

1 Authors: Evelyn Belien, Sergio Rossi, Hubert Morin, Annie Deslauriers
2 Title: High resolution analysis of stem radius variations in black spruce subjected to rain exclusion for
3 three summers.
4 Affiliation and address: Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555
5 Boulevard de l'Université, Chicoutimi (QC), G7H2B1, Canada
6 Corresponding author: Evelyn.Belien@uqac.ca, (418) 545 5011 post 2330

7 **Abstract**

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

20 **Keywords**

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

22 **Key message**

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

25 **Author contributions**

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

27 SR; Data analysis and interpretation, critical manuscript revision.

28 HM; Conception of the study, critical manuscript revision.

29 AD; Conception of the study, critical manuscript revision.

30 **Introduction**

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

42 Despite the improving knowledge about the global reaction of forests to drought and changing precipitation
43 regimes (Beier et al. 2012; Choat et al. 2012) and numerous studies on the drought effects on tree growth in natural
44 and controlled environments (D'Orangeville et al. 2013; Eilmann et al. 2009; Rossi et al. 2009; Swidrak et al. 2011),
45 the impacts of repeated prolonged summer droughts on mature black spruce (*Picea mariana* (Mill.) BSP) trees still
46 remain largely unknown. Previous studies have focused mainly on the effects of drought in Europe (Bréda et al.
47 2006) and tropical regions (Phillips et al. 2009), but because of its high latitude, the response of the boreal forest to
48 climate warming and drought may be different from other biomes in the world (Soja et al. 2007). Black spruce, the
49 conifer characterizing the boreal forest of the northern hemisphere, has the ability to grow on a wide range of soil

50 conditions and is well adapted to grow under conditions of low nutrient availability and waterlogged soils
51 (Lamhamedi and Bernier 1994). Since water is normally is not a limiting factor in its distribution area, black spruce
52 may be particularly vulnerable to drought.

53 Automatic dendrometers can provide useful information on the seasonal and daily patterns of stem
54 contraction and expansion and can be used to study water relations and drought responses of trees (Améglio et al.
55 2001; Drew and Downes 2009; Giovannelli et al. 2007). Seasonal changes in stem radius variations have been
56 classified according to rehydration patterns, showing a period of stem shrinking in winter, followed by rehydration
57 and growth in spring and summer (Tardif et al. 2001; Turcotte et al. 2009). In summer, daily stem radius variations
58 are mainly driven by transpiration and soil water content; shrinking takes place during the day, followed by
59 expansion due to rehydration at night. Daily variations in winter are driven by temperature changes, when shrinking
60 takes place during cooling and expansion during temperature increases (Sevanto et al. 2006). It was hypothesized by
61 Giovanelli et al. (2007) that, at the beginning of drought periods, there is a decline in tree water status as shown by
62 larger stem contractions. Daily stem expansion is positively related to the amount of precipitation (Deslauriers et al.
63 2003a; Deslauriers et al. 2007; Turcotte et al. 2011) while a decrease in soil water content results in larger daily
64 amplitudes and more stem shrinking (Intrigliolo and Castel 2006; Sevanto et al. 2005). Experiments on wood
65 (Zweifel et al. 2000) and on living trees (De Schepper et al. 2012) showed that stem radius variations are mainly
66 determined by water content changes in the elastic bark tissues. Stem shrinkage can be a signal of an internal water
67 deficit, which may later alter different physiological processes. For example, stomatal conductance may be inhibited
68 and photosynthesis and cell division decline after a continued hydrological stress (Abe et al. 2003; Chaves et al.
69 2003)

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

- 77 radius variations by decreasing the total stem expansion and (II) the characteristics of the daily cycles by increasing
- 78 the amplitude of contraction.

