Repeated spring precipitation shortage alters individual growth patterns in Scots pine forests in the Western Alps

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Repeated spring precipitation shortage alters individual growth patterns in Scots pine forests in the Western Alps

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Key message

In the inner-Alpine Aosta Valley, severe growth reductions occurred in Scots pine stands during 1987-1993 and 2003-2005. Trees more sensitive to May precipitation exhibited stronger growth decline during these periods.

Abstract

Over the last decades, Scots pine (*Pinus sylvestris* L.) decline has involved large areas in the European Alps. Although the species is supposed to be drought-resistant, increased temperatures and droughts are often indicated as predisposing causes of the decline. Nevertheless, the exact climate conditions that initiate the decline, and the reasons why they differentially affect individual trees, are largely unknown. Our aims were to identify climate constraints on Scots pine growth, and elucidate the effect of individual characteristics, such as tree age, size, crown condition, mistletoe occurrence, competition, and sensitivity to climate, on tree growth decline and recovery after repeated climatic stress. We analysed 232 trees in four second-growth stands located at 985 to 1350 m a.s.l. in the inner-Alpine Aosta Valley, NW Italy. Multi-year growth declines, occurred in 1987-1993 and 2003-2005, were related to repeated May precipitation shortage, while temperatures and summer precipitations played a minor role. Growth decline was stronger in the stand at lower elevation and with higher competition intensity. At the individual scale, trees more sensitive to May precipitation exhibited lower growth rates during both dry periods, but not a faster recovery. In the lower elevation stand, tree growth decline was significantly related to both crown transparency and mistletoe abundance, which was almost absent in the other stands. We conclude that future variations in the spring precipitation regime could threaten Scots pine more than warming *per se*, in inner-Alpine valleys around 1000-1400 m a.s.l. Still, different individual sensitivity to precipitation will likely result in patchy patterns of healthy and declining trees within the same stand.

Keywords Climate change; competition; crown; decline; *Pinus sylvestris*; tree ring.

Introduction

Scots pine (*Pinus sylvestris* L.) is the most widespread tree species in Europe, covering more than 20 million hectares from Siberia and Northern Fennoscandia to Southern Europe. During the 20th century, the species has considerably expanded in the European Alps due to its early-seral character, i.e., a capacity to colonize abandoned fields and grasslands (Barbero et al. 1990). In inner-Alpine valleys characterized by continental climate, a peculiar tolerance to a wide range of climatic and edaphic stressors (Richardson 1998) allows the species to grow on southerly-exposed slopes where other species are limited by concomitant low winter and high summer temperatures, and summer rain shortage (Vacchiano et al. 2012). Therefore, in the continental sectors, Scots pine can be considered both an early- and late-seral species (Ozenda 1985). However, over the last 20 years, an increasing number of studies have reported a decline of Scots pine in inner-Alpine valleys, especially at medium and low elevations, e.g., in the Austrian Inn Valley (Oberhuber 2001), Swiss Valais (Bigler et al. 2006), Southern France (Thabeet et al. 2009), and Italy's Aosta Valley (Vacchiano et al. 2012). Symptoms of the decline include stem growth reduction, crown defoliation, and mortality, eventually leading to shifts in species composition in favour of other species such as downy oak (*Quercus pubescens* Willd.) (Weber et al. 2007; Rigling et al. 2013; Vacchiano and Motta 2015).

Different biotic agents, including mistletoe (*Viscum album* L.), insects, nematodes, and fungi have been locally found to act as contributing factors (Manion 1981) for Scots pine defoliation and mortality (Dobbertin and Rigling 2006; Polomski et al. 2006; Wermelinger et al. 2008; Gonthier et al. 2010). However, on a broader scale, increased temperatures and more frequent droughts are indicated as the main drivers (predisposing and inciting factors) of the decline (Rebetez and Dobbertin 2004). Current climate change scenarios predict further year-round warming in Southern Europe (IPCC 2013; Jacob et al. 2014), which will likely exacerbate summer moisture deficits and aggravate drought effects on forest ecosystems (Allen et al. 2010). On the other hand, precipitation forecasts are less clearcut, especially in the Alpine region: precipitations may decrease in summer, but changes in spring and fall are expected to be less pronounced (Gobiet et al. 2014), with uncertain consequences on forest ecosystems (Lindner et al. 2014). Finally, extreme climate events, such as droughts and/or heat waves, are expected to increase in Southwestern Europe (IPCC 2013). Single-year droughts certainly affect forest ecosystems (Bréda et al. 2006), but on drought-adapted species such as Scots pine they generally cause short-term growth reduction followed by recovery, at least in healthy trees (Pichler and Oberhuber 2007; Eilmann and Rigling 2012; Eilmann et al. 2013). On the opposite, repeated droughts lead to irreversible alterations in the xylem hydraulic system (Hereş et al. 2014), and to progressive depletion of stored carbohydrates (Rigling et al. 2013). This process negatively affects tree metabolism and resistance to pathogens that are the actual mortality agents, and can lead to tree death up to several years or even decades after the event (Bigler et al. 2006; Hereş et al. 2014).

