

The effect of rainfall and competition intensity on forest response to drought: lessons learned from a dry extreme

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Abstract We investigated forest responses to global warming by observing: (1) planted *Pinus halepensis* forests, (2) an aridity gradient—with annual precipitation (P) ranging from ~300 to ~700 mm, and (3) periods of wet and dry climate that included the driest period during at least the last 110 years. We examined: (1) how the length of climatic integration periods to which trees are most responsive varies in space and time, (2) the extent to which competition modulates growth decline during drought (2011) and subsequent recovery (2012) years. The temporal scale of rainfall that was most influential

on growth shortened in progressing southward, and in the drier than in the wetter period. Long-term underground water storage, as reflected in the relationship of growth to multiple-year rainfall, remained significant up to the point where $P \approx 500$ mm. Under drier conditions ($P < 500$ mm) in both space and time, influential rainfall scales shortened, probably reflecting a diminishing role of water storage. These drier locations are the first from which the species would be likely to retreat if global warming intensified. Competition appeared to set an upper limit to growth, while growth variation among individual trees increased as competition-intensity decreased. That upper limit increased in 2012 compared with 2011. The observed insensitivity of slow-growing trees to competition implies that mortality risk may be density independent, when even any potential for higher soil moisture availability in open stands is lost to evapotranspiration before it can benefit tree growth.

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Introduction

Extreme climatic events, superimposed on persistent warming and drying of the weather, have become more frequent in the Mediterranean region (Hoerling et al. 2012). Climatic projections associated with global warming scenarios indicate a similar trend (Giorgi and Lionello 2008), with aridity expected to shift northwards and/or to higher altitudes (Jump et al. 2009). Water availability is the main limiting factor for vegetation in the Mediterranean region (Pigott and Pigott 1993), therefore this trend has profound

implications for functioning of vegetation: increased incidence of performance decline and mortality events in forests have already been reported, both in this region (Korner et al. 2005; Carnicer et al. 2011; Sanchez-Salguero et al. 2012) and worldwide (Allen et al. 2010), in the last few decades. Knowledge of the spatial and temporal determinants of responses of the main forest tree species to climatic changes is, therefore, important for predicting and, possibly, alleviating forest decline.

It is well known that, in many cases, radial growth of trees integrates the effects of previous year(s) climatic and ecological conditions (Fritts 1976), which are expressed in temporally autocorrelated series of tree-ring widths. Such integration may result from buffered and/or accumulative behavior of the temporal variation in the resources the tree utilizes; behavior expressed in: the physiological [e.g., carbon balance (Niinemets 2010)] and structural [e.g., foliage amount (Galiano et al. 2011); xylem integrity (Brodrribb et al. 2010)] state of the tree itself, or of its immediate environment [e.g., soil/bedrock water storage (Breshears et al. 2009)]. Regarding the latter, moisture stored in deep soil layers and in bedrock can play an important role in the survival of vegetation in dry climates (Raz-Yaseef et al. 2010; Schwinning 2010). Such moisture domains are within reach of tree roots (Zwieńiecki and Newton 1995), relatively safe from evaporative loss (Newman et al. 1997), and may be quantitatively substantial (Querejeta et al. 2007; Breshears et al. 2009; Schwinning 2010). Thus, they potentially may serve as a moisture resource for trees, which fluctuates over multi-annual periods.

The dominant low-elevation conifer in the Mediterranean is *Pinus halepensis* s.l. (Schiller 2000). Diverging trends of performance were recently observed among *P. halepensis* forests in relatively humid (Linares et al. 2011) and arid (Sarris et al. 2011) parts of its distribution, as well as along climatic gradients (Vicente-Serrano et al. 2010b; Dorman et al. 2013b). Differences among responses to drought events may be, at least partially, due to differing time scales over which vegetation is sensitive to drought stress (Pasho et al. 2011; Levesque et al. 2013; Vicente-Serrano et al. 2013). Characterization of the dominant time scales over which drought influences forest performance could, therefore, be critical for early detection of forest decline and mortality events.

Indeed, under past exposures to drought intensification, growth of *P. halepensis* s.l. in Greece has been found to shift from seasonal to multi-annual influences of previous rainfall (Sarris et al. 2007), as occurred during the extremely dry decades in the region at the end of the twentieth century (Sarris et al. 2011). It has been hypothesized that dependence on longer rainfall-integration periods expressed increasing utilization of deep moisture pools by the drought-stressed trees (Sarris et al. 2007), and this hypothesis was supported by interpretations of carbon and oxygen isotope signals in tree rings (Sarris et al. 2013).

Such effects have also been noticed for other low-elevation conifers in the central Mediterranean region, e.g., *Pinus pinea* (Mazza and Manetti 2013).

Pinus halepensis s.l. populations in Israel include a large portion of the moisture conditions within which the species can survive: from relatively moist conditions (~800 mm annual rainfall) in the north to very dry (~250 mm) in the south. The southernmost populations are of special interest (Grunzweig et al. 2003; Maseyk et al. 2008a, b) since they are very close to the species' survival limits and beyond the limit of its natural distribution. *P. halepensis* is considered the most drought resistant of the Mediterranean pines (Schiller 2000), thanks to physiological adjustments associated with drought avoidance (Klein et al. 2011). Nevertheless, its populations in southern Israel recently exhibited high mortality rates, reaching even 90 % in some locations (Dorman et al. 2013a). Thus, they were ideal for testing the hypothesis that multi-annual accumulated rainfall drives growth under severe drought stress, possibly related to forest die-back caused by depletion of deeper-ground moisture pools.

In addition to effects of climate, forest performance is affected by structural attributes such as tree density. Competition intensity is generally negatively related to growth (Linares et al. 2010), although not in all cases (e.g., Julio Camarero et al. 2011; Granda et al. 2013). Density may significantly interact with climatic conditions and with location along a climatic gradient, which suggests enhanced detrimental effects of high density in drought years (Sanchez-Salguero et al. 2013) and at the dry edges of forest distributions (Gomez-Aparicio et al. 2011; Coll et al. 2013). However, the density at which further thinning would not increase water availability for the remaining trees remains unknown (Ungar et al. 2013).

Extreme drought events may present important tipping points in forest ecosystems (Penuelas et al. 2001; Breda and Badeau 2008). Thus, improved understanding of the sources of variability in the effect of density on tree response to drought requires bridging the gap between regional (Carnicer et al. 2011; Gomez-Aparicio et al. 2011) and more local studies (Pasho et al. 2012; Sanchez-Salguero et al. 2013). Whereas in the former, multivariate effects have been characterized along wide climatic gradients on the basis of forest inventory data, studies in the latter enable analysis of growth responses to specific climatic events by means of a dendro-ecological approach based on annual resolution radial growth trajectories.

