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Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance

David Montwé · Heinrich Spiecker · Andreas Hamann

Abstract To select suitable planting stock for reforestation under uncertain future climates, information about tolerances of genotypes to different climate conditions is necessary. One useful approach is to combine dendrochronological research with common garden experiments to quantify genotype by environment interactions observed over time. Here, we assess the response of Douglas-fir provenances planted in a common environment to climate variation over five decades using tree-ring analysis and historic height data. A rare drought event that affected growth in the year of 1985 provided the opportunity to study how mature Douglas-fir provenances differ in resilience and resistance to drought conditions and whether there are trade-offs with long-term productivity. We found that overall growth performance of provenances originating from drier and colder environments within the coastal range was below average and correlated with interannual variation in temperature. Productive provenances originated primarily from moist and warm areas and their annual increments co-varied strongly with summer precipitation and summer drought indices. Further, provenances with below average growth were able to recover more quickly from the drought event of 1985, but did not show stronger drought resistance than coastal sources. Our results provide evidence for trade-offs between productivity and drought resilience and show that sources originating from moist locations are more dependent on favorable growing conditions in the summer. We conclude that selecting drought-resilient planting stock as an adaptation strategy for climate change is possible, but it would entail reductions in productivity.

Keywords Drought response · Resilience · Plasticity · Adaptation · Assisted migration · Tree-rings

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Introduction

Climate change projections for the Pacific Northwest of Canada and the USA suggest an increase in temperature of approximately 2 °C by the 2050s and of 3.0 °C by the 2080s, while annual precipitation is expected to remain similar. However, seasonal precipitation patterns might shift towards an increase in the winter and a decrease in the summer. Together with rising evapotranspiration due to higher temperatures, this might lead to exacerbated drought conditions during the growing season (Mote and Salathé 2010). The rate of change is expected to exceed the rate at which tree species can adapt to changing environmental conditions (Aitken et al. 2008). Observed climate trends over the last several decades have been closely following climate change projections for the Pacific Northwest (Mote and Salathé 2010), and it has been inferred that conifers of the temperate zone are already lagging behind their optimal climate niches (Loarie et al. 2009). Moving genotypes north in latitude and upwards in elevation has therefore been suggested as a measure to help Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) populations keep pace with climate change (St. Clair and Howe 2007; Rehfeldt et al. 2014).

The large natural range of Douglas-fir includes a multitude of environmental conditions from the coastal rainforests of Washington and British Columbia to the very dry areas in

southern latitudes and east of the Cascade Mountains (Little 1971). In these diverse environments, different selection pressures act upon populations, causing evolutionary adaptations to local conditions (Aitken et al. 2008). The rationale behind assisted migration is to utilize existing populations that are adapted to projected climatic conditions. Uncertainty about risks and unintended consequences that could potentially exceed the benefits of assisted migration are the major concerns preventing such measures from being implemented (e.g., Ricciardi and Simberloff 2009). Provenance trials, where seeds from multiple locations have been planted at sites representing different environments, can serve to make such inferences (e.g., Schmidtling 1994; Carter 1996; Mátyás 1996; Leites et al. 2012). As drought events are likely to become more frequent and severe, the drought tolerance of Douglas-fir populations is relevant for the development of climate change adaptation strategies for this species. Already, it has been recommended to move Douglas-fir planting stock hundreds of kilometers northward in western North America (St. Clair and Howe 2007; Gray and Hamann 2013) and, most recently, this has even been highlighted as an issue for consideration in Europe, where Douglas-fir is an important introduced species (Isaac-Renton et al. 2014).

The seedling stage is often considered to be most sensitive to environmental stress, and the main level at which adaptation through natural selection takes place (Lawrence et al. 1962; St. Clair and Howe 2007). Accordingly, drought tolerance of Douglas-fir has been assessed extensively with experiments where seedlings grown in greenhouses were exposed to artificial drought stress or where vulnerability of the xylem to drought-induced cavitation was assessed (Kavanagh et al. 1999). Seedlings from the coastal variety *menziesii* have been found to be less resistant against drought and more vulnerable to cavitation (Ferrell and Woodard 1966; Pharis and Ferrell 1966; Kavanagh et al. 1999; Valladares et al. 2007). In turn, seedlings from the interior variety *glauca* have been found to be more drought resistant and less vulnerable to failure of the water-conducting system. Within the coastal variety, differences in drought tolerance were found as well: Seedlings from a seed source at the southern end of Oregon were more drought tolerant than seedlings from northern Oregon and Vancouver Island. Even within a single seed source, higher drought tolerance was found on a southern slope than on a northern slope (Ferrell and Woodard 1966).

In mature trees, drought is considered one of the main drivers of mortality and a key contributing factor to secondary damage through insects and diseases (Allen et al. 2010). It is therefore necessary to evaluate if adaptive traits of drought tolerance found in seedlings can also be found in mature trees. The information on the response of mature trees to past environmental conditions is stored in tree-rings and can be revealed using methods of dendrochronology. In France,

Martinez-Meier et al. (2008) found higher survival of Douglas-fir trees with tree-rings of higher wood density. Consequentially, Dalla-Salda et al. (2009) and Dalla-Salda et al. (2011) demonstrated genetic differences and a link between wood density, cavitation resistance, and growth performance of mature Douglas-fir clones under the severe pan-European drought event of 2003. For the same drought year, but in a genetic trial in Germany, Jansen et al. (2012) showed that provenances from the interior were least affected by this drought event. However, seeds of the interior variety consistently show lower productivity when tested against the coastal variety (see Isaac-Renton et al. 2014 for a meta-analysis). This sharp separation is strongly limiting the applicability of seed transfers.

