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Title: High resolution analysis of stem radius variations in black spruce subjected to rain exclusion for three summers.

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Abstract

In the near future, climate warming is expected to produce more severe and frequent periods of drought with consequent water stresses for boreal species. In this paper, we present a high resolution analysis of chronologies of stem radius variations in black spruce under rain exclusion. Prolonged rain exclusions were applied for three consecutive summers to trees on four sites along a latitudinal gradient. The stem radius variations of control and treated trees were monitored year-round at an hourly resolution with automatic point dendrometers. The seasonal patterns of shrinking and swelling were analyzed using a sequential analysis technique and the daily patterns of contraction and expansion were extracted. Overall, the treated trees followed their daily cycles of contraction and expansion during the rain exclusions and no cumulative difference in stem expansion was observed over the three years. Trees subjected to rain exclusion showed larger stem contractions in summer on three out of four sites and larger winter contractions were observed on the northern sites. This study shows that a repeated summer drought does not necessarily lead to a direct evident stress reaction, showing the resilience of the boreal forest.

Keywords

Picea mariana, Dendrometer, Drought, Boreal forest, Stress, Climate change

Key message

Repeated droughts resulted in increased stem shrinking in some sites and years, but did not lead to a pronounced stress reaction in the stem radius variations of mature black spruce.

Author contributions

EB; Data collection, data analysis and interpretation, manuscript writing.

SR; Data analysis and interpretation, critical manuscript revision.

HM; Conception of the study, critical manuscript revision.

AD; Conception of the study, critical manuscript revision.

Introduction

The boreal forest is characterized by cold temperatures, therefore water evaporation is generally low and soils often remain wet throughout the growing season. As a result, growth of boreal species is strongly related to abundant water supply and the trees are adjusted to living in high moisture conditions (Hofgaard et al. 1999; Huang et al. 2010). These conditions could partially change in the future as climatic models for Eastern Canada predict increases in temperature and precipitation in the next 50 years (IPCC 2007; Plummer et al. 2006). The increase in precipitation will occur mainly in winter in the form of snowfall, while extreme conditions with drought events should be experienced in spring and summer, when the main plant growth processes take place (Burke et al. 2006; Zhang et al. 2000). It is likely that more precipitation in winter will not be adequate to balance enhanced evapotranspiration due to increasing temperatures, resulting in soil moisture content declines and more frequent and longer drought periods (Easterling et al. 2000; Motha and Baier 2005). These droughts may dramatically contribute to the effects of climate change on tree growth and mortality in the Canadian forest (Peng et al. 2011).

Despite the improving knowledge about the global reaction of forests to drought and changing precipitation regimes (Beier et al. 2012; Choat et al. 2012) and numerous studies on the drought effects on tree growth in natural and controlled environments (D'Orangeville et al. 2013; Eilmann et al. 2009; Rossi et al. 2009; Swidrak et al. 2011), the impacts of repeated prolonged summer droughts on mature black spruce (*Picea mariana* (Mill.) BSP) trees still remain largely unknown. Previous studies have focused mainly on the effects of drought in Europe (Bréda et al. 2006) and tropical regions (Phillips et al. 2009), but because of its high latitude, the response of the boreal forest to climate warming and drought may be different from other biomes in the world (Soja et al. 2007). Black spruce, the conifer characterizing the boreal forest of the northern hemisphere, has the ability to grow on a wide range of soil conditions and is well adapted to grow under conditions of low nutrient availability and waterlogged soils (Lamhamedi and Bernier 1994). Since water is normally is not a limiting factor in its distribution area, black spruce may be particularly vulnerable to drought.

