1 Title

2 Douglas-fir climate sensitivity at two contrasting sites along the southern limit of the European

- 3 planting range
- 4

5 Author

- 6 Cristiano Castaldi¹, Maurizio Marchi^{1*}, Giorgio Vacchiano², Piermaria Corona¹
- 7 ¹CREA Research Centre for Forestry and Wood, Viale S. Margherita 80, 52100 Arezzo, Italy
- 8 ²Università degli Studi di Milano, DISAA. Via Celoria 2, 20133 Milano, Italy

9

10 Corresponding author

- 11 Maurizio Marchi, +393498387082 maurizio.marchi85@gmail.com
- 12

13 Abstract

Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) is an interesting exotic tree species planted 14 across a large part of Europe during the last century. In both experimental trials and conventional 15 16 forest plantations, the species has demonstrated high growth rate and valuable timber quality, with high phenotypic plasticity. This study aimed to investigate climate-growth relationships of Douglas-17 fir inat two Italian sites with a contrasting climate regime. A Mediterranean area in Southern Italy 18 19 (Mercurella site) and a cooler and moister one in the Northern Apennines without summer aridity (Acquerino) were selected as study sites. The relationship between tree-ring chronologies and 20 monthly climatic variables was investigated by mean and moving correlation analysis. The 21 minimumLate winter temperatures of (February and March) play a key role for Douglas fir at both 22 sites, with a positive effect on growth. At the northern site, Douglas fir experiences also a high 23 sensitivity to late summer temperatures (negative correlation) and spring-summer precipitation 24 (positive correlation). On the whole, the species demonstrates high growth rates at southern 25 26 latitudes even in Europe and in- Mediterranean environment, with low sensitivity to climatic Page 1 out of 27

- 27 fluctuation. However, further common garden experiments should be planned in order to test
- 28 adaptation and the interaction between genetic and environment of the second or third generation

29 seeds from old stands across the whole Europe.

30

31 Keywords

32 Pseudotsuga menziesii; tree ring analysis; dendroclimatology; forest plantations; exotic forest

33 species

Page 2 out of 27

34 Introduction

Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) is one of the most promising exotic tree species 35 in Europe, first introduced from North America more than 150 years ago (Isaac-Renton et al., 2014; 36 Schmid et al., 2014) and currently distributed in almost all European countries for high-quality 37 38 timber production (Hermann and Lavender, 1999). During the first years of its experimentation, every European country was used to work separately by collecting seed from the native range 39 independently, mainly according to local climate and experts knowledge. Afterwards, during the 40 second half of XX century, the adaptive traits of 180 provenances of Douglas fir were tested within 41 the IUFRO (International Union of Forest Research Organizations) 1969-70 experimental network 42 (Eilmann et al., 2013), which still represents one of the more extensive and standardized 43 experimental trials in Europe for Douglas fir. The "pure seed" collected from almost the whole 44 native range was there also compared with some "second-generation provenances" (i.e., from 45 plantations in the European introduction range that had already reached reproductive age) were 46 tested, showing high productivity, sometimes even higher than the American seeds (Ducci and 47 Tocci, 1987). However, direct comparisons of the growth response of such introduced provenances 48 to contrasting climates have not been carried out so far. Nevertheless, provenance trials 49 demonstrated that, under favourable climatic conditions, Douglas-fir grows faster than native 50 conifers, e.g. Scots pine (Pinus sylvestris L.) or European larch (Larix decidua Miller) in forest 51 stands (Eilmann and Rigling, 2012). The high degree of genetic variability and plasticity that 52 Douglas fir exhibits and due to its huge natural range, has allowed European countries to 53 successfully test its use, from Mediterranean to continental Europe (Brus et al., 2012; Eilmann et 54 al., 2013; Howe et al., 2010). Very recently, Hintsteiner et al. (2018) also showed that the detection 55 of the correct provenance of old Douglas fir stands in Europe could be very difficult. In this sense, a 56 connection between performances in native and introduced zones is generally hard. 57

A variety of empirical and experimental approaches has been exploited to assess plant response to
 climate variability and climate change over large geographic areas (Bréda et al., 2006; Chen et al.,

60 2010). Examples are provenance trials or common gardens (Lipow et al., 2003; Rehfeldt et al., 2014), empirical analyses of growth and mortality by permanent forest inventory plots (Marchi, 61 2019; Poschenrieder et al., 2018; Stephenson et al., 2014), remote sensing and detection of net 62 primary productivity (Fassnacht et al., 2014; Smith et al., 2008) as well as dendrochronological 63 analysis of growth-climate correlations from tree ring time series (Avanzi et al., 2019; Eilmann and 64 Rigling, 2012; Mazza et al., 2018). The latter type of data might improve knowledge on species 65 requirements to adjust predictions of growth simulators even on Douglas fir trees outside its native 66 67 range (Castaldi et al., 2017) and evaluatepredict the trees' response to long-term climate variations. In particular, dendrochronological climate-growth response models may help to evaluate the trees' 68 response to past climate variations and to forecast future ecosystem responses to climate change, 69 especially when analysing the same species under different climatic conditions (Corona, 2016; 70 71 Härdtle et al., 2014). If a species shows local growth acclimation, i.e. it responds differently when grown under different climates (Case and Peterson, 2005), provenances with a higher tolerance of 72 warm and dry conditions may play an important role in climate change adaptation, as they would 73 probably acclimate well when translocated to northern latitudes or higher elevations that are about 74 75 to experience a warming climate trend (Hampe and Petit, 2005). Actually knowledge of available genotypes as well as information on the genetic structure of forest tree systems and populations is 76 fundamental to cope with a changing climate, understanding long-term adaptation processes and 77 78 balancing statistical models properly (Benito Garzón et al., 2019; Piotti et al., 2017). In its native range, Douglas fir's growth is positively affected by precipitation, especially between 79 80 May and September, often referred as its-in-the "growing season" (Case and Peterson, 2005) and negatively by winter cold spells and snowpack depth (Littell et al., 2008). Sensitivity to growing 81 82 season temperatures generally shifts from negative to positive with increasing elevation. However, even at the northernmost/highest sites, precipitation limits Douglas-fir radial growth more than 83 84 temperatures (Griesbauer and Green, 2010), and sThen summer drought is the main limiting factor 85 for both coastal (i.e. *viridis*) and interior (i.e. glauca) varieties also in Europe (Vejpustková and