It is presumed that thinning could reduce between-tree competition for soil water (McDowell et al. 2006) and thus enhance the trees' adaptive capacity to withstand drought stress (Breda and Badeau 2008; Kerhoulas et al. 2013; Sanchez-Salguero et al. 2013). Recognizing the maximal benefit from thinning, in terms of drought resistance and resilience, for a given tree species in different environmental

Table 1 Geographical and structural characteristics of the ten study sites

Site ^a	T. (C.)	Latitude/longitude	Elev.	Planted	DBH ^b	Height ^b	Density ^b	Mortality ^b
S0	25 (50)	31.38N/34.86E	438	1961	19.4 ± 0.3	10.2 ± 0.3	188.3 ± 11.5	78
S1	30 (60)	31.38N/34.86E	469	1967	20.6 ± 0.3	12.1 ± 0.2	311.7 ± 16.3	2
S2	28 (56)	31.37N/34.85E	409	1969	12.6 ± 0.2	8.4 ± 0.1	373.0 ± 12.6	25
S3	27 (54)	31.42N/34.85E	372	1968	16.0 ± 0.3	11.3 ± 0.2	527.2 ± 13.6	1
C1	29 (58)	31.82N/35.01E	337	1965	22.0 ± 0.6	15.7 ± 0.3	384.6 ± 22.2	2
C2	30 (60)	31.80N/34.99E	328	1962	21.3 ± 0.3	13.5 ± 0.4	336.5 ± 10.6	1
C3	26 (52)	31.78N/34.98E	378	1964	31.2 ± 0.6	16.7 ± 0.4	202.3 ± 14.1	8
N1	25 (50)	33.01N/35.54E	384	1960	35.1 ± 0.9	23.2 ± 0.5	187.3 ± 14.0	2
N2	29 (58)	32.99N/35.48E	678	1960	31.3 ± 1.2	17.5 ± 0.4	278.5 ± 23.1	1
N3	26 (52)	32.95N/35.49E	604	1967	39.6 ± 0.6	19.9 ± 0.4	167.4 ± 10.5	0

T. Sample size of trees, C. sample size of cores, Elev. elevation (m)

^a Sample for site S0 included living and dead trees; samples for the other nine sites included living trees only

^b Averages ± SE (except for mortality) among either the sampled (“focal”) trees [diameter at breast height (DBH; cm), tree height (Height; m)] or those in the 8-m-radius circles around them [density (trees ha⁻¹), mortality (%)]

settings, is essential for sustainable forest management (Ungar et al. 2013; Olivar et al. 2014). The climatic gradient in Israel is steep, but, nevertheless is synchronized with respect to the temporal sequences of climatic deviations, and homogeneous with respect to forest structure in planted *P. halepensis* forests. It therefore provides an excellent opportunity to compare the modulating effects of competition on decline and recovery following a specific drought event, among different positions along this climatic gradient.

In the present study, dendro-ecological methods and quasi-manipulation experiments based on natural variation (i.e., comparison between wet and dry climatic periods) were used to fill in key pieces missing from the puzzle of how semi-arid forests respond to extreme drought, and how competition intensity modulates this response. Our specific study questions were:

1. How does the length of the climatic integration period to which trees are most responsive vary in space, i.e., at different positions along a steep climatic gradient, and in time, i.e., during a relatively wet compared with an extremely dry period?
2. To what extent does competition between trees within a stand modulate growth decline during a drought year and growth recovery in the following wet year, and how do these effects change along a steep climatic gradient?

Materials and methods

Study sites

Nine sites, located in three regions (three sites per region)—south (S1–S3), center (C1–C3) and north (N1–N3)—along

a rainfall gradient with southwardly increasing aridity, were chosen for dendrochronological sampling (Table 1; Figs. S1, S2). An additional site (S0), which exhibited the highest tree mortality levels (78 %) encountered during preliminary field trips, was also sampled in order to contrast the growth rates observed in the nine main sites with those observed under apparently extreme conditions. For site selection, the following criteria were applied: (1) planted forest comprising >80 % *P. halepensis*; (2) planting year during the 1960s; (3) south-facing aspect; (4) similar lithology; and (5) pairwise proximity (i.e., <10-km spacing between each pair of adjacent sites within a region). All ten eventually chosen sites were located on chalk bedrock, the prevailing rock type within Israeli planted forests. Species composition and planting dates were obtained from the Israeli Forest Service geographic information system layer. Aspect data were based on a 25-m digital elevation model layer of Israel (Hall and Cleave 1988). Rock type data were based on 1:50,000 geological maps (Geological Survey of Israel).

Climate data

Daily data of precipitation (*P*), minimum temperature ($T_{\min.}$), and maximum temperature ($T_{\max.}$) were obtained from three meteorological stations (Table 2; Figs. S1, S3). Two additional stations (Fig. S1) were used to interpolate missing daily $T_{\min.}$ and $T_{\max.}$ values in regions S and C, where they involved, respectively, 6 and 5 % of days (Fig. S4). This procedure was our only means of obtaining complete time series of *P*, $T_{\min.}$ and $T_{\max.}$ for the three studied regions. Values were interpolated by using linear regression models (Sarris et al. 2014), based on days when both “predictor” and “predicted” stations operated, i.e., ~17,000 and ~15,000 days in regions S and C,

Table 2 Characteristics of the main three meteorological stations used to monitor climatic conditions in the studied regions and average conditions for 1966–2012

Variable	Season	South ^a	Center ^a	North
Latitude/longitude		31.38N/34.87E	31.72N/34.98E	32.98N/35.51E
Elevation (m)		460	353	930
Distance ^b		1.1, 1.1, 2.9, 5.0	10.7, 8.6, 5.6	4.5, 2.5, 4.0
<i>P</i> (mm)	Fall	43.8	76.6	109.6
	Winter	194.7	338.7	446.9
	Spring	60.5	98.8	135.3
	Summer	0.3	0.0	1.3
	Annual	299.3	514.1	693.0
<i>T</i> _{min.} (°C)	Fall	15.8	17.4	14.4
	Winter	8.0	10.0	5.0
	Spring	11.9	13.3	10.5
	Summer	18.4	20.0	18.3
	Annual	13.5	15.1	12.1
<i>T</i> _{max.} (°C)	Fall	26.8	27.7	22.9
	Winter	16.2	17.3	10.7
	Spring	24.0	24.4	19.5
	Summer	31.7	31.9	29.3
	Annual	24.7	25.3	20.6

P Precipitation, *T* Temperature, *min.* minimum, *max.* maximum

^a Missing daily temperature values for the south and central stations (5–6 %) were interpolated based on two additional stations. See Fig. S1 for station locations, Figs. S4, S5 and text for details

^b Distance (km) from the meteorological station to sites 0–3 (*South*) or sites 1–3 (*Center* and *North*), respectively (Fig. S1)

respectively (Fig. S5). The agreement within station pairs was very high (Fig. S4), with R^2 -values of 0.99 and 0.96 for $T_{\max.}$, and 0.88 and 0.89 for $T_{\min.}$, in S and C, respectively (Fig. S5).