79 **Methodology**

80 *Study sites*

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

88 *Experimental design*

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

99 *Data collection*

100 Stem radius variations were measured at about 1.3m height with automatic point dendrometers
101 (Agricultural Electronics Corp., Tucson, Arizona) from May 2010 to October 2012. Dendrometers were based on a
102 precision linear variable differential transducer enclosed in an aluminum housing and fixed on the tree with
103 stainless steel rods having a thermal linear expansion coefficient of $17 \mu\text{m}\cdot\text{m}^{-1}\cdot^{\circ}\text{C}^{-1}$. With this equipment, the
104 percentage of metal expansion was less than 1% of stem variation. A sensing rod held against the surface of the bark

105 measured the radius variations, which in our monitoring represented the overall variation in size of xylem and
106 phloem together. The sensitivity of dendrometers to temperature and humidity was negligible due to the use of
107 dimensionally stable compounds in their manufacture and the dead bark was partially removed to minimize error
108 due to hygroscopic thickness variations. As the stem changed in size, the core of the transducer moved and
109 translated the displacement in an electrical signal. Measurements were taken every 15 min and stored in CR-10X
110 dataloggers (Campbell Scientific Corporation) providing precise and high-resolution data of radius variation over
111 time.

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

119 *Data analysis*

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

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

130 represents a moment when the values are either below or above the overall average. CUSUM chart chronologies
131 were drawn up for the three consecutive growing seasons.

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

137 **Results**

138 *Weather and site characteristics*

139 All sites had a typical boreal climate, but since they are located along a latitudinal gradient there were
140 differences in the local climate. The mean annual temperature ranged from 0.90 °C in the northern site (DAN) to
141 4.16 °C in the southern site (SIM). Rain occurred regularly throughout the summer on all sites, with SIM having the
142 highest and BER the lowest total amount (Fig. I). However, soil moisture content in BER was higher than on the
143 other sites due to the higher water holding capacity of the soil. The lowest values of soil moisture content were
144 observed in SIM during the summer of 2010; overall this site had the highest seasonal variations in soil water
145 content. MIS and DAN, the two northern sites, had intermediate soil moisture contents with fewer fluctuations,
146 indicating a more constant water supply in the soil. In winter there was a gradual reduction of the soil water content,
147 with MIS attaining the lowest values.

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

154 *Stem radius variations*

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

163 discrepancy between the control and treated trees appeared when the winter shrinking started, whereas in BER and
164 SIM both curves already separated during the summer drought.

165

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

173

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

180 **Discussion**

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

187
188 An increase in daily stem contraction in summer may be a reliable indicator of early water stress
189 (Giovannelli et al. 2007; Intrigliolo and Castel 2006). In the first and second year of the rain exclusion there was no
190 difference in the amplitude of contraction and expansion between the control and treated trees along the latitudinal
191 gradient. The increase in stem contraction during the third year indicates that there could be a cumulative effect of
192 drought on the water status of the plant. When soil water is unlimited stem contractions can be explained by changes
193 in vapour pressure deficit (Devine and Harrington 2011). However, stem shrinking becomes a function of water
194 availability when the soil water content is inadequate to recharge the stem overnight. Stem contraction occurs when
195 water is lost from the bark tissues due to transpiration, but not immediately replaced via soil water uptake. The water
196 loss takes place mainly in the living, physiologically active parts of the stem (Zweifel et al. 2000), when occurring in
197 summer this can have a potential impact on cell division and development and other metabolic processes.

198
199 Increased summer shrinking was not observed in DAN, the northern site with the lowest temperatures and
200 shorter growing season of the four plots (Boulouf Lugo et al. 2012). In this site a high soil water table was observed
201 throughout the summer. There is thus a lower transpirational demand and slower tree growth. It was shown by
202 McLaughlin et al. (2003) that slower growing trees may be less sensitive to drought than fast growing trees.
203 However, with climate change however, temperatures are expected to rise, mainly at higher latitudes, which may
204 result in disproportionate variations in stem size with latitude.