Formattato: Tipo di carattere: Times New Roman, Corsivo

Formattato: Tipo di carattere: Times New Roman, Corsivo

Page 4 out of 27

86 Čihák, 2019) but highly vulnerable to eExceptional and recurrent drought often stress the species more than native ones species (Thurm et al., 2016), especially on less fertile soils (Sergent et al., 87 88 2014). However, particularly when in association with beech and Norway spruce, growth of Douglas fir iIn Europe, may be also promoted by warm winters, due to the fact that thanks to active 89 photosynthesis may be active even in winter months (Chen et al., 2010), possibly combined with 90 the benefit of additional water supply after snowmelt. This issue has been detected in association 91 with beech and Norway spruce (Schmid et al., 2014). As a consequence, when compared to native 92 European tree species, Douglas fir has high potential to cope with warmer climates, and can 93 outcome them in virtue of a higher resistance and faster recovery from drought. 94

95 The aim of this paper is to analyse the strength and spatio-temporal stability of the relationship 96 between radial growth of Douglas fir and main climatic drivers under Mediterranean environment. 97 The growth-climate response of Douglas fir at two plantations sites in Italy with contrasting climate 98 regimes is here analysed and discussed.

99

100 Materials and methods

101 Study sites

Italy is one of the countries were Douglas fir was extensively tested by both IUFRO programs and 102 national experimentation since 1922 (Castaldi et al., 2017). The two study sites here selected 103 (Figure 1) were Acquerino in the northern Apennines (44°0'38.97" N, 11°0'25.47" E) and 104 Mercurella in the southern Apennines (39°20'11.55" N, 16°4'49.42" E). Both sites are characterized 105 by pure artificial plantations of Douglas fir established around 1940s, with similar elevation (900 106 107 and 835 m a.s.l., respectively). Just few information were available on the genotype of planting 108 materials. According to literature and information available in the archives, both stands were established by 3-year-old seedlings form the nursery of Vallombrosa with "Italian" seeds collected 109 form mature trees with unknown origin (probably form Washington, Oregon or California) around 110 1930 (Avolio and Bernardini, 2000). 111

Page 5 out of 27

112 The two sites are characterized by mild climate with average mean summer-temperatures in Summer (June-July-August) around 20°C which is close to the temperature known to be the 113 ecological optimum for Douglas fir growth (Wang et al., 2012). On the other hand, the two sites 114 display different climatic regimes, mainly due to a different latitude and distance from the 115 116 Mediterranean sea. The southernmost site (Mercurella) has a warmer and drier climate (warmtemperate, Cs zone according to Köppen-Geiger classification), with a mean annual temperature of 117 13.1°C and annual precipitation of 936 mm. The northern site (Acquerino) is cooler (mean annual 118 119 temperature = 9.8 °C) and wetter (mean annual precipitation = 1437 mm). According to Metzger et al. (2013) Acquerino and Mercurella sites fall within the J (cool temperate and moist) and K (warm 120 temperate and mesic) bioclimatic belts, respectively. These two sites do not represent the full range 121 of climatic conditions throughout the native range of Douglas-fir in the Pacific Northwest of the 122 123 United States. However, the northern site has a substantially longer humid period during winter and spring, while the southern site is subject to a three-month summer aridity. In our hypothesis, such 124 differences should be sufficient to highlight differences in local acclimation (Aitken et al., 2008). 125



126

127



Page 6 out of 27

distribution of Douglas fir in Europe (Brus et al. 2012). The red line is mean temperature and blue
line is precipitation. Blue area: wet period; red dotted area: dry period.

131

According to the soil database of Italy (Costantini et al., 2014), the area of Acquerino is mainly 132 characterized by Cambisols (Dystric and Calcaric) while Mercurella by Haplic Umbrisols. No 133 significant disturbance has been documented to affect either the sites since planting (e.g., 134 windthrow or pests). The two analysed sites have also similar tree density (Table 1); this suggested 135 136 also a similar silvicultural history i.e. no thinning was recorded in the last decades in either the sites. However, the effect of diverging site fertility was evident, with a top height of 43.5 m at Acquerino 137 138 and 36.9 m at Mercurella. Top height was also used as a proxy of soil nutrient condition given the unavailability of soil samples. 139

140

141 Table 1. Stand characteristics at the two investigated sites.

	Acquerino	Mercurella
Elevation (m)	900	835
Distance from the sea (km)	63.8	3.4
Trees (ha ⁻¹)	247	294
Basal area (m ² ha ⁻¹)	111.8	90.4
Mean DBH (cm)	75.9	62.5
Stand top height (m)	43.5	36.9