Potential evapotranspiration (PET) was estimated on the basis of $T_{\min.}$, $T_{\max.}$ and latitude, according to Hargreaves (1994). Monthly *P* and PET values were then used to calculate the standardized precipitation-evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010a), which is a site-specific drought indicator that expresses standardized deviations from the average monthly water balance (P –PET); it offers several advantages: (1) the standardization process permits comparison in time and space (Vicente-Serrano et al. 2010a), (2) inclusion of temperature data in the SPEI formulation takes into account the role of warming-induced drought stress (Adams et al. 2009), and (3) the multi-scalar nature of droughts may be expressed by calculating SPEI for different time scales (Pasho et al. 2011). Thus, the SPEI served the following purposes in the present study: (1) it delineated drought periods; and (2) it served as an inclusive indicator of drought severity, encompassing its two main components, i.e., *P* and PET. A 12-month integration period, i.e., SPEI12 (Fig. 1), was chosen for (1) in the light of a previous study in which a stronger response of *P. halepensis* to cumulative droughts over 11 months was detected (Pasho et al. 2011).

The main analysis of climatic conditions (Tables 2, S1; Figs. 1d–f, S3) was based on 47 hydrological seasons (1965/1966–2011/2012), which is the longest period over

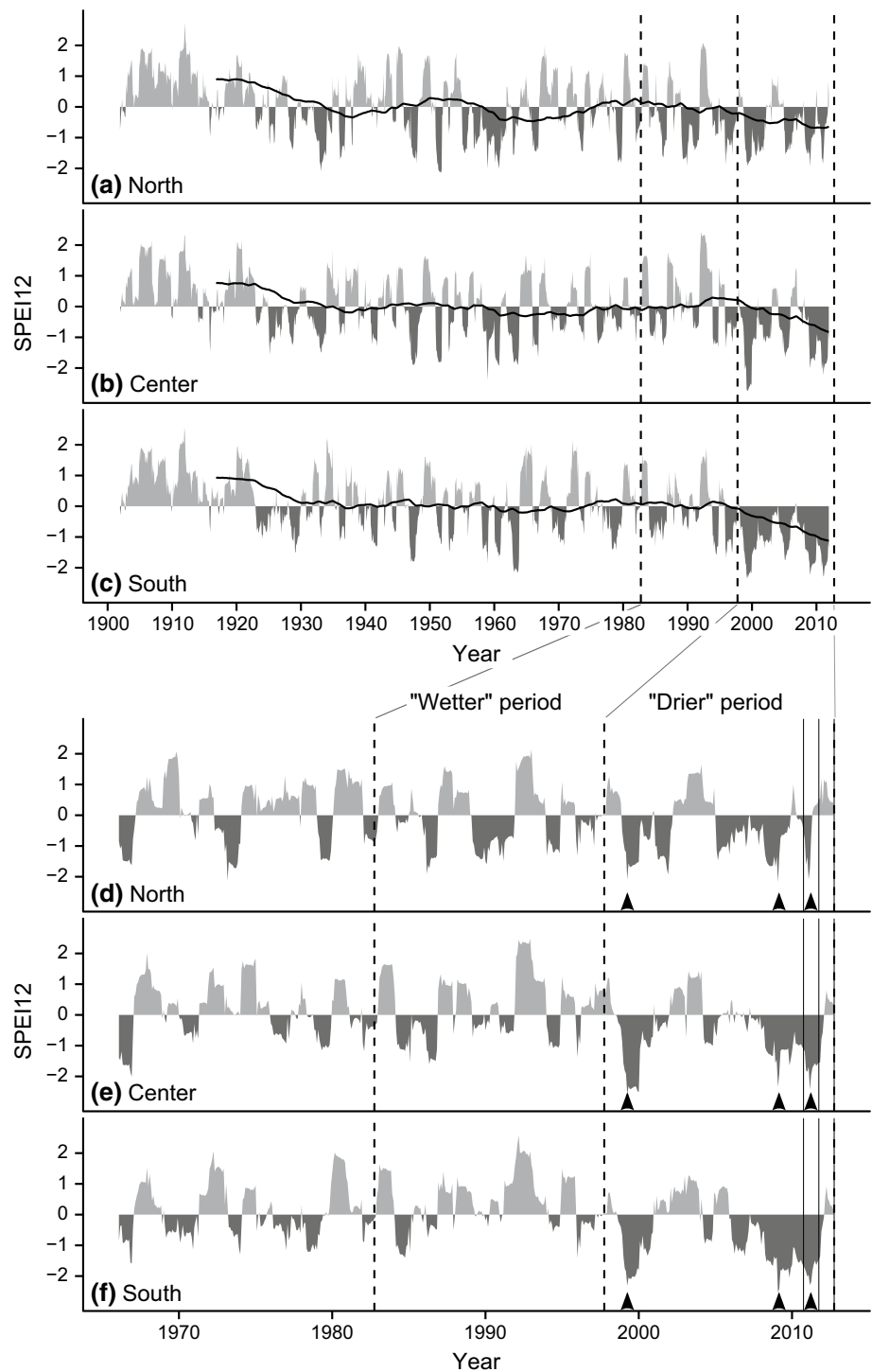
which *P*, $T_{\min.}$ and $T_{\max.}$ data were available from meteorological stations in all three studied regions. In order to provide a broader perspective on the analyzed time frame, we also evaluated SPEI12 evolution over a 110-year period (Fig. 1a–c). The data were downloaded from the global SPEI data base (<http://sac.csic.es/spei/>), which covers the period 1901–2011, for three 0.5° grid cells (north—32°45′N, 35°45′E; center—31°45′N, 34°45′E; and south—31°15′N, 34°45′E).

Field measurements and sampling

Field measurements and dendrochronological sampling took place from autumn 2012 up to and including spring 2013. In each of the nine main sites (S1–3, C1–3, N1–3), 30 “focal” trees were randomly selected from among the living, unsuppressed, i.e., not overshadowed by their neighbours, individuals. In site S0 there were few living trees (Table 1); therefore 27 focal trees were selected, of which eight were alive and 19 dead. Two wood cores were extracted at breast height from opposite sides of each focal tree, by using an increment borer.

All trees located within 8 m (Linares et al. 2010) from a focal tree were considered “neighbours.” We recorded the diameter at breast height (DBH) of each focal tree and its neighbors(s), the distance of each neighbor from its respective focal tree, and the height of each focal tree. Woody species other than *P. halepensis* or regenerated *P. halepensis* individuals were very rare in all sites (Fig. S2) (Osem et al. 2009, 2013).