Even under the most pessimistic climate change scenarios, the Pacific Northwest of North America will not experience precipitation levels found in the interior today. Therefore, the environmental variation within the coastal range appears to be more promising for finding a better match (Fig. 1). Ideally, planting stock selected for a projected warmer climate would be drought tolerant and productive. In this study, we selected eight provenances from the coastal distribution of Douglas-fir in one of the oldest reciprocal provenance trials in western North America. The sample represents a wide range of moisture and temperature conditions, and each provenance sample is based on up to 89 parent trees collected throughout an area of approximately 1200 km^2 to characterize a locally adapted population. Our first objective is to assess the relationship between growth and interannual variation in moisture conditions throughout the lifetime of this trial using tree-rings. The second objective is to infer underlying adaptive strategies from metrics of drought resilience and resistance including plastic wood structural response. The third objective is to quantify the trade-off between productivity and drought tolerance of provenances.

Materials and methods

Study site and experimental design

The experimental site is part of the *Pacific Northwest Region Douglas-fir provenance trial* and is located in the Canadian province of British Columbia (Ching and Bever 1960). The site is part of the Malcolm Knapp Research Forest of the University of British Columbia (decimal lat 49.2641°; decimal long −122.5732° at an elevation of approximately 170 m a.s.l). This site is characterized by a maritime climate, with an annual mean precipitation of approximately 2150 mm, of which 480 mm fall between May and September. The mean annual air temperature is 9.5 and 15.8 °C during the growing season (May to September). The soil is a Humo-Ferric Podzol originating from plutonic hornblende granodiorite and quartz
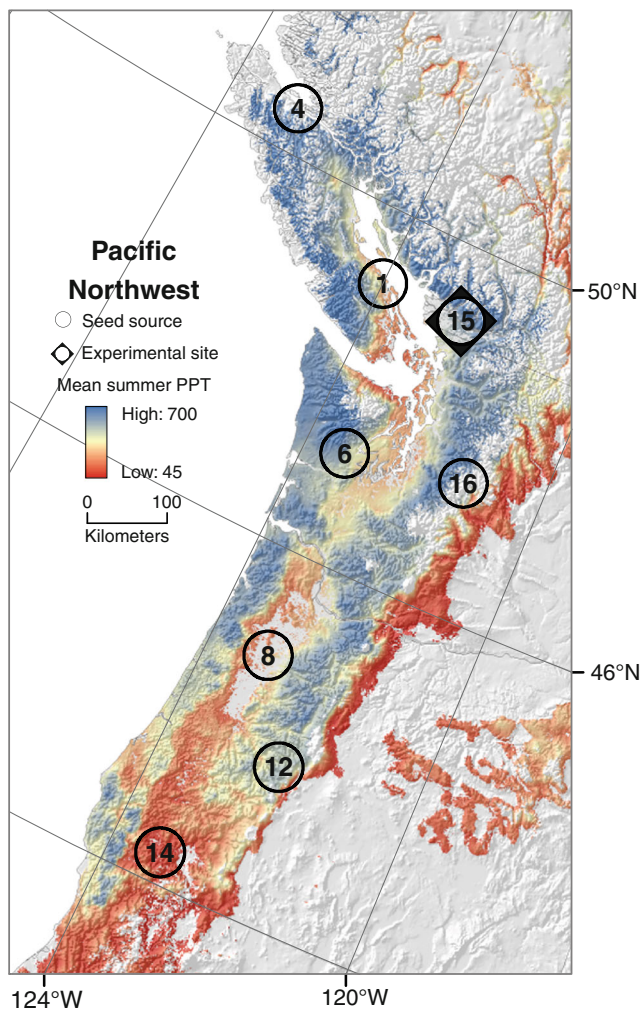
Fig. 1 Geographic locations of provenances and the experimental site in the Pacific Northwest of Canada and the USA. *Black circles* represent seed source locations. The experimental site is indicated by a *black diamond*. Mean summer precipitation is displayed within the outline of the Douglas-fir distribution

experimental site and climate normals for the seed source locations (1961–1990) was obtained with *ClimateWNA* (Hamann et al. 2013). With over 1200 km^2, the seed collection areas for this trial were unusually large (White and Ching 1985). Therefore, climate data extracted for the respective test site locations might not reliably represent the climate niche of the sampled population. Therefore, we extracted climate normals for a 30-km radius around the test site coordinates, which were subsequently averaged (Table 1).

Measurements

Historic height and diameter data of the studied provenance trial was obtained from the *Center of Forest Provenance Data* (*http://cenforgen.forestry.oregonstate.edu/*). In addition, current diameter at breast height and top height were measured in 2012. Top height was assessed using a laser rangefinder (TruPulse 360R, Laser Technology Inc., USA). Based on height and diameter growth until 1982 and 2012, volume per hectare was estimated in accordance to Wykoff et al. (1982) for a hypothetical stem density of 400 per hectare. Depending on the slope, two to four increment cores were extracted from each sample tree. To avoid reaction wood, cores were only taken in directions perpendicular to slope. Cores were labeled with a pencil and stored in plastic straws. At the end of each day in the field, we removed the cores from the straws to allow them to dry, thereby reducing the risk of molding. In our tree-ring laboratory in Freiburg, Germany, cores were glued on fluted multiplex boards. These boards were mounted on glass plates, and the surface was prepared using an ultra-precise, diamond fly cutter (Kugler F500, Kugler GmbH, Salem, Germany). Subsequently, samples were scanned at high resolution, and then tree-ring width and the percentage of latewood were measured using the standard tree-ring software *Windendro* (Regent Instruments Canada Inc. 2012).

