Tree-growth analyses to estimate tree species’ drought tolerance

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Climate change is challenging forestry management and practices. Among other things, tree species with the ability to cope with more extreme climate conditions have to be identified. However, while environmental factors may severely limit tree growth or even cause tree death, assessing a tree species’ potential for surviving future aggravated environmental conditions is rather demanding. The aim of this study was to find a tree-ring-based method suitable for identifying very drought-tolerant species, particularly potential substitute species for Scots pine (Pinus sylvestris L.) in Valais. In this inner-Alpine valley, Scots pine used to be the dominating species for dry forests, but today it suffers from high drought-induced mortality. We investigate the growth response of two native tree species, Scots pine and European larch (Larix decidua Mill.), and two non-native species, black pine (Pinus nigra Arnold) and Douglas fir (Pseudotsuga menziesii Mirb. var. menziesii), to drought. This involved analysing how the radial increment of these species responded to increasing water shortage (abandonment of irrigation) and to increasingly frequent drought years. Black pine and Douglas fir are able to cope with drought better than Scots pine and larch, as they show relatively high radial growth even after irrigation has been stopped and a plastic growth response to drought years. European larch does not seem to be able to cope with these dry conditions as it lacks the ability to recover from drought years. The analysis of trees’ short-term response to extreme climate events seems to be the most promising and suitable method for detecting how tolerant a tree species is towards drought. However, combining all the methods used in this study provides a complete picture of how water shortage could limit species.

Keywords: afforestation, breakpoints, climate change, drought tolerance, growth dynamics.

Introduction

Climate change poses challenges for forestry management and practices to find how best to maintain forests under aggravated climatic conditions. Water shortages as a result of climate change, in particular, are likely to become a major factor limiting species distribution and establishment in the near future (IPCC 2007). Already today, drought is thought to be an important factor leading to increased tree mortality, forest decline and rapid decline-induced vegetation shifts (Breshears et al. 2005, Gitlin et al. 2006, Allen et al. 2010). Hence, substitute species that are able to fulfil the current socio-economic requirements of forests must be considered, in particular, at the current boundaries of tree species’ distribution (Bolte et al. 2009).

Drought-induced mortality can be brought about by two main mechanisms. First, the xylem may dysfunction as a result of extensive cavitation, which can be caused by a single extreme drought event. Second, stored carbohydrates may progressively deplete due to reduced photosynthetic activity under chronic drought (Bréda et al. 2006, McDowell et al. 2008). However, until now there has been no conclusive evidence to support either of the two theories, and more studies on the temporal dynamics of growth limitations are needed (Hartmann 2011). Retrospective analyses using tree-ring data seem to be valuable for studying the dynamics of growth limited by drought, as tree rings are formed with a lower priority than, e.g., buds and roots, and are therefore more sensitive to climate variations (Waring 1987). This means that tree rings...
can serve as reliable indicators of a progressive depletion of carbohydrate stores, and consequently, the drought response and lag effects of trees can be analysed. The great value of using tree-ring data for studying carbohydrate storage depletion was recently demonstrated in a study on stable isotopes in tree rings, which found a close relationship between wood formation and the carbohydrates produced at the same time. These results suggest that, under chronic drought conditions stored carbohydrates are not much involved in the wood formation process, possibly because their availability is reduced under drought (Eilmann et al. 2010).

In inner-Alpine valleys, increasingly frequent droughts are thought to be the main factor limiting tree growth and a key factor triggering the mortality of Scots pine (*Pinus sylvestris* L.), which is the species that dominates the dry forests at lower elevations (Rigling et al. 2003, Dobbertin et al. 2005, Bigler et al. 2006). Pubescent oak (*Quercus pubescens* Willd.) has been considered as a possible substitute species for Scots pine on dry sites (Eilmann et al. 2006, Weber et al. 2007), but recent analyses indicate that pubescent oak might also soon reach its physiological limitations if water shortages become more severe (Eilmann et al. 2009). The dry forests are, however, very important for the local communities since they protect the villages and infrastructure against natural hazards such as rock fall or avalanches. Thus, to maintain the vital function of these protection forests in future, potential substitute species for Scots pine need to be found. The main challenge for forestry in the near future thus seems to be the question of how to identify potential substitute species that are more capable of coping with the increasing drought conditions in the inner-Alpine valleys.