Fig. 1 A cumulative standardized precipitation–evapotranspiration index (SPEI) over the previous 12-month period (*SPEI12*) as a function of month, based on two data sources, **a–c** 0.5° pixels from the global SPEI database for 1901–2011 (see <http://sac.csic.es/spei/>) and **d–f** local meteorological stations’ data for 1966–2012 (see Fig. S1; Table 2), in three regions: **a, d** north, **b, e** center and **c, f** south. The SPEI is a standardized variable; values above zero denote water surplus, values below zero denote water deficit. **a–c** A 15-year moving average of *SPEI12* (positioned at the end of each consecutive 15-year period) is shown as a black solid line. **d–f** The 2011 and 2012 seasons are marked with vertical lines; extreme drought conditions (*SPEI12* < -2) during the studied period (1983–2012) are marked with arrows



Competition index

The intensity of competition around each focal tree was expressed as a distance- and size-dependent competition index (CI) (Linares et al. 2010). The CI of a focal tree (*f*) is the sum of *N* quotients (*N* = the number of neighbours) between the ratio DBH_n/DBH_f and $dist_{fn}$, where DBH_n and DBH_f are DBH values of the neighbor and focal trees,

respectively, and $dist_{fn}$ is the distance from the focal tree to the corresponding neighbor tree, as follows:

$$CI = \sum_{n=1}^N \frac{DBH_n/DBH_f}{dist_{fn}}$$

The effect of CI on tree growth was examined for the last 2 years—2011 and 2012—which happened to form

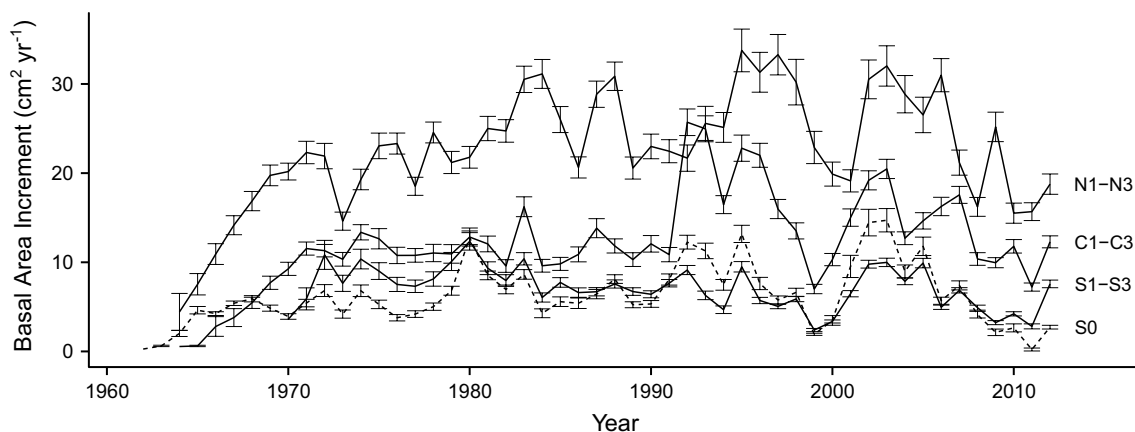


Fig. 2 Basal area increment (BAI) of *Pinus halepensis* as function of year (yr) in the three regions, and in the high-mortality site in the southern region (S0). Values are averages \pm SE, based on 80, 85, and

85 trees for the north (N1–N3), center (C1–C3) and south (S1–S3) regions, respectively, and on 25 trees for the S0 site

a sequence of a drought and a wet year, respectively (see “Results”), enabling us to explicitly address the effects of competition on drought-induced growth decline and subsequent recovery.

Dendrochronological methods

Cores were sanded with increasingly fine sandpaper until tree rings were clearly visible under a binocular microscope. Tree ring width (TRW) was measured to an accuracy of 0.01 mm with a LINTAB 6 measuring device (Rinntech, Heidelberg). In 47 cores (7.9 %) a missing ring could be confidently “interpolated” on the basis of cautious cross-dating against the second core from the same tree (Fig. S6) and the site chronology. These interpolated rings were given the value of 0 mm. In 24 cores (4.0 %) the existence of a missing ring was inferred, but its position could not be unambiguously determined, or the core could not be cross-dated because of tree damage. All 34 cores (5.7 %) from the 17 trees of which at least one core belonged to the latter group were excluded from the analysis. For the remaining 280 trees, average TRW series were calculated based on the two intact cores per tree (Weber et al. 2008).

The last year of growth was 2012, except for the dead trees from site S0, for which the latest year used was that in which a tree ring was present on both cores of the given tree. About half (48 %) of the 54 cores collected in site S0 thus ended at one of the years in the last sequence of drought years (2008–2011) (Fig. 1d–f); the rest ended either earlier (1998–2007; 28 %) or later (2012; 24 %).

To exclude trees having uncharacteristic growth pattern because of damage, agreement of each tree’s TRW series with the corresponding site mean series was evaluated according to the Gleichläufigkeit (Glk) value and its significance. The Glk is a classic time-series agreement

measure based on a sign test—a test that measures the year-to-year agreement between the interval trends of two chronologies, based on the sign of year-to-year growth change and expressed as a percentage (Eckstein and Bauch 1969). Only five trees did not have significant ($p < 0.05$) agreement with their site mean series; these trees were discarded from the analysis. Thus, the final sample (Table 1) consisted of 275 average TRW series from individual trees, i.e., from 92.6 % of the sampled trees.

Detrending by fitting flexible curves (e.g., splines) to the TRW series, followed by removal of autocorrelation from the residual series by means of autoregressive modeling, is a frequently adopted practice in tree ring research (e.g., Pasho et al. 2011), which is intended to emphasize the high-frequency, i.e., year-to-year, component of growth variation. However, it also removes an uncontrolled amount of low-frequency variability (Frank et al. 2007), which is exactly the kind of variability we would expect when growth processes integrate climatic conditions over several years. We thus decided to retain any climate-related low-frequency signals in our tree ring data (Sarris et al. 2014). Therefore, we chose to remove only the trend of decreasing ring width with increasing tree age and size (Biondi and Qeadan 2008), by converting TRW to basal area increment (BAI) values (Fig. 2). The BAI is considered biologically more meaningful than TRW because, by definition, it may express change in resistance to drought of the tree hydraulic system (Brodribb et al. 2010), and it was shown to outperform TRW for evaluating overall tree growth (Biondi and Qeadan 2008), as related to tree mortality (Bigler and Bugmann 2004) and competition intensity (Weber et al. 2008). BAI was extensively used as the primary indicator of trees physiological state in studies examining trees responses to competition (e.g., Linares et al. 2010) and/or

to drought (e.g., Jump et al. 2006), while more refined traits of annual tree rings, e.g., earlywood and latewood widths (Pasho et al. 2012) or isotopic composition (e.g., Levesque

et al. 2013), are used to obtain supplementary physiological information. The BAI was calculated as follows:

$$BAI_t = \pi(R_t^2 - R_{t-1}^2)$$

where R_t and R_{t-1} , respectively, are the stem radii at breast height at the end and at the beginning of annual ring formation. The radius was derived by summing all TRW values, from the pith outwards. If the pith was not reached by the borer, the calculated distance from the pith to the first measured ring, based on each site average, was added at the beginning of the series and removed after calculation of the BAI series (Martin-Benito et al. 2011). Finally, regional average BAI chronologies from the last 30 years (1983–2012), when growth patterns had already stabilized after the establishment phase (Fig. 2), were used for analysis of climatic effects on forest growth in each region.