Assessment of the relationship between growth and climate

Data analysis and illustration was performed in the *R*-programming environment (R Development Core Team 2013). To remove the dimension-related trend in tree-ring width series, widths were transformed into basal area increments using the *bai.out*-function of the *dplr*-package (Bunn 2008). To explore the relationship between weather at the trial site and secondary growth, we correlated annual growth to yearly climate data. For this analysis, only the years from 1970 to 2011 were used to avoid the impact of various influences on the early growth years following the establishment of the trial. The remaining trend in the basal area increment series was removed using a smoothing spline implemented in the *detrend*-function of the *dplr*-package. The spline was calculated with a 30-year frequency threshold of 50 %. The standardized growth series were subsequently averaged by provenance. To evaluate the reliability of the

diorite. The experiment was established in 1959 at 16 locations throughout the Pacific Northwest using seedlings grown for 2 years in the nursery (Ching 1965). The trial is reciprocal, with each of the 16 seed origins also having an experimental site close by. At each of the sites, the trial was laid out as a complete randomized block design with four replications, allocated to two plantations about 1 km from each other. Each block is about 1.15 ha in area and consists of 16 plots.

In each plot, 121 trees were planted in the spring of 1959 at 2.4×2.4 m spacing. Only the innermost 49 trees were intended for measurements, while the surrounding trees serve as buffer to the surrounding plots. Overall, we sampled 124 trees. Being usually well supplied with precipitation, the experimental site was affected by an unusual drought in the year of 1985. This drought event occurred in the first half of the growing season, which is known to be most important for Douglas-fir growth (Chen et al. 2010). Annual climate data for the

Table 1 Eight provenances characterized by elevation in m (*Elev*), mean annual precipitation in mm (*MAP*), mean summer precipitation (*MSP*), mean driest month precipitation (MDMP), mean annual temperature in degrees Celsius (*MAT*), mean summer temperature (*MST*), mean warmest month temperature (MWMT), annual heat moisture index (*AHM*), mean summer heat moisture index (*SHM*)

Prov.	Elev.	MAP	MSP	MDMP	MAT	MST	MWMT	AHM	SHM
P1	840	2734	177	47	6.5	13.6	15.1	6.3	40.6
P4	150	2786	240	68	8.4	14.9	15.9	6.7	30.6
P6	90	2077	135	32	10.3	16.7	17.6	10.2	59.9
P8	60	1159	72	14	11.2	18.0	19.0	18.4	113.8
P12	580	1410	112	16	11.0	17.5	19.0	15.0	77.6
P14	910	953	51	10	10.1	17.7	19.0	22.1	162.5
P15	180	2313	264	81	9.2	16.2	17.1	8.4	33.6
P16	1120	2263	194	51	5.1	12.8	14.2	7.0	41.8

derived chronologies, we calculated the average mean inter-serial correlation (ISC) and the expressed population signal (EPS) in accordance to Fritts (2001) and Wigley et al. (1984). ISC measures the strength of the common signal in a chronology and is therefore an indicator of its consistency. EPS is a measure of how well the sampled chronology represents a theoretical population with a finite number of trees. In addition, we calculated average first-order autocorrelation (AC), which indicates the influence of the previous year on the current year's growth. Pearson's correlation coefficient was calculated between mean chronologies and climate variables representing precipitation, temperature, and drought indices for winter, spring, summer, and fall.

Assessment of plastic responses to drought

To analyze the impact of the 1985 drought event, we utilize a concept introduced by Lloret et al. (2011), where several indicators serve as a measure of plastic response to drought: *Resistance* is defined as rate of reduction in growth during drought and is calculated by division of growth in the drought year by the growth rate of a pre-drought period. *Recovery* is a measure for the ability of a tree to recover from the disturbance and is calculated by division of the growth rate during drought by the growth rate of the post-drought period. The ability to achieve pre-drought performance is defined as *Resilience* and is therefore calculated as the ratio between post- and pre-drought performance. *Relative Resilience* is defined as resilience weighted by the damage experienced during the disturbance and is calculated by subtracting the value of *Resistance* from the value of *Resilience*. The reference period ideally represents normal growth conditions, without major disturbances (Lloret et al. 2011). Therefore, as a pre-drought reference period, we defined the years from 1980 to 1984. Five years following the disturbance were defined as post-drought period.

Statistical analysis

Because the experiment was laid out as a complete randomized block design, we used ANOVAs to test the significance of differences between provenances in drought tolerance indicators, latewood proportions, height, diameter, and volume. The analysis was done using the *lmer*-function for mixed models from the package *lme4* (Bates et al. 2013) in combination with the package *lmerTest* (Kuznetsova et al. 2013). Provenance was specified as a fixed effect, and block was specified as a random effect. The *glht*-function with a *Bonferroni* adjustment to *p*-values, implemented in the *multicomp*-package, was used to control experiment-wise α-levels in post-hoc tests (Hothorn et al. 2008). The relationships between volume per hectare, height, diameter at breast height and provenance climate were explored using linear and polynomial models with the *lm*-function of the *r-base* package. Similarly, the relationship between volume per hectare and drought response was assessed. Best fit was determined by selecting the model with the lowest Akaike's information criterion. An *F*-test, implemented in the *lm*-function, was used to test for significance of the coefficients of determination. Confidence intervals (95 %) were calculated and illustrated using the *geom_smooth*-function of the *ggplot2*-package (Wickham 2011).

