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Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains

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Extreme climatic events are key factors in initiating gradual or sudden changes in forest ecosystems through the promotion of severe, tree-killing disturbances such as fire, blowdown, and widespread insect outbreaks. In contrast to these climatically-incited disturbances, little is known about the more direct effect of drought on tree mortality, especially in high-elevation forests. Therefore projections of drought-induced mortality under future climatic conditions remain uncertain. For a subalpine forest landscape in the Rocky Mountains of northern Colorado (USA), we quantified lag effects of drought on mortality of Engelmann spruce *Picea engelmannii*, subalpine fir *Abies lasiocarpa*, and lodgepole pine *Pinus contorta*. For the period 1910–2004, we related death dates of 164 crossdated dead trees to early-season and late-season droughts. Following early-season droughts, spruce mortality increased over five years and fir mortality increased sharply over 11 years. Following late-season droughts, spruce showed a small increase in mortality within one year, whereas fir showed a consistent period of increased mortality over two years. Pine mortality was not affected by drought. Low pre-drought radial growth rates predisposed spruce and fir to drought-related mortality. Spruce and fir trees that died during a recent drought (2000–2004) had significantly lower pre-drought growth rates than live neighbour trees. Overall, we found large interspecific differences in drought-related mortality with fir showing the strongest effect followed by spruce and pine. This direct influence of climatic variability on differential tree mortality has the potential for driving large-scale changes in subalpine forests of the Rocky Mountains.

Extreme climatic events such as droughts, heat waves, frosts, and windstorms often initiate gradual or sudden changes in forest ecosystems (Innes 1998, Diffenbaugh et al. 2005). Processes of forest dynamics may be affected in non-linear and unpredictable ways by climatic events, especially with respect to tree mortality, as trees may be buffered from moderately poor conditions but be susceptible to extreme conditions (Lloyd and Graumlich 1997). Climatic events often directly or indirectly promote intense, widespread disturbances in subalpine forests of the Rocky Mountains: fire is associated with severe drought, blowdown is caused by extreme wind events, and insect outbreaks often follow drought and/or blowdown (Romme and Despain 1989, Veblen et al. 1989, Kulakowski and Veblen 2002, Bebi et al. 2003, Sibold and Veblen 2006). These disturbances result in large patches of tree mortality, which dramatically change forest composition and structure, and alter susceptibility to subsequent disturbances (Veblen et al. 1994, Bigler et al. 2005). Unlike these proximate causes of disturbance-induced tree mortality, less is known about drought as a relatively direct cause of tree death in subalpine forests (Donnegan and Rebertus 1999). In temperate latitudes, relationships between tree mortality and drought often have been investigated in dry woodlands, near ecotones with non-arboreal vegetation or at low elevations (Clinton et al. 1993, Villalba and Veblen 1998). However, the link between climate variability and fine-scale tree mortality for some widespread forest types such as subalpine forests in the US West is not well understood (Lloyd and Graumlich 1997).

Relationships of tree mortality to drought are complex and difficult to predict (Hanson and Weltzin

2000, Breshears and Allen 2002, Breshears et al. 2005) because climate variation both acts directly on trees to produce physiological stress and also may affect other mortality agents such as insects and diseases (Bréda et al. 2006). Potential interactions between drought and biotic mortality agents often make it difficult to determine the proximate cause of tree death. Species-specific differences in responses to the physiological stress triggered by drought and/or to biotic agents of mortality may result in differential mortality among tree species which in turn may result in shifts in species composition (Clinton et al. 1993, Elliott and Swank 1994, Mueller et al. 2005). Although tree mortality has been observed to increase during or following single droughts (Peterken and Mountford 1996) and tree mortality responses to timing and length of droughts have been shown to be non-linear (Innes 1998, Hanson and Weltzin 2000, Bigler et al. 2006), there is little quantitative work on lag effects of droughts over a longer time frame.

The major objectives of the present study are to reconstruct the temporal distribution of tree mortality and to quantify lag effects of drought on tree mortality in a subalpine forest of the Rocky Mountains in northern Colorado, USA. We focus on three dominant tree species, i.e. Engelmann spruce *Picea engelmannii*, subalpine fir *Abies lasiocarpa* and lodgepole pine *Pinus contorta* var. *latifolia*. The following three questions are addressed in this study. First, does tree mortality increase during and following drought years (i.e. years with increased water deficit)? Ecophysiological studies suggest major differences in the hydraulic properties among the three tree species, particularly pine showing greater water use efficiency than spruce or fir (Knapp and Smith 1981). Consequently, we hypothesise for spruce and fir increased mortality during the drought year and during following years (Peterken and Mountford 1996, Pedersen 1998). Second, do early-season droughts have a different effect on tree mortality than late-season droughts? Drought that occurs in the beginning of the growing season may affect tree growth and mortality differently than drought that occurs late in the growing season, because physiological activities of trees change during the growing season (Hanson and Weltzin 2000, Martínez-Vilalta et al. 2002). Third, do decreased growth rates prior to drought predispose trees to mortality? Previous studies have shown that stressed trees are more likely to be killed during and following drought (Pedersen 1998, Ogle et al. 2000). Answering these questions will allow a better understanding of climate effects on forest dynamics in these widely distributed, subalpine forest ecosystems.