Table 3 Effects of four climatic variables, at seasonal to annual scales, on average basal area increment (BAI) per region, for the period 1983–2012

Variable	Scale	South	Center	North
P	Fall	0.26 (+)		
	Winter	0.45 (+)	0.41 (+)	
	Spring ^a			0.19 (+)
	Annual	0.71 (+)	0.56 (+)	0.18 (+)
SPEI	Fall			
	Winter	0.50 (+)	0.41 (+)	
	Spring ^a			0.20 (+)
	Annual	0.70 (+)	0.58 (+)	0.22 (+)
$T_{min.}$	Fall	0.14 (–)		
	Winter	0.28 (–)	0.25 (–)	
	Spring		0.26 (–)	0.24 (–)
	Summer			0.14 (–)
	Annual	0.25 (–)	0.23 (–)	0.21 (–)
$T_{max.}$	Fall	0.19 (–)		
	Winter	0.35 (–)	0.35 (–)	
	Spring	0.14 (–)	0.33 (–)	0.17 (–)
	Summer			
	Annual	0.33 (–)	0.36 (–)	0.17 (–)

Values are R^2 of linear regressions with the *sign* of the slope estimate in parentheses, positive (+) or negative (–). Cells where the effects were not significant ($p > 0.05$) are left blank. For other abbreviations, see Tables 1 and 2

^a The effects of summer P and the standardized precipitation-evapotranspiration index (SPEI) were not examined because P is negligible in that season (Table 2), therefore the effect of P is meaningless and that of SPEI is reduced to the effect of $T_{min.}$ and $T_{max.}$

Statistical analysis

Climatic trends (Table S1; Fig. S3) and effects of climatic conditions on BAI (Table 3; Figs. 3, S7, S8) were evaluated at various time scales by using linear regression; more specifically, by using the estimates and p -values of the terms in a given model, and the fractions of variance explained by that model (R^2). Quantile regression (Cade and Noon 2003) was used to examine the effect of CI on BAI (Table 4; Fig. 4), where a non-homogeneous relationship was detected (see “Results”).

Statistical analyses were done with the R software (R Development Core Team 2013). The quantreg package (Koenker 2013) was used for fitting quantile regression models; the SPEI package (Beguería and Vicente-Serrano 2013) for calculating PET and SPEI, and the dplR package (Bunn 2008) for calculating Glk.

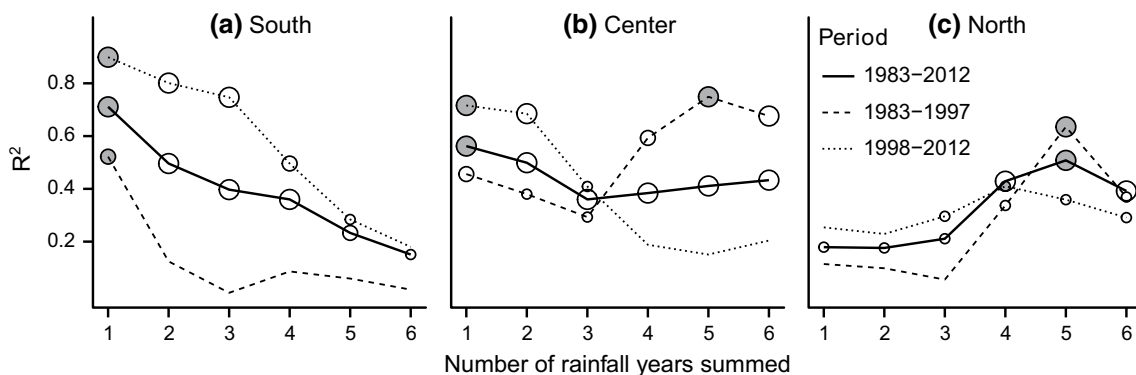


Fig. 3 R^2 -values from linear regression of tree growth (BAI) as function of rainfall amount, for different rainfall integration time-scales (1–6 years) and for three periods (1983–1997, 1998–2012, and 1983–2012), in each of the three regions: **a** south, **b** center and **c** north. Rainfall effects on BAI were positive in all cases. Significant effects

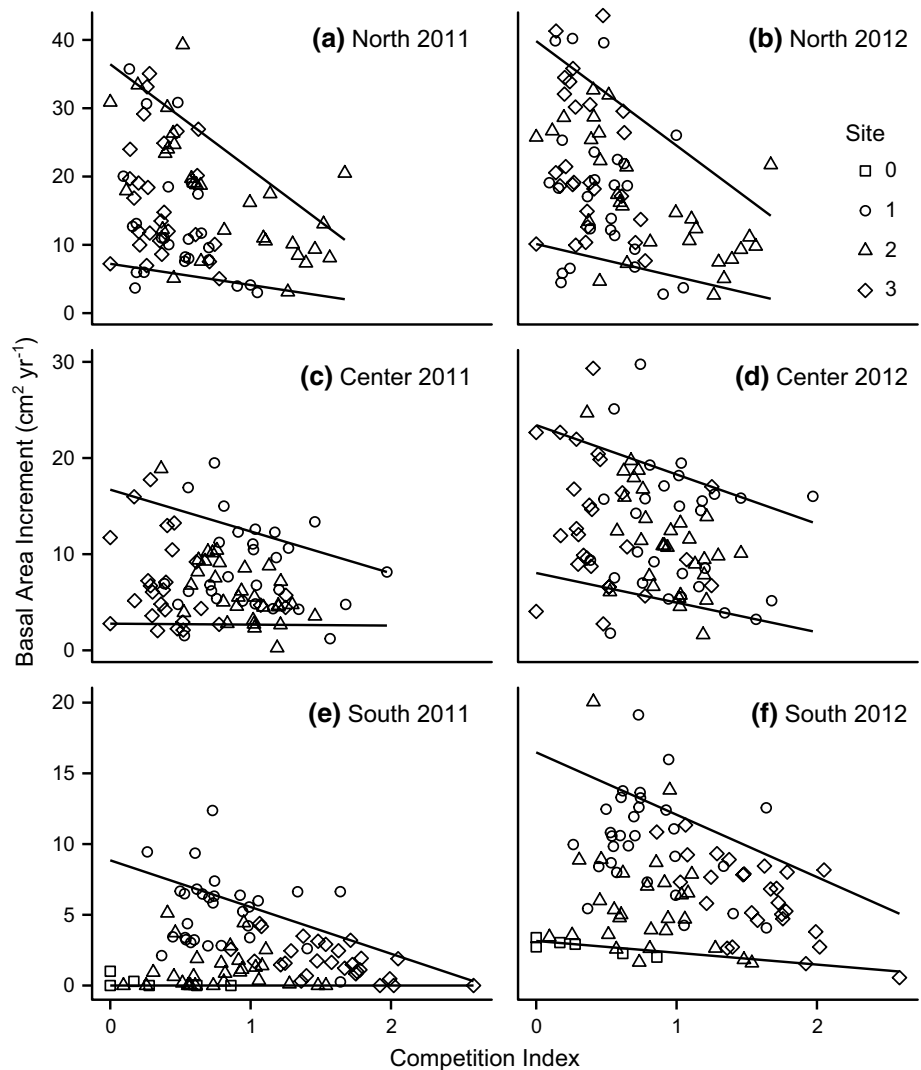
of rainfall are marked with empty circles, with circle size proportional to significance level [$p < 0.001$ (large), $p < 0.01$ (intermediate), $p < 0.05$ (small)]. The integration period that produced the highest R^2 in each region/period combination is marked with a filled circle