Results

Genetic pre-programming of height, diameter, and volume

Volume per hectare was significantly different between provenances at ages 24 and 54 ($p=0.013$ and $p<0.001$, respectively). This was mainly attributed to differences in height ($p<0.001$ for age 24 and $p<0.001$ for age 54). Diameter at breast height was significantly different at age 24 ($p=0.041$), but not at age 54 ($p=0.17$). The local provenance, *P15*, performed best at ages 24 and 54, while *P14* and *P16* showed low productivity at both

ages. *P12* was an average performer at age 24 but dropped to the lowest rank by age 54. The relationship between general growth (height, diameter at breast height, and volume) and temperature at the seed origin appears to express the second-degree polynomial shape of a response function (Fig. 2, left column). This relationship is most pronounced for mean temperature of the warmest month. Provenances from colder and warmer environments seem to be less productive, which again is mainly attributed to differences in height. Precipitation at the seed origin appears to be linearly related to height, volume, and less strongly, to diameter at breast height (Fig. 2, right column). The rainfall minimum throughout the growing season seems to most strongly determine growth performance. Provenances from dry environments show lower growth.

Moisture conditions over five decades of growth

Deviations of summer precipitation and a summer drought indicator from the normal conditions of 1961 to 1990 are shown in Fig. 3a. Gray bars represent monthly summer

Fig. 2 The relationships between growth variables at age 54 (height, diameter at breast height, and volume per hectare), mean warmest month temperature (°C), and mean driest month (mm) at the seed source location are displayed here. *Error bars* represent the standard error of the mean. Confidence intervals (95 %) of the regression line are indicated as a *gray ribbon*

precipitation, and the thin black bars indicate summer drought conditions. Exceptional water deficits at the site are therefore revealed when the gray bars and the black bars fall significantly below the baseline. An exceptional event first occurred in the growing season of 1960 with no precipitation recorded in July; only 1 year after the seedlings had been planted. This drought was, however, moderated by 140 mm of precipitation in August. In the following years, severe water deficits occurred especially in 1965 and 1967. In 1967, after a wet May, June, and July, precipitation was absent and temperatures were high in August, leading to a high drought index for this year. The year of 1985 represents the most severe early summer drought event in the lifetime of the experiment. Precipitation was 35 % below average in June and culminated in July with a precipitation sum 95 % below normal. The cumulative drought index fell below 70 % of normal conditions. Towards the end of our observation period, less severe drought events occurred in 1998, 2002, 2003, 2006, and 2009. To assess resilience to drought in detail, we concentrate on the drought of 1985 and the growth episodes before and after this event.

Dependence of growth on climatic conditions

The series of basal area increments shown in Fig. 3b indicate a general trend from small increments close to the pith to larger increments formed about 10 years after the seedlings were planted. In the following decades, basal area increments remained stable until the end of our observation period. However, the annual increments followed moisture conditions to some degree. This appears to be especially pronounced in 1985 and, to a lesser extent, in 1993, 2006, and 2009. The provenances in Fig. 3b are colored by decreasing volume growth after 54 years from black to gray. The local seed source (*P15*) shows superior basal area increments from the beginning of the experiment. This pattern is only broken after the drought year of 1985, when a short-lasting rank change occurred with two less productive provenances (*P14* and *P16*).