The direct way to detect potential substitute species is to focus on the mortality rates of the tree species and opt for the species with the lowest mortality (Allen et al. 2010). Another possibility is to detect growth limitations due to climatic conditions by analysing tree rings and using correlative analysis of growth responses to climate (e.g., Rigling et al. 2002, Weber et al. 2007, Eilmann et al. 2009). This correlative method has, however, the disadvantage that it is based on time series over several decades. Thus, multiple severe drought years are not considered, despite their importance for tree growth and survival (Bigler et al. 2006).

In this study, we analyse the radial growth response to water shortage of four tree species, two native to the central Alps and two non-native species. The native species were Scots pine (*P. sylvestris* L.) and European larch (*Larix decidua* Mill.). Scots pine range from dry low elevation up to the tree-line, while European larch is more common at higher altitudes. These two native species are compared with the two non-native species black pine (*Pinus nigra* Arnold) and Douglas fir (*Pseudotsuga menziesii* Mirb. var. *menziesii*). The present study was conducted with even-aged trees in a 40-year-old afforestation in the dry Swiss Rhone valley. The aims of the study were:

- to identify possible substitute species with a potential to replace Scots pine on the driest sites of its distribution area; and
- to establish a procedure for assessing the potential of tree species to cope with dry conditions.

Different tree-ring-based methods were tested to find the most suitable for identifying species with a high drought tolerance. First, we compared the level of increment under dry conditions. Second, we analysed trees’ long-term (decadal) growth responses to detect any effects of decreasing water availability by stopping the irrigation. Third, we focused on the impact of drought years analysing the mid-term (based on a 4-year period) growth depressions caused by drought years, the short-term (annual) growth depressions in the drought years and the trees’ recovery afterwards.

### Materials and methods

#### Study site

To compare tree species’ responses to drought, the following requirements need to be fulfilled: (i) to diminish side effects, all species need to grow under similar site conditions and experience the same stand history; (ii) to minimize age bias, the selected trees need to be even-aged; (iii) to avoid overestimating the effect of drought on tree growth, tree growth in the juvenile phase, including the strong age-related decrease, should be omitted for the analysis of growth changes.

This study was therefore conducted in an even-aged afforestation (46°19′N, 7°44′E), located in the dry central part of the Swiss Rhone valley near the village of Gampel (Canton Valais), where all selected trees grow under the same site conditions. The afforestation site is situated between the valley floor (650 m a.s.l.) and 700 m a.s.l. on a 55% south-exposed slope. The shallow soil with a depth of 9 cm is characterized as Rendzic Leptosol type, with limestone as the parent material. The average tree height is 15 m (~10 m for European larch, ~14 m for Scots pine, ~15 m for black pine and ~20 m for Douglas fir). The tree diameter at breast height ranges from 18 cm (European larch and Scots pine; standard deviation: SD*European larch* = 5 cm, SD*Scots pine* = 2 cm) to 24 cm (black pine; SD = 4 cm) or 27 cm (Douglas fir; SD = 6 cm). The climate is continental, with an annual mean temperature of 9.2 °C, based on measurements for the period 1961–90 made by MeteoSwiss at the Sion weather station (492 m a.s.l., 30 km away from the study site). The annual mean precipitation sum measured for the period 1961–90 at the MeteoSwiss weather station in Visp (640 m a.s.l., 10 km away from the study site) was 660 mm.
The afforestation was set up in 1970 with Scots pine, European larch, black pine and Douglas fir planted in groups. All trees were planted equally far apart from each other. Thus, the stand density should be comparable for all species. However, this might not be absolutely true for Scots pine, which might grow in spots with a slightly lower tree density due to past mortality events. To facilitate species establishment in this dry environment, the local forest service regularly irrigated the whole site after periods without rainfall within the vegetation period with an artificial irrigation system from 1970 to 1992.