142

143 Sampling method and tree-ring series preparation

In order to derive comparable data, the sampling size was differently designed according to sites' characteristics. Indeed, while Mercurella is a pure experimental forest plot approximately 1 hectare wide, the Acquerino plantation covers about 30 hectares. For this reason the same number of dominant trees (20) was sampled within each site. Firstly 20 points were randomly thrown across each site. Then the dominant Douglas-fir tree nearest to each point was cored twice on the crossslope sides at 130 cm stem height with an angle of 90° between samples. Cores were fixed on a wooden support to be transported in the lab, prepared and measured with 0.01 mm precision using

Page 7 out of 27

LINTAB6[®]. Tree ring series were cross-dated using TSAP-WIN software and an average single ring-width series was obtained for each sampled tree. Finally a site mean chronology was obtained averaging all the single-tree series. Each cored tree was also measured for diameter at breast height (DBH) and total height.

Each cross-dated series was standardized separately by a double detrending procedure to isolate the 155 156 climatic signal: a negative exponential curve was first applied to remove age trends, then a spline function (50% cut-off and 10 years) was fitted to emphasize higher frequency inter-annual climatic 157 158 variance (Biondi and Qeadan, 2008; Mazza et al., 2018; Yamaguchi et al., 1991). Autoregressive modelling was performed on each detrended ring-width series to check for the existence of 159 160 significant (p<0.05) first-order temporal autocorrelation. Residual series were finally averaged using a bi-weight robust mean to obtain residual site chronologies, upon which all subsequent 161 162 analyses were based. The quality of the sampling procedure was checked by analysing the expressed population signal (EPS), a measure of how well the mean chronology represents the 163 sampled population. 164

165

166 Climate-growth relationships analysis

As meteorological stations nearest to the study sites did not provide continuous and consistent data, 167 monthly precipitation and temperatures (maximum and minimum) from 1901 to current time were 168 169 obtained from the Climate Explorer (http://climexp.knmi.nl) portal (Trouet and Van Oldenborgh, 2013) for the 1x1° cell where each site was located. The three-month Standardized Precipitation and 170 171 Evaporation Index (SPEI) was also calculated for each site, using the SPEI package (Maca and Pech, 2016) for the R statistical language. As minimum and maximum monthly temperatures were 172 highly correlated in both sites (Pearson's r = 0.982 and 0.993, respectively in Acquerino and 173 Mercurella), only the latter was used in subsequent analyses. 174

The influence of climate on tree-ring growth was investigated using mean correlation functions(CF) and moving correlation functions (MCF). While the first method is used to evaluate the most Page 8 out of 27

177 influential climatic drivers during the whole life-span of the trees, the second is computed on a moving window with a smaller width to assess the change in growth response through time (Biondi 178 and Waikul, 2004; Marchi et al., 2015) (Biondi and Waikul, 2004; Marchi et al., 2015). We used a 179 30-year moving window, which satisfied the conditions whereby sample size is less than 80% of all 180 181 available years and more than twice the number of predictors (Biondi and Waikul, 2004). Maximum 182 temperature, total precipitation and SPEI were computed at a monthly resolution from May of the previous year (t-1) to September of the year of growth (t), so as to include the autumn and winter 183 184 before ring formation. Significant Pearson's correlations between residual site chronologies and climate variables were detected using the 95th percentile range method without bootstrap 185 186 resampling. The R packages dplR (Bunn et al., 2017) and treeclim (Zang and Biondi, 2015) were used for tree ring series management and analysis. 187

188

189 Results

The individuals selected at the two sites were on average 68 and 70 years old, with 78 and 76 years which were counted for the two oldest individuals respectively. The average diameter of cored trees was 69 and 73 cm, respectively. Mean sensitivity was 0.125 at both sites with a mean ring width between 4 and 5 mm.yr⁻¹ (Table 2). Of all individual raw tree-ring series (Figure 2), 60% at Acquerino and 85% at Mercurella could be fitted by a negative exponential curve; for the others, a linear decreasing or horizontal fit was used in the first detrending.

196

197 Table 2. Statistical parameters of mean tree-ring width chronologies for the two investigated sites.

	Acquerino	Mercurella
Mean DBH, cored trees (cm)	69.4 ±5.1	73.1 ±4.7
Length of site chronology (years)	78	76
Mean sampling depth (number of cores)	14.9 ±4.5	16.3 ±2.2
Mean sensitivity	0.121 ±0.03	0.127 ± 0.04
Mean ring width (mm)	4.969 ±1.66	4.031 ±1.83
Expressed population signal (EPS)	0.926	0.918
Mean interseries correlation (RBAR)	0.418 ±0.11	0.365±0.12

Page 9 out of 27

	Signal-to-noise ratio	12.452	10.544
	First-order autocorrelation after indexing (chrono)	-0.144	0.179
198			

As evidenced by Figure 2, a negative pointer year was clearly evident for the Mercurella site in 1981-1982. A negative pointer year is defined as an extremely narrow tree ring width (TRW) with growth reduction exceeding 40% compared with the average TRW in the previous four years. Moreover, we have a very big ring in 1980 followed by two very small ring width in 1981 and 1982. This was connected to exceptional long growing season in 1980 and a heavy frost event in autumn. This event seriously damaged trees' needles and two years occurred for the species to regenerate the crown.