The inter-serial correlation (ISC) of basal area increment chronologies varies between 0.70 and 0.79, which indicates sufficient reliability for further analysis (Table 2). Likewise, the expressed population signal (EPS) values all exceeded 0.85, which is the threshold of acceptability. The autocorrelation (AC) is also high, indicating carryover effects from the previous years' growth. Climate-growth correlations show that for most provenances, basal area growth at the site was strongly related to precipitation during the summer months of June, July, and August (Table 3). The variation of precipitation of the previous winter, spring, and current-year fall was not correlated with growth increments. This is expressed most strongly for the local provenance, *P15*, which also responded most strongly to the SHM summer drought indicator. The annual drought indicator, annual heat-moisture index (AHM), is not significantly
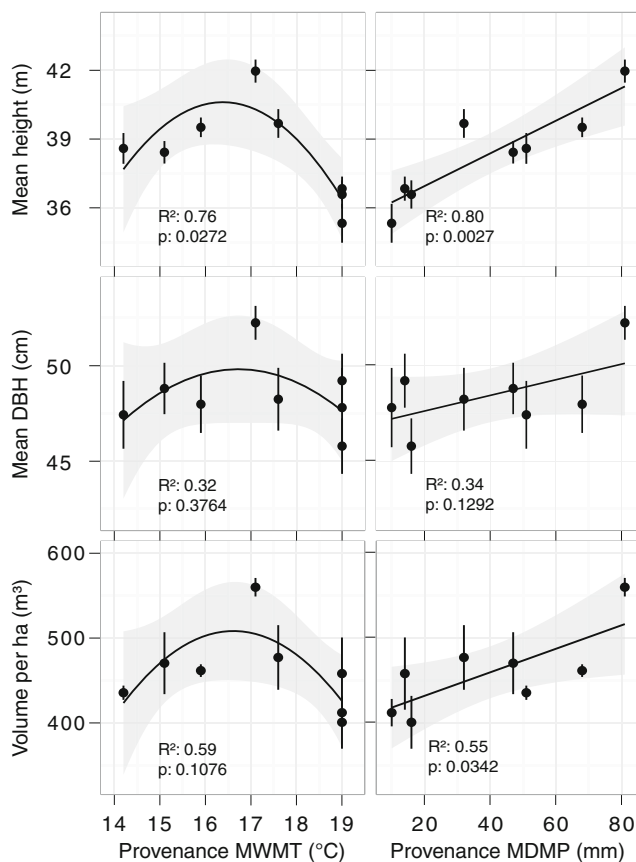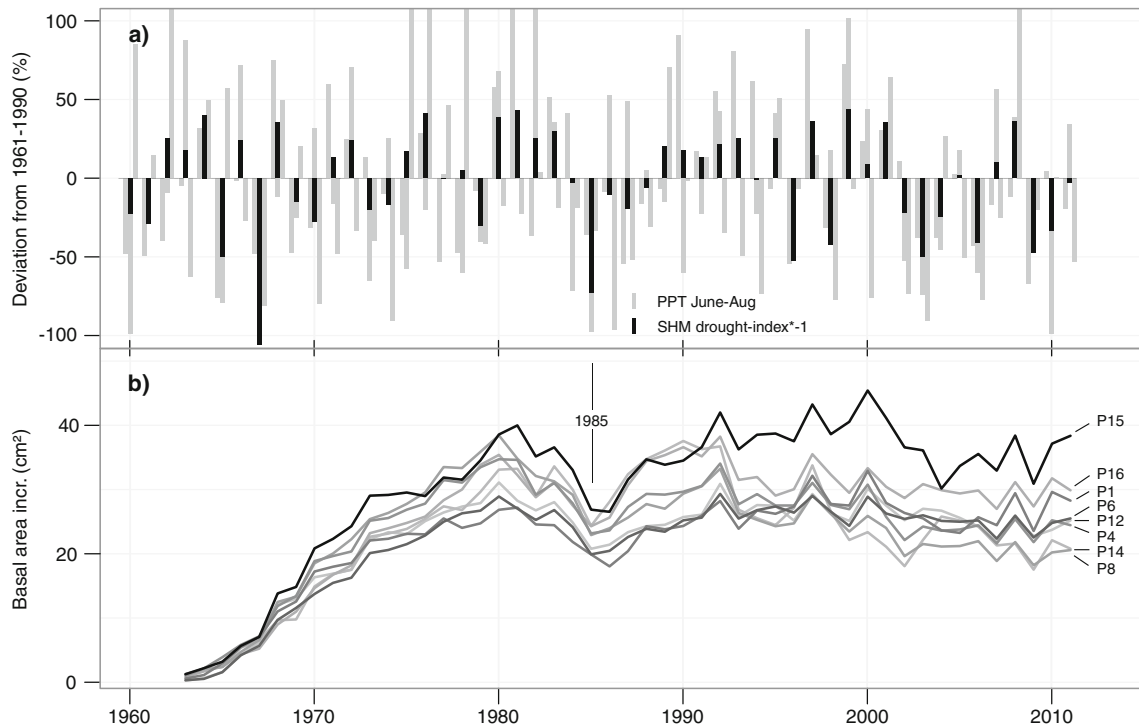
Fig. 3 In the *upper panel* (**a**), *bars* represent deviations of summer (June–August) precipitation over the entire lifetime of the trial, relative to the 1961–1990 climate normal period. Positive values indicate above average moisture conditions, while negative values indicate dry summer months. The deviations of the SHM drought index (relative to the normal of $\overline{x}$1961–1990) are indicated by *thin dark bars*. The SHM index is inversed for convenience. Unusual drought events are indicated by negative deviations. Basal area increments for eight provenances are displayed in the *lower panel* (**b**). The color ramp indicates productivity after 54 years of growth at the test site: *Dark colors* indicate high productivity, *bright colors* indicate low productivity

correlated with growth of any of the provenances, indicating that moisture conditions during the summer are the limiting factor for growth at this test site. The provenances *P14* and *P16*, however, do not show a significant correlation with summer precipitation or summer drought. Instead, growth of these seed sources seems to be related to the length of the growing season, indicated by the positive correlation with spring and fall temperatures.

Resilience and productivity

The drought event of 1985 caused an immediate reduction in basal area growth ranging between 20 and 31 % as compared to the five year pre-drought reference period (Table 4). A provenance from the dry Willamette Valley in Oregon (*P8*) has the strongest reduction, while *P1* from a drier eastern part of Vancouver Island was least affected. While provenances did not differ significantly in the resistance metric ($p=0.113$), statistically significant differences ($\alpha=0.05$) were found for recovery ($p=0.01$), resilience ($p=<0.001$), and relative resilience ($p=0.002$). The southernmost and driest provenance, *P14*, and the high elevation source from the Cascade Mountains, *P16*, exhibited the fastest recovery and highest resilience. The local seed source, *P15*, showed average recovery and resilience. These indicators were especially low for *P8* and *P1*, followed by *P6* and *P4*. Resilience of provenances to this single drought event was found to be strongly related ($R^2=0.74$, $p=0.006$) to the correlation between basal area increments and summer drought (SHM index) in the 42-year period of our climate-growth analysis (Table 3). Within tree-rings, two provenances with fast recovery and high resilience were found to have significantly larger proportions of latewood in the five-year period prior to the drought event ($p=0.02$) and in the year the drought occurred ($p=<0.001$). In the drought year, the proportion of latewood was reduced across all provenances, but most pronounced for the productive provenances (Table 5). In