**Climate analyses**

To assess water availability for tree growth, we calculated a monthly drought index \( DI = P - \text{potET} \) based on precipitation sums \( P \) and the potential evapotranspiration \( \text{potET} \) according to Thornthwaite (1948). To compare annual water availability with tree growth, the drought index was averaged for the relevant months for tree growth (from July of the previous year to September of the current year, see Eilmann et al. 2009). A year was considered as a ‘drought year’ if the averaged drought index was \(< -25 \text{ mm} \) (cf. drought index in Figure 1). Since no information on the amount of irrigation water was available, we focused on drought years after the irrigation was abandoned (1993–2008). Thus, based on the annual drought index, four drought years were selected with the following most severe drought indices: \( DI_{1996} = -30.9 \text{ mm} \); \( DI_{1998} = -32.3 \text{ mm} \); \( DI_{2003} = -27.3 \text{ mm} \) and \( DI_{2004} = -29.9 \text{ mm} \) (cf. Figure 1). Hence, two pairs of successive drought years were analysed: the pair 1996/1998 occurred shortly after the irrigation was shut down in 1992, before the trees had adapted to drought. In contrast, the second pair of drought years, 2003/2004, occurred 11 and 12 years after the irrigation was terminated. By the time the second drought period had set in, the trees had adjusted their phenotype to increased water shortage (Rigling et al. 2003, Eilmann et al. 2009).

**Sampling and data analysis**

In spring 2009, two increment cores (diameter: 5 mm; length: from bark to pith) from 15 dominant trees per species were sampled at breast height (1.3 m). To avoid compression wood, the cores were taken at a 60° angle from the slope. The surfaces of the cores were planed off with a core-microtome (WSL, Birmensdorf, Switzerland), and chalk was inserted in the cell lumina to allow a better contrast for further analyses. The tree-ring, earlywood and latewood widths were measured separately using a combination of a Lintab digital positioning table and the software TSAP-Win (both Rinntech, Heidelberg, Germany). The measurements made on the two cores per tree were averaged and arranged in a tree chronology. As Fritts (2001) also found, the tree-ring and earlywood widths developed in a very similar way. Thus, we focused in this study on the tree-ring and latewood widths (referred to collectively as the ‘radial increment’).

Mean chronologies and the range for each parameter were calculated for each species. In addition, we calculated standard dendrochronological statistical values, including the autocorrelation, which indicates how much tree-ring formation of the current year was influenced by the tree-ring formation of the previous year, mean sensitivity, i.e., the year-to-year variation in

![Figure 1. Tree-ring and latewood chronologies per species, together with the annual drought index series, DI (averaged for the period in July of the previous year to September of the current year). Important drought years are marked with arrows. The period with occasional irrigation is indicated by the shaded area with the DI in grey, as it might not represent the real water availability as the amount of irrigation water was not quantified and therefore not included in the index.](image-url)
the mean chronology, as well as an overall average of the tree-ring or latewood width and the standard deviation. These characteristics were calculated separately for the irrigation and the non-irrigation period (up to and including 1992 and after 1992). For each species we calculated the common tree-ring signal (Rbar) as the inter-series correlation for the entire period (1975 to 2008).