Page 10 out of 27



207 Figure 2. Raw individual chronologies at Acquerino (above) and Mercurella (below).

208

Over the analysed time period the residual ring-width site chronologies (Figure 3) had a mean interseries correlation (RBAR) of 0.42 and 0.36, negligible first-order autocorrelation, and an EPS much higher than 0.85, value generally accepted as minimum threshold to detect valid climatic correlations and indicating a common macro-environmental influence on growth (Wigley et al., 1984).

214

Page 11 out of 27



Figure 3. Residual site chronologies at Acquerino (above) and Mercurella (below) – biweighted
mean of individual series after detrending individual series with a negative exponential (or linear)
and a 10-year spline smoother.

219

Both sites exhibited a significant climatic trend during the second half of the last century (p of the regression slope <0.05) as a drying trend at the northern site of Acquerino, and a warming trend at Mercurella (Figure 4). Many significant correlations between growth and climate variables were found by CF (Figure 5). At Acquerino, maximum temperature was significant in July of the year prior to growth, February (positive correlation) and during the mid- and late summer of the growth year (July, August, September - negative correlation). Precipitation showed a negative correlation with growth in October and November of the previous year (t-1), and positive in May and July of

Page 12 out of 27

the current year. Summer SPEI (July-October) had a positive effect on growth with a lag of one year, and a negative effect (July) of growth of the current year. Less months were detected as significant at Mercurella. Ring width showed a significantly negative correlation with maximum temperatures in October (t-1) and July. Positive correlation arose only with temperatures in the winter of the year of growth t (February and March). Precipitation showed only significantly negative correlation with growth in December (t-1), while a negative effect on growth was detected for SPEI on June (t-1).

234









241 correlations, p < 0.05, are marked by black bars)

The MCF analysis highlighted several periods with significant correlation between ring width and climate, but not all the correlations were stable over time. At Acquerino, spring and summer

Page 15 out of 27

245 temperatures were rarely significant, but February and also March as long as the period 1958-1988 were highlighted as stable positive correlation. The average maximum September temperatures of 246 September became relevant in the last decades for growth of the current year, and in the period 247 1955-1991 for growth of the following year. This could be seen as a possible a prolonging of 248 vegetative season. In the first part of study period, maximum temperature of the previous May also 249 had a positive influence on tree ring width (Figure 6). Correlations with water availability were also 250 unstable, with a positive influence of previous year precipitation shifting from September to June, 251 and of current year from July to May. Summer drought (measured by SPEI) had generally a 252 negative effect on growth, but this was significant only in recent years. On the contrary, a 253 significantly positive effect of water availability in previous summer was detected for the first part 254 of the study period. At Mercurella, MCF evidenced similar relationships with growth, i.e., a stable 255 256 positive influence of February/March maximum temperature, a negative influence of December (t-1) precipitation and positive influence of September (t-1) precipitations, and a generally positive 257 effect of water availability (positive SPEI) in the year before growth. An additional relevant effect 258 was the negative influence of July maximum temperature on current year growth, which has been 259 260 significant since 1960. Possible impacts on growth trends might also be addressed to water supply as reserve in soil; the two stands are growing on different soil types: While Cambisols characterize 261 Acquerino, Haplich Umbrisols (more humid) characterise Mercurella. 262

263

Page 16 out of 27



265 Figure 6. Moving correlation functions (MCF) between ring width and climatic variables
266 (significant correlations, p<0.05, are marked by stars)

267

268 Discussion

The Mediterranean basin represents the southern edge of Douglas fir's introduction range in Europe and here, under both a Mediterranean <u>(Mercurella)</u> and <u>a more a less drycontinental-like</u> climate (Acquerino), late winter (February and March) is recognised as a key season for Douglas fir growth.

Page 17 out of 27

272 On the basis of the obtained empirical evidence our findings may confirmexplain the successful introduction of such valuable exotic forest tree species even at the southern limits of Europe. As 273 overall, the low sensitivity of the species we calculated with our sampling was almost the half of the 274 value generally found for Abies alba Mill. or Fagus sylvatica L. in Italy (Mazza et al., 2014; Rita et 275 276 al., 2014)-which represents the Italian native tree species generally growing in similar climatic conditions to those our stands were located. This aspect might suggest a low interaction between 277 278 climate and tree species, i.e. growth trends are often uncorrelated with the climate. The positive correlation between growth and February-March temperatures, which has been detected also by 279 other studies in Europe (e.g. Thurm et al., 2016), highlights that some cambial activity is possible 280 even in winter, an important adaptive trait of many conifer species (Gričar et al., 2015). The absence 281 of frost events during winter might favour growth of the species in the growing season. For instance 282 283 the negative pointer year we found around 1980s was mainly addressed to an intense foliar damage trees experienced during the winter, which probably limited photosynthesis in the first part of the 284 following growing season. Then, summer temperature in the year of growth is found to be a limiting 285 286 factor under both climate regimes here considered; the fact that summer temperature in the previous 287 year have instead positive influence might be related to faster organic matter turnover and higher 288 resource availability for growth in the following year.