However, even in areas with high mortality, declining and vigorous pine trees can co-occur in the same stand (Bigler et al. 2006), suggesting that individual tree characteristics influence decline. In this context, analysis at the individual tree level can increase our understanding of processes behind tree response to long-term stress. Extensive literature reports on the influence of tree age (Carrer and Urbinati 2004), size (Mérian and Lebourgeois 2011), and local competition intensity (Pichler and Oberhuber 2007) on growth response to inter-annual climate variations, but tree-level response to multi-year or repeated climatic stress has been scarcely investigated (Thabeet et al. 2009; Walter et al. 2013).

To investigate Scots pine response to multi-year stress, we analysed growth patterns of 232 trees in four stands located at different elevations (985 to 1350 m a.s.l.) along the east-west axis of the

Aosta Valley (NW Italy), one of the driest valleys in the Alps. In this region, land use change has considerably increased forest cover over the last 50 years (+30%, Garbarino et al. 2006), mainly due to expansion of early-seral species such as Scots pine. However, Scots pine forests have recently displayed a quick loss of vitality (Gonthier et al. 2010; Vacchiano et al. 2012). The specific objectives of our analysis were: (1) to identify climatic conditions that determined multi-year growth decline in Scots pine stands in the period 1965-2005; (2) to assess the influence of site, stand, tree age, size, competition, and sensitivity to climate on individual tree growth decline and recovery after repeated climatic stress; and (3) to test whether crown transparency as an indicator of tree vitality, and mistletoe as an inciting mortality agent, are related to the ability of trees to respond to climatic stress.

Material and Methods

Study area and sampling

The study area covers the Aosta Valley region in Northwestern Italy (Fig. 1). Climate is warm-summer continental, with mean annual temperature at the bottom of the valley (Aosta, 45°26’ N, 7°11’ E, 583 m a.s.l.) of 10.9 °C (years 1961-1990; Biancotti et al. 1998). Mean temperature in January and July may differ by as much as 22°C. Mean annual precipitation in the central valley is scarce (494 mm in Aosta, years 1961–1990) compared to other Alpine valleys, and water deficit may occur at low elevations from June to September. Winter precipitation usually comes as snow. Aosta Valley exhibits both crystalline (granites) and metamorphic bedrocks, but most landscape is covered by quaternary deposits of glacial, gravitative, or colluvial origin.

Scots pine forests occur on 5,372 ha on both acidic and basic substrates of well-exposed slopes, from the valley bottom up to 1900 m a.s.l. (Vacchiano et al. 2014). Depending on successional stage and climatic factors, species composition may range from 100% pine (especially on recently disturbed sites or on dry, south-facing slopes) to mixtures with other conifers (*Larix decidua* Mill., *Picea abies* L. Karst., *Abies alba* Mill., *Pinus uncinata* Mill.) or broadleaves (*Quercus pubescens* Willd., *Fagus sylvatica* L., *Quercus petraea* (Mattus.) Liebl., *Castanea sativa* Mill.).

In 2005 we selected four Scots pine stands along the east-west axis of the Region: one at Challand-Saint-Anselme (hereafter Chal), two at Saint Denis (SD1 and SD2), and one at Morgex (Morg) (Table 1, Fig. 1). All stands originated by natural encroachment after the abandonment of pastures and meadows in the past century. All of them exhibited visual symptoms of decline such as a wide range of crown transparencies. In each stand, we established a 70x70m monitoring plot, where all living trees with diameter at breast height (dbh) > 4 cm were identified, labelled, and mapped. For each tree, we measured dbh, tree height, and crown radii in four orthogonal directions, which were then used to calculate crown area, approximated as an ellipse. Furthermore, we assessed crown transparency on a scale from 0 (healthy crown) to 100 (completely defoliated) by comparison with visual field guides (Müller and Stierlin 1990; Dobbertin et al. 2004), and recorded mistletoe abundance on a scale from 0 (absent) to 3 (abundant) (Dobbertin and Rigling 2006). One increment core was taken at breast height from all living trees within a concentric 50x50 m subplot, to avoid edge effects in the calculation of competition indices (Castagneri et al. 2008).