Automatic dendrometers can provide useful information on the seasonal and daily patterns of stem contraction and expansion and can be used to study water relations and drought responses of trees (Améglio et al. 2001; Drew and Downes 2009; Giovannelli et al. 2007). Seasonal changes in stem radius variations have been classified according to rehydration patterns, showing a period of stem shrinking in winter, followed by rehydration and growth in spring and summer (Tardif et al. 2001; Turcotte et al. 2009). In summer, daily stem radius variations are mainly driven by transpiration and soil water content; shrinking takes place during the day, followed by expansion due to rehydration at night. Daily variations in winter are driven by temperature changes, when shrinking takes place during cooling and expansion during temperature increases (Sevanto et al. 2006). It was hypothesized by Giovanelli et al. (2007) that, at the beginning of drought periods, there is a decline in tree water status as shown by larger stem contractions. Daily stem expansion is positively related to the amount of precipitation (Deslauriers et al. 2003a; Deslauriers et al. 2007; Turcotte et al. 2011) while a decrease in soil water content results in larger daily amplitudes and more stem shrinking (Intrigliolo and Castel 2006; Sevanto et al. 2005). Experiments on wood (Zweifel et al. 2000) and on living trees (De Schepper et al. 2012) showed that stem radius variations are mainly determined by water content changes in the elastic bark tissues. Stem shrinkage can be a signal of an internal water deficit, which may later alter different physiological processes. For example, stomatal conductance may be inhibited and photosynthesis and cell division decline after a continued hydrological stress (Abe et al. 2003; Chaves et al. 2003)

In this paper, we present an analysis of stem radius variation chronologies collected over three years at four sites located along a latitudinal gradient. A prolonged summer drought was applied each year on all sites. This allowed us to study the effects of summer drought both during its occurrence and in the following winter and spring. We analysed the seasonal patterns of shrinking and rehydration throughout the years using a sequential analysis technique (Page 1961). At a higher resolution, the daily patterns of contraction and expansion were extracted (Deslauriers et al. 2003b) and compared between the trees subjected to rain exclusions and a control group. It was expected that a repeated summer drought applied to mature black spruce trees would affect (I) the seasonal stem radius variations by decreasing the total stem expansion and (II) the characteristics of the daily cycles by increasing the amplitude of contraction.

Methodology

Study sites

The study was conducted on black spruce in the boreal forest of the Saguenay-Lac-Saint-Jean region, Quebec, Canada. Four permanent plots [Simoncouche (abbreviated as SIM), Bernatchez (BER), Mistassibi (MIS) and Camp Daniel (DAN)] were installed in mature, even-aged stands located along a latitudinal and altitudinal gradient to cover a wide range of tree growth dynamics. The climate was typical boreal with cold winters and cool summers with abundant precipitation (Table 1). Soils were podzolic with different depths among sites. The organic layer in SIM ranged between 10 and 20 cm, with the maximum rooting depth limited by a shallow bedrock. In the other sites, the organic layer was deeper and attained 20-40 cm.

Experimental design

In each site, ten dominant or co-dominant trees with upright stems and similar growth rates were chosen, five control and five treated trees. The selection was based on proximity among the treated trees to allow the installation of the equipment for rain exclusion on the same group of individuals. Trees with polycormic stems, partially dead crowns, reaction wood or evident damage due to parasites were avoided. Plastic transparent under-canopy roofs were installed during late May-early June to exclude the treated trees from precipitation in 2010, 2011 and 2012. The majority of the root system of black spruce is localized within a distance of 90-200 cm from the stem collar (Polomski and Kuhn 1998). Accordingly, the plastic roofs extended for at least three meters from the stem of each tree and drained the rain into sinking points in the soil to avoid water flowing back towards the stem as much as possible. The plastic roofs were removed in September to ensure the winter survival of trees. The control trees were left untreated.

Data collection

Stem radius variations were measured at about 1.3m height with automatic point dendrometers (Agricultural Electronics Corp., Tucson, Arizona) from May 2010 to October 2012. Dendrometers were based on a precision linear variable differential transducer enclosed in an aluminum housing and fixed on the tree with stainless steel rods having a thermal linear expansion coefficient of 17 $\mu m \cdot m^{-1} \cdot °C^{-1}$. With this equipment, the percentage of metal expansion was less than 1% of stem variation. A sensing rod held against the surface of the bark measured the radius variations, which in our monitoring represented the overall variation in size of xylem and phloem together. The sensitivity of dendrometers to temperature and humidity was negligible due to the use of dimensionally stable compounds in their manufacture and the dead bark was partially removed to minimize error due to hygroscopic thickness variations. As the stem changed in size, the core of the transducer moved and translated the displacement in an electrical signal. Measurements were taken every 15 min and stored in CR-10X dataloggers (Campbell Scientific Corporation) providing precise and high-resolution data of radius variation over time.