Structural changes or significant breaks in the radial increment were analysed for the species chronologies over the entire observation period from 1975 to 2008. Therefore, we calculated the empirical fluctuation processes according to an OLS-based CUSUM-test (a CUMulative SUM-test based on ordinary least squares residuals). If the null hypothesis, namely the regression coefficient, does not change over time and the species chronology for latewood or tree-ring width is statistically stable, had to be rejected as a result of the OLS-based CUSUM-test, the location (in this case the years of the breakpoints) and the optimal number of breakpoints were selected according to the Bayesian information criterion. For this breakpoint analysis, the strucchange package in R was used (for details, see Zeileis et al. (2003)).

The lag effects of water shortage on tree growth were quantified by testing the mean radial increment of the 4 years prior to the first drought year (1996 or 2003) of the pair (pre\_mean) against the mean radial increment in the 4 years after the second drought event (1998 or 2004) of the pair (post\_mean), using a Wilcoxon rank sum test. The percentage change in radial increment after the second drought year was also calculated.

In addition, short-term changes in the radial increment due to a drought year were analysed, as was the speed of recovery after the drought year. The drop in radial increment in the first drought year of the pair (1996 and 2003) was tested against the radial increment in the 4 years prior to the first drought year of the pair (pre 1 to pre 4). In addition, we tested the radial increment in the second drought year of the pair (1998 or 2004) against the radial increment in the following 4 years (post 1 to post 4). For this analysis, a multiple comparison test after Kruskal–Wallis (pgirmess package in R) was used.

## Results

### Long-term analysis

The radial increment (latewood and tree-ring width) decreased with decreasing water availability as indicated by the similarity between the increment curves and the drought index (Figure 1). This was most apparent during drought years. By far, the highest increment of all species was in Douglas fir, followed by black pine and Scots pine (Table 1). This was consistent for both the irrigated and non-irrigated periods and remained unchanged in drought years. Only European larch changed its rank: during the irrigation period up to and including 1992 (Figure 1), its level of increment was similar to that of black pine. After the irrigation was abandoned, however, it rapidly dropped to the lowest level of increment of all species (Table 1). Thus, European larch showed by far the most negative growth response to soil-water deficiency.

Comparing the statistical characteristics of the time series for latewood and tree-ring width before and after the irrigation stop (up to and including 1992 vs. after 1992, see Table 1) clear differences were found with decreasing autocorrelation and increasing sensitivity after 1992. European larch was the most sensitive of all species after the irrigation was stopped. It also had the lowest mean inter-series correlation (Rbar, calculated for the whole period (1975–2008); Table 1). All other species showed similarly high inter-series correlations.

Long-term changes in the level of increment, so-called breakpoints, were found in the mean chronologies of all species (Figure 2). Up to three breakpoints occurred in the tree-ring chronologies; the first in 1980 (or 1979 in European larch), the second in 1985 (or 1986 in European larch) and the third in 1995. For Douglas fir the first breakpoint (around 1980) was missing, and it underwent only two structural changes.