Methodological approach

Radial growth is a good indicator of tree vitality and reaction to environmental stress (Dobbertin 2005). Furthermore, in contrast to other tree vitality indices such as crown transparency, ring measurement is objective, repeatable, and retrospective (on the whole tree life-span). We analysed tree-ring series to assess individual tree response to inter-annual climate variations, and identified protracted growth decline periods. Then we analyzed tree response to inter-annual climate variations (ring width-climate correlations) and to prolonged stress (i.e. growth rates during and after the identified decline periods) using tree age, size, competition, mistletoe abundance, and crown transparency as covariates.

Ring-width analysis

Tree cores were prepared using standard dendrochronological techniques (Speer 2010). Tree rings were measured to the nearest 0.01 mm and cross-dated using TsapWin (Rinntech, Germany). Cross-dating accuracy was checked using COFECHA (Holmes 1983). Sample size showed an abrupt reduction prior to 1965, thus 1965-2005 was identified as the investigation period. Series not entirely overlapping with this period, and those poorly cross-dating, were excluded from the analyses. Raw ring width (RW) and basal area increment (BAI) series were built for 54 trees for SD1, 66 for SD2, 73 for Morg, and 39 for Chal, for a total of 232 series across the study sites.

To assess inter-annual growth variations, we removed age-size related trends on RW series by a double-detrending process using the DetrendeR package (Campelo et al. 2012) for the R statistical framework 3.1 (R Development Core Team 2014). Detrending was based on a cubic spline with 50% frequency response at wavelength of 200 years, followed by a cubic spline function with 32 years response (Fritts 1976); we computed detrended ring width by dividing raw RW by the value fitted with the splines. We then calculated mean sensitivity (MS) of detrended series to assess high-frequency variations (Fritts 1976), first-order autocorrelation (AC) to measure the influence of previous year's growth on the current ring, and mean correlation between trees (Rbar) to measure the common growth forcing among trees within each plot.

Finally, mean chronologies were calculated for each plot as the bi-weight robust mean of detrended individual series (Cook 1985).

Tree-level competition

To assess the competitive status of each tree, we computed distance-dependent and distance-independent individual-tree based competition indices (CIs) (Tab. 2). We tested different radii (5, 7 and 9 m) of the zone of influence (i.e., the circular area surrounding the subject tree where competitors are selected) to compute distance-dependent CIs. Moreover, different weights were applied to species other than Scots pine to account for possible variations in the competitive pressure of interspecific competitors. Specifically, due to the high number of species in the four plots, some of which represented by few individuals, we gathered them in two groups: conifers (5 species) and broadleaves (13 species). To test if conifer and/or broadleaf interspecific competitors had higher or lower competitive pressure on focus trees (always Scots pines) compared to intraspecific competitors (weight = 1), we assigned different weights to trees belonging to the two groups: 0.5 to test for lower (half) competitive pressure; 1 for same pressure; 2 for higher (double) pressure. All possible combinations were tested. The predictive ability of each combination of CI, zone of influence, and weighting scheme was tested by a linear regression against cumulative BAI of each tree in the ten years before measurement (Castagneri et al. 2008). Both predictors and dependent variables were log-transformed to normalize error distributions. The combination of competition index, radius of the zone of influence, and weighting scheme producing the highest correlation with BAI (i.e., competition importance) and steepest regression slope (i.e., competition intensity) was used in subsequent analyses.

Climate-growth relationships

The influence of climate on the inter-annual growth variability in the four site chronologies (years 1965-2005) was assessed by bootstrap correlations using the bootRes package (Zang and Biondi 2013) for R. Climate variables entered in correlations included: monthly mean temperature and precipitations sum from May of the previous year to September of the ring formation year, both retrieved from the CRU TS 3.21 dataset (Harris et al. 2014) accessed via the KMNI climate explorer (http://climexp.knmi.nl); the self-calibrating Palmer Drought Severity Index (sc-PDSI, CRU TS 3.21 dataset); the ratio between precipitation and potential evapotranspiration (P/PET) according to Thornthwaite (1948); and the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010) based on a 6-month integration period. As PET (and P/PET) was null for winter months due to temperature below 0, while sc-PDSI and SPEI are incremental, i.e., they incorporate the value of the previous months, these were computed only for the growing season (April-August) of the ring formation year.

Multi-year growth declines and recovery

Tree growth response to prolonged stress was assessed as follows: (1) for each year in the period 1965-2005, we calculated the number of trees with lower-than-average BAI. Decline periods were identified as those where two or more consecutive years had lower-than-average BAI in at least 2/3 of trees. (2) For each of these periods, we computed individual tree growth decline as the ratio between BAI during the period and BAI in the previous five years, and (3) individual growth recovery as the ratio between BAI in the five years after and BAI during the decline period (Martín-Benito et al. 2008). We then assessed climate anomalies of each decline and recovery period (i.e., differences in monthly temperature, precipitation, P/PET, sc-PDSI and SPEI in decline and recovery periods compared to the reference period), and whether individual growth decline and recovery differed among stands (Kruskal-Wallis median test, with Mann-Whitney pairwise comparisons).