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

208

209 In winter, the daily amplitudes of contraction and expansion are usually smaller than in summer and are
210 mainly driven by temperature (Sevanto et al. 2006). Daily winter cycles are reversed as compared to summer cycles,
211 shrinking occurs during the night when temperatures drop because water leaves the elastic bark tissues to prevent
212 cell damage due to freezing (Zweifel and Häsler 2000), while expansion takes place when the temperature increases
213 during the day. As in summer, winter shrinking is related to water loss and is thus an indicator of the tree water
214 status (Loris et al. 1999; Zweifel and Häsler 2000). Transpiration demands may still be high in late winter and early
215 spring, especially on warmer days, but water uptake by roots is very limited due to low soil temperatures (Loris et al.
216 1999). The trees depend on their sap reserves to meet winter transpiration demands (Boyce et al. 1991) but the water
217 losses cannot immediately be compensated (Sevanto et al. 2006). The drier soils in the treated sites are usually
218 colder because of their lower heat conductance and the trees may have a lower internally stored water reserve due to
219 the drought treatment, causing the larger stem shrinkage during winter. More periods of drought may induce
220 physiological consequences such as inhibition of early spring photosynthesis. This effect may be mitigated by rising
221 temperatures, which were not simulated in this experiment, due to an increase in photosynthesis and an earlier start
222 of the growing season (Sevanto et al. 2006). On the other hand, higher temperature may lead to higher evaporation
223 in winter, resulting in even more water loss and stem desiccation. Water losses that occurred in winter are usually
224 compensated during early spring rehydration, when cycles contain a freeze-induced contraction and a thaw induced
225 expansion (Turcotte et al. 2009). The treated trees consequently have a larger spring rehydration in DAN and MIS,
226 the sites experiencing a larger winter shrinkage.

227

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

234

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

245 **Conclusion**

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

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

260

261 **Acknowledgments**

262 This work was funded by the Natural Sciences and Engineering Research Council of Canada and the
263 Consortium Ouranos. The authors thank F. Gionest and J-G. Girard for their technical support and A. Garside for
264 checking the English text. The authors declare that they have no conflict of interest.

265 **Tables**

266 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

267

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

Site	Cumulative expansion (mm)	
	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