Material and methods

Study area

The study area is located near Cameron Pass in Roosevelt National Forest in northern Colorado (USA) and extends over 11 × 5.8 km (centered on 40°33′N, 105°50′W). Elevation ranges from 2930 to 3320 m a.s.l. (above sea level). The dominant tree species in these subalpine forests are Engelmann spruce, subalpine fir, lodgepole pine and quaking aspen *Populus tremuloides*. Based on data from climate stations in Colorado (see next section and Appendix A1), we estimated for the study area (mean elevation 3141 m a.s.l.) mean temperatures of −10.1°C in January and 10.8°C in July. The estimated annual precipitation is 697 mm. Monthly precipitation decreases from 81.2 mm in April to 45.5 mm in June, and from 60.0 mm in July to a minimum of 43.3 mm in October.

Climate data and calculation of water deficits

Monthly means of temperature and precipitation from nine climate stations in the region were corrected for elevation in the study area using monthly lapse rates (Appendix A1). We calculated monthly temperature and precipitation values for the Cameron Pass study area by interpolation using an inverse-distance weighting scheme among the nine climate stations (Appendix A1). Drought (i.e. abnormally low precipitation over an extended period of time) is linked to water stress of plants via depletion of soil water (Bréda et al. 2006). We calculated water deficits using a water balance model based on a modified Thornthwaite method (Willmott et al. 1985; Appendix A2). Unlike the Palmer drought severity index (PDSI), which is an index of water deficit scaled to the climate of a region, raw water deficits may be interpreted relative to the total amount of precipitation required to ameliorate the drought.

We used cumulative water deficits from January through July to represent early-season deficits and cumulative water deficits from January through December to represent late-season deficits. Early-season deficits develop at the beginning of the growing season (June to July) and are influenced by snow pack in late spring (precipitation from March to May) and rainfall in June and July. Late-season deficits often begin as early-season deficits and continue during summer and fall or may be initiated by low precipitation and high temperatures in the late growing season (August to October) and early winter (Appendix A2, Fig. A2.1).

Sample sites and sampling design

Sixteen sample sites were selected in the study area including sites dominated mainly by spruce and fir, but also pine (Table 1). Sites were selected to cover different elevations, aspects, and slopes. In transects of approximately 10 to 50 m width and variable length, all dead, standing trees ≥ 20 cm DBH (diameter at breast height) were sampled. The common mode of tree mortality at these study sites was not related to widespread disturbances such as insect outbreaks or blowdown that create large patches of dead trees (Veblen et al. 1991, Mast and Veblen 1994). We extracted two increment cores at breast height from opposite sides of each tree. Stem sections showing evidence of eroded wood were avoided. About 10% of all dead, standing trees found in the field could not be cored because of rotten wood. Fallen trees were generally too decayed for sampling (Mast and Veblen 1994). For each dead tree, we also cored a live neighbour tree of the same species and of similar DBH for comparison of radial growth rates of pairs of dead and live trees. For each dead and live tree, we noted UTM (Universal Transverse Mercator; zone 13) coordinates using a GPS receiver, elevation, aspect, slope steepness, and DBH. In the field, each dead tree was assigned to a decay class (A = some needles present; B = some twigs remaining but no needles; C = some branches left; D = only the bole remaining).

Processing of increment cores and tree-ring series

Increment cores were processed following standard procedures in dendrochronology. We measured tree rings using a Velmex measurement system with a precision of 0.01 mm. Master chronologies, which integrate the climate signal of several trees in a region, were used to match growth patterns of the sampled trees. Site- and species-specific master chronologies were developed by adding trees cored in 2004 to existing chronologies from sites nearby the study area, which originally ended in 1986 (Veblen unpubl.). Based on these new master chronologies, we used the software COFECHA to quantitatively crossdate the series from the dead trees and to check the quality of the measured tree-ring series of both dead and live trees (Holmes 1983). Finally, the crossdated tree-ring series were compared visually with master chronologies.

Dead trees that were identified in the field were double-checked for species identification using wood-anatomical characteristics. Cores that could not be crossdated or that showed evidence of eroded tree rings at the outermost ring were not used in the analyses. We obtained a reliable estimate of the calendar year of the outermost ring from 172 trees of 278 sampled dead trees (all species = 61.9%; spruce = 54.7%, fir = 77.0%, pine = 40.5%); 164 of these trees died after 1909 and were used in the following analyses. If two cores were available and yielded different years for the

Table 1. Description of sample sites.