Individual tree responses

To investigate factors influencing individual response to inter-annual climatic variations (i.e., ring width-climate correlation coefficients for the most significant climate factors), and individual growth decline and recovery after prolonged stress (response variables), we used a linear mixed model approach, with site as a random factor (in both intercept and slope). Growth decline and recovery were squared-root transformed, while correlation coefficients were processed by Fisher z-transformation. Independent variables were tree size characteristics (dbh, height, and crown area), tree age, and competitive status (CI). In the models for growth decline and recovery, we included as predictors the tree response to inter-annual climatic variations, and growth decline and recovery in the periods preceding the one being analysed. The effect of each independent variable was tested first by univariate models, which allowed the identification of significant predictors. Successively, the latter were used in multivariate models to assess their relative influence on response variables. Linear mixed effects models were fitted using the package lme4 (Bates et al. 2014) for R.

Finally, we computed generalized linear models (with log-link function and gamma distribution) to assess the effect of independent variables, plus mistletoe infection where present, on individual crown transparency in the four stands.

Results

Stand characteristics and competitive status

In the four stands, Scots pine accounted for 75% (SD1) to 100% (SD2) of the total basal area (Table 1). Other species were mainly downy oak at SD1, downy oak and other broadleaves at Morg, and larch at Chal. SD1 had the highest total stand density but the lowest basal area and quadratic mean diameter (QMD). Trees at SD1 were also shorter and younger than in the other plots.

Among different competition indices, the highest correlation with BAI was produced by CAI (Table 2). Most indices performed better when computed on a 7 m-radius area of influence. Performance of CIs did not improve when using different weighting coefficients for interspecific competitors. Despite having the lowest basal area, SD1 showed the highest correlation and steepest linear regression coefficient between BAI and CAI, indicating higher importance and intensity of competition at the local scale.

Climate-growth relationships

Tree-ring series in SD1 showed the highest mean sensitivity, while in Chal they had the highest Rbar (Table 1). In all stands, inter-annual growth variations were strongly affected by spring and early summer climatic conditions of the ring formation year (Fig. 2), while the climate of other seasons had a moderate and inconsistent influence (Supplementary Fig. 1). Spring and summer temperature had a negligible effect on growth at SD1 and Morg. A moderately positive effect of April temperature emerged at SD2, and a negative effect of May and August temperatures at Chal. May precipitation (or May P/PET in SD1) was the most important factor, and significantly affected individual growth in 74% of trees (80% at SD1, 82% at SD2, 65% at Morg, 70% at Chal). Precipitation in other spring and summer months had little influence. Ring-width correlation with sc-PDSI and SPEI indicated that SD1 was the site most affected by April to August water deficit.

Growth decline and recovery periods

During the investigation period 1965-2005, there were 13 years with at least 2/3 of trees showing reduced growth rates (i.e., annual BAI lower than average) (Fig. 3 and 4). The first three years (1965, 1968 and 1976) were isolated events, while the remaining ten clustered in two periods: 1987-1993, where growth was reduced in almost all trees, and 2003-2005. As ring-series ended in 2005, it was not possible to calculate recovery after 2003-2005.

May temperature during decline (1987-1993 and 2003-2005) and recovery (1994-1998) periods was above the 1965-2005 average (Fig. 5), indicating a general warming over the last decades. May precipitations and P/PET were much lower than average in the growth decline years (except precipitation in 1988), with a negative peak in 1991. May precipitation during the recovery period (1994-1998) was above average, except for 1998, while P/PET was below average, due to high temperatures. Sc-PDSI and SPEI in May evidenced normal conditions during 1987-1993 and drought in 2003-2005, while 1994-1998 period was quite wet. During April and summer months (June, July and August), temperatures were above average in both the decline and recovery periods, while precipitations had no evident reduction during 1987-1993 (Supplementary Fig. 2). sc-PDSI was consistent with a 2003-2005 drought, whereas conditions during 1987-1993 were close to average.

All plots experienced a severe growth reduction in 1987-1993 (Fig. 6), but SD1 showed the most dramatic decline ($p < 0.001$, Kruskal-Wallis median test with Mann-Whitney pairwise comparison). Trees at SD1 also experienced the strongest growth recovery among all sites during 1994-1998, while in Morg recovery was poor. The 2003-2005 growth decline was less severe than the previous in all plots. Again, growth reduction was stronger in SD1, while trees in SD2 did not show any decline.