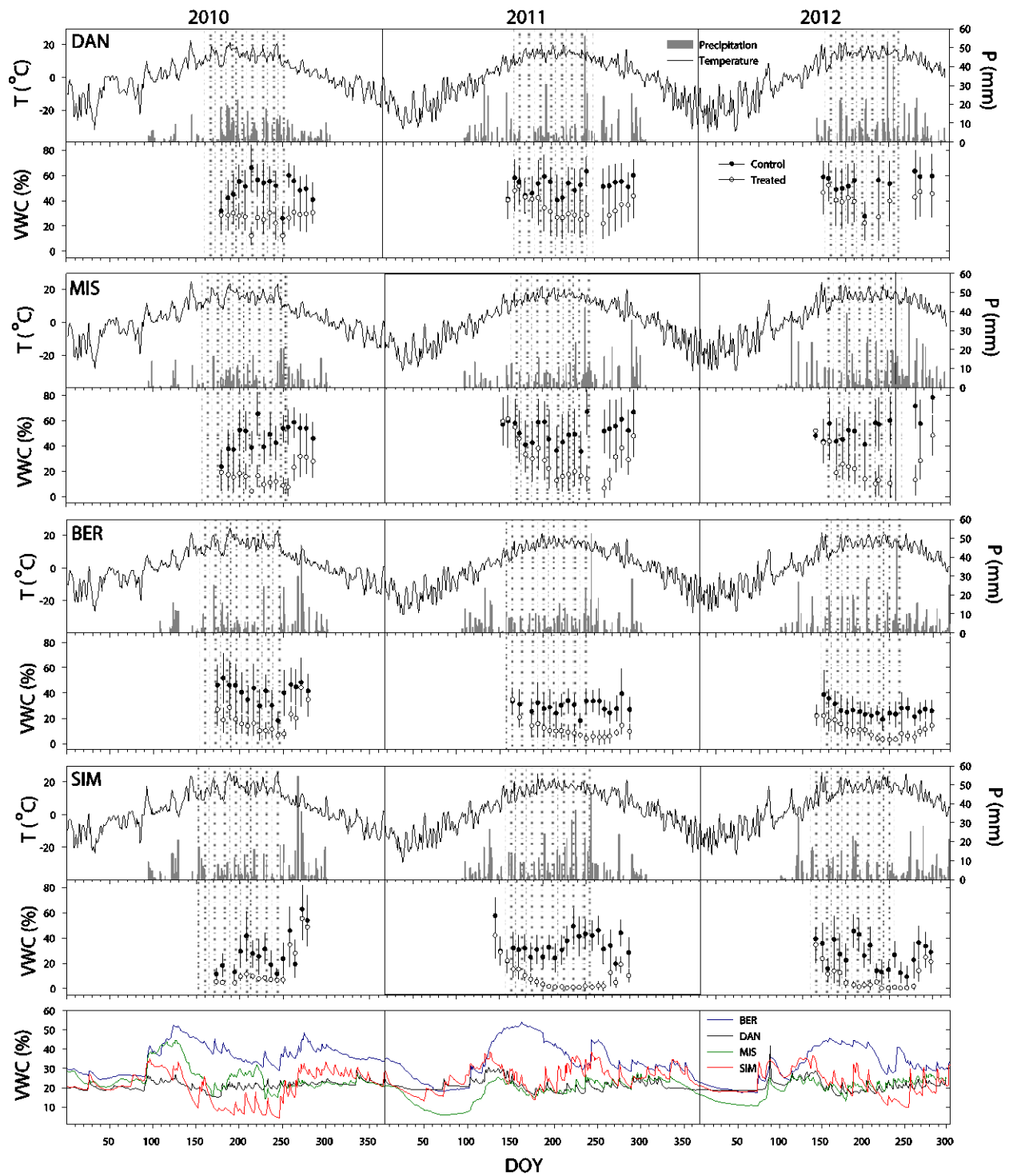
269

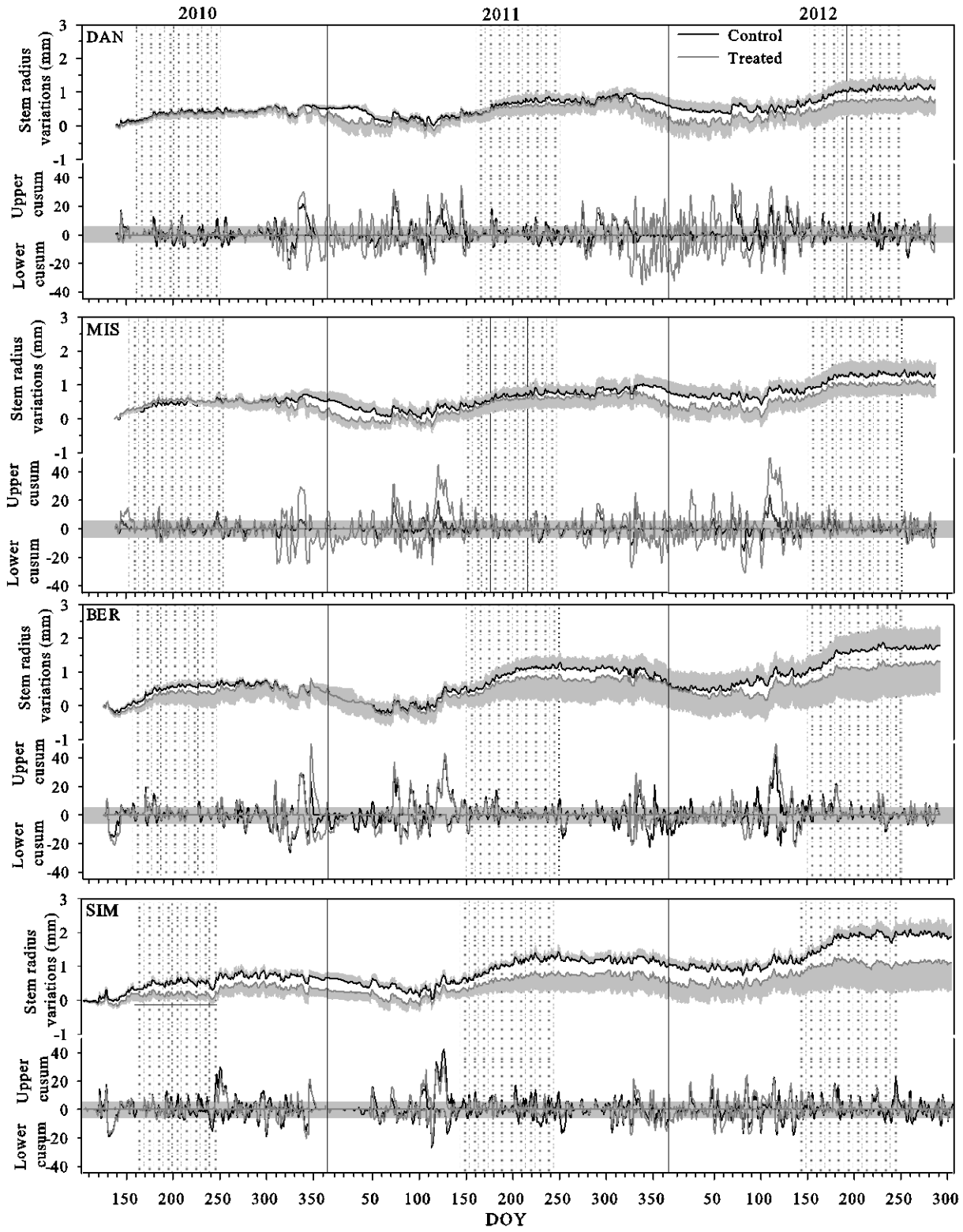
270 **Figures**

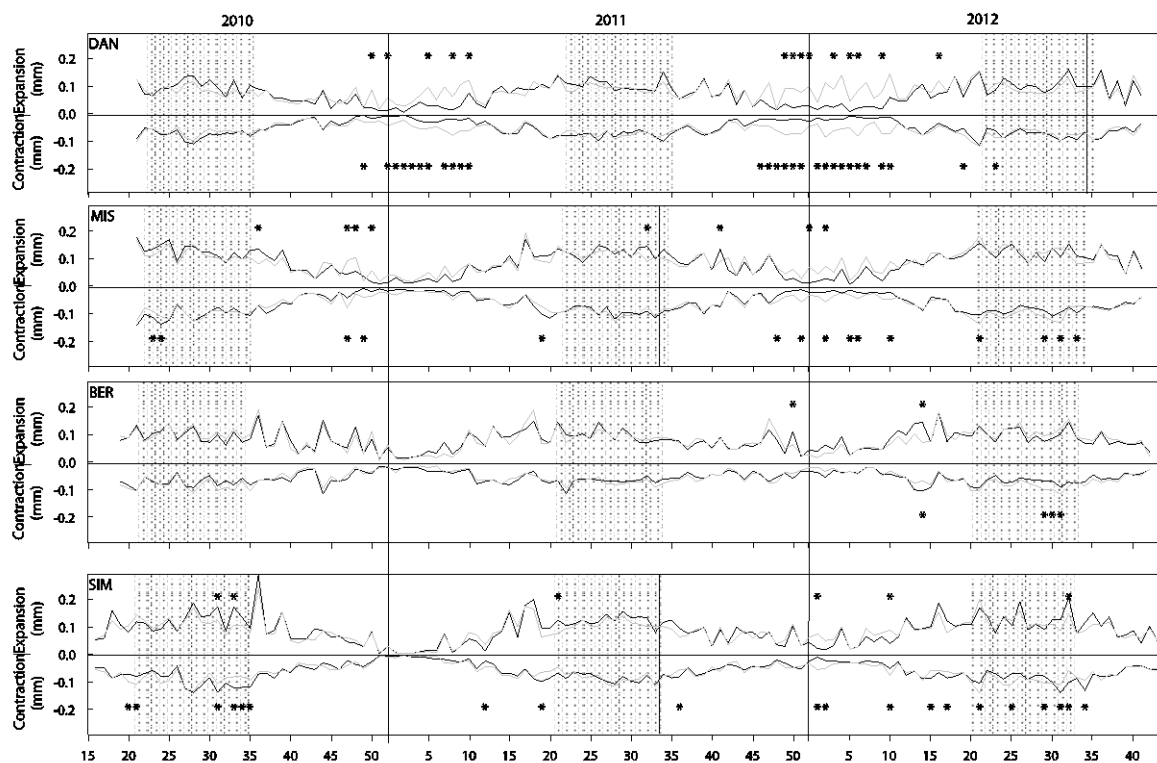
271 Fig. 1: Top: Daily air temperature (T, black curve) and precipitation (P, grey bars) for each site. Volumetric water
 272 content of the soil (VWC) in the treated (open circles) and control (solid circles) plots with the standard deviation.
 273 Bottom: Volumetric water content of the control sites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

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

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







284

285 **References**

286 Abe, H., Nakai, T., Utsumi, Y. and Kagawa, A., 2003. Temporal water deficit and wood formation in
 287 *Cryptomeria japonica*. *Tree Physiology*, 23(12): 859-863.