Summer precipitation was recognized as a limitinginfluencing factor only at the northern location 289 (Acquerino), suggesting local acclimation, and a different temporal regulation of photosynthesis 290 and physiological activity for the southernmost provenance. On the other hand, high precipitation in 291 autumn preceding growth has a negative effect on productivity at both sites. This might seem 292 counter intuitive, but can be explained by a complementary effect of rain versus snow. Rain gauges 293 are generally not able to measure both snow and rain; measurements of low rainfall in late autumn 294 and early winter months might "hide" snowfall (relatively frequent at both sites), which is 295 beneficial to next year's growth via increased water availability in the soil after snowmelt (Littell et 296 al., 2008). 297

Page 18 out of 27

298 The current-year growing conditions are mainly able to influence latewood growth whereas earlywood growth is influenced by antecedent and current-year conditions (Eilmann and Rigling, 299 2012; Watson and Luckman, 2002). In this case and regarding water balance, previous year drought 300 was found to strongly limit growth (probably via an influence on earlywood formation) only at 301 Acquerino, where usually no aridity occurs during the summer, and the soil is more fertile (top see 302 803 height at age 70, Table 1). Only one month of significant correlation between TRW and with SPEI has been detected at Mercurella. Recent studies have found Douglas fir to be vulnerable to 304 exceptional and recurrent drought episodes only on low fertility sites (Sergent et al., 2014), which is 305 the opposite to what we have found. However, Mercurella is both dryer and hotter than Acquerino 306 and closer to the seaside. In this particular environment trees might have deal with low water 307 availability and moisture deficit by local acclimation. Such effect may be stronger than what 308 309 implied by soil characteristics. Another possibility might consider this skill as already included in the genotype of the trees and not expressed in other zones (Mathys et al., 2014). This represents a 310 potential research question which should be addressed with adequate molecular techniques. Indeed, 311 the genetic provenance of old Douglas fir stands in Europe is rarely known and only recently 312 addressed by means of dedicate sampling procedures and nuclear markers (Hintsteiner et al., 2018). 313 In our study the only information available is that both stands were established by 3 year old 314 seedlings form the nursery of Vallombrosa with "Italian" seeds collected form mature trees with 315 unknown origin (probably form Washington, Oregon or California) around 1930 (Avolio and 316 317 Bernardini, 2000)In this framework, it remains unknown whether instead the smaller top height at 318 the southern site is a result of some resistance (i.e. productivity trade-off of the southern provenance). To solve this, common garden experiments with such provenance might be pursued to 319 evaluate the productive performance of this seed source under different climate regimes. Actually 320 the growth response to climatic conditions in the previous year and winter based on tree-ring width 321 time series measured at an annual time step is supposed to be maintained. This aspect might open 322

Page 19 out of 27

new research scenarios for other studies where second-stage seed sources from such old Douglas firstands might represent a valuable potential for forest management in Italy.

Testing provenance materials and monitoring the growth response of rear-edge populations in warm 325 and dry climates is fundamental for adaptive forest management in Europe (Provan and Maggs, 326 2012). Under such perspective, this study could represent an opportunity to derive useful insight on 327 328 this exotic species in Europe. Actually, climate is challenging for plant growth across the whole Europe, both in the warm-temperate zone due to summer aridity periods with increasing 329 temperatures, and in wetter areas that are undergoing significant drying trends. Under this scenario, 330 acclimated old populations of Douglas fir showing high growth plasticity and tolerance to drought 331 (Boiffin et al., 2017; Isaac-Renton et al., 2014) may be seen as to have a good potential for timber 332 supply in Europe (Rais et al., 2014; Sergent et al., 2014). The role of active forest management may 333 be relevant in this end, since the stand structure can have a deep influence on the mitigation of 334 water stress, also in the case of Douglas fir (Mazza et al., 2018; Rebetez et al., 2006). 335

The MCF analysis showed a quite complicated framework where just few correlations were stable 336 and dominant. Indeed this aspect was not surprising given the nature of the relationship: an exotic 337 338 species introduced in a new environment. The analysis detected that the strength and significance of most correlations with Douglas fir growth against temperature, precipitation, and SPEI shifted from 339 months in the year prior to growth to those in the year when growth occurs. At Acquerino, late 340 summer temperature became significantly limiting only after the year 1970 (and after 1960 at 341 Mercurella). Anyway this aspect should not be addressed to a possible adaptation of the species. 342 The negative correlations of growth with summer temperature in the recent decades suggest that 343 temperatures have increased and are now at or above the temperature optimum for growth i.e. 344 around 20°C (Briffa et al., 2001). No consistent sign could be found for any divergence-like 345 weakening of tree responses to temperature in recent decades (Briffa et al., 1998; Wigley et al., 346 1984). The most important month for winter temperature shifted from March to February also at 347 Acquerino, and for summer precipitation from July to May as a possible consequence of the 348 Page 20 out of 27

anticipation of growing season onset and precipitation reduction induced by climate change. Also, at Mercurella, the previous years' drought has maintained its importance throughout the study period, which may again reflect the interaction between climate and soil in determining tree growth (i.e., a higher water availability may compensate for the limitation of a poor soil by increasing the resources available to the tree in the following year).

354

355 Conclusions

After almost 100 years of experimentation, Douglas fir has demonstrated a relevant potential for 356 timber production across Europe. The species is probably there to stay, and many countries are 857 358 currently implementing silviculture aiming to regenerate the species naturally. Known as a droughttolerant species, Douglas fir has in fact demonstrated a high acclimation capacity when grown in 359 360 warm and dry climates (southern provenances). It is relevant to highlight that the Mercurella stand 361 here examined represents the southernmost plantation at the southern limit of European planting range of Douglas fir. Late winter temperatures play here a key role for Douglas fir growth, while 362 precipitation has a lower effect. However, the differences in potential maximum productivity 863 864 between southern and northern Mediterranean provenances have to be further assessed. Given the 865 adaptive capacity of this species to European climate, current plantations may be considered as a elimate smart seed sources to establish new populations with high adaptive capacity under future 366 867 climate change. However, further common garden experiments should be planned in order to 368 properly test adaptation of the second or third generation seed generated by old Douglas fir stands 369 across Europe. An interesting study could compare adaptation of this species in both zones, the Pacific North West and Europe, collecting seeds from both and to test them with a novel field trial 370 network to be established in both areas. In our opinion, further experimental should be welcomed 371 such as the IUFRO 1960s experimentation as well as the EUDIREC (Grant agreement ID: 372 FAIR950909) project. 373

