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Short communication

Amount vs. temporal pattern: On the importance of intra-annual climatic conditions on tree growth in a dry environment

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ABSTRACT

Forests in semi-arid regions are at particular risk for climate change impacts. Although it has been recently acknowledged that vulnerability to climate change depends on changes in climatic variability and the occurrence of extreme events, and not just the mean climatic conditions, the relative importance of such effects remains largely unexamined. In the present study we investigated the effects of intra-annual rainfall distribution characteristics, as opposed to total rainfall amount, on tree growth. More specifically, proportion of large rain events and dry season length – two climatic characteristics considered key to the survival of planted *Pinus halepensis* forests in a semi-arid region – were evaluated based on a tree-rings dataset. Dry season length did not have a significant effect on growth, highlighting the high resilience of this species when facing harsh climatic conditions. Proportion of large rain events had a positive effect on growth under dry conditions, as expected. The magnitude of this effect was relatively small, compared to that of total rainfall amount. Nevertheless, an increase in the proportion of large rain events as a result of climate change may potentially balance the decline in its total amount, in terms of trees growth rate, to an extent quantifiable using our statistical model predictions.

Forests in semi-arid regions of mid-latitudes are an example of an ecosystem where negative effects of climate change are already underway (Allen et al. 2010; Steinkamp and Hickler, 2015), with widespread mortality events reducing forest cover and increasing the potential for soil erosion. It has been recently acknowledged that vulnerability of plants to climate change will largely depend on changes in climatic variability and the occurrence of extreme events, and not just the mean climatic conditions (Smith, 2011; Reyer et al. 2013). For example, precipitation events, as well as drought, are predicted to become more extreme, potentially changing soil water distribution across different depths in a way which benefits deeper-rooted woody plants (Kulmatiski and Beard, 2013). Increased climatic variability, however, may also translate to a higher probability of long periods of drought, which may negatively affect perennial species even if the total amount of precipitation is unchanged. For instance, in highly seasonal semi-arid climates tree mortality can occur when dry season length (DSL) surpasses the physiological tolerance threshold of the given tree species (Breshears et al. 2009; Klein et al. 2014). Nevertheless, the consequences of changes in the hydrological regime to vegetation productivity have mainly been limited to theoretical examination, at least for woody plants (Anderegg et al. 2013).

Dendrochronology can provide a retrospective characterization of year-to-year growth variation of trees, making it the most suitable tool for studying climate-growth relationships. Taking into account concurrent climatic conditions, dendrochronological studies have long ago established the link between tree growth processes and limiting climatic factors, one of them being water availability, with varying degree of sensitivity according to the timing of the climatic stress. A recently adopted practice in tree rings research is also taking into account the duration, or time-scale, over which climatic state is observed (Vicente-Serrano et al. 2013). Nevertheless, only a monthly resolution is generally considered (e.g. annual rainfall sum, last 3-months mean temperature in January, etc.). An alternative way of characterizing water availability conditions in a more comprehensive manner involves

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taking one step further and constructing soil water content (SWC) models, fed with detailed climatic data regarding precipitation and potential evapotranspiration (PET). SWC prediction, however, is frequently also based on monthly data (e.g. Lebourgeois et al. 2013) or aggregated to such prior to the contrasting with tree growth (e.g. Michelot et al. 2012). Moreover, SWC models inevitably rely on numerous assumptions, such as soil water holding capacity and maximal transpiration rate, which are difficult to verify, especially for trees (Granier et al. 1999). Thus, climatic characteristics that address higher-than-monthly resolution or characterize timing rather than amount, such as the proportion of large rain events (LRE) and DSL (respectively) largely remain unexamined.

Pinus halepensis is a relatively drought-resistant pine species naturally found in the western Mediterranean region, with a few isolated populations in the eastern Mediterranean. It was also extensively planted, including in semi-arid environments where climate is drier than encountered within the natural distribution range (de Luis et al. 2013). One such region is southern Israel, where planted forests of the species grow under average annual rainfall amounts (P) of 250–350 mm (Schiller and Atzmon, 2009). Recent dendrochronological studies conducted in the region implied that P is the principal climatic variable affecting performance of *P. halepensis*, rather than rainfall amounts over shorter (monthly) or longer (multi-annual) time scales, or other factors such as temperature (Maseyk et al. 2011; Dorman et al. in press-a). Because P is much lower than PET, lack of deep ground infiltration and formation of deep roots may limit the influence of multiple years' rainfall on tree growth. On the other hand, due to the relative insignificance of other limiting factors, all rainfall is potentially utilized for growth, and thus rainfall in no particular month or season is more important than the whole annual sum (Sarris et al. 2007; Dorman et al. in press-a).