Individual tree response

In all plots, tree growth was positively affected by May precipitation. However, the effect of May precipitation on intra-annual growth variations during 1965-2005 was not significantly affected by tree age, size, or competitive status (Table 3). Growth decline in 1987-1993 was more severe in suppressed trees (those with high CIs) and in trees more sensitive to May precipitation in the previous years (Table 4), especially at SD1 and SD2 (Fig. 7). No variable appeared to influence growth recovery in 1994-1998, while growth decline in 2003-2005 was more severe in young trees and, consistently with the previous stress period, in those more sensitive to precipitation in the previous years (Tables 3 and 4, Fig. 7).

Crown transparency

SD1 exhibited the highest crown transparency among all stands (Fig. 8). Furthermore, several trees in SD1 were infested by mistletoe (79%), whereas its occurrence was sporadic in SD2 (2%) and null in the other stands. Considering all stands together, we found a scarce influence of competition and tree characteristics on crown transparency (Table 3). Crown area had a negative effect on crown transparency, but could not discern whether small crowns were more defoliated, or defoliation reduced crown size. Individual tree growth decline in 2003-2005 was not related to crown transparency at SD2, Morg, and Chal (results not shown), but it was at SD1 (Table 5). Furthermore, mistletoe at SD1 was more abundant in trees with higher transparency – but again, causation between the two variables could be either direction.

Discussion

Climate influence on Scots pine growth

Scots pine is characterized by great ecological plasticity, which allows the species to grow in a variety of environmental conditions. In Northern Europe, radial growth is mainly limited by temperature during the short growing season (Gunnarson and Linderholm 2002), while in Central and Southern Europe growth is often controlled by water availability in April, May, June or July-August, depending on the region (Zang et al. 2012; Panayotov et al. 2013; Schuster and Oberhuber 2013; Morán-López et al. 2014; Merlin et al. 2015). In all analysed stands, May precipitation was the main climate factor influencing Scots pine growth, while precipitation and summer temperature, often indicated as major climate stressors in dry sites, had a negligible effect. Recent studies on Scots pine cambial activity on similar environmental conditions could help interpreting the observed patterns. In the dry valley of the Inn River (Austria), Gruber et al. (2010) and Swidrak et al. (2014) evidenced that cambial activity in Scots pine lasts from early/mid-April to the end of June/early July, with a peak cell production in early to mid-May. Similarly, Eilmann et al. (2013) indicated that tree rings in Valais (Switzerland) are mostly completed already in June, before the dry period occurs in July and August. We can therefore assume that, in the analysed sites, rings are mostly formed in May, when temperature is relatively low and, generally, does not determine high evapotranspiration. Thus, May precipitation is the limiting factor here. Summer climate has a negligible effect, as most of xylem cells differentiate before June.

Here, we provided empirical evidence that reduced May precipitations over several years induced prolonged growth depressions, being very reduced during both 1987-1993 and 2003-2005, and abundant in the recovery period 1994-1998. On the other hand May temperature, and summer precipitations and temperatures, were neither unusual during 1987-1993, nor favourable in the successive recovery period, indicating a secondary role of such climate factors. This result is critical for the definition of climatic stress for the species. Increased temperature, heat waves and summer drought events are often indicated as a major threat for forest ecosystems (Allen et al. 2010; Huang et al. 2015), but do not seem to have influenced Scots pine growth in the inner-Alpine Aosta Valley. However, we cannot exclude influence of warming and summer droughts on other tree physiological processes (e.g., root growth, Brunner et al. 2009; nonstructural carbohydrates accumulation, Galiano et al. 2011), or on biotic agents of Scots pine decline (e.g., insects and nematodes, Rebetez and Dobbertin 2004; mistletoe, Dobbertin et al. 2005).

After dry years, when May precipitation returned to average values, Scots pine trees recovered rapidly. In the five years following the drought of 1987-1993, growth increased by 40% (Morg) to 130% (SD1). In 1995, almost 2/3 of trees showed higher-than-average growth. Good recovery capacity indicates adaptation of the species to climate variations, especially in the site more affected by drought (SD1).

Individual tree response

The classical dendrochronological method is based on the selection of large, healthy, and possibly isolated trees to create a mean chronology representative of the population (Schweingruber et al. 1990). However, over the last decade, an increased interest in the individual response to climate emerged (Carrer 2011). Each tree has its own characteristics, and experiences different ecological conditions, which can potentially influence tree response to environmental variations (Tessier et al. 1997; Castagneri and Motta 2009). We observed a large variability in Scots pine individual response to climate, growth decline during stress periods, growth recovery, and crown transparency. However, the investigated tree characteristics scarcely explained such differences. Tree age was the only characteristic that partially influenced growth decline, but with no generalized effects. Indeed, age influenced growth decline during 2003-2005, but had neither influence during the former event, nor affected growth recovery and crown transparency. In past studies, tree characteristics such as age, stem diameter, height, and crown size have been shown to affect tree response to inter-annual climate variations, but observations were not consistent (e.g., for age effect see Szeicz and MacDonald 1994; Carrer and Urbinati 2004; Esper et al. 2008; Dorado Liñán et al. 2012; Rozas 2014). Our data suggest that the influence of tree characteristics on growth responses to climate (both inter-annual variations and long-term stress) depends on the peculiar characteristics of the stand, species, and climate event (Merlin et al. 2015), and a general pattern cannot be defined.