374

Page 21 out of 27

- 575 Funding: this study was conducted with financial support from the RGV-FAO project funded by
- the Italian Minister of Agricultural, Food and Forestry Policies. Cristiano Castaldi has received the
- 377 support by University of Tuscia (Italy) as Ph.D. student.
- 878 Maurizio Marchi was funded by EU, in the framework of the Horizon 2020 B4EST project
- "Adaptive BREEDING for productive, sustainable and resilient FORESTs under climate change",
- 380 UE Grant Agreement 773383 (http://b4est.eu/).
- 381
- 382 Conflict of Interest: the authors declare that no conflict of interest exists
- 383

384 References

- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration
 or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111.
 https://doi.org/10.1111/j.1752-4571.2007.00013.x
- Avanzi, C., Piermattei, A., Piotti, A., Büntgen, U., Heer, K., Opgenoorth, L., Spanu, I., Urbinati, C.,
 Vendramin, G.G., Leonardi, S., 2019. Disentangling the effects of spatial proximity and
 genetic similarity on individual growth performances in Norway spruce natural populations.
 Sci. Total Environ. 650, 493–504. https://doi.org/10.1016/j.scitotenv.2018.08.348
- Avolio, S., Bernardini, V., 2000. La parcella sperimentale N. 412 di douglasia verde di Pavari nella
 Catena Costiera calabra a settant'anni dall'impianto [The experimental plot N. 412 of green
 Douglas fir in the coastal mountain chain after seventy years from its establishment]. Ann.
 Silvic. Res. 31, 119–136.
- Benito Garzón, M., Robson, T.M., Hampe, A., 2019. ΔTraitSDM: species distribution models that
 account for local adaptation and phenotypic plasticity. New Phytol.
 https://doi.org/10.1111/nph.15716
- Biondi, F., Qeadan, F., 2008. A Theory-Driven Approach to Tree-Ring Standardization: Defining the
 Biological Trend from Expected Basal Area Increment. Tree-Ring Res. 64, 81–96.
 https://doi.org/10.3959/2008-6.1
- Biondi, F., Waikul, K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of
 climate signals in tree-ring chronologies. Comput. Geosci. 30, 303–311.
 https://doi.org/10.1016/j.cageo.2003.11.004
- Boiffin, J., Badeau, V., Bréda, N., 2017. Species distribution models may misdirect assisted
 migration: insights from the introduction of Douglas-fir to Europe. Ecol. Appl. 27, 446–457.
 https://doi.org/10.1002/eap.1448

Page 22 out of 27

- Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe
 drought : a review of ecophysiological responses , adaptation processes and long-term
 consequences. Ann. For. Sci. 63, 625–644. https://doi.org/10.1051/forest
- 411 Briffa, K.R., Osborn, T.J., Schweingruber, F.H., Harris, I.C., Jones, P.D., Shiyatov, S.G., Vaganov,
 412 E.A., 2001. Low-frequency temperature variations from a northern tree ring density network. J.
 413 Geophys. Res. 106, 2929. https://doi.org/10.1029/2000JD900617
- Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G., Vaganov, E.A., 1998.
 Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature 391,
 678–682. https://doi.org/10.1038/35596
- Brus, D.J., Hengeveld, G.M., Walvoort, D.J.J., Goedhart, P.W., Heidema, A.H., Nabuurs, G.J.,
 Gunia, K., 2012. Statistical mapping of tree species over Europe. Eur. J. For. Res. 131, 145–
 157. https://doi.org/10.1007/s10342-011-0513-5
- Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2017.
 Dendrochronology Program Library in R. https://doi.org/10.1016/j.dendro.2008.01.002
- Case, M.J., Peterson, D.L., 2005. Fine-scale variability in growth-climate relationships of Douglasfir, North Cascade Range, Washington. Can. J. For. Res. 35, 2743–2755.
 https://doi.org/10.1139/x05-191
- Castaldi, C., Vacchiano, G., Marchi, M., Corona, P., 2017. Projecting Nonnative Douglas Fir
 Plantations in Southern Europe with the Forest Vegetation Simulator. For. Sci. 63, 101–110.
 https://doi.org/http://dx.doi.org/10.5849/forsci.16-048
- Chen, P.Y., Welsh, C., Hamann, A., 2010. Geographic variation in growth response of Douglas-fir to
 interannual climate variability and projected climate change. Glob. Chang. Biol. 16, 3374–
 3385. https://doi.org/10.1111/j.1365-2486.2010.02166.x
- Corona, P., 2016. Consolidating new paradigms in large-scale monitoring and assessment of forest
 ecosystems. Environ. Res. 144, 8–14. https://doi.org/10.1016/j.envres.2015.10.017
- Costantini, E., Barbetti, R., Fantappiè, M., L'Abate, G., Lorenzetti, R., Napoli, R., Marchetti, A.,
 Rivieccio, R., 2014. The soil map of Italy A hierarchy of geodatabases, from soil regions to
 sub-systems, in: GlobalSoilMap Basis of the Global Spatial Soil Information System. pp. 109–
 112. https://doi.org/10.1201/b16500-23
- 437 Ducci, F., Tocci, A., 1987. Primi risultati della sperimentazione IUFRO 1969-70 su Pseudotsuga
 438 menziesii (Mirb.) Franco nell'appennino centro-settentrionale [First results of IUFRO/1969-70
 439 experimentation on Pseudotsuga menziesii (Mirb.) Franco in Northern and Central Apennines].
 440 Ann. dell'Istituto Sper. per la Selvic. 18, 215–289.
- 441 Eilmann, B., de Vries, S.M.G., den Ouden, J., Mohren, G.M.J., Sauren, P., Sass-Klaassen, U., 2013.
- 442 Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir
- 443 (Pseudotsuga menziesii (Mirb.)) provenances. For. Ecol. Manage. 302, 133–143.
- 444 https://doi.org/10.1016/j.foreco.2013.03.031