A detailed hydrological investigation of the planted forests' ecosystem conducted in the region (Raz-Yaseef et al. 2010, 2012) suggested that forest productivity was more strongly dependent on the proportion of rainfall occurring as part of intensive (>30 mm) storms (P_{30}/P; see below) leading to relatively deep infiltration, than on P. It was also proposed that DSL plays an important role in tree survival – since it determines the amount of time trees are exposed to a zero transpirable SWC regime – given the initial water availability attained by the end of the wet season and the time span until the following wet season begins (Klein et al. 2014). However, both above-mentioned hypotheses are based on a limited time frame (4–5 years), thus the significance and relative importance of the suggested effects could not be examined.

The purpose of the present study is to investigate the relative importance of P_{30}/P and DSL, as opposed to P, for *P. halepensis* tree growth in semi-arid regions. This is achieved by combining (1) simple climatic indices (addressing specific timing- and intensity-related climatic characteristics), the biological importance of which has been previously recognized, with (2) a comprehensive tree-rings dataset spanning a time-frame of 30 years. The results are also ultimately intended to aid in the prediction of forest response to future climatic changes, by highlighting the relative importance of intra-annual rainfall distribution as opposed to its total amount.

The studied area (see Fig. 1 in Dorman et al. in press-b) included planted monoculture *P. halepensis* stands in Lahav and Dvira forests in southern Israel. The climate in this area is semi-arid (average annual rainfall of ~300 mm), and highly seasonal (5 consecutive months with <2.5 mm rainfall depth). Three sites were randomly selected within the area of Lahav and Dvira forests for dendrochronological sampling. All sites were located on south-facing slopes (to test responses of trees to elevated drought stress as such slopes are drier due to higher solar radiation load) of similar lithology, and were of similar age (43–45 years old in 2012).

Dendrochronological sampling was conducted during autumn 2011–spring 2012. In each of the three sites, 30 living unsuppressed, i.e., not overshadowed by their neighbors, trees were randomly selected (Fig. A.1). Two wood cores were extracted from opposite sides of each tree at breast height using an increment borer. Cores were sanded using increasingly fine sanding paper until tree rings were clearly visible under a binocular microscope. Tree Ring Width (TRW) was measured to an accuracy of 0.01 mm using a LINTAB 6 measuring device (Rinntech, Heidelberg, Germany). Five trees with damaged cores or un-datable missing rings were removed from the analysis. Finally, TRW values were converted to Basal Area Increment (BAI) values (Biondi and Qeadan, 2008), and average BAI chronologies were calculated per tree. Structural characteristics of the sites (tree dimensions, density and mortality) are provided in Dorman et al. (in press-b). Records from the last 30 years of tree growth (1983–2012), when growth patterns had already stabilized after the establishment phase (Fig. A.2), were used for analysis of climatic effects on forest growth in each region. The final dataset included 2549 BAI records, from 85 trees over 30 years.

To characterize climatic conditions in the studied area, daily precipitation records for the period 1953–2012 were obtained from the standard meteorological station “Lahav” bordering Lahav forest (31.38N/34.87E). Climatic conditions were characterized using three variables: P, P_{30}/P and DSL. P for the year *t* was defined as the rainfall sum over the respective hydrological year (1st of August in year *t-1* until 31st of July in year *t*). LRE were defined as consecutive runs of rainy days with the total amount of rainfall >30 mm. Annual sum of rainfall during LRE (P_{30}) was divided by P to obtain P_{30}/P (Fig. 1). The onset and the end of the wet season were considered the days when 10% and 90% of the annual rainfall amount have been accumulated, respectively. Accordingly, the DSL for year *t* has been defined as the period of time between the end of the wet season in year *t-1* and the onset of the wet season of year *t-1* (Fig. 1).

A Linear Mixed-Effects Model has been constructed to consider the effects of fixed (P, P_{30}/P and DSL) and random (site and tree-within-site) effects on BAI. The most parsimonious model has been selected according to the Akaike Information Criterion (AIC). For easier interpretation of the model (Table 1), predicted BAI was calculated for an array of climatic settings encompassing the range of observed condition in 1983–2012 (Fig. 2). Model fitting was done in R (R Core Team, 2014), using package nlme (Pinheiro et al. 2014).