Site	Coordinates (easting/northing)	Elevation (m)	Aspect (°)	Slope (°)	DBH (cm)	Age (years)	n dead (spruce)	n dead (fir)	n dead (pine)
Box Canyon, L, A	429714/4490287	3060	7	27	25.5	251	11	12	0
Corral Creek, L, A	434589/4485838	3110	163	13	29.0	–	3	1	7
Corral Creek, L, B	433788/4486804	3250	158	18	34.9	203	6	0	8
Corral Creek, R, A	433554/4485500	3082	342	15	36.9	190	11	1	3
Corral Creek, R, B	432437/4485334	3224	18	10	34.7	–	7	7	0
Montgomery Pass, A	425449/4488633	3082	91	12	38.3	199	14	9	0
Montgomery Pass, B	423667/4488003	3312	352	10	38.7	410	22	1	0
Poudre River, L, A	434525/4488453	2943	287	8	29.9	305	9	9	0
Poudre River, L, B	434575/4488109	3015	345	20	35.8	367	16	5	0
South Trail, L, B	431832/4491027	3055	40	18	28.3	194	1	6	15
Trap Creek, L, A	429743/4488376	3179	75	12	31.5	205	4	7	1
Trap Creek, L, B	429632/4488653	3221	99	23	33.6	170	4	5	1
Trap Creek, R, A	430116/4488131	3200	297	13	30.1	270	4	9	0
Trap Creek, R, B	429936/4487249	3264	276	8	30.7	181	0	13	0
Zimmerman Lake, L, A	425554/4487254	3120	309	11	32.1	192	12	9	2
Zimmerman Lake, L, B	426868/4487024	3265	294	17	34.6	212	4	19	0

Site = name of sample site followed by L or R (orographic left or right side of valley) followed by A or B (A, lower site; B, upper site); coordinates = easting and northing in UTM (Universal Transverse Mercator) coordinates; elevation = elevation above sea level; aspect = aspect of slope; slope = slope steepness; DBH = average tree diameter at breast height; age = average tree age at breast height; n dead (spruce) = number of dead spruce; n dead (fir) = number of dead fir; n dead (pine) = number of dead pine. Values for coordinates, elevation, aspect, slope, DBH, and age are average values based on dead trees sampled at each site (' – ' for sites with <4 trees).

outermost ring, we assumed the year of tree death to be the more recent year. To accurately estimate tree age at breast height, we used Duncan's (1989) geometric method to estimate the number of missing rings between pith and first complete tree ring. Tree ages of cores only with <20 missing rings between pith and first complete ring were considered. Average tree ages at breast height were used to roughly describe stand ages (Table 1).

Bivariate event date analysis

To analyse effects of increased water deficits (hereafter "drought") on tree mortality, we applied a temporal modification of spatial point pattern analysis for one-dimensional, bivariate data (Ripley 1976, Diggle et al. 1995). Point pattern analysis using Ripley's K function is a common method to analyse spatial data in ecology (Wiegand and Moloney 2004). Recently, multivariate point pattern analysis has been adapted to the study of event date associations for the analysis of synchrony of fires from multiple sedimentary records (Gavin et al. 2006). In our study, we further adapted the application of Ripley's K to examine a one-directional process in time (i.e. bivariate event date analysis), and test the hypotheses that tree mortality events coincide with or follow drought events using variable time lags.

The number of mortality events (M) during and following drought events (D) was counted and scaled for different lags t, using a minor modification of the bivariate K function:

$$K_{DM}(t) = \frac{T}{n_D n_M} \sum_{i=1}^{n_D} \sum_{j=1}^{n_M} I\left[(M_j - D_i) \le t | M_j \ge D_i\right] \tag{1}$$

where t is time (years), T is the length of the record, n_D and n_M are the number of drought and mortality events, M_j and D_i are times of mortality events j and drought events i, and the identity function I counts the number of mortality events during and following drought years (see the example in Appendix A3). The inference of causality between these two processes is valid because we consider the condition that mortality events have to occur on the same year as or after drought.

To remove the time dependence of $K_{DM}(t)$, the L function was derived as $L_{DM}(t) = K_{DM}(t) - t$. $L_{DM}(t)$ is directly related to the expected additional number of events within lag t compared to a random distribution. Values of L above an upper confidence limit indicate association or synchrony between the two records (i.e. there is greater mortality than expected during and following drought), values of L below a lower confidence limit indicate asynchrony (i.e. there is less mortality than expected during and following drought), and values of L between the two confidence limits indicate independence. Because we hypothesised that mortality increases following drought, we evaluated only positive associations. The L function was calculated for 1000 Monte-Carlo simulations to derive 95% and 99% confidence envelopes. Monte-Carlo simulations are based on randomising drought years (without replacement). This approach results in valid tests even if the underlying process of tree mortality is non-stationary (Results; Diggle 2003). The power of this method in detecting relationships between two causally-related records is illustrated in Appendix A3.

Analysis of event date associations between mortality and drought

We defined drought years by applying thresholds to time series of cumulative water deficit over each year. Drought events were selected based on late-season water deficits (cumulative water deficit from January through December; hereafter "late-season drought") or early-season water deficits (cumulative water deficit from January through July; hereafter "early-season drought"). We selected a range of severity of late-season and early-season drought. Late-season droughts examined were based on thresholds of 70, 80 and 90 mm water deficit, yielding series of 30, 19 and 11 years, respectively. Early-season droughts were based on thresholds of 30 and 40 mm water deficit, yielding series of 11 and 5 events, respectively (Appendix A2). Event date analyses were performed for all combinations of mortality events (by species) and drought events (by threshold level).