Page 23 out of 27

445	Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species' drought tolerance.
446	Tree Physiol. 32, 178–187. https://doi.org/10.1093/treephys/tps004

- Fassnacht, F.E., Hartig, F., Latifi, H., Berger, C., Hernández, J., Corvalán, P., Koch, B., 2014.
 Importance of sample size, data type and prediction method for remote sensing-based
 estimations of aboveground forest biomass. Remote Sens. Environ. 154, 102–114.
- 450 https://doi.org/10.1016/j.rse.2014.07.028
- Gričar, J., Prislan, P., de Luis, M., Gryc, V., Hacurová, J., Vavrčík, H., Čufar, K., 2015. Plasticity in
 variation of xylem and phloem cell characteristics of Norway spruce under different local
 conditions. Front. Plant Sci. 6, 1–14. https://doi.org/10.3389/fpls.2015.00730
- Griesbauer, H.P., Green, D.S., 2010. Assessing the climatic sensitivity of Douglas-fir at its northern
 range margins in British Columbia, Canada. Trees 24, 375–389.
 https://doi.org/10.1007/s00468-009-0407-z
- Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: The rear edge matters.
 Ecol. Lett. 8, 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x
- Härdtle, W., Niemeyer, T., Fichtner, A., Li, Y., Ries, C., Schuldt, A., Walmsley, D., von Oheimb, G.,
 2014. Climate imprints on tree-ring δ15N signatures of sessile oak (Quercus petraea Liebl.) on
 soils with contrasting water availability. Ecol. Indic. 45, 45–50.
- 462 https://doi.org/10.1016/j.ecolind.2014.03.015
- 463 Hermann, R.K., Lavender, D.P., 1999. Douglas-fir planted forests. New For. 17, 53–70.
 464 https://doi.org/10.1023/A:1006581028080
- Hintsteiner, W.J., van Loo, M., Neophytou, C., Schueler, S., Hasenauer, H., 2018. The geographic
 origin of old Douglas-fir stands growing in Central Europe. Eur. J. For. Res. 0, 1–15.
 https://doi.org/10.1007/s10342-018-1115-2
- Howe, G.T., Jayawickrama, K., Cherry, M., Johnson, G.R., Wheeler, N.C., 2010. Breeding DouglasFir, in: Plant Breeding Reviews. John Wiley & Sons, Inc., Oxford, UK, pp. 245–353.
 https://doi.org/10.1002/9780470650349.ch6
- Isaac-Renton, M.G., Roberts, D.R., Hamann, A., Spiecker, H., 2014. Douglas-fir plantations in
 Europe: A retrospective test of assisted migration to address climate change. Glob. Chang.
 Biol. 20, 2607–2617. https://doi.org/10.1111/gcb.12604
- Lipow, S.R., Johnson, G.R., St. Clair, J.B., Jayawickrama, K.J., 2003. The role of tree improvement
 programs for Ex situ gene conservation of coastal Douglas-fir in the Pacific Northwest. For.
 Genet. 10, 111–120.
- Littell, J.S., Peterson, D.L., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: Water
 limits tree growth from stand to region. Ecol. Monogr. 78, 349–368.
- 479 https://doi.org/10.1890/07-0712.1
- Maca, P., Pech, P., 2016. Forecasting SPEI and SPI Drought Indices Using the Integrated Artificial
 Neural Networks. Comput. Intell. Neurosci. 1–17.