Table 2 This table shows the number of sample trees (*N* trees) and dendrochronological statistics for each provenance: Inter-serial correlation (*ISC*), expressed population signal (*EPS*) and average autocorrelation (*AC*)

Prov.	*N* trees	ISC	EPS	AC
P1	16	0.78	0.93	0.63
P4	16	0.79	0.95	0.71
P6	16	0.75	0.91	0.72
P8	14	0.79	0.93	0.72
P12	16	0.76	0.92	0.69
P14	15	0.70	0.92	0.72
P15	16	0.76	0.95	0.67
P16	15	0.74	0.92	0.77

Table 3 The correlation coefficients show the relationship between detrended basal area increment series for eight provenances and seasonal climate variables at the test site

		Provenances ordered by productivity at age 54							
Variables		P15	P6	P1	P4	P8	P16	P14	P12
Temperature	Winter	0.14	0.17	0.09	0.17	0.15	0.15	0.14	0.23
	Spring	0.07	0.16	−0.01	0.24	0.22	0.36*	0.42**	0.18
	Summer	−0.32*	−0.11	−0.24	−0.12	−0.09	0.00	0.07	−0.13
	Fall	0.32*	0.33*	0.23	0.37*	0.31	0.45**	0.32*	0.29
Precipitation	Winter	0.14	0.08	0.07	−0.01	0.09	0.03	0.1	0.03
	Spring	−0.06	−0.11	−0.08	−0.14	−0.09	−0.11	0	−0.16
	Summer	0.52**	0.38*	0.45**	0.37*	0.45**	0.25	0.17	0.36*
	Fall	0.04	0.03	0.03	0.05	0.04	0.05	0.09	0.02
Drought	AHM	−0.11	−0.03	−0.08	−0.09	−0.02	−0.1	−0.18	−0.02
	SHM	−0.51**	−0.40**	−0.42**	−0.37*	−0.42**	−0.26	−0.21	−0.37*

Monthly temperature and precipitation data was averaged for winter (Dec.–Feb.), spring (Mar.–May), summer (Jun.–Aug.), and fall (Sep.–Nov.). Drought is indicated by an annual (*AHM*) and summer heat moisture index (*SHM*). Provenances are ordered by descending productivity from left to right

Significance codes *$p<0.05$; **$p<0.01$

the recovery period from 1986 to 1990, differences between provenances disappeared ($p=0.052$), while the latewood proportion generally increased.

In Fig. 4, resilience to the 1985 drought event is plotted against volume per hectare at age 24. It appears that resilience is strongly dependent on productivity: Provenances *P14* and *P16* were the least productive before the drought event and also had the highest resilience to drought. The variation within the remaining provenances is low, with similar productivity and resilience at that point in time. In Fig. 5, volume per hectare at age 54 is plotted against the correlation between summer precipitation and basal area increments. After more than five decades, the local seed source *P15* emerged as the most productive provenance, and it also shows the strongest relationship between growth and summer precipitation. In turn, the least productive provenances, *P14*, *P16*, and *P12*, appear to be less dependent on mean summer precipitation.

Discussion

Plasticity correlates with productivity

Growth performance of provenances across temperature gradients has been found to be lowest at the edges of the distribution, forming a polynomial response function (Rehfeldt et al. 1999; Wang et al. 2006). The relationships found in this study indicate that provenances from sites with more extreme temperatures, as well as provenances from environments with dry summers, perform below average. The highly plastic interannual response of the productive provenances compared to the less variable growth of the less productive provenances point to different adaptive strategies within the coastal population. Low precipitation during the summer appears to be a key limiting factor for highly productive provenances. However, these provenances are also able to transform favorable moisture conditions into growth. In environments without frequent severe drought events, competition for light

Table 4 Indicator values for resistance, recovery, resilience, and relative resilience for eight provenances ordered from high to low productivity

	P15	P6	P1	P4	P8	P16	P14	P12
Resistance	0.73 a	0.75 a	0.80 a	0.74 a	0.69 a	0.78 a	0.77 a	0.74 a
	(0.03)	(0.04)	(0.03)	(0.02)	(0.01)	(0.02)	(0.05)	(0.04)
Recovery	1.23 abc	1.2 ab	1.13 a	1.22 abc	1.18 ab	1.35 bc	1.42 c	1.17 ab
	(0.10)	(0.10)	(0.09)	(0.07)	(0.07)	(0.04)	(0.10)	(0.07)
Resilience	0.90 a	0.90 a	0.89 a	0.90 a	0.82 a	1.05 b	1.07 b	0.87 a
	(0.07)	(0.07)	(0.05)	(0.05)	(0.06)	(0.04)	(0.05)	(0.05)
Relative resilience	0.16 ab	0.15 a	0.09 a	0.16 a	0.12 a	0.27 bc	0.31 c	0.12 a
	(0.07)	(0.07)	(0.06)	(0.05)	(0.05)	(0.03)	(0.06)	(0.05)

Standard error of the mean is provided in parentheses. Different letters behind the values indicate significant differences between provenances ($\alpha=0.05$)