 288 Améglio, T., Cochard, H. and Ewers, F.W., 2001. Stem diameter variations and cold hardiness in walnut
 289 trees. *Journal of Experimental Botany*, 52(364): 2135-2142.
 290 Beier, C. et al., 2012. Precipitation manipulation experiments - challenges and recommendations for the
 291 future. *Ecology Letters*, 15(8): 899-911.
 292 Belien, E., Rossi, S., Morin, H. and Deslauriers, A., 2012. Xylogenesis in black spruce subjected to rain
 293 exclusion in the field. *Canadian Journal of Forest Research-Revue Canadienne De Recherche
 294 Forestiere*, 42(7): 1306-1315.
 295 Boulouf Lugo, J., Deslauriers, A. and Rossi, S., 2012. Duration of xylogenesis in black spruce lengthened
 296 between 1950 and 2010. *Annals of Botany*, 110(6): 1099-1108.
 297 Boyce, R.L., Friedland, A.J., Webb, E.T. and Herrick, G.T., 1991. Modeling the effect of winter climate on
 298 high-elevation red spruce shoot water contents. *Forest science.*, 37(6): 1567-1580.
 299 Bréda, N., Huc, R., Granier, A. and Dreyer, E., 2006. Temperate forest trees and stands under severe
 300 drought: a review of ecophysiological responses, adaptation processes and long-term
 301 consequences. *Annals of Forest Science*, 63(6): 625-644.
 302 Burke, E.J., Brown, S.J. and Christidis, N., 2006. Modeling the recent evolution of global drought and
 303 projections for the twenty-first century with the hadley centre climate model. *Journal of
 304 Hydrometeorology*, 7(5): 1113-1125.
 305 Chaves, M.M., Maroco, J.P. and Pereira, J.S., 2003. Understanding plant responses to drought - from
 306 genes to the whole plant. *Functional Plant Biology*, 30(3): 239-264.