Table 4 Summaries of quantile regression models (10 and 90 % quantiles, i.e., $\tau = 0.1$ and 0.9, respectively) for BAI as function of the competition index (CI), for 2 years in three regions

Term	τ	Region	2011			2012		
			Value	SE	p	Value	SE	p
Intercept	0.1	North	7.22	2.47	0.005	10.12	3.02	0.001
		Center	2.77	1.38	0.047	8.04	2.32	0.001
		South	0	0.66	1	3.15	1.12	0.006
	0.9	North	36.43	3.18	<0.001	39.82	3.11	<0.001
		Center	16.71	2.23	<0.001	23.42	2.34	<0.001
		South	8.85	1.19	<0.001	16.48	1.87	<0.001
CI	0.1	North	-3.1	3.19	0.335	-4.8	3.69	0.198
		Center	-0.1	1.45	0.946	-3.08	2.51	0.224
		South	0	0.52	1	-0.83	0.89	0.353
	0.9	North	-15.39	3.66	<0.001	-15.3	3.98	<0.001
		Center	-4.35	2.17	0.049	-5.13	2.51	0.044
		South	-3.3	0.86	<0.001	-4.41	1.44	0.003

Estimates, SE and significance of the intercept and slope terms were obtained from 12 quantile regression models. The respective 12 fitted lines are shown in Fig. 4
Significant ($p < 0.05$) effects are marked in bold

Fig. 4 BAI as a function of competition index, separately for three regions, **a, b** north, **c, d** center and **e, f** south, and 2 years, **a, c, e** the dry year 2011, and **b, d, f** the wet year 2012. Each point represents an individual tree. Quantile regression lines are drawn for each combination of region, year, and quantile (10 and 90 %). **a–f** Lower line 10 % Quantile, upper line 90 % quantile. See Table 4 for statistics of the 12 respective models. Note that y-axis' ranges differ among panels



Results

Climatic trends

Based on the global SPEI database, the most recent 15-year period has been the driest all three regions have experienced during the last 110 years (Fig. 1a–c). Meteorological station data show that three instances of extreme drought conditions ($\text{SPEI}_{12} < -2$) have been observed during the last 30 years (1983–2012), and that they occurred in the same years (1999, 2009, and 2011) in all three regions (Fig. 1d–f). Notably, these years were concentrated into the second (“drier”) half (1998–2012) of the studied period. However, the durations of extreme droughts differed between regions: in the north, each lasted only 1 month, i.e., 1 month satisfied the criterion $\text{SPEI}_{12} < -2$, whereas longer extremely dry periods were observed in the center (10, 1, and 1 months) and south (7, 3, and 3 months in 1999, 2009 and 2011, respectively).

Annual and seasonal rainfall amounts did not show significant temporal trends, except for a decrease in spring rainfall ($p < 0.05$) in the central and northern regions (Table S1; Fig. S3). Temperature (T_{\min} and T_{\max}), however, significantly increased in all three regions, at annual ($p < 0.001$) (Fig. S3) and, in most cases, also seasonal (Table S1) scales. In all regions the steepest rate of temperature increase was observed in summer. For example, the estimated warming rates in the south were 0.051 and 0.054 °C year⁻¹ (Table S1), summing over 47 years to increases of 2.4 and 2.5 °C in T_{\min} and T_{\max} , respectively.

Missing rings

The percentages of cores having at least one missing ring were higher in the south than in the center and north (Table S2). Almost all identified missing rings were associated with the year 2011 (Table S2), and the lowest growth rate among all combinations of sites and years was observed in the high-mortality site S0 in 2011. Six living trees from that site were the only ones for which the 2011 tree ring could be dated on both sampled cores; four of them had a ring missing from the 2011 position, the other two had BAI of 0.30 and 1.00 cm² year⁻¹, giving an average BAI of only 0.22 cm² for that year (Fig. 2). This observation expresses the potentially devastating impact of the 2011 drought on tree growth processes, as well as the association of low growth rates with high mortality risk.

Climate–growth relationships at seasonal to annual scales

In all cases with significant ($p < 0.05$) effects of climatic variables on BAI, the effects of P and SPEI were positive, whereas the effects of T_{\min} and T_{\max} were negative

(Table 3). Annual P had a stronger effect on BAI than seasonal P in the south and center, whereas in the north the effect of annual P was slightly lower than that of spring P . The temperature terms accounted for variation in BAI to similar, relatively small degrees (14–36 %) in all regions, whereas rainfall accounted for it to higher, more variable, degrees (18–71 %).

The importance of the total annual rainfall was further demonstrated by comparing the effects of total rainfall among all possible 12-month annual integration periods. Rainfall totals in the seven 12-month periods that include November–April (which is when ~ 95 % of rainfall occurs, in all three regions) had the highest and relatively constant influence on BAI (Fig. S7). The period November–October was chosen for all subsequent analyses, because, on “average,” it produced slightly higher R^2 -values, among regions (0.48 vs. 0.47–0.48; Fig. S7); however, it was noted that each of the seven alternative periods produced essentially identical results.