Analysis of pre-drought radial growth rates

Drought might be more likely to kill trees that are weakened or otherwise predisposed to death by a variety of long-term factors such as competition or low nutrient availability (Manion 1981). Because radial growth rates (i.e. tree-ring widths) are related to tree vigour (Dobbertin 2005), we examined if trees that died during recent droughts had lower pre-drought growth rates than surviving trees. Since radial growth rates tend to decline as tree diameters increase, we compared only pairs of recently dead and live trees of similar DBH. Trees that died between 2000 and 2004, which included several years of drought, were compared with their live neighbours. Differences between average pre-drought growth rates over two 5-year periods (1990–1994, 1995–1999) were tested between dead and live trees using a Wilcoxon signed rank test for paired samples (Zar 1999). Only spruce and fir were analysed, because no pine died after 1999. Growth rates were calculated using the first core extracted of each tree or the core with the later death date. Before comparing growth rates, we tested the assumption of similar DBH and age of dead and live trees. There were no significant differences between DBHs of the pairs of spruce compared (V = 25, p = 0.078, median dead trees = 41.00 cm, median live trees = 37.25 cm, n = 8 pairs; Wilcoxon signed rank test for paired samples, exact p-values for tied ranks) or of fir (V = 71.5, p = 0.072, median dead trees = 25.00 cm, median live trees = 26.75 cm, n = 14 pairs). Similarly, for the age distributions of dead versus live trees, there were no significant differences for spruce (V = 22, p = 0.219, median dead trees = 238 years, median live trees = 237.5 years, n = 7 pairs) or for fir (V = 57.5, p = 0.157, median dead trees = 211.5 years, median live trees = 158.5 years, n = 12 pairs).

Results

Relationships between mortality frequencies and drought

Between 1910 and 2004, 64 spruce, 85 fir, and 15 pine died that were crossdated (Fig. 1). Trees often died in clusters with two to six consecutive years of increased tree mortality, particularly fir (Fig. 1b), but also spruce (Fig. 1a). Up to four or five spruce or fir trees died in the same year (2002 and 2003). The number of dead trees increased over time, but more so for spruce and fir than for pine (Fig. 1; slopes β of Poisson regression of effect of time on mortality frequency: spruce, β = 0.0258; fir, β = 0.0239; pine, β = 0.0127; standard errors are not reported because of temporal autocorrelation).

Drought years with the five highest late-season water deficits (based on cumulative water deficits through December) occurred in 1978, 1994, 1944, 1939, and 1996 (in decreasing order of intensity; Fig. 1 and A2.1b). The five most severe early-season droughts based on cumulative water deficits through July occurred during the last 27 years in 1994, 1978, 2002, 2000, and 1980 (in decreasing order of intensity; Fig. 1 and A2.1b). Visual inspection of the water deficit and mortality time series showed that particularly between 1978 and 2004, periods of increased late-season or early-season water deficits coincided with increased tree mortality (Fig. 1). This association was more pronounced for fir than for spruce. These relationships are explored more quantitatively below.

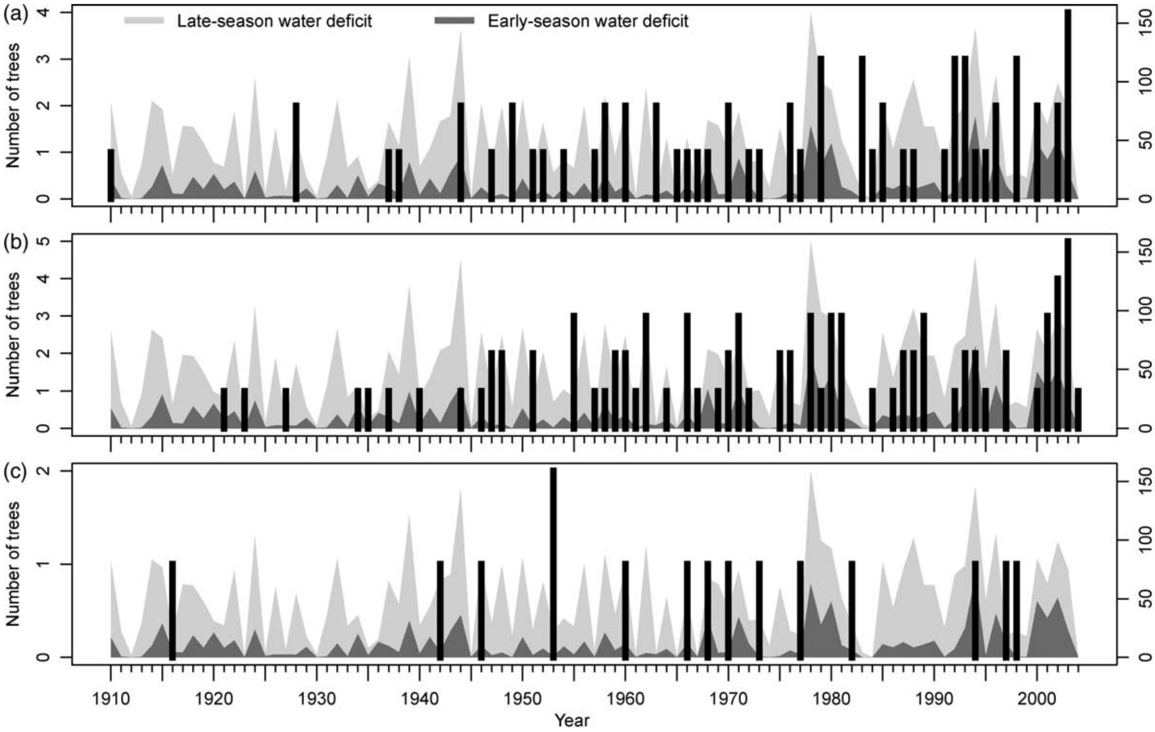

Fig. 1. Tree deaths and water deficits from 1910 to 2004. Numbers of dead trees per year are shown as black bars (left y axis). In the background are late-season water deficits (cumulative water deficits from January through December; light grey) and early-season water deficits (cumulative water deficits from January through July; dark grey) (right y axis); large water deficits correspond to high water stress. Mortality frequencies are shown for: a) spruce (n = 64); b) fir (n = 85); and c) pine (n = 15).