A weather station was present in a canopy gap in the proximity of the study plots on all sites. Rainfall and temperature data was recorded every 15 min and stored as hourly sums or means respectively using CR10X dataloggers (Campbell Scientific Corporation). The volumetric water content (VWC) of the soil was measured weekly with a portable device (Fieldscout TDR 100) in four points at a distance of 1 m from the collar of each tree and continuously with a fixed sensor at the weather station at a depth between 12-20 cm using a time domain reflectometry soil moisture meter (TDR). All VWC measurements were divided by the maximum observed value of the site to standardize results.

Data analysis

Hourly means of the stem radius variations were taken and irregularities were removed from the raw data with a 4-degree smoothing using the EXPAND procedure in SAS (Deslauriers et al 2011). The difference between the total stem expansion of treated and control trees was tested using a simple t-test for the dendrometer value at the last day of the measurements.

Daily means were taken from the chronology of daily stem radius variations and the growth trend was removed by subtracting the previous value from each value. Positive and negative shifts in the daily mean stem radius variations over the three years were studied using cumulative sum (CUSUM) charts, which represents a running total of deviations from a reference value (Page 1961). The positive and negative cumulative sum of the deviations of the sample values greater than k standard errors from the target mean are calculated and plotted. An upward or downward out-of-control state is detected when the CUSUM chart exceeds the decision interval and represents a moment when the values are either below or above the overall average. CUSUM chart chronologies were drawn up for the three consecutive growing seasons.

The stem-cycle approach was used to determine and characterize the phases of contraction and expansion, where contraction was defined as the period from the first maximum of the cycle to the minimum and expansion was the total period from the minimum to the next maximum. The amplitude of contraction and expansion was extracted for each cycle and weekly means were used to study the cycle characteristics. Differences between the treatments were tested with a sliced ANOVA within each week on the time series of amplitudes.

Results

Weather and site characteristics

All sites had a typical boreal climate, but since they are located along a latitudinal gradient there were differences in the local climate. The mean annual temperature ranged from 0.90 °C in the northern site (DAN) to 4.16 °C in the southern site (SIM). Rain occurred regularly throughout the summer on all sites, with SIM having the highest and BER the lowest total amount (Fig. I). However, soil moisture content in BER was higher than on the other sites due to the higher water holding capacity of the soil. The lowest values of soil moisture content were observed in SIM during the summer of 2010; overall this site had the highest seasonal variations in soil water content. MIS and DAN, the two northern sites, had intermediate soil moisture contents with fewer fluctuations, indicating a more constant water supply in the soil. In winter there was a gradual reduction of the soil water content, with MIS attaining the lowest values.

A clear increase in soil moisture content can be seen during snowmelt from the end of March, followed by a decrease with fluctuations during summer (Fig. I). During the three periods of rain exclusion the soil moisture content around the treated trees decreased quickly after the installation of the roofs and then stayed at continuously low values until the removal of the roofs. The two southern sites became the driest during the periods of exclusion. The soils had recuperated up to the same values as the control plots at the start of the second and third season of exclusion. Snow usually melted first in SIM at the end of April and then in May on the other sites.

Stem radius variations

Diurnal and seasonal trends can be found in the stem radius variations. Over the three years, all sites showed characteristic seasonal patterns in both treatments. The stem radius gradually increased as from the end of April until mid-July, when stem increase reduced and a plateau was reached. In winter stem shrinking occurred roughly from November until mid-March, this period of winter shrinking started earlier in the northern sites (Fig. II). The cumulative stem expansion after the three years of the experiment ranged from 2.07mm in SIM to 0.89mm in MIS and was lower in the rain excluded trees as compared with the control trees. No clear latitudinal or altitudinal trend was observed. The percentage difference between treated and control trees was larger in SIM (38%) and smaller in MIS (8%) (Table 2). This difference was not significant on any of the sites. In MIS and DAN the discrepancy between the control and treated trees appeared when the winter shrinking started, whereas in BER and SIM both curves already separated during the summer drought.