Table 5 Latewood-proportions of tree-rings prior to the drought event (mean of 1980–1984), the drought event itself (1985) and after the drought year (mean of 1986–1990) for eight provenances ordered by decreasing productivity from left to right

Latewood proportion

Variable	P15	P6	P1	P4	P8	P16	P14	P12
Pre drought	33.6 a	37.8 ab	37.7 ab	38.4 ab	39.1 ab	40.0 b	40.1 b	39.1 ab
	(1.06)	(1.49)	(1.6)	(1.59)	(1.06)	(1.21)	(1.23)	(1.44)
Drought year	27.2 b	31.8 ab	36.2 abc	33.5 abc	32.9 abc	37.4 ac	38.8 c	32.2 ab
	(0.99)	(1.72)	(1.83)	(1.46)	(1.10)	(1.10)	(1.22)	(1.98)
Post drought	36.9 a	41.2 ab	39.7 ab	40.1 ab	42.3 b	41.6 ab	40.6 ab	40.4 ab
	(0.99)	(1.51)	(1.30)	(1.46)	(0.80)	(1.09)	(0.98)	(1.25)

The standard error of the mean is displayed in parentheses. Different letters behind the values are indicating significant differences between provenances ($\alpha = 0.05$)

might be under stronger selection pressure than competition for water (Hartmann 2011). Natural selection might have favored traits contributing to faster growth and therefore an advantage in competition for light. In contrast, the less productive provenances can benefit from precipitation only to a limited extent. In dry environments, natural selection might favor investments into safety mechanisms such as cavitation-resistant water-conducting systems (Hacke and Sperry 2001) or drought avoidance by early bud break and bud set (St. Clair et al. 2005). Under drought conditions, productive provenances might fail to regulate stomata accordingly and suffer from cavitation in the efficient but vulnerable water-conducting system (Bréda et al. 2006). This could also explain

the delayed recovery observed in this study, as the sustained damage has to be overcome first.

Although the less productive provenances are rather independent of moisture conditions during the summer and therefore appear to be a safer alternative for a drier future, they are limited in other metrics: temperature in spring and fall appear to be especially limiting factors based on their high correlations with growth. Specifically, low temperatures during the beginning and end of the growing season limit growth of these provenances. Similarly, investments into safety mechanisms could contribute to growth limitations of the drought-resilient provenances. Denser wood has been found to be more resistant against drought-induced cavitation (Hacke et al. 2001). A higher proportion of latewood is closely correlated with higher
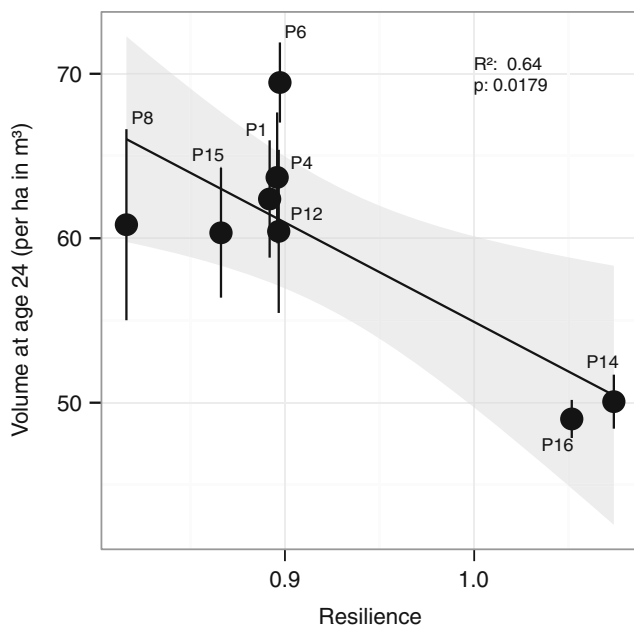

Fig. 4 Relationship between volume per hectare in 1982 (age 24) and resilience to the drought of 1985. *Error bars* represent the standard error of the mean. Confidence intervals (95 %) of the linear regression line are indicated as a *gray ribbon*
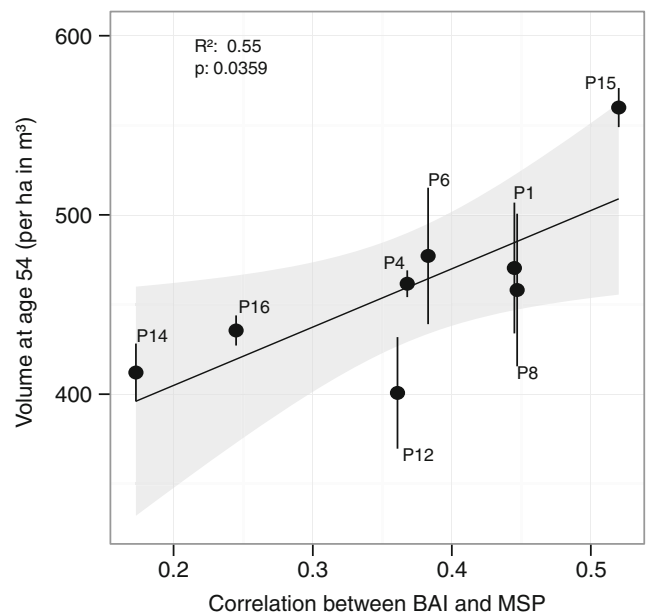