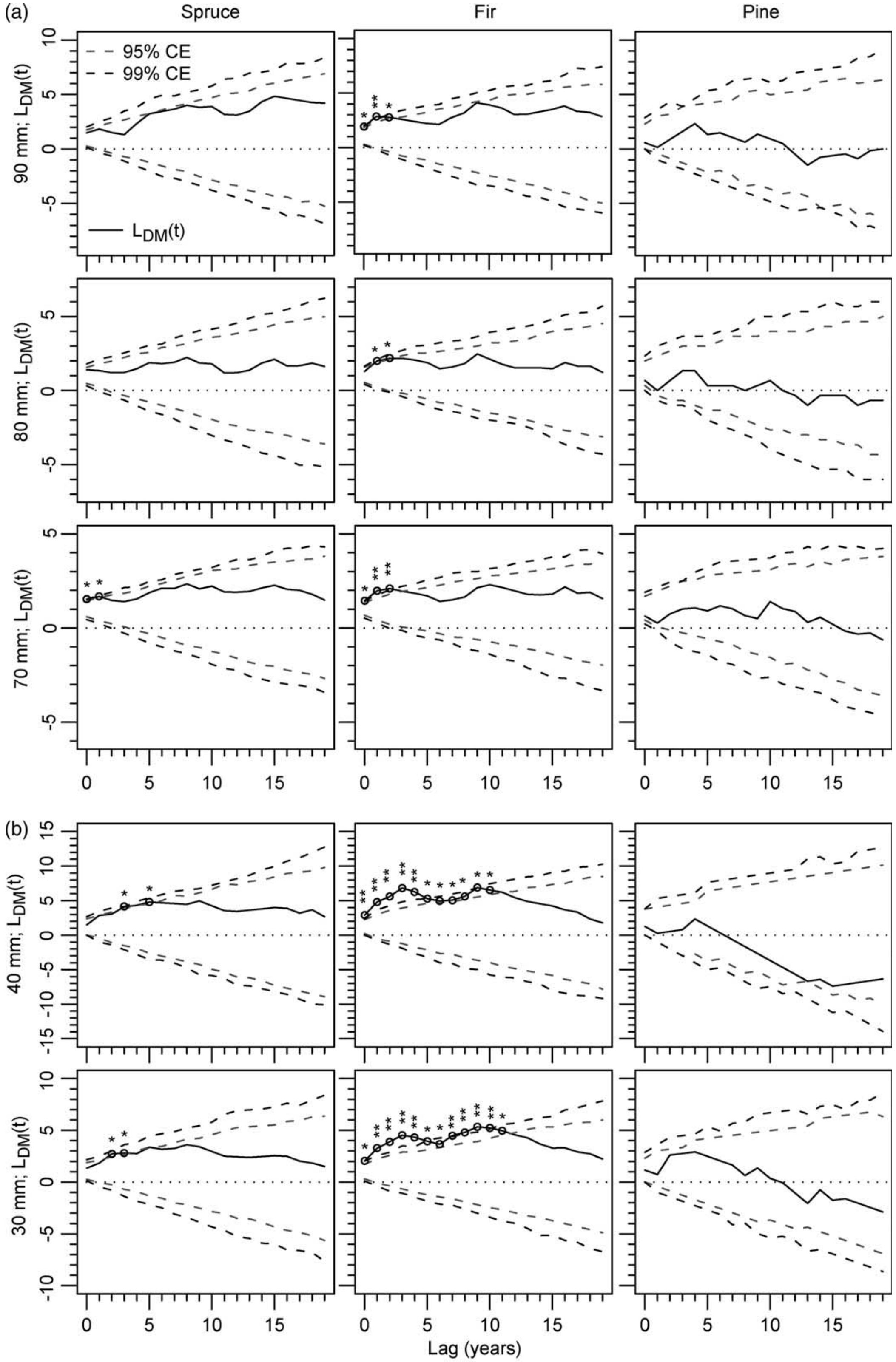

Fig. 2 (*Continued*)

Analysis of event date associations between mortality and drought

Late-season droughts resulted in significantly increased mortality of spruce within one year and of fir within two years (Fig. 2a). Using different thresholds, fir showed a more consistent and stronger drought-mortality association than spruce. Early-season droughts increased mortality of spruce within five years, whereas fir mortality was strongly increased up to 11 years (Fig. 2b). For both spruce and fir, the drought-mortality association showed no significant lags for higher thresholds of late-season droughts, which included only a small number of drought years. For lower thresholds of early-season droughts (i.e. including a large number of mild drought years), the associated mortality of fir declined sharply (results not shown). Mortality of pine was not affected by either late- or early-season droughts.