On all sites and treatments, amplitudes of expansion and contraction were largest in summer; they became smaller during winter and started increasing again in early spring. During the summers of 2011 and 2012 the control trees in DAN showed larger upward shifts compared with the treated trees (Fig. II). During the last summer of rain exclusion, the contractions in MIS and BER were larger in the treated trees, but the amplitude of expansion was the same as in the control trees (Fig. III). Also in SIM, there were larger summer contractions in the treated trees, but towards the end of the exclusion the amplitude of the contraction decreased (Fig. III). More upward shifts were seen in the control trees in SIM during summer, but in winter both treatments largely followed the same pattern (Fig. II).

The drought treatment did not only affected the stem radius variations during the growing season but also had an impact in the following winter. In the northern sites, DAN and MIS, winter expansion and contraction were larger in the treated trees than in the control trees (Fig. III). This also happened sporadically during the second winter in SIM. The higher winter fluctuations in the CUSUM charts show that in DAN and MIS the winter shrinkage was stronger in the treated trees (Fig. II). This stronger shrinkage was followed by a larger rehydration in spring meaning that winter stem dehydration was greater in the north, for the excluded trees.

Discussion

We studied three-year chronologies of stem radius variations in black spruce trees excluded from summer precipitation. The prolonged summer droughts did not cause a significant difference in the cumulative stem expansion of black spruce over the three years, but it is clear from Fig. II that the expansion in the treated trees was lower on all sites. The second hypothesis, that there would be larger contractions in the treated trees, was partially confirmed. Larger contractions were observed in summer during the third year in three out of the four sites, in both winters in MIS and DAN and a few times in the second winter in SIM.

An increase in daily stem contraction in summer may be a reliable indicator of early water stress (Giovannelli et al. 2007; Intrigliolo and Castel 2006). In the first and second year of the rain exclusion there was no difference in the amplitude of contraction and expansion between the control and treated trees along the latitudinal gradient. The increase in stem contraction during the third year indicates that there could be a cumulative effect of drought on the water status of the plant. When soil water is unlimited stem contractions can be explained by changes in vapour pressure deficit (Devine and Harrington 2011). However, stem shrinking becomes a function of water availability when the soil water content is inadequate to recharge the stem overnight. Stem contraction occurs when water is lost from the bark tissues due to transpiration, but not immediately replaced via soil water uptake. The water loss takes place mainly in the living, physiologically active parts of the stem (Zweifel et al. 2000), when occurring in summer this can have a potential impact on cell division and development and other metabolic processes.

Increased summer shrinking was not observed in DAN, the northern site with the lowest temperatures and shorter growing season of the four plots (Boulouf Lugo et al. 2012). In this site a high soil water table was observed throughout the summer. There is thus a lower transpirational demand and slower tree growth. It was shown by McLaughlin et al. (2003) that slower growing trees may be less sensitive to drought than fast growing trees. However, with climate change however, temperatures are expected to rise, mainly at higher latitudes, which may result in disproportionate variations in stem size with latitude.

In SIM, the stem contractions, but also the expansions, of the treated trees decreased towards the end of the third exclusion period, resulting in a lower daily fluctuation. This may imply that the trees could rehydrate less during the night, meaning that there was less water available to lose during transpiration.