Beside tree characteristics, also inter-tree competition can influence tree response to climate, as it affects light and water availability, resource uptake, and growth efficiency (Gersonde and O'Hara 2005; Castagneri and Motta 2009). It is often assumed that trees in denser stands have a weaker climate signal (Schweingruber et al. 1990), as supported by comparative studies (Hurteau et al. 2007; Castagneri et al. 2012). However, high competition can increase sensitivity to drought as it exacerbates water stress (Martín-Benito et al. 2011; Martìnez-Vilalta et al. 2012; Madrigal-González and Zavala 2014). In his seminal work on tree decline diseases, Manion (1981) indicated competition as a slow "predisposing" factor, while particularly dry years can be the "contributing" or "inciting" cause of mortality of weakened trees. This was partially confirmed by our results, as SD1 was at the same time the stand with more intense competition (despite a low basal area), the most sensitive to summer drought, and the most affected by prolonged climate stress. At the tree level, however, the effect of competition on climate-growth relationships was less clear. Competition appeared to exacerbate drought effects during 1987-1993, but did not influence growth recovery, nor decline in 2003-2005. As discussed for age/size effect, we believe that competition-drought interactions at the tree level are extremely complex and do not comply with general rules, as shown by the inconsistence of previous findings (Piutti and Cescatti 1997; Pichler and Oberhuber 2007; Martín-Benito et al. 2008; Camarero et al. 2011; Rozas 2014).

In the analysed stands, trees more sensitive to May precipitation (during the years previous the droughts) had lower growth rates in 1987-1993 and 2003-2005. However, they were not able to recover faster than other trees during 1994-1998. Therefore, high correlation between growth and climate did not indicate high tree plasticity, i.e., a capacity to reduce growth under unfavourable climate and to take advantage of positive conditions. Instead, within stands, some trees were simply more susceptible to precipitation shortage. Individual difference could be possibly related to genetics (Taeger et al. 2013), morphology (e.g., the wood anatomy, Hereş et al. 2014; root system architecture, Mickovski and Ennos 2002), physiology (e.g., carbon storage in sapwood and needles, Camarero et al. 2015), or micro-site soil conditions (Gruber et al. 2010).

Crown conditions

Crown transparency is widely used to monitor anthropogenic, soil, or climate stress in forest stands. Still, to date, it has been scarcely used to investigate individual response to stress. As both tree growth and crown transparency are not cause-specific indicators of stress, their assessment may complement each other (Dobbertin 2005; Camarero et al. 2015). Among the four investigated stands, the highest crown transparency was found at SD1, where repeated May droughts had the strongest effect on growth. Here, we also observed a relationship between individual growth decline and crown transparency, suggesting that these stress indicators were responding to a common limiting factor, i.e. spring water availability, while tree characteristics and perceived competition played a minor role. SD1 was also affected by mistletoe, which occurred only sporadically in the other stands. Within the stand, trees with high infestation had the highest crown transparency (as observed by Dobbertin and Rigling 2006). In accordance to Rigling et al. (2010), we did not observe a direct effect of mistletoe on growth decline, but rather crown degradation, enhanced by mistletoe infection, can result in higher sensitivity to drought stress.

Conclusion and future perspectives

Along the east-west axis of the inner-Alpine Aosta Valley, at elevations between 985 and 1350 m a.s.l., repeated precipitation shortage in May caused prolonged growth reductions in Scots pine second-growth stands, while there was no evidence of summer climate constraint on growth patterns. However, we cannot exclude that the forecasted general warming (IPCC 2013) will increase Scots pine sensitivity to May precipitation, as we observed more severe growth reductions at lower elevations. The species is certainly adapted to water stress, and able to recover even after seven years of precipitation shortage. Nevertheless, in the most stressful condition (dense stands at low elevation), prolonged reductions of growth and high crown transparency aggravated by mistletoe infestation can compromise tree functioning and increase mortality risk (Bigler et al. 2006; Rigling et al. 2010; Hereş et al. 2012). Thinning to reduce competition for water could moderate drought stress, and thus Scots pine decline (Rigling et al. 2013; Fernández-de-Uña et al. 2015). Otherwise, similarly to what forecasted for other Alpine valleys, we can expect pine to be replaced by more drought tolerant species such as downy oak (Weber et al. 2007; Vacchiano and Motta 2015). However, uncertainty in future precipitation regime in the Alpine area (IPCC 2013) complicates predictions of species performance in the next decades.