307 Choat, B. et al., 2012. Global convergence in the vulnerability of forests to drought. *Nature*, 491(7426):
308 752-+.

309 D'Orangeville, L., Cote, B., Houle, D. and Morin, H., 2013. The effects of throughfall exclusion on
310 xylogenesis of balsam fir. *Tree Physiology*, 33(5): 516-26.

311 De Schepper, V., van Dusschoten, D., Copini, P., Jahnke, S. and Steppe, K., 2012. MRI links stem water
312 content to stem diameter variations in transpiring trees. *Journal of Experimental Botany*, 63(7):
313 2645-2653.

314 Deslauriers, A., Morin, H., Urbinati, C. and Carrer, M., 2003a. Daily weather response of balsam fir (*Abies*
315 *balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of
316 Quebec (Canada). *Trees - Structure and Function*, 17(6): 477-484.

317 Deslauriers, A., Rossi, S. and Anfodillo, T., 2007. Dendrometer and intra-annual tree growth: what kind
318 of information can be inferred? *Dendrochronologia*, 25(2): 113-124.

319 Deslauriers, A., Rossi, S., Turcotte, A., Morin, H. and Krause, C., 2003b. A three-step procedure in SAS to
320 analyze the time series from automatic dendrometers. *Dendrochronologia*, 29(3): 151-161.

321 Devine, W.D. and Harrington, C.A., 2011. Factors affecting diurnal stem contraction in young Douglas-fir.
322 *Agricultural and Forest Meteorology*, 151(3): 414-419.

323 Drew, D.M. and Downes, G.M., 2009. The use of precision dendrometers in research on daily stem size
324 and wood property variation: A review. *Dendrochronologia*, 27(2): 159-U7.

325 Drobyshev, I., Simard, M., Bergeron, Y. and Hofgaard, A., 2010. Does soil organic layer thickness affect
326 climate-growth relationships in the black spruce boreal ecosystem? *Ecosystems*, 13(4): 556-574.

327 Easterling, D.R. et al., 2000. Climate extremes: Observations, modeling, and impacts. *Science*, 289(5487):
328 2068-2074.

329 Eilmann, B., Zweifel, R., Buchmann, N., Fonti, P. and Rigling, A., 2009. Drought-induced adaptation of the
330 xylem in Scots pine and pubescent oak. *Tree Physiology*, 29(8): 1011-1020.

331 Giovannelli, A. et al., 2007. Evaluation of drought response of two poplar clones (*populus x canadensis*
332 *monch* 'i-214' and *p-deltoides* marsh. 'dvina') through high resolution analysis of stem growth.
333 *Journal of Experimental Botany*, 58(10): 2673-2683.

334 Hofgaard, A., Tardif, J. and Bergeron, Y., 1999. Dendroclimatic response of *Picea mariana* and *Pinus*
335 *banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. *Canadian Journal of*
336 *Forest Research*, 29(9): 1333-1346.

337 Huang, J. et al., 2010. Radial growth response of four dominant boreal tree species to climate along a
338 latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology*, 16(2): 711-
339 731.

340 Intrigliolo, D.S. and Castel, J.R., 2006. Usefulness of diurnal trunk shrinkage as a water stress indicator in
341 plum trees. *Tree Physiology*, 26(3): 303-311.

342 IPCC, 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the*
343 *Fourth Assessment Report of the Intergovernmental Panel on Climate Change.*

344 Lamhamedi, M.S. and Bernier, P.Y., 1994. Ecophysiology and field performance of black spruce (*Picea-*
345 *mariana*)- A review. *Annales des Sciences Forestières*, 51(6): 529-551.

346 Loris, K., Havranek, W.M. and Wieser, G., 1999. The ecological significance of thickness changes in stem,
347 branches and twigs of *Pinus cembra* L. during winter. *Phyton*, 39(Eurosilva): 117-122.