In winter, the daily amplitudes of contraction and expansion are usually smaller than in summer and are mainly driven by temperature (Sevanto et al. 2006). Daily winter cycles are reversed as compared to summer cycles, shrinking occurs during the night when temperatures drop because water leaves the elastic bark tissues to prevent cell damage due to freezing (Zweifel and Häsler 2000), while expansion takes place when the temperature increases during the day. As in summer, winter shrinking is related to water loss and is thus an indicator of the tree water status (Loris et al. 1999; Zweifel and Häsler 2000). Transpiration demands may still be high in late winter and early spring, especially on warmer days, but water uptake by roots is very limited due to low soil temperatures (Loris et al. 1999). The trees depend on their sap reserves to meet winter transpiration demands (Boyce et al. 1991) but the water losses cannot immediately be compensated (Sevanto et al. 2006). The drier soils in the treated sites are usually colder because of their lower heat conductance and the trees may have a lower internally stored water reserve due to the drought treatment, causing the larger stem shrinkage during winter. More periods of drought may induce physiological consequences such as inhibition of early spring photosynthesis. This effect may be mitigated by rising temperatures, which were not simulated in this experiment, due to an increase in photosynthesis and an earlier start of the growing season (Sevanto et al. 2006). On the other hand, higher temperature may lead to higher evaporation in winter, resulting in even more water loss and stem desiccation. Water losses that occurred in winter are usually compensated during early spring rehydration, when cycles contain a freeze-induced contraction and a thaw induced expansion (Turcotte et al. 2009). The treated trees consequently have a larger spring rehydration in DAN and MIS, the sites experiencing a larger winter shrinkage.

Dendrometers represent both stem growth and water-related changes in stem size. It was found earlier that the amount of cells produced and the cell size were not affected by the drought treatment in MIS, BER and DAN (Belien et al. 2012). The cumulative difference in stem expansion between the treatments is therefore mainly water related. For SIM it should be kept in mind that the growth of the treated trees was already lower before the start of the experiment (Belien et al. 2012). This was accounted for in the analysis of shrinking and expansion patterns by removing the growth trend.

Water deficit is normally never an issue in these forests, especially in the northern sites, where the soil water content stays more or less stable throughout the summer. The northern sites have thicker organic soil layers, giving them generally wetter conditions but making them more susceptible to extreme climatic event such as droughts (Drobyshev et al. 2010). The soil of the southern site, SIM has a lower water holding capacity due to a thinner organic soil layer. The results of our investigation demonstrated how important it is to include different sites when studying water relations, since environmental factors may play a role in the effect of the drought treatment on the stem radius variations. Stem radius variations are not only influenced by the amount of soil water available, but also by vapour pressure deficit, solar radiation and maximum temperature (Deslauriers et al. 2003a; Deslauriers et al. 2007; Devine and Harrington 2011). These environmental variables were not altered in this experiment, even though they are also expected to differ under future climate change.

Conclusion

Previous studies showed the usefulness of dendrometers to assess the water status and drought reactions of trees (Giovannelli et al. 2007; Oberhuber and Gruber 2010; Zweifel et al. 2005). However, these studies were done on younger plants or only during the growing season. To our knowledge a long term drought experiment, in which trees were monitored throughout the year has never been performed before. This study was conducted on a large temporal and spatial scale. The four sites cover a large part of the latitudinal range of the commercial boreal forest and our sample was constituted of mature trees living in their natural environment. The manipulative experiment was repeated over three consecutive summers and the following winters, producing mid-term chronologies of high temporal resolution.

In spite of the repeated summer drought treatments, there was surprisingly no clear overall stress reaction of the trees to the treatment. Moreover, they kept following daily and seasonal cycles of hydration and dehydration. We showed that when studying the effect of drought one should not only look at the tree response during the treatment, but also in the following winter. When studying mature trees' reaction to a modification of the environment such as rain exclusion, it is important to repeat the experiment for several years on the same trees to monitor the long-term effects on stem radius variations and water status.

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Tables

Table 1: Location and climatic characteristics of the four study sites during the three years of the experiment.

Site	Latitude	Longitude	Mean annual temperature (°C)	Maximum temperature (°C)	Minimum temperature (°C)	April-October precipitation
DAN	50°41′N	72°11′W	0.90	29.90	-40.81	610.80
MIS	49°43′N	71°56′W	2.78	30.80	-35.34	630.30
BER	48°51′N	70°20′W	2.19	29.26	-35.40	608.30
SIM	48°12′N	71°14′W	4.16	30.30	-31.13	664.37

Table 2: Cumulative stem expansion (mm) after the three years of rain exclusion.