Analysis of pre-drought radial growth rates

Recent droughts during 2000 to 2004 (Fig. 1) provided the opportunity to compare pre-drought growth rates of trees that died during this period ($n = 8$ spruce and 14 fir) to neighboring live trees (Fig. 3). We found significantly lower growth rates during 1990 to 1994 for trees that subsequently died than for live trees for spruce ($V = 0$, $p = 0.008$) and for fir ($V = 17$, $p = 0.025$), as well as for the period 1995 to 1999 for spruce ($V = 0$, $p = 0.008$) and for fir ($V = 16$, $p = 0.020$).

Discussion

Long-lasting lag effects of drought on tree mortality

Tree mortality in the subalpine forests of the Rocky Mountains is strongly affected by drought during the current year as well as during years following a drought (Fig. 1). The relationship between water deficits and tree mortality is particularly evident between 1978 and 2004, when the most severe water deficits occurred. There are also strong interspecific differences in the effects of drought on mortality: subalpine fir showed the strongest and most persistent drought-mortality association, whereas Engelmann spruce showed a weaker association and lodgepole pine showed no such association (Fig. 2). While this is the first retrospective study in the Rocky Mountains to show a lagged drought-mortality association, other studies have found similarly lagged effects of 15 to 20 years for oak (*Quercus*) species in the Midwest (USA) (Pedersen 1998) and for European beech *Fagus sylvatica* in England (Peterken and Mountford 1996).

Lag effects of drought on tree mortality differ with the seasonality of the drought as revealed by bivariate event date analysis (Fig. 2). Particularly for fir, mortality is more strongly related to early-season drought (i.e. moisture shortages through July) than to late-season drought (i.e. moisture shortages through the growing season and into the dormant season). Fir mortality was strongly increased for 11 years following early-season drought, and only for two years following late-season drought. For spruce, early- and late-season droughts resulted in increased mortality for five years and one year, respectively (Fig. 2). The seasonal effect of drought on differential tree mortality of spruce and fir is probably related to different ecophysiological traits of the two species (Knapp and Smith 1981). Drought that already exists early in the growing period (i.e. during a time when meristematic activity starts at high elevation) may have stronger effects on fir mortality than drought either late in the growing season or after growth cessation (i.e. September to December). One possible mechanism responsible for increased mortality to early-season drought may be related to seasonal changes in stomatal behaviour, which has been found for fir (Knapp and Smith 1981, Pataki et al. 2000). Similarly, seasonal effect of drought on mortality was also observed for deciduous broadleaf forests in the eastern US (Hanson and Weltzin 2000).

Explanations of lagged tree mortality following drought

We suggest several possible explanations for increased mortality up to 11 years following drought (Bréda et al. 2006). Severe drought can cause cavitations and xylem dysfunction, which affect a tree's physiology over several years (Tyree and Sperry 1988, Hanson and Weltzin 2000). During drought, trees react with stomatal closure to prevent water loss and cavitation as well as reduced leaf area and/or assimilation, which

Fig. 2. Bivariate event date analysis for tree mortality and drought. Different thresholds were used to select years with more or less severe drought. The L(t) function (transform of Ripley's K) is shown for lags of 0 to 19 years (black line), separately for spruce ($n = 64$), fir ($n = 85$), and pine ($n = 15$). Confidence envelopes (95% and 99% CE; dashed lines) are based on 1000 Monte-Carlo simulations. Significant lags are encircled and denoted with **($p < 0.01$) and *($p < 0.05$) indicating increased mortality during or after drought within a lag of t years. (a) Late-season droughts (thresholds of late-season water deficits: 90 mm, $n = 11$; 80 mm, $n = 19$; 70 mm, $n = 30$); (b) early-season droughts (thresholds of early-season water deficits: 40 mm, $n = 5$; 30 mm, $n = 11$).