During the whole period of climatic data availability (1953–2012), average P in the studied region was 292 mm, about half of which fell during LRE (average $P_{30}/P = 0.53$). The average wet season started on November 29th and ended on March 17th. DSL varied between 207 and 357 days, with the average being 258 days. According to linear regression, there was no significant change over time ($p > 0.1$) in any of the three variables (P, P_{30}/P, DSL).

The most parsimonious model of tree growth included only P, P_{30}/P and their interaction (Table 1). This means that DSL had no substantial effect on growth. BAI was strongly and positively affected by P (Fig. 2). The effect of P_{30}/P was more complicated, due to the $P \times P_{30}/P$ interaction. P_{30}/P had a positive effect on growth under relatively dry conditions, and a negative effect under relatively wet conditions (Fig. 2). For example, under average conditions ($P = 300$ mm), predicted BAI was 6.7% higher under an intensive rainfall regime compared to a less intensive one (P_{30}/P increase from 0.44 to 0.65; the 25% and 75% quantiles of the variation observed during 1983–2012). Under drier conditions ($P = 200$ mm) the beneficial effect of LRE was much more substantial (BAI increase by 22.7%). Under more humid conditions ($P = 400$ mm), however, the same increase in LRE led to −1.4%

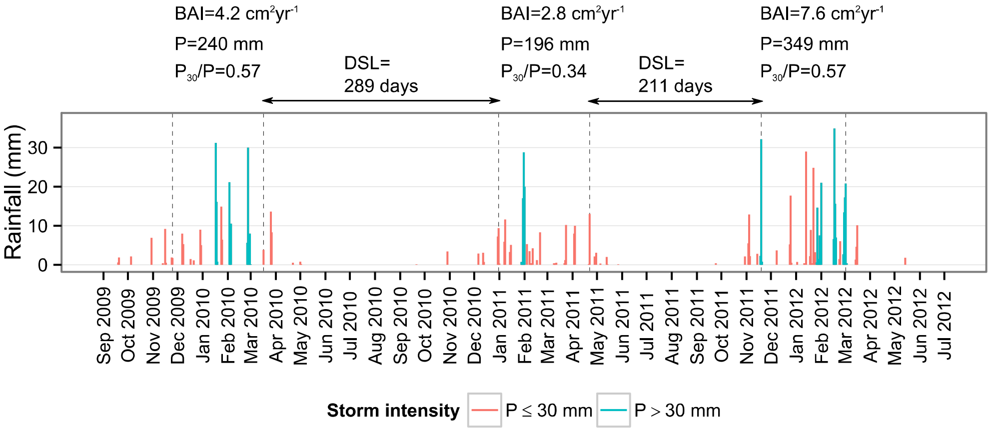

Fig. 1. An example of intra-annual rainfall characteristics calculation. Daily rainfall amount is plotted as function of time for three rainfall seasons: 2010, 2011 and 2012. Rainfall during large rain events (LRE) (P_{30}; consecutive rainfall days summing to >30 mm) and all other events are marked with blue and red, respectively. The dates when 10% (onset) and 90% (end) of rainfall has accumulated for a given season are marked with dashed vertical lines. Dry season length (DSL) is the time interval between end of the previous season and the onset of the current one. Average observed Basal Area Increment (BAI) among the studied 85 trees is also specified for each of the three years. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Final model of Basal Area Increment (BAI) as function of rainfall amount (P) and proportion of large rain events (LRE) (P_{30}/P).

	Value	Std. Error	t-value	p-value
(Intercept)	−4.26	1.512	−2.81	0.0049
P	0.03	0.003	11.96	<0.001
P_{30}/P	10.04	1.55	6.48	<0.001
$P \times P_{30}/P$	−0.03	0.005	−5.59	<0.001

change in BAI. The effect of P, though, was more extensive than that of P_{30}/P. For example, under average P_{30}/P conditions (0.54, during 1983–2012), increasing P (from 241 to 367 mm, which also correspond to the 25% and 75% quantiles) increased predicted BAI by 41.4%.