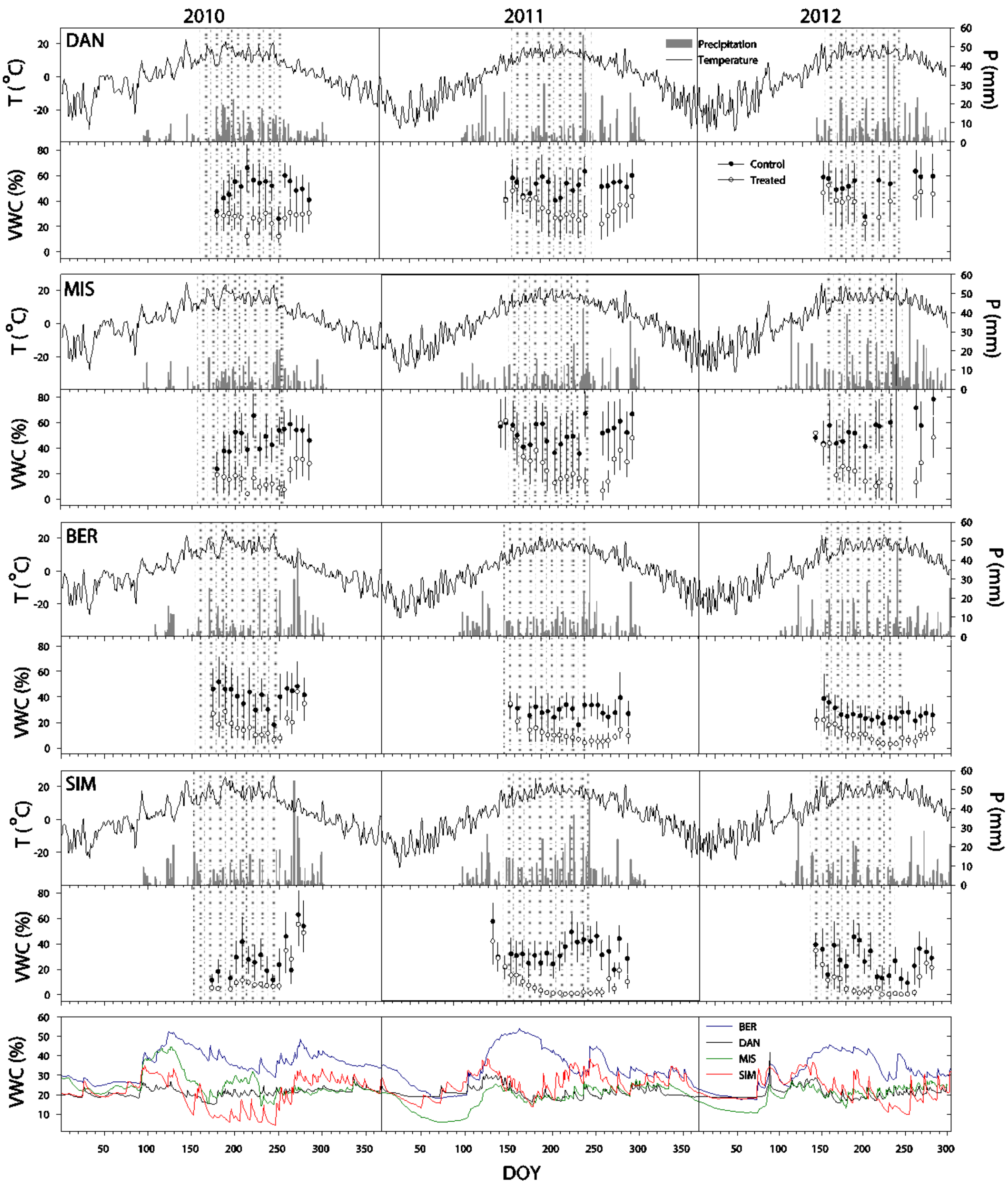
	Cumulative expansion (mm)	
Site	**Control**	**Treated**
DAN	1.96±0.44	1.47±0.97
MIS	1.10±0.24	0.89±0.31
BER	1.31±0.33	1.21±0.37
SIM	2.07±0.36	1.28±0.88