### Table 1: Descriptive statistics of tree-ring and latewood widths.

<table>
<thead>
<tr>
<th>Tree-ring width</th>
<th>Mean [1/100 mm]</th>
<th>SD [1/100 mm]</th>
<th>$r_{\text{auto}}$</th>
<th>$S_{\text{mean}}$</th>
<th>Rbar</th>
<th>Latwood width</th>
<th>Mean [1/100 mm]</th>
<th>SD [1/100 mm]</th>
<th>$r_{\text{auto}}$</th>
<th>$S_{\text{mean}}$</th>
<th>Rbar</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scots pine</td>
<td>281</td>
<td>111</td>
<td>0.79</td>
<td>0.17</td>
<td></td>
<td>Scots pine</td>
<td>45</td>
<td>16</td>
<td>0.63</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>black pine</td>
<td>337</td>
<td>116</td>
<td>0.92</td>
<td>0.11</td>
<td></td>
<td>black pine</td>
<td>70</td>
<td>17</td>
<td>0.50</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td>Douglas fir</td>
<td>417</td>
<td>72</td>
<td>0.25</td>
<td>0.16</td>
<td></td>
<td>Douglas fir</td>
<td>96</td>
<td>17</td>
<td>0.45</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td>European larch</td>
<td>345</td>
<td>170</td>
<td>0.89</td>
<td>0.21</td>
<td></td>
<td>European larch</td>
<td>64</td>
<td>19</td>
<td>0.62</td>
<td>0.16</td>
<td></td>
</tr>
<tr>
<td>Scots pine</td>
<td>121</td>
<td>48</td>
<td>0.56</td>
<td>0.32</td>
<td>0.87</td>
<td>Scots pine</td>
<td>26</td>
<td>12</td>
<td>0.32</td>
<td>0.42</td>
<td>0.60</td>
</tr>
<tr>
<td>black pine</td>
<td>182</td>
<td>52</td>
<td>0.17</td>
<td>0.26</td>
<td>0.85</td>
<td>black pine</td>
<td>54</td>
<td>18</td>
<td>-0.18</td>
<td>0.39</td>
<td>0.47</td>
</tr>
<tr>
<td>Douglas fir</td>
<td>260</td>
<td>81</td>
<td>0.43</td>
<td>0.25</td>
<td>0.73</td>
<td>Douglas fir</td>
<td>83</td>
<td>30</td>
<td>0.19</td>
<td>0.37</td>
<td>0.56</td>
</tr>
<tr>
<td>European larch</td>
<td>97</td>
<td>54</td>
<td>0.39</td>
<td>0.45</td>
<td>0.67</td>
<td>European larch</td>
<td>27</td>
<td>14</td>
<td>0.47</td>
<td>0.45</td>
<td>0.39</td>
</tr>
</tbody>
</table>

Calculations were made separately for the periods with occasional irrigation up to & including 1992 and after 1992, with the exception of Rbar, which was calculated for the whole period (1975 to 1992). Abbreviations: SD = standard deviation, $r_{\text{auto}}$ = autocorrelation coefficient, $S_{\text{mean}}$ = mean sensitivity, Rbar = mean inter-series correlation.
In the latewood chronologies, up to two breakpoints were found (Figure 2). While Douglas fir showed no structural changes at all, one breakpoint was found for black pine and two in Scots pine and European larch. The first breakpoint occurred in 1979 in European larch and in 1984 in Scots pine. The second occurred 1 or 2 years after the irrigation was stopped, in 1993 and 1994, respectively. The only breakpoint in black pine occurred at the same time as the first one in Scots pine in 1984.

**Drought year analysis**

The tree growth of all species was substantially reduced in all drought years (Figure 1). Consequently, the narrowest increment in many trees was found in the 1998 drought year. For tree-ring width, in Scots pine it was in 9 out of 15 trees, in black pine 11 out of 15, in Douglas fir 11 out of 15 and in European larch it was 5 out of 15. For latewood width, in Scots pine it was 9 out of 15, in black pine 8 out of 15, in Douglas fir 8 out of 15 and in European larch 4 out of 15.

To assess the effects of the drought years on trees’ midterm growth, we compared the radial increment in the 4 years before and after the drought years (Table 2), and found the strongest reduction in tree-ring width in European larch (−66%) followed by Scots pine (−56%), in particular after the 1996/1998 drought years. In general, the decrease in tree-ring width was more severe after the 1996/1998 drought than after the 2003/2004 drought period. However, after the drought years 2003/2004, the growth of the two

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Figure 2. Tree-ring and latewood chronologies per species (black curve) with corresponding breakpoints (vertical lines). The average increment between two breakpoints is given by the white curve. The range of distribution is darkly tinted.
pine species, Scots pine and black pine, was significantly reduced.

In latewood width, significant mid-term changes after drought years were fewer and less severe than in tree-ring width (Table 2). But as with tree-ring width, the increment reduction in latewood was again most evident in larch (−59%) and in Scots pine (−36%). Douglas fir was the only species that did not show any significant mid-term change in latewood width. Significant reductions in latewood width were found in the two pine species after 2003/2004 and in larch after 1996/1998.