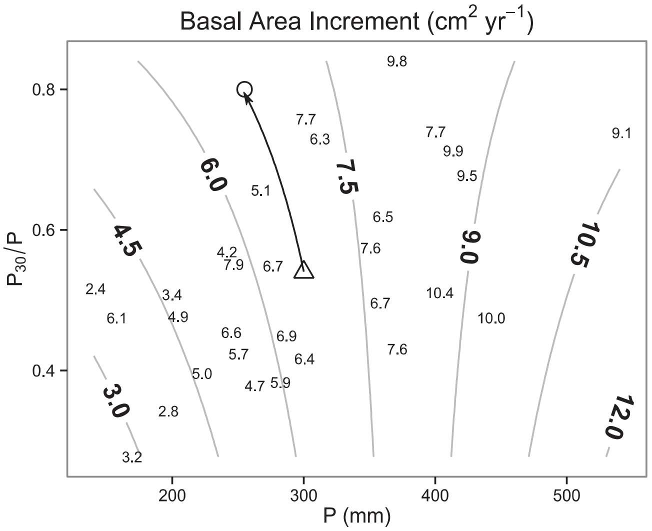

Fig. 2. Observed and predicted Basal Area Increment (BAI) as function of rainfall amount (P) and proportion of large rain events (LRE) (P_{30}/P). Numbers mark average observed BAI (among 85 trees) during the period 1983–2012. Contours show predictions according to the model described in Table 1. The triangle symbol (△) marks average observed conditions during the period 1983–2012 in terms of P and P_{30}/P, producing a predicted BAI of 6.7 $cm^2\ yr^{-1}$; the arrow and the circle symbol (○) display that a 15% reduction in P may be compensated by a 48% increase in P_{30}/P in order to retain the same BAI.

We have assessed the relative importance of two key characteristics of intra-annual rainfall distribution, as opposed to its total amount, in a semi-arid planted forest of *P. halepensis*. It has been shown that forest growth is mostly determined by total annual rainfall amount and to a lesser extent by the proportion of LRE. Under dry conditions, the predicted effect of LRE proportion was positive.

Global warming scenarios suggest that total rainfall amount will be reduced, but extreme events frequency may increase, e.g. in the Mediterranean (Giorgi and Lionello, 2008). The magnitude of change for each driver of tree growth will likely determine the outcome for semi-arid forests, with rainfall intensity increase potentially balancing the decline in its total amount. For example, a 15% decline in annual rainfall (which corresponds to the median projection for 2080–2100 under the RCP4.5 scenario for the studied region) (Stocker et al. 2013) will need to be counterbalanced by a 48% increase in the proportion of LRE for BAI not to decline (Fig. 2). Future studies are necessary to measure the relative probability of decrease in total rainfall amount as opposed to increase in LRE in the studied region, in light of the predicted tree growth changes for each scenario (Fig. 2).

Our results support the idea that rainfall intensity is an important climatic factor to forest functioning via its effect on infiltration depth (Raz-Yaseef et al. 2010, 2012; Klein et al. 2011). The claim that P_{30}/P is more important than P itself (Raz-Yaseef et al. 2012), however, is not supported – at least with respect to individual tree growth. It may be true that the share of tree transpiration out of overall evapotranspiration at the ecosystem level (Raz-Yaseef et al. 2012) benefits the most from a high proportion of LRE. Yet, growth and survival of individual trees ultimately depends on the absolute quantity of resources they are exposed to (i.e. P), and the “efficiency” with which these resources are provided (i.e. P_{30}/P) can only help so much. In general, sap flow measurements are advantageous for studying fine-grained (day-to-day) temporal variation in trees functioning in response to drought, and for understanding the water budget of various forest ecosystem components (Raz-Yaseef et al. 2012; Klein et al. 2014). Dendrochronology, on the other hand, provides a wider perspective on the climate-growth relationship of individual trees, by exposing their responses to a comprehensive set of climatic conditions encountered in the past (Sarris et al. 2007; Vicente-Serrano et al. 2013).

The lack of DSL effect on growth of *P. halepensis* highlights the high resilience of the species when facing harsh climatic conditions. The isohydric physiological adaptation of *P. halepensis*, i.e. the ability to efficiently moderate water loss via stomata closure at times of drought, results in very high plasticity in terms of growing season length and timing (Klein et al. 2011, 2013). It is also possible, however, that our results underestimate the true DSL effect on tree growth due to the fact that only living trees were sampled (Lloret et al. 2011; Dorman et al. in press-b).

In summary, the present study demonstrated how physiological insights from extensive yet short-term studies can be contrasted with long-term climatic and dendrochronological data, for statistically evaluating the relative importance of intra-annual climatic effects for the given species. Such efforts are crucial to expand our currently limited understanding of the link between climatic conditions, present and future, and forest mortality risk (Anderegg et al. 2013).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2015.03.002.

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