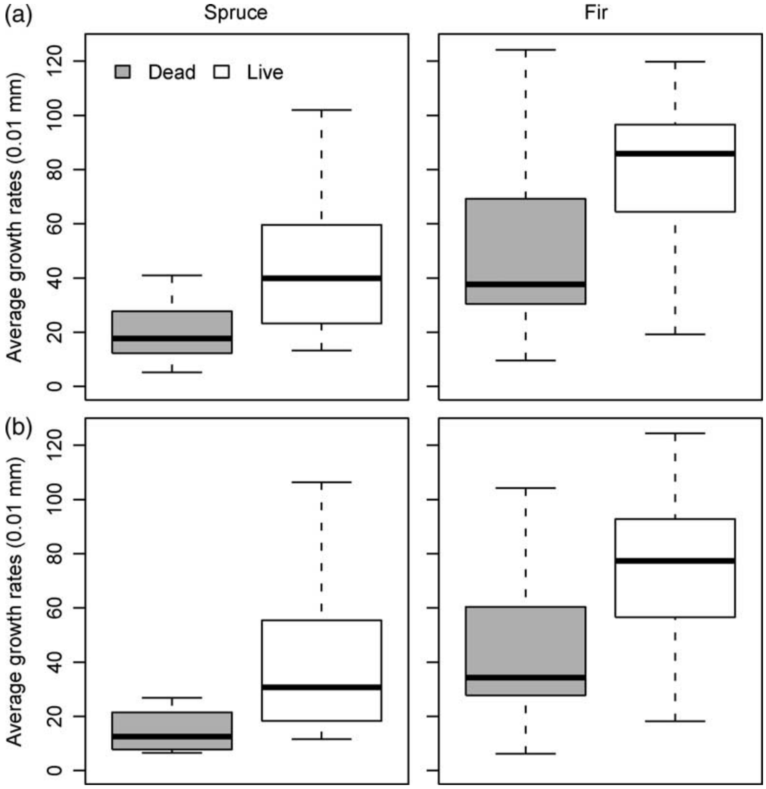

Fig. 3. Comparison of pre-drought growth rates. Boxplots of average radial growth rates for spruce (n = 8) and fir (n = 14), separately for dead and live trees. (a) Period 1990–1994, (b) period 1995–1999.

reduces carbohydrate reserves and growth rates in the drought year and in following years (Tyree and Sperry 1988, Irvine et al. 1998, Bréda et al. 2006). Sustained low and rapidly decreasing growth rates in turn are associated with increased likelihood of tree mortality (Bigler and Bugmann 2004). Such stressed trees may be predisposed to insect attack (Allen and Breshears 1998) and phytopathogens such as Armillaria root disease (*Armillaria* spp.; Clinton et al. 1993, Cherubini et al. 2002). These contributing factors may also have pronounced interspecific effects. For example, subalpine fir is known to be generally less decay-resistant than spruce and more susceptible to fungi such as annosum root disease *Heterobasidion annosum*, which is often followed by fir engraver beetles *Scolytus ventralis* (Mast and Veblen 1994, Worrall et al. 2004).

Just as drought may predispose trees to additional stresses and declining growth, these same stresses or long-term stress factors such as competition may predispose trees to die during subsequent drought (Manion 1981). We found that reduced pre-drought radial growth rates for both spruce and fir strongly increases the risk of tree mortality (Fig. 3). Decreased growth rates of trees prior to drought-incited mortality have also been observed in a range of other forest ecosystems (Pedersen 1998, Ogle et al. 2000, Suarez et al. 2004, Bigler et al. 2006).

Susceptibility to drought differs among subalpine tree species

A previous dendrochronological study of the growth-climate relationship in subalpine spruce-fir forests showed a higher dependence of fir than spruce on moisture availability, but this difference was pronounced on mesic and humid sites while very minor on the driest microsites such as south aspects (Villalba et al. 1994). Spruce seems to be better adapted to extreme conditions than fir, the latter being rare on drier sites (Peet 2000). Pine grows better under warmer and drier conditions (Villalba et al. 1994), and in our study area, pine has a preference for dry, south-facing slopes (Table 1), which suggests lower susceptibility to drought than for spruce or fir.

Ecophysiological studies have found decreasing leaf conductance from fir to pine to spruce, and decreasing minimum xylem potential from pine to fir to spruce (Knapp and Smith 1981). Both high leaf conductance and high minimum xylem potential are adaptations to drought (Tyree and Ewers 1991, Bréda et al. 2006).

Overall, pine is a more efficient water conserver and less vulnerable to drought than spruce or fir, because of better stomatal control under dry conditions (Knapp and Smith 1981). Diurnal and seasonal changes might further explain differences among the three species, e.g. increasing leaf conductance for spruce throughout the day or spruce showing the smallest decrease of leaf conductance through the summer (Knapp and Smith 1981).

Potential methodological effects on drought-mortality relationships

Our finding of a population-wide pattern of drought-induced tree mortality and increased mortality over the most recent decades is not likely an artifact of sampling. Specifically, there are multiple lines of evidence that suggest little bias in the construction of the long-term patterns in tree death dates. First, loss of standing dead trees due to total decay and thus censoring earlier death dates can be ruled out because the wood of trees found in the field was generally well preserved due to the dry-cool climate. Dead wood turnover times for fallen spruce, fir, and pine have been estimated to be species independent and to range between 340 and 800 years (Kueppers and Harte 2005). In our study, only relatively large, standing trees were sampled and only trees that died after 1909 were included in the analysis (Donnegan and Rebertus 1999).

Second, we evaluated the possibility that dead trees not included in the analysis (i.e. fallen trees, undated trees or trees with eroded tree rings) might have biased the distributions of mortality frequencies (Table 2). In general, there were not large numbers of fallen dead trees in the stands (Donnegan and Rebertus 1999, Kueppers et al. 2004). Because annual fall rate is relatively low (between 0.7% and 1.5% for beetle-killed Engelmann spruce in similar forests in Colorado; Mielke 1950, Schmid and Hinds 1974) and because decay rates of standing dead trees are even lower than those for fallen dead trees, it is likely that the death dates of fallen trees are much older than those determined for the standing dead trees. For the standing dead trees that we sampled, we assumed decay class to be a rough proxy of time since tree death. We tallied the number of dated and undated trees by species and decay class, and we calculated the quantiles of the death dates of the dated trees for each species and decay class. Given the wide distribution of death dates in decay classes B and C (Table 2) and assuming that the undated trees show a similar distribution, we suggest that adding these undated spruce, fir, and pine trees to the data set would not significantly shift the temporal distribution of mortality frequencies (Fig. 1).