The analysis of short-term (=annual) growth changes in tree-ring width revealed that recovery after drought years was strongest (Table 4) and fastest (Table 3) in black pine. The greatest decrease in tree-ring width during drought years was in Scots pine; while its recovery was quite successful, it was delayed by 3–4 years after the second drought year. Douglas fir also recovered with a delay of 3 years after the second drought year. European larch responded least to drought years but then also showed no signs of recovery in the following years.

Regarding the differences between the two pairs of drought years, the decrease in tree-ring width was most pronounced before the drought period 1996/1998 (Table 3; P < 0.001 for Scots pine, black pine and Douglas fir, P < 0.01 for European larch). However, all species except for European larch recovered after 1998 and showed significantly higher increments in the post-years than in the drought year itself.
Table 4: Overview of the ranking of drought tolerances as a result of the different analyses.

<table>
<thead>
<tr>
<th>Tree ring width</th>
<th>Scots pine Black pine Douglas fir European larch</th>
<th>Latewood width</th>
<th>Scots pine Black pine Douglas fir European larch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fig. 1</td>
<td>level of increment [1/100 mm]</td>
<td></td>
<td>level of increment [1/100 mm]</td>
</tr>
<tr>
<td></td>
<td>121 182 260 97</td>
<td></td>
<td>26 54 83 27</td>
</tr>
<tr>
<td></td>
<td>rank sum</td>
<td></td>
<td>rank sum</td>
</tr>
<tr>
<td></td>
<td>33 2 3 3</td>
<td></td>
<td>38 3 2 3</td>
</tr>
<tr>
<td></td>
<td>weighted rank sum</td>
<td></td>
<td>weighted rank sum</td>
</tr>
<tr>
<td></td>
<td>73 51 51 10</td>
<td></td>
<td>83 143 33 33</td>
</tr>
</tbody>
</table>

The superscripts specify the rank of the species according to their tolerance of drought, where "1" indicates the species with the highest drought tolerance, and "4" the species with the lowest drought tolerance. In the mid-term changes (Table 2), significant changes on the 99% level were weighted with one, and changes significant on the 99.9% level with two. The weighted rank sum was calculated using weighting factors based on how important the different methods were for estimating species’ drought tolerance (level of increment = 0; long-term changes = 0.5; mid-term changes = 0.25; short-term changes = 0.75). In the mortality analysis and the conclusion, the species furthest on the left has the highest drought tolerance and the species furthest on the right has the lowest. “No difference between two species” in their drought tolerance was tagged with /; “a slight decrease” with >; and “a very strong difference” with >>.

(P < 0.001). In 2003/2004, the decrease in tree-ring width was less pronounced (P < 0.01 only for Douglas fir). As a consequence, the recovery was also least pronounced.

Latewood width was clearly reduced during each drought year (P < 0.001), but also recovered afterwards (P < 0.001), although not in all species. Hence, unlike with tree-ring width, no clear difference between the drought years in the 1990s and in the following decade was found. As with tree-ring width, black pine recovered best (Table 4, 160%), followed by Scots pine (135%), which showed a strong growth reduction in each drought year, but also a clear recovery afterwards. In contrast, Douglas fir and European larch recovered only slightly (33%), with marked delay.

Discussion

Species tolerance towards drought

The growth of Douglas fir and black pine seemed to be less limited by the prevailing dry conditions in Valais than that of Scots pine and European larch, as the persistence of larger increments indicates (Figure 1). The lower impact of drought on the tree growth of Douglas fir and black pine is most apparent when looking at the response of latewood width, where neither showed any significant growth reduction after irrigation was stopped (Figure 2). The absence of growth breaks in response to water shortage indicates that Douglas fir and black pine were less sensitive to increased drought conditions than Scots pine and larch. This might be due to them having a more effective stomatal control mechanism, as described by Grieu et al. (1988), Lassoie and Salo, (1981) for Douglas fir and Lebourgeois et al. (1998) for black pine.

