majority of the larch progenys. This is in agreement with the results of Gricar et al. (2015) and suggests that the earlywood tracheids are more stable in their structure to maintain optimal water conduction under variable environmental conditions. To illustrate this trait of adaptation, the range of tracheid lengths in the hybrid larch progenies is 4-6 mm (late plus earlywood cells), suggesting a large variability in cell lengths. But in the standard deviation of the measured values and the ranges, there are no significant differences compared to the European larch.

At the trunk height of 6.5 m compared to breast height shorter tracheids were formed on average. This is in line with the findings of Chalk (1930), who described a decrease in tracheid length with increasing trunk height within the same tree ring.

Chalk (1930), Bisset et al. (1951), Fujiwara and Yang (2000) and Fabisiak and Fabisiak (2021) were able to prove a decrease in tracheid lengths with increasing tree ring width in trees of Sitka spruce and Scots pine and Maritime pine (Bisset et al. 1951). However, the present investigation does not allow any statements to be made regarding a correlation between tree ring width and cell length, as no measurements of tree ring widths were carried out in the present context. But it can be assumed that the higher radial growth of the hybrid larches, which Wolf et al. (2021) determined, seems to have no negative effect on the tracheid lengths as the hybrid larch progeniess ‘Graupa 68’, ‘Marienberg’, ‘Cunnersdorf II’ and ‘Fichtelberg’ achieved higher mean values at the respective sites compared to the European larch. A comparable observation for larch couldn’t be extracted from the literature.

The growth site is an important influencing factor in order to be able to exploit the potential of hybrid larch progenys (Wolf et al., 2021). The results of the Tukey HSD test illustrate the site-dependent differences in the tracheid lengths of the larch progenies. With the exception of "Marienberg", no significant differences were found between the experimental plots. This result seems to be contrasting to the results of Hering (1994) and Wolf et al. (2021), who described the influence of the genetic component, which in combination with the site-dependent environmental influences has an effect on the tracheid lengths. Nevertheless, in some cases there were considerable differences in performance between the different experimental plots. For example, progeny 'Frauenstein I' on the corresponding plot has 14 % longer tracheids than the European larch, whereas on the Bad Liebenstein plot tracheids were on average 3 % shorter. The differences in performance, which affect the preference of progenies within a site, may be due to genotype-environment interactions, which cause genotypes to react differently to different environmental conditions (Hering, 1994). Furthermore, adaptation to site conditions cannot be excluded. There is a positive correlation between tracheid length and hydraulic susceptibility (Sellin, 1991). The larger the water-conducting cells are, the more likely it is that air embolisms occur within the tracheids, which reduce the hydraulic conductivity of the xylem. Conversely, there is a positive correlation of hydraulic conductivity with the length and width of the tracheids, as the flow resistance within the stem is reduced (Rosner et al., 2007, Gonzalez-Benecke et al., 2010). The survival of trees depends significantly on the ability of the xylem to maintain the water supply of the tree crown under variable environmental conditions (Zwieniecki and Secchi, 2015). Consequently, the physiological aspect of cell sizes has a limiting effect on the site suitability of hybrid larches. The cross progenies with smaller tracheids are more suitable for dry sites in order to avoid air embolisms within the cells. On the other hand, the progenies with a large average tracheid length are suitable for moist sites in order to benefit from the advantages of increased hydraulic conductivity.

The Leubnitz and Bad Liebenstein sites have higher annual mean temperatures, but the Frauenstein and Bärenstein sites have the higher precipitation totals. According to Antonova and Stasova (1997), temperature has the greatest climatic influence on the formation of the wood cells. This is largely confirmed by the comparisons between the experimental plots. More precisely, with the exception of the hybrid larch 'Frauenstein I', the trees of the progenies 'Hasselburg', 'Graupa 68' and 'Marienberg' on the experimental plot Bad Liebenstein formed the longest tracheids on average at the age of 11 to 17 years. This could be due to the higher annual mean temperature as maintaining factor of this plot. However, the European larch 'Hasselburg' shows a contradicting behavior. Thus, the sample trees on the Leubnitz plot developed the shortest tracheids, although this plot has the highest average temperature of 8.1 °C. Nevertheless, an indication of the influence of high temperatures on cell size, possibly combined with drought stress, is probably given by the observation that cell length decreased on some test plots in 2015. Following a vegetation period with comparatively high temperatures in 2014, spring and especially July 2015 are characterised by again temperatures above the long-term average.

Marchal et al. (2017) described an effect of precipitation on the growth performance of hybrid larches. With increasing water availability, they observed an increasing superiority of the hybrid larches over the parent species. These statements contradict the results, as the greatest difference between European larch and hybrid larch was determined on the Leubnitz plot, which also has the lowest annual precipitation. However, besides the European larch, only the hybrid larch 'Graupa 68' is located on this plot.

But, regarding only 'Hasselburg', a slight trend of increased cell length with increasing precipitation can be observed. Unfortunately, this trend cannot be verified due to a lack of samples from the other test sites.

To check a possible association between tracheid width and length, the data of the Bad Liebenstein and Leubnitz test plots were pooled. We found a slight positive trend for the latewood, which might indicate that the larger the cell width, the longer the cells seem to be. For earlywood an opposite trend was found, that means the larger the diameter, the shorter the cells.

This interesting result might be interpreted to mean that in spring the limited carbohydrate resource (limited photosynthetic products due to needle sprouting in spring) is used to form large-lumened but shorter tracheids. In contrast, the small-lumen tracheids differentiated at the end of the growing season seem to become somewhat longer with increasing diameter, as sufficient assimilates are now available.

Conclusion

The investigations show that significantly longer tracheids of the larch progeny are found in the latewood, which confirms the investigation of former studies, that describe significant differences in cell size between the early and latewood of trees and also hybrid larches. Furthermore, a negative correlation of tracheid lengths with stem height was found, which assumes a significant decrease in cell length with increasing trunk height. Although the sample trees of the progenies grew on the same site and were of the same age, they differed significantly from each other in terms of cell lengths. This finding reflects the hypothesis of significant differences between individual sample trees of the same progeny and highlights the phenotypic plasticity of this morphological trait. Furthermore, it was found that the tracheid lengths of the larch progenys of 11 to 17 years cambial age generally experience a significant increase. From our results we conclude that source-sink relationships play an important role in cell morphogenesis.

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