Fig. 5 Volume per hectare plotted against the correlation between basal area increments and mean summer precipitation (MSP) at the test site. Low values indicate a weak relationship and high values a strong relationship. *Error bars* represent the standard error of the mean. Confidence intervals (95 %) of the linear regression line are indicated as a *gray ribbon*

wood density (Lachenbruch et al. 2010). Therefore, wood density can serve as an indicator for drought tolerance in tree breeding programs for a drier future, as noted by Dalla-Salda et al. (2009, 2011). Earlywood, on the other hand, accounts for the major part of water conductivity in tree-rings (Domec 2002). Thus, the higher the proportion of latewood, the lower the probability of hydraulic failure of the water transport system. As the latewood proportion was related to drought resilience in this experiment, our results indicate that drought tolerance in coastal Douglas-fir is at least to some degree related to a trade-off between safety and efficiency of the hydraulic pipeline. The increased production of latewood in the recovery period indicates a mechanism of acclimation to drought. The reduction of latewood proportions in the drought year appears to be contrary to such a mechanism. However, drought can force trees to shut down growth for the season (Nilsson and Wiklund 1992), resulting in reduced latewood production.

Moving provenances to enhance resilience of Douglas-fir forests

Our results indicate that mature Douglas-fir provenances from sources throughout the coastal range differ in resilience to drought events. These seed sources could be used to improve resilience of Douglas-fir in areas where drought conditions are expected to become more prominent. Our results also indicate, however, that drought resilience is related to significantly lower growth performance. This confirms Eilmann et al. (2013) who assessed drought resistance of mature Douglas-fir provenances in the Netherlands. They found more southern provenances to be more drought resistant but less productive at the same time. In our study, this relationship becomes especially evident when comparing the low performing, drought-tolerant provenances P14 and P16 to the thriving local population P15. The productivity of provenance P14, for instance, is 28 % lower than the the productivity of the local seed source P15. On the surface, then, the P14 and P16 seed sources would not appear to be suitable candidates for planting despite their higher level of drought resilience. The forest management implications of these results are, however, more complex. The long rotations of coastal Douglas-fir imply that seed stock chosen today based on present data may become suboptimal as climates change. For example, severe drought events may increase in frequency due to decreased summer precipitation and increased evapotranspiration: what was once a historic once-in-a-century drought could occur every decade (Christidis et al. 2014). Such a change in frequency would likely reduce the productivity of historically productive provenances (P15) and instead favor the safety-oriented provenances (P14, P16). In addition, the provenances P14 and P16 are expected to increase productivity under a warming climate since their growth is positively correlated with spring and fall temperatures (Table 3).

We found comparatively drought-tolerant provenances from throughout the range of coastal Douglas-fir, including some unexpected results. For example, the performance of provenance P8 was counter-intuitive: Coming from the summer-dry Willamette Valley in Oregon, we expected that this provenance would show an adaptation to drought that would lead to above average performance in the drought event of 1985. This expected result could not be found. However, the low resilience of P8 is in fact consistent with the general relationship between growth and drought resilience found in this trial, as P8 was among the top performers prior to the drought event. It also confirms Ferrell and Woodard (1966) who found low drought tolerance in seedlings from this area. Similarly, the scaling of resilience and productivity can also be observed for P12. In eastern Washington, we found a provenance (P16) that showed superior resilience to drought, which appears to be unexpected based on the rather cold and wet climate at the seed origin. Similar results were also observed in a set of 35 Douglas-fir provenances from Washington, Oregon, and California by Bansal et al. (2014), who found that genotypes from cooler environments were more drought resistant. Prevention of hydraulic failure in the xylem pipeline induced by frost-thaw events requires structural adaptations of the xylem pipeline similar to those required for the prevention of embolisms caused by drought (Hacke and Sperry 2001; Mayr et al. 2006; Schreiber et al. 2011, 2013). This could be a possible explanation for the high drought tolerance of provenances from cold origins. Therefore, the influence of source climate on drought resilience appears to be more complex, and it may be misleading to rely on broad geographic location alone when selecting drought-tolerant planting material.

The results presented here are limited to conditions represented by the study site and stand. The experimental site was chosen to represent typical environmental conditions of Douglas-fir forests in coastal British Columbia and Washington. Therefore, one should be careful when extrapolating these results to sites with different environmental conditions. Local populations may be adapted to additional factors other than climate, such as soils, mycorrhiza, photoperiod, or the pressures of pests and pathogens. When transferring drought-adapted planting stock, maladaptation to these additional factors can potentially counteract the benefits (Aitken and Whitlock 2013). However, there is strong indication that current Douglas-fir forests in the Pacific Northwest are already maladapted (St. Clair and Howe 2007) and that more frequent droughts on water-limited sites could compromise growth performance in the future (Chen et al. 2010). However, given the significant reduction in productivity associated with drought resilience, land managers should carefully assess local site and climatic conditions and target water-limited planting sites with drought-resilient seed sources. On sites with sufficient water availability, selecting more drought-tolerant genotypes to address future climate change may be

counterproductive (Chen et al. 2010). At which point *P14* and *P16* become more productive to plant than the local seed source will depend on the magnitude of climate change: whether the long-term increases through an extended growing season can counterbalance the substantial short-term reduction in volume growth is uncertain. In our study, the local provenance *P15* did not show sustained reductions in growth following drought and remained a top performer under a wide range of interannual variation in climate conditions. Therefore, local planting material should not be ruled out as a viable choice within a larger strategy to address climate change.

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