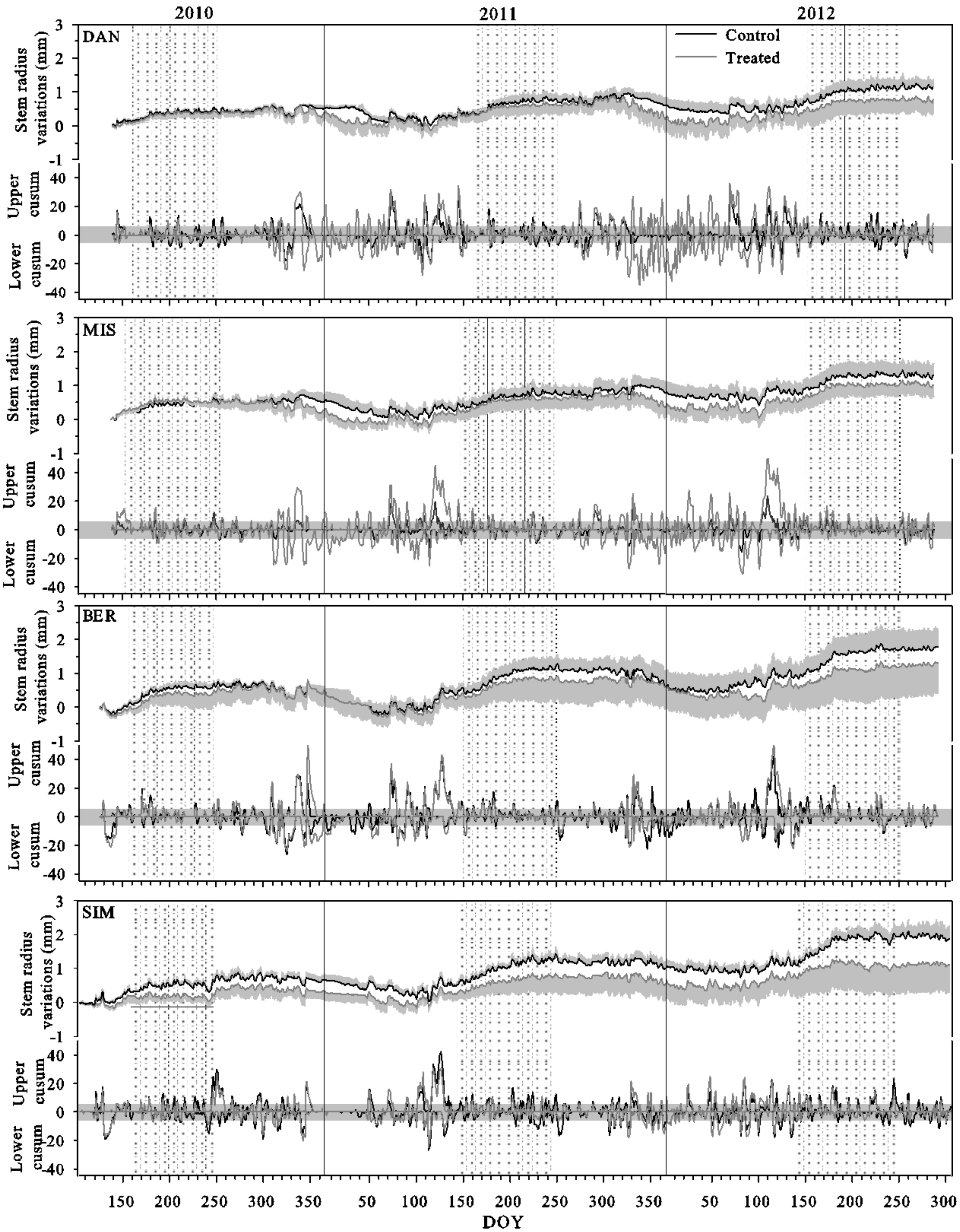
Figures

Fig. 1: Top: Daily air temperature (T, black curve) and precipitation (P, grey bars) for each site. Volumetric water content of the soil (VWC) in the treated (open circles) and control (solid circles) plots with the standard deviation. Bottom: Volumetric water content of the control sites over the entire study period. The shaded background represents the periods of the rain exclusion treatment

Fig. 2: Daily means and standard deviations (grey bars) of the stem radius variations of the treated (grey lines) and control trees (black lines). High and low-sided CUSUM charts for the daily stem radius variations, where the high sided only uses the positive values and the low-sided only the negative values, for control (black lines) and treated (grey lines) trees.