348 McLaughlin, S.B., Wullschleger, S.D. and Nosal, M., 2003. Diurnal and seasonal changes in stem
349 increment and water use by yellow poplar trees in response to environmental stress. *Tree*
350 *Physiology*, 23(16): 1125-1136.

351 Motha, R.P. and Baier, W., 2005. Impacts of present and future climate change and climate variability on
352 agriculture in the temperate regions: North America. *Climatic Change*, 70(1-2): 137-164.

353 Oberhuber, W. and Gruber, A., 2010. Climatic influences on intra-annual stem radial increment of *Pinus*
354 *sylvestris* (L.) exposed to drought. *Trees-Structure and Function*, 24(5): 887-898.

355 Page, E.S., 1961. Cumulative sum charts. *Technometrics*, 3(1): 1-8.
356 Peng, C. et al., 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal
357 forests. *Nature Climate Change*, 1(9): 467-471.
358 Phillips, O.L. et al., 2009. Drought sensitivity of the Amazon rainforest. *Science*, 323(5919): 1344-1347.
359 Plummer, D.A. et al., 2006. Climate and climate change over north America as simulated by the
360 Canadian RCM. *Journal of Climate*, 19(13): 3112-3132.
361 Rossi, S., Simard, S., Rathgeber, C.B.K., Deslauriers, A. and De Zan, C., 2009. Effects of a 20-day-long dry
362 period on cambial and apical meristem growth in *Abies balsamea* seedlings. *Trees-Structure and*
363 *Function*, 23(1): 85-93.
364 Sevanto, S. et al., 2005. Relationships between diurnal xylem diameter variation and environmental
365 factors in Scots pine. *Boreal Environment Research*, 10(5): 447-458.
366 Sevanto, S. et al., 2006. Wintertime photosynthesis and water uptake in a boreal forest. *Tree Physiology*,
367 26(6): 749-757.
368 Soja, A.J. et al., 2007. Climate-induced boreal forest change: Predictions versus current observations.
369 *Global and Planetary Change*, 56(3-4): 274-296.
370 Swidrak, I., Gruber, A., Kofler, W. and Oberhuber, W., 2011. Effects of environmental conditions on
371 onset of xylem growth in *Pinus sylvestris* under drought. *Tree Physiology*, 31(5): 483-493.
372 Tardif, J., Flannigan, M. and Bergeron, Y., 2001. An analysis of the daily radial activity of 7 boreal tree
373 species, Northwestern Quebec. *Environmental Monitoring and Assessment*, 67(1-2): 141-160.
374 Turcotte, A., Morin, H., Krause, C., Deslauriers, A. and Thibeault-Martel, M., 2009. The timing of spring
375 rehydration and its relation with the onset of wood formation in black spruce. *Agricultural and*
376 *Forest Meteorology*, 149(9): 1403-1409.
377 Turcotte, A., Rossi, S., Deslauriers, A., Krause, C. and Morin, H., 2011. Dynamics of depletion and
378 replenishment of water storage in stem and roots of black spruce measured by dendrometers.
379 *Frontiers*, 2(21): 1-8.
380 Zhang, X.B., Vincent, L.A., Hogg, W.D. and Niitsoo, A., 2000. Temperature and precipitation trends in
381 Canada during the 20th century. *Atmosphere-Ocean*, 38(3): 395-429.
382 Zweifel, R. and Häsler, R., 2000. Frost-induced reversible shrinkage of bark of mature subalpine conifers.
383 *Agricultural and Forest Meteorology*, 102: 213-222.
384 Zweifel, R., Item, H. and Häsler, R., 2000. Stem radius changes and their relation to stored water in
385 stems of young Norway spruce. *Trees - Structure and Function*, 15(1): 50-57.
386 Zweifel, R., Zimmermann, L. and Newbery, D.M., 2005. Modeling tree water deficit from microclimate:
387 an approach to quantifying drought stress. *Tree Physiology*, 25(2): 147-156.
388