The effect of drought years also seems to be less severe for black pine and Douglas fir as these species showed a less distinct lag effect in the reduction of tree growth after drought years than Scots pine and European larch (Table 2). Black pine showed by far the most plastic response to drought years, with the fastest and most pronounced recovery (Tables 3 and 4). Fast recovery is a clear survival advantage, and multiple drought years are not expected to have an exacerbating effect on the performance of black pine.

In contrast to Douglas fir and black pine, Scots pine closes its stomata at an early stage under heat and drought conditions (Zweifel et al. 2009), thus significantly reducing its photosynthetic activity (Ciais et al. 2005, Rennenberg et al. 2006, Granier et al. 2007, Reichstein et al. 2007). This might be the reason for the relatively strong growth limitation for Scots pine compared with Douglas fir and black pine. Not only did Scots pine show the greatest tree-ring depression during drought years (Table 3) and a marked mid-term growth restriction in the years following the drought event (Table 2), but it also recovered well after drought years, albeit with some delay (Tables 3 and 4). Scots pine might lack the ability to survive on the driest sites if the severity and frequency of drought increase...
because it does not recover fast enough from drought. As Bigler et al. (2006) showed, there is an increased mortality risk for Scots pine after repeated drought years.

Of the four species studied, European larch suffered most from drought. Its increment reduced markedly in response to the irrigation stop (Figure 2) and to the drought years in the 1990s (Table 2), and it failed to recover after severe drought (Tables 3 and 4). The afforestation was first established without any water limitation (with irregular irrigation until 1992), but in 1996 the European larch trees were suddenly exposed to drought and showed no signs of recovery during subsequent years. European larch, thus, seems to be maladjusted to the dry conditions and frequent drought years typical at low altitudes in Valais. The trees’ poor performance in response to drought might be due to them having an ineffective control mechanism for dealing with water loss (Anfodillo et al. 1998) or to the disadvantages of annually reproducing its foliage (Migliavacca et al. 2008).

The importance of drought as a limiting factor for tree growth in the inner-Alpine dry valleys was underlined by the fact that all tree species investigated responded sensitively to reduced water availability (Figure 1), in accordance with other studies (Martinez-Meier et al. 2008) on Douglas fir, Martin-Benito et al. (2008) on black pine, Eilmann et al. (2006, 2011) on Scots pine and Anfodillo et al. (1998) on European larch. In addition, we found that growth significantly reduced after irrigation was stopped (Figure 2), as Eilmann et al. (2009) and Rigling et al. (2003) also showed. However, in our study the response of tree-ring width to the irrigation being stopped did not occur immediately, probably because this coincided with a period between 1992 and 1995 of improved water availability, when drought index increased (Figure 1). In fact, 1996 was the first time in the study period when tree growth was effectively limited by drought, and the first year (after the breakpoint) when significantly reduced tree-ring widths were observed for all species (Figure 2). As a result, the growth depressions observed in the 1996/1998 drought years were more distinct than in the drought years in 2003/2004 (see mid- and short-term changes, Tables 2 and 3).

The main reason why trees respond in a less pronounced way to the severe drought in 2003/2004 than in 1996/1998 could be that the tree phenotype successfully adjusted during subsequent 11 years after the irrigation was stopped. One mechanism that may be involved in such a phenological adjustment is that the altered carbon allocation favours root growth shifting the zone of maximal water uptake further below the surface (Ericsson et al. 1996, Pühe 2003). This shift the carbon allocation leads to a deeper rooting system, which allows the trees to reach a better water supply from deeper water pools during subsequent drought years when the topsoil dries out. Another important mechanism that enables a tree to adjust to increased drought is to reduce its green biomass by shedding