In the south and center, either annual P or annual SPEI had the closest fits to the average BAI pattern, whereas in the north T_{\min} had the same effect magnitude as P and SPEI (Table 3). The R^2 -values for the effects of annual P and SPEI were very similar—differing by 0.01–0.04 R^2 “units,” with a similar “average” R^2 of 0.48–0.50 in the three regions. This suggests that use of the more complex SPEI (which is based on P , T_{\min} , T_{\max} , and latitude) offered no advantage over the use of P alone. In accordance with the principle of parsimony (Johnson and Omland 2004), we chose to proceed with the simpler variable (i.e., P) that accounted for the same amount of variation in tree growth.

Multi-annual rainfall effect on growth

When the whole studied period (1983–2012) was examined, multiple-year rainfall was found to have less influence on tree growth than shorter integration periods with progression from north to south (Figs. 3, S8), in contrast to what could be expected based on previous studies (see “Introduction”). Annual rainfall had the highest effect on BAI in the south and center, whereas in the north the most influential scale was 5 years (Figs. 3, S8). Furthermore, in parallel with the lengthening of the influential rainfall integration period, the percentage of BAI variation accounted for by rainfall amount decreased in absolute terms (Fig. 3) in progressing from the south (71 %; 1 year) through the center (56 %; 1 year) to the north (51 %; 5 years).

The responses to climate also differed when the “wetter” (1983–1997) and “drier” (1998–2012) halves (Fig. 1d–f) of the studied period were compared (Fig. 3). In the south, annual rainfall was most influential in both periods, but its effect was higher in the drier period ($R^2 = 0.90$) than in the wetter one ($R^2 = 0.52$). In the center, 5-year rainfall was

most influential in the wetter period ($R^2 = 0.75$), whereas annual rainfall became most influential in the drier period ($R^2 = 0.72$). In the north, the most influential scales were 5 ($R^2 = 0.64$) and 4 ($R^2 = 0.41$) years in the wetter and drier periods, respectively. Thus, a drastic transition in the rainfall-integration periods that accounted for growth was only observed in the center, as the climate shifted to drier conditions.

Competition effect on growth

A heteroscedastic (i.e., heterogeneous statistical variances) pattern was evident in the relationship between CI and BAI, characterized by decreasing variation in BAI among sampled trees, with increasing CI (Fig. 4). Within a given moisture regime, competition appeared to set the upper limit that growth could reach, whereas BAI variation decreased as CI increased. Consequently, we were interested in statistically testing whether the likelihood of observing extreme values of growth (very high or very low BAI) was related to competition. We used quantile regression to separately assess the effects of competition on the lower and upper parts of the BAI distribution (Cade and Noon 2003), specifically the upper and lower deciles, i.e., the 10 and 90 % quantiles (Table 4; Fig. 4).

The slopes, i.e., CI effects (Table 4) of the 10 % quantile regressions were not significantly different from zero in all regions and both years ($p > 0.1$), but the intercepts of the 10 % quantile regressions were significantly ($p < 0.05$) different from zero in all cases except for 2011 in the south ($p > 0.1$). In other words, the “lower level” that BAI reached was constant, consistently uninfluenced by competition. That lower level of BAI was generally higher than zero, except for 2011 in the south (Fig. 4e).

As for the 90 % quantile regressions, both the slope and intercept terms were significantly ($p < 0.05$) different from zero in all cases, and all slopes were negative (Table 4; Fig. 4). In other words, CI had a negative effect on the “upper level” that BAI reached, in all regions and both years. Interestingly, the effect was strongest in the north, where the 90 % quantile of BAI decreased by $15 \text{ cm}^2 \text{ year}^{-1}$ per unit CI, compared with $3\text{--}5 \text{ cm}^2 \text{ year}^{-1}$ in the south and center (Table 4).

The upper limit of BAI variation increased during the wet year 2012 compared with the very dry one of 2011 in all three regions (Table 4; Fig. 4), and the change was more pronounced towards drier areas. From 2011 to 2012, the estimated 90 % BAI quantile at zero competition (i.e., the intercept term in the 90 % quantile regression model) increased from 8.9 to $16.5 \text{ cm}^2 \text{ year}^{-1}$ in the south, compared with an increase from 16.7 to $23.4 \text{ cm}^2 \text{ year}^{-1}$ in the center, and from 36.4 to $39.8 \text{ cm}^2 \text{ year}^{-1}$ in the north (Table 4).

The implication of these results is that the range of observed BAI values decreased as CI increased. The clearest example of this phenomenon was observed during the drought year 2011 in the south, where the 10 and 90 % regression lines meet at CI of 2.7, at BAI of 0, and cross the x -axis at BAI of 0 and $8.9 \text{ cm}^2 \text{ year}^{-1}$, respectively (Table 4; Fig. 4e). In other words, zero growth was expected in all trees experiencing intense competition ($\text{CI} > 2.7$), whereas under minimal competition pressure ($\text{CI} = 0$) BAI values varying between 0 and $8.9 \text{ cm}^2 \text{ year}^{-1}$ could be expected.

Discussion

Rainfall effect at the annual to multi-annual scales

The limiting effect of storage capacity on vegetation is expected to be maximized in regions where $P \approx \text{PET}$, on an annual scale, since the water budget is mainly limited by energy in wetter regions and by precipitation in drier regions (Milly 1994; Schwinning 2010). Although the entire studied area falls into the $P < \text{PET}$ category, the average annual water balance ($P - \text{PET}$) was most negative in the south, at $-1,096 \text{ mm}$, compared with -858 mm in the center and -470 mm in the north (during 1983–2012). Therefore the potential importance of multi-annual rainfall is theoretically expected to increase from south to north, as indeed has been observed in the present study (see below).

The importance of the single-year integration period of rainfall in explaining tree growth in the southern region (Maseyk et al. 2011), which is extremely dry for *P. halepensis*, could be associated with the very negative water balance, which leads to loss of most of the annual rainfall during the same year (Raz-Yaseef et al. 2012; Ungar et al. 2013). It was previously shown that the proportion of annual rainfall transpired by a planted *P. halepensis* stand increases with progress from a relatively humid to a relatively arid region. In a region having 280-mm average annual rainfall—Yatir Forest, adjacent to our southern sites—transpiration of the *P. halepensis* trees amounted to 80 % of annual rainfall (Schiller and Cohen 1998), compared with 69 % in a 700-mm year^{-1} region (Ramat Hanadiv) (Schiller and Cohen 1995). Subsequent studies in Yatir Forest found lower proportions: 49–66 % in 2004–2006 (Klein et al. 2013; Ungar et al. 2013); 37 % in 2007 (Raz-Yaseef et al. 2010) and 57 % in 2010 (Klein et al. 2014). The reduction is attributed to thinning from 600 to 300 trees ha^{-1} , which took place in 1994 (Ungar et al. 2013). However, it was also found that surface runoff and deep drainage were negligible (Raz-Yaseef et al. 2010). Therefore, most of the “remaining” rainfall water is lost to the atmosphere each year through interception or through

evapotranspiration from the soil and the herbaceous understory vegetation (Ungar et al. 2013). Thus, the potential for water to be stored and carried over from one year to the next is expected to be low in that region.