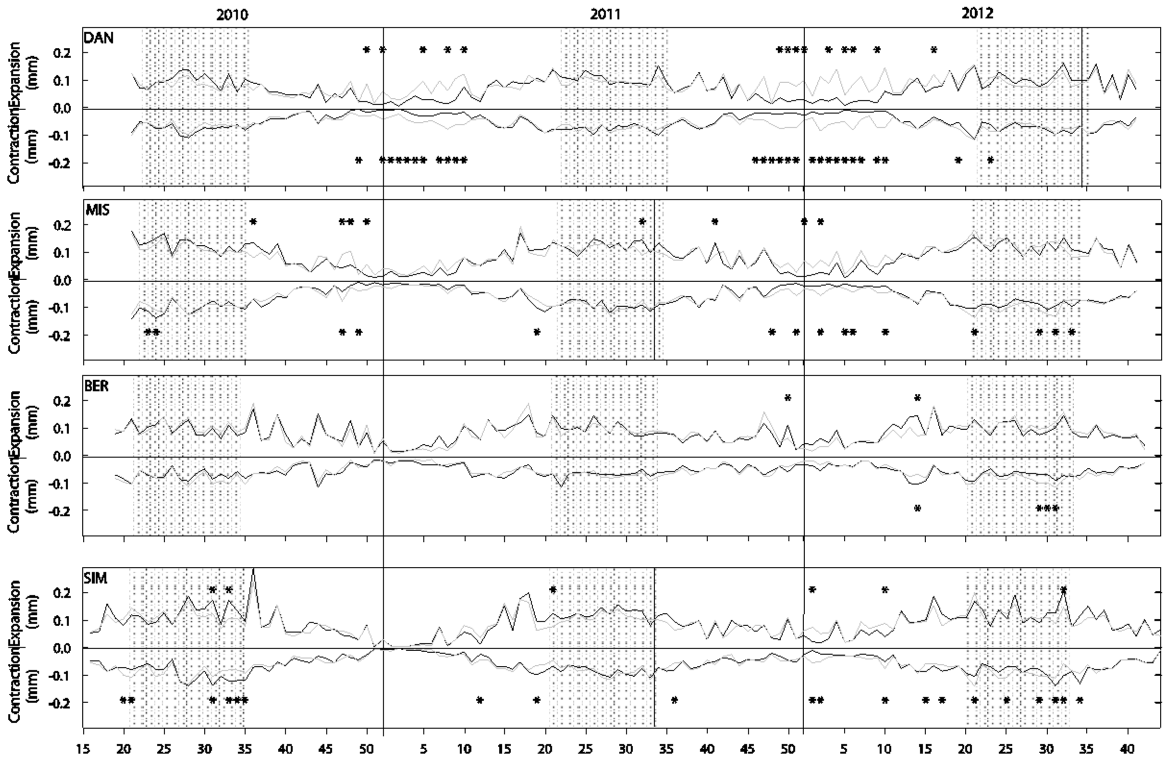
Fig. 3: Weekly means of the daily contraction and expansion for the treated (grey lines) and control (black lines) trees. Significant differences ($p<0.05$) are indicated with an asterisk. The shaded background indicates the periods of rain exclusion


2010
2011
2012
DAN
MIS
BER
SIM
T (°C)
P (mm)
VWC (%)
Precipitation
Temperature
Control
Treated
BER
DAN
MIS
SIM
DOY



2010
2011
2012
DAN
MIS
BER
SIM
Control
Treated
Stem radius variations (mm)
Upper cusum
Lower cusum
DOY

283



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