Our individual-level analysis showed that trees more sensitive to inter-annual precipitation variations had lower growth rates than other trees during repeated precipitation shortages, but were not able to recover faster, i.e., they were less able to cope with adverse climate conditions. However, we did not identify a unique tree characteristic influencing tree response to climate. Extensive literature suggests that individual size/age/competition effect on response to climate is related to specific site, stand, and climate conditions. More detailed analyses on Scots pine tree genetics, and on physiological adjustment to stress, could shed light on why trees within a stand respond differently to climate stress. Future variations in spring precipitation regime in the Alps, which is less predictable compared to temperature (IPCC 2013), could threaten Scots pine in inner-Alpine valleys at elevation around 1000-1400 m a.s.l. Still, different individual sensitivity to precipitation will probably result in patchy patterns, with healthy trees close to individuals with declining growth rates, and defoliated crowns infested by mistletoe.

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Author contribution statement

DC conceived the study, contributed to data acquisition, and drafted the manuscript. AB contributed to climate analysis and manuscript preparation. RM was the principal investigator of the scientific project, contributed to result interpretation, and provided critical revision of the manuscript. GV was responsible for study design and acquisition of data, and contributed to analysis on competition and manuscript preparation.

Conflict of interest

The authors declare that they have no conflict of interest

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FIGURE CAPTIONS

Fig. 1 Location of the four study sites, Challand-Saint-Anselme (Chal), Saint Denis low (SD1) and high (SD2) elevation, Morgex (Morg), and the Region's capital city (Aosta), within the Aosta Valley Region, Northwestern Italy. Green indicates forested area

Fig. 2 Bootstrap correlation coefficients between the four stand chronologies and April to August climate variables. TEMP = temperature, PRCP = precipitation, P/PET = ratio between precipitation and potential evapotranspiration, sc-PDSI = self-calibrating Palmer Drought Severity Index, SPEI = Standardized Precipitation Evapotranspiration Index. Dark bars indicate correlation coefficients significant at $p < 0.05$

Fig. 3 Mean Basal Area Increment (BAI) in the four study sites during 1965-2005

Fig. 4 Percentage of trees with annual BAI below the 1965-2005 average (all plots). Years with more than 2/3 of trees with BAI lower than average are indicated with red bars

Fig. 5 May climate anomalies in 1987-1993, 1994-1998, and 2003-2005 relative to the reference period 1965-2005 (equal to 1). TEMP = temperature, PRCP = precipitation, P/PET = ratio between precipitation and potential evapotranspiration, sc-PDSI = self-calibrating Palmer Drought Severity Index, SPEI = Standardized Precipitation Evapotranspiration Index

Fig. 6 Median growth (BAI) decline in 1987-1993, 2003-2005, and recovery in 1994-1998. Different letters indicate different growth response between stands in the same period, according to Kruskal-Wallis median test with Mann-Whitney pairwise comparisons

Fig. 7 Relationship between individual tree growth decline in 1987-1993 (a) and 2003-2005 (b), and response to May precipitation in the previous period in the four stands

Fig. 8 Percentage crown transparency in the four study stands during 2005

SUPPLEMENTARY FIGURE CAPTIONS

Fig. 1 Bootstrap correlation coefficients between the four stand chronologies and climate variables from May of the previous year to September of the ring formation year. Dark bars indicate correlation coefficients significant at $p < 0.05$

Fig. 2 April, June, July and August climate anomalies in 1987-1993, 1994-1998, and 2003-2005 relative to the reference period 1965-2005 (equal to 1). TEMP = temperature, PRCP = precipitation, P/PET = ratio between precipitation and potential evapotranspiration, PDSI = self-calibrating Palmer Drought Severity Index, SPEI = Standardized Precipitation Evapotranspiration Index

Table 1 Site and stand characteristics, and tree-ring statistics, for the four stands

	Site			Stand							Chronology			
	Elevation m a.s.l.	Slope %	Aspect	Trees pine n	Trees total n	BA pine m^2	BA total m^2	QMD pine cm	Height pine m	Age pine years	Cores n	MS	AR	Rba
SD1	985	62	SW	876	1400	13.6	18.0	12.8	6.4	60	54	0.394	0.386	0.45
SD2	1350	34	SW	929	929	35.7	35.7	22.1	11.9	124	66	0.240	0.417	0.36
Morg	1090	77	S	610	824	34.1	36.8	23.8	13.5	95	73	0.252	0.404	0.36
Chal	1115	40	W	573	724	35.3	42.3	27.3	15.6	95	39	0.263	0.369	0.50