In the more humid regions, i.e., center and north, the potential for water to accumulate in deep soil/bedrock layers may be higher, as suggested by the effect of multi-annual accumulated rainfall on tree growth. The shorter influential rainfall-integration periods in the “drier” half of the studied period than in its “wetter” half, are also in accordance with the latter expectation. The higher drought stress during the drier period could result in depletion of water accumulated in deeper layers from previous years, leading to trees’ dependence on shorter rainfall-integration periods. Thus, as could be expected, the transition from longer to shorter integration periods was most pronounced in the central region (Fig. 3), which experiences moderate dryness. In the south, single-year rainfall was already the most influential factor from the beginning of the studied period; therefore drought only increased the impact of the loss of annual rainfall. In the north, rainfall reduction may have had a relatively minor effect, compared with that in the other regions, because the water balance in this region is the least negative (Fig. S3), and recent droughts were the mildest (Fig. 1).

Our estimate for the threshold of the transition towards dependence on annual rainfall was $P \approx 500$ mm (or $P-PET \approx -850$ mm), because the dramatic shift in the influential integration periods (from 5 years to annual; Fig. 3b) was observed in the center, where P decreased from 563 to 438 mm (or $P-PET$ from -788 to -895 mm) between 1983–1997 and 1998–2012. In the north and south, average P (and $P-PET$) values were outside of that range in both periods (higher and lower, respectively) and, indeed, no prominent changes in the lengths of influential rainfall-integration periods were observed in these two regions. The region-dependent disruption of carry-over effects may be a valuable target for future research (Granda et al. 2013), since the shortening of time scales at which climatic influences on tree growth occur implies that more immediate response to drought would be expected; the latter needs to be incorporated into predictions of forest responses to drought (Vicente-Serrano et al. 2013).

Sarris et al. (2007) have shown that on the island of Samos (Greece), which experienced gradual rainfall decline, *P. halepensis* s.l. depended on 4–6 years of rainfall during 1994–2000, when average annual precipitation was 659 mm; during the previous wetter period, shorter integration periods were more influential. These results are in accordance with our present findings, in light of the hypothesis regarding the dependence of the importance of storage capacity on the annual water balance. During 1994–2000 Samos received rainfall amounts similar to those of

northern Israel (659 and 693 mm, respectively), and similar integration periods (4–6 and 4–5 years, respectively) were found to have the most influence on tree growth in both cases. The earlier period in Samos was wetter (842 mm in 1951–1977), therefore it could be that the importance of storage and, therefore, of multi-annual rainfall was again reduced, because the limiting effect of water availability on tree growth was weaker (Schwinning 2010). This is in agreement with findings for another tree species growing in a relatively humid environment (Levesque et al. 2013), where greater utilization of water from deeper soil layers was indicated at a relatively xeric site (701-mm annual rainfall) than at a relatively mesic one (1,184 mm).

In light of our present findings, together with those from Greece (Sarris et al. 2007, 2011, 2013), we suggest that along the aridity gradient in eastern Mediterranean *P. halepensis* forests, influential drought scales are multi-annual under intermediate water-balance conditions, and that they contract towards annual scales under either drier or wetter conditions, in space (along climatic gradients) and in time (under alternating wetter and drier climatic conditions). By artificially extending the geographical range of the species, the planted forests may, therefore, provide a valuable demonstration of the processes that will occur at the xeric limit of the natural distribution of *P. halepensis* s.l. in the future, under global climate change.

Effect of competition

The non-homogeneous variability of competition effect on tree growth was in accordance with the concept of multiple limiting factors operating in the studied system (Cade and Noon 2003). In other words, the degree of responsiveness to competition varied among trees from different “portions” of the BAI variation; whereas the fast-growing trees were sensitive to competition, and therefore more likely to occur in low-competition neighborhoods, the slow-growing trees were insensitive, and therefore equally likely to occur under all competition intensities (Fig. 4). The insensitivity to competition of the slowest growing trees, as well as the lack of association between tree density and mortality among sites (Table 1), thus indicate that mortality risk may be density independent, contrariwise to the traditional assumption (e.g., Linares et al. 2010).

The *P. halepensis* forests in Israel were mostly planted on shallow soil, because areas of deeper soil were utilized for agriculture. For example, average soil depths in Lahav (where sites S0–S2 are located) and Yatir (~ 15 km to the east) forests are 30–35 cm (Schiller 1972). Under such conditions, the differences in tree growth and performance are significantly affected by the differences in storage capacity of the subsoil materials (Schiller 1982), which can be substantial (Schwinning 2010, 2013). For

example, the development of *P. halepensis* was similarly good on marl and chalk (which our study sites are located on) in a 200- to 300-mm-rainfall area to that on limestone or dolomite in a 500- to 600-mm area, probably because of the contributions to water retention of the higher porosity and lower permeability of the former (Schiller 1982).

We hypothesize that the structure of the soil/bedrock complex, in addition to modifying water storage, may change the nature of competition for water. When soil water storage is mainly limited to shallow soil/bedrock interfaces, trees' zones of influence may be much less under their own control, i.e., with a fixed water-harvesting area surrounding each tree, but instead may be determined by the frequency of suitable bedrock fissures (Schwinning 2010, 2013). It is even possible for pathways for roots through rocks to be so scarce that roots of different individuals will rarely come into close contact except in the soil horizon (Schwinning 2013). Further research is necessary to examine whether slow growth and insensitivity to competition, at both the individual-tree and site levels, may characterize locations of low-capacity and/or fragmented water pools in deep soil layers.

It is important to note that the present study addressed only unsuppressed trees; therefore, the range of competition intensities (Fig. 4) does not include the most extreme competition conditions. However, extrapolation of our results shows that the probability of observing high growth rates in suppressed trees was very low, regardless of local habitat quality; with regard to the drought year 2011 in the south as an extreme example, zero growth was expected in all trees at CI > 2.7 (Fig. 4e). The association of lower growth rates with increased mortality risk was established in numerous studies (e.g., Suarez et al. 2004; Bigler et al. 2007). It was also shown that tree ring production may stop some years before actual tree death, as defined by lack of green foliage (Cherubini et al. 2002). Very narrow or missing tree rings, therefore, express the most extreme degrees of stress along that continuum, likely indicating high mortality risk for those individual trees (Sarris et al. 2007; Novak et al. 2011).

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