Page 24 out of 27

- Marchi, M., 2019. Nonlinear versus linearised model on stand density model fitting and stand
 density index calculation: analysis of coefficients estimation via simulation. J. For. Res.
- 484 https://doi.org/10.1007/s11676-019-00967-0
- Marchi, M., Castaldi, C., Merlini, P., Nocentini, S., Ducci, F., 2015. Stand structure and influence of
 climate on growth trends of a Marginal forest population of Pinus nigra spp. nigra. Ann. Silvic.
 Res. 39, 100–110. https://doi.org/10.12899/asr-1066
- Mathys, A., Coops, N.C., Waring, R.H., 2014. Soil water availability effects on the distribution of
 20 tree species in western North America. For. Ecol. Manage.
- Mazza, G., Gallucci, V., Manetti, M.C., Urbinati, C., 2014. Climate–growth relationships of silver
 fir (Abies alba Mill.) in marginal populations of Central Italy. Dendrochronologia 32, 181–190.
 https://doi.org/10.1016/j.dendro.2014.04.004
- Mazza, G., Sarris, D., Chiavetta, U., Ferrara, R.M., Rana, G., 2018. An intra-stand approach to
 identify intra-annual growth responses to climate in Pinus nigra subsp. laricio Poiret trees from
 southern Italy. For. Ecol. Manage. 425, 9–20. https://doi.org/10.1016/j.foreco.2018.05.029
- Piotti, A., Leonarduzzi, C., Postolache, D., Bagnoli, F., Spanu, I., Brousseau, L., Urbinati, C.,
 Leonardi, S., Vendramin, G.G., Urfm, U.R., 2017. Unexpected scenarios from Mediterranean
 refugial areas : disentangling complex demographic dynamics along the Apennine distribution
 of silver fir. J. Biogeogr. 44, 1547–1558. https://doi.org/10.1111/jbi.13011
- Poschenrieder, W., Biber, P., Pretzsch, H., 2018. An Inventory-Based Regeneration Biomass Model
 to Initialize Landscape Scale Simulation Scenarios. Forests 9, 212.
 https://doi.org/10.3390/f9040212
- Provan, J., Maggs, C.A., 2012. Unique genetic variation at a species' rear edge is under threat from
 global climate change. Proc. Biol. Sci. 279, 39–47. https://doi.org/10.1098/rspb.2011.0536
- Rais, A., van de Kuilen, J.-W.G., Pretzsch, H., 2014. Growth reaction patterns of tree height,
 diameter, and volume of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) under acute
- drought stress in Southern Germany. Eur. J. For. Res. 133, 1043–1056.
- 508 https://doi.org/10.1007/s10342-014-0821-7
- Rebetez, M., Mayer, H., Dupont, O., 2006. Heat and drought 2003 in Europe: a climate synthesis.
 Ann. For. Sci. 63, 569–577. https://doi.org/10.1051/forest
- 511 Rehfeldt, G.E., Jaquish, B.C., López-upton, J., Sáenz-romero, C., St, J.B., Leites, L.P., Joyce, D.G.,
- 512 2014. Comparative genetic responses to climate for the varieties of Pinus ponderosa and
- 513 Pseudotsuga menziesii : Realized climate niches. For. Ecol. Manage. 324, 138–146.
- 514 https://doi.org/10.1016/j.foreco.2014.02.041
- 515 Rita, A., Gentilesca, T., Ripullone, F., Todaro, L., Borghetti, M., 2014. Differential climate-growth
- relationships in Abies alba Mill. and Fagus sylvatica L. in Mediterranean mountain forests.
- 517 Dendrochronologia 32, 220–229. https://doi.org/10.1016/j.dendro.2014.04.001

Page 25 out of 27

- Schmid, M., Pautasso, M., Holdenrieder, O., 2014. Ecological consequences of Douglas fir
 (Pseudotsuga menziesii) cultivation in Europe. Eur. J. For. Res. 133, 13–29.
- 520 https://doi.org/10.1007/s10342-013-0745-7
- Sergent, A.S., Rozenberg, P., Bréda, N., 2014. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. Ann. For. Sci. 71, 697–708.
 https://doi.org/10.1007/s13595-012-0220-5
- Smith, B., Knorr, W., Widlowski, J.-L., Pinty, B., Gobron, N., 2008. Combining remote sensing data
 with process modelling to monitor boreal conifer forest carbon balances. For. Ecol. Manage.
 255, 3985–3994. https://doi.org/10.1016/j.foreco.2008.03.056
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A.,
 Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong,
 G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z.,
- 530 Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.R., Malizia, A., Malizia, L.R.,
- 531 Pabst, R.J., Pongpattananurak, N., Su, S.H., Sun, I.F., Tan, S., Thomas, D., Van Mantgem, P.J.,
- 532 Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases
- continuously with tree size. Nature 507, 90–93. https://doi.org/10.1038/nature12914
- Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem
 growth. For. Ecol. Manage. 376, 205–220. https://doi.org/10.1016/j.foreco.2016.06.020
- Trouet, V., Van Oldenborgh, G.J., 2013. KNMI Climate Explorer: A Web-Based Research Tool for
 High-Resolution Paleoclimatology. Tree-Ring Res. 69, 3–13. https://doi.org/10.3959/1536 1098-69.1.3
- Vejpustková, M., Čihák, T., 2019. Climate Response of Douglas Fir Reveals Recently Increased
 Sensitivity to Drought Stress in Central Europe. Forests 10, 97.
 https://doi.org/10.3390/f10020097
- Wang, T., Campbell, E.M., O'Neill, G.A., Aitken, S.N., 2012. Projecting future distributions of
 ecosystem climate niches: Uncertainties and management applications. For. Ecol. Manage.
 279, 128–140. https://doi.org/10.1016/j.foreco.2012.05.034
- 545 Watson, E., Luckman, B.H., 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine
 546 tree-ring chronologies from the southern Canadian Cordillera. Can. J. For. Res. 32, 1858–1874.
 547 https://doi.org/10.1139/x02-096
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the Average Value of Correlated Time Series,
 with Applications in Dendroclimatology and Hydrometeorology. J. Clim. Appl. Meteorol.
 https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2
- Yamaguchi, D.K., Cook, E.R., Kairiukstis, L.A., 1991. Methods of Dendrochronology, Applications
 in the Environmental Sciences. Arct. Alp. Res. 23, 120. https://doi.org/10.2307/1551446
- Zang, C., Biondi, F., 2015. Treeclim: An R package for the numerical calibration of proxy-climate relationships. Ecography (Cop.). 38, 431–436. https://doi.org/10.1111/ecog.01335
- 555

Page 26 out of 27

Page 27 out of 27