**Suitability of the methods used to detect drought tolerance**

An even-aged afforestation is ideal for a comparative study on species’ drought tolerance as no interference with differing site conditions and age trends need to be considered. However, for a detailed analysis of the effect of drought years on tree growth (mid- and short-term analyses) the focus must be on the mature phase of tree growth only, since tree growth is more stable during this phase. In this study, we made a trend analysis to check for significant trends (data not shown). From 1995 onwards we found no negative growth trend. The only exception was black pine showing a slightly but non-significant negative trend (compare Figure 1 and Figure 2). However, black pine was the species showing the best recovery after drought years. We are thus convinced that the growth response to drought years is not confounded by an age trend.

In contrast, in the juvenile phase, a decrease in the rate of tree growth is strongly age related (Figures 1 and 2 before 1985). Even if the investigation period is short (<10 years as in our analysis), increment decreases are also age related. Thus, if juvenile growth is considered the effect of the drought year will always be overestimated.

Interpreting for tree species’ drought tolerance is still challenging. The methods used in this study varied in how suitable they were for identifying species that are able to cope well with increased drought, and we ranked the methods we tested according to their suitability (see Table 4):

(i) The best method for assessing species’ drought tolerance we found was to analyse the short-term (annual) changes triggered by drought years (Table 3, weight = 0.75), as this reveals the direct hampering effect of tree growth during a drought year as well as the pace of subsequent recovery. High plasticity, i.e., fast recovery after drought years, is a significant advantage and a strong indicator of species ability to cope with frequent droughts. Since severe drought years like that in 2003 are likely to be more frequent in future (Schär et al. 2004), this analysis provides a first indication of the potential of a tree species for dealing with the extremely dry conditions expected in the inner-Alpine valleys.

(ii) Breakpoint analysis (Figure 2, weight = 0.5), which reveals significant growth changes on a long-term scale, is an appropriate indicator for drought tolerance as it reveals continuous limitations on tree growth due to decreasing water availability. The latewood width of Douglas fir and black pine, however, showed no breakpoint under
increasingly severe drought conditions, which suggests that the growth of these species is less dependent on water availability. Thus, breakpoint analysis provides more information on the ability of a tree species to cope with increased water shortage in the long term than, e.g., the analysis of the level of increment alone.

(iii) The analysis of mid-term (4 years before and after the drought year) changes after drought years (Table 2, weight = 0.25) allows a quantification of the lag effects on tree growth according to drought years. However, in slow-growing trees such as European larch (see 2003/2004 in Table 2), the growth reduction is less pronounced. Therefore, less severe growth reduction per se may not necessarily be a sign of high drought tolerance as it may also arise from trees’ inability to recover from previous droughts.

(iv) The level of increment (Table 1, Figure 1) can give a first impression of how well trees cope with chronic drought. However, a high increment does not necessarily indicate that the tree is well adjusted to site conditions as a high growth rate might reduce the lifetime of a tree, as Bigler and Veblen (2009) suggested. Hence, the level of increment cannot be used as a proxy for species’ tolerance to drought and was therefore ignored in our final ranking (Table 4).

Conclusion

Our study demonstrates that tree rings reveal information not only about how much a species might be limited by certain site conditions but also about its potential to endure. The two non-native species, Douglas fir and black pine, appeared to cope better with chronic drought and drought years than Scots pine or European larch. This result is confirmed by the relatively high mortality rate in Scots pine during the last 30 years in Valais and the increases in crown dieback and mortality rates in European larch during recent years. In contrast, no mortality in black pine and Douglas fir at the study site has been observed to date.

The aim of this study was to find the best tree-ring-based methods for identifying species with a high drought tolerance. We found that short-term analyses are most suitable for assessing species’ potential to cope with drought. However, we still recommend using a procedure that combines all the methods used in this study as this will provide a more coherent picture of the responses of tree species to chronic drought and severe drought events.

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References


Tree physiological responses to drought