For site characteristics, Elevation is the mean plot elevation, Slope is the mean percent slope, and Aspect is the main exposition. For stand characteristics, all referred to one hectare, Trees pine is the number of Scots pine trees, Trees total is the total tree number (i.e., including all the species), BA pine is Basal Area of Scots pine, BA total is the total Basal Area, QMD pine is the quadratic mean diameter of Scots pine, Height pine is the mean height of all Scots pine trees, Age pine is the mean number of years at breast height, estimated to the pith, of the cored Scots pine trees. For tree-ring series, it is reported the number of successfully cross-dated cores, the mean sensitivity (MS), the autocorrelation (AC), and the mean correlation between trees (Rbar)

Table 2 Competition indices (CIs) with corresponding equations, and correlations (Pearson's R) with individual tree BAI over the last 10 years in the four stands. For CAI, linear regression slope is also reported in brackets

Index	Source	Variables	Equation	SD1	SD2	Morg	Chal
Voronoi	Daniels et al. (1986)	Distance	-	0.44	0.19	0.26	0.42
BAL	Wykoff (1990)	Basal Area	$\frac{\sum_{j=1}^{n} BA_j}{BA_i^2}$	0.15	0.28	-0.03	0.17
Hegyi	Hegyi (1974)	Distance, dbh	$\sum_{j=1}^{n}\frac{D_j}{D_i\cdot\left(L_{ij}+1\right)}$	-0.63	-0.33	-0.49	-0.41
PK	Pukkala and Kolström (1987)	Distance, height	$\sum_{j=1}^{n}\arctan\frac{\left(H_j-H_i\right)}{L_{ij}}$	-0.07	-0.30	-0.49	0.02
CCS	Alvarez Taboada et al. (2003)	Distance, crown area	$\sum_{j=1}^{n}\frac{A_j}{A_i\cdot L_{ij}}$	-0.66	-0.41	-0.53	-0.51
CAI	Castagneri et al. (2008)	Dist., crown area, height	$\sum_{j=1}^{n}\frac{\left(\frac{A_j\cdot H_j}{A_i\cdot H_i}\right)}{L_{ij}}$	-0.68 (-0.41)	-0.47 (-0.25)	-0.60 (-0.39)	-0.58 (-0.30)

In the equations, n is the number of competitors, D_i the subject tree dbh (cm), D_j the competitor tree dbh (cm), BA_i the subject tree basal area (cm^2), BA_j the competitor tree basal area (cm^2), L_{ij} the distance between competitor and subject tree (m), H_i the subject tree height (m), H_j the competitor tree height (m), A_i the subject tree crown area (m^2), A_j the competitor tree crown area (m^2)

Table 3 Parameter estimates of univariate linear mixed models of tree response to May precipitation (R. May prec), growth decline in 1987-1993 (BAI 87_93), recovery in 1994-1998 (BAI 94_98), and decline in 2003-2005 (BAI 03_05), and of univariate generalized linear models of crown transparency (Transparency)

	R. May prec	BAI 87_93	BAI 94_98	BAI 03_05	Transparency
Age	-0.008	0.003	-0.011	**0.013***	-0.011
DBH	-0.014	0.029	-0.048	0.014	-0.042
Height	-0.001	0.001	-0.001	0.001	0.001
Crown area	0.019	0.208	0.012	0.176	**-0.575***
Comp. index	-0.065	**-0.221***	-0.174	-0.036	-0.333
R. May prec.		**-1.741***	1.141	**-1.823****	-0.585
BAI 87_93			-1.966	-0.098	
BAI 94_98				-0.673	
BAI 03_05					-0.644

Bold indicates significant predictors at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 4 Parameter estimates of linear mixed models (multivariate) of growth decline in 1987-1993 (BAI 87_93, Model 1) and in 2003-2005 (BAI 03_05, Model 2). Comp. index is the individual CAI value; R. May prec is tree response to May precipitation; Age is tree age

	Estimate	Std. Err.	Sig.	AIC
Model 1 (BAI 87_93)				-336.4
Comp. index	-0.024	0.008	**	
R. May prec.	-0.179	0.077	*	
Model 2 (BAI 03_05)				-310.6
Age	0.001	0.0003	*	
R. May prec.	-0.156	0.0595	**	

* indicates $p < 0.05$, ** indicates $p < 0.01$

Table 5 Parameter estimates of generalized linear model (multivariate) of crown transparency at SD1 (Model 3). Mistletoe is percent infestation of mistletoe on the tree; BAI 03_05 is growth decline in 2003-2005

	Estimate	Std. Err.	Sig.	AIC
Model 3 (transparency)				181.3
Mistletoe	0.0748	0.0298	*	
BAI03_05	-0.2558	0.0986	*	

* indicates $p < 0.05$