Last, it is unlikely that death dates were greatly affected by an undetected yet widespread disturbance such as primary insect attacks, phytopathogens, blowdown, or rock fall. While these factors may have contributed to some individual death dates, the dispersion of sampling across many sites implies that regional drought was the primary mortality factor.

We also believe there is negligible error in determining the short-term (i.e. year-to-year) patterns in mortality dates. We assumed that tree death, as determined by the outer visible tree ring of a core, is the earliest possible year of tree death. Because trees can have missing or partial tree rings prior to death, the actual lag

Table 2. Comparison of death dates by species and decay class for dated and undated trees.

Tree species	Total (n)	Observed number of trees in each decay class				Death dates (year) of dated trees in each decay class‡ (5%, 50%, 95% quantiles)		
		A	B	C	D	A	B	C
Engelmann spruce								
Dated	70	1	53	16	0	–, 2002, –	1941, 1983, 2003	1887, 1941, 1969
Undated	58	0	24	32	2			
Subalpine fir								
Dated*	86	16	66	4	0	1995, 2002, 2003	1924, 1970, 1994	1941, 1954, 1968
Undated	26	1	19	6	0			
Lodgepole pine								
Dated	15	0	10	5	0		1953, 1974, 1998	1921, 1946, 1972
Undated	22	2	8	12	0			

‡Quantiles were not calculated for decay classes that did not include any trees. 5% and 95% quantiles of death dates were only calculated for decay classes with ≥4 dead trees.

*One dated fir tree was excluded in this analysis, because the information on the decay class was missing.

Shown for each tree species are the total number of dead trees (dated = dated trees without eroded tree rings; undated = undated trees or trees with eroded tree rings) and for each decay class (A = some needles present; B = some twigs remaining but no needles; C = some branches left; D = only the bole remaining) the observed number of dead trees. For dated, dead trees, the 5%, 50%, and 95% quantiles of death dates are shown.

effect of drought on tree mortality might be slightly longer than indicated by the results of bivariate event date analysis. Since generally two cores per tree were used, which were taken from different sides of the stem, the estimates of tree death dates are relatively robust. For example, the differences between the death dates from the two cores of each tree showed that 21 of 47 spruce (44.7%) and 40 of 61 fir (65.6%) differ by zero or one year. Thirty-five of 47 spruce (74.5%) and 55 of 61 fir (90.2%) show a difference of zero to four years. These results indicate that most trees die a relatively rapid death once growth production ceased in one part of the stem. Observations in permanent plots in subalpine spruce-fir stands showed that tree-ring production typically ceased one to three years before actual tree death (Mast and Veblen 1994). Nevertheless, we acknowledge that the impossibility of precisely determining the year of death for all trees is a potential source of error in determining lag effects.

Implications of current and changing climate on drought-induced tree mortality

A direct link of climate variability to tree mortality has the potential for driving large-scale changes in subalpine forests. Scenarios of climate change for the 21st century in the Colorado Rocky Mountains project an increased frequency of extremely hot days, increased length of heat waves, and a decrease of root zone soil moisture during summer months (Stohlgren et al. 2004, Diffenbaugh et al. 2005). Drought effects in forests have been suggested to be alleviated under elevated, atmospheric CO_2 concentrations (Hanson and Weltzin 2000, Martínez-Vilalta et al. 2002), more so for deciduous trees than for conifers (Leuzinger et al. 2005), related to reduced stomatal opening and increased water use efficiency. However, CO_2-induced reduction of water stress has recently been shown to be relatively small based on experimental field studies of deciduous tree species exposed to exceptionally severe drought (Leuzinger et al. 2005).

Drought effects could substantially affect vegetation and carbon cycling in the 17 000 km^2 of subalpine spruce-fir forests in the central and southern Rocky Mountains (Alexander 1987). In the most severe case, increased drought would result in widespread tree mortality and large-scale shifts in vegetation boundaries, as documented underway in the southwestern US (Allen and Breshears 1998, Hanson and Weltzin 2000, Breshears et al. 2005). However, in subalpine forest ecosystems drought-induced shifts of species composition are not only dependent on tree mortality processes, but also on climatic influences on regeneration and growth processes. Increased tree mortality might result in more regeneration in some forest stands and compensatory growth of surviving trees, which in turn might offset drought-induced losses of carbon.

Our study shows that drought is an essential factor involved in differential mortality of co-occurring subalpine tree species, but it is presumably just one element in a series of potentially interacting mortality factors. Proximate causes of tree death are notoriously difficult to determine (Manion 1981) and it is likely that increases in tree mortality associated with drought may also involve increased susceptibility of trees to disease and insect attack. A better understanding of the effects of drought on subalpine forest ecosystems and carbon cycling under current climate is a prerequisite to predicting potential effects of increasing frequency and intensity of drought under changing climate.

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References

Alexander, R. R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. – USDA For. Serv. Agric. Handbook, No. 659.

Allen, C. D. and Breshears, D. D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. – Proc. Natl Acad. Sci. USA 95: 14839–14842.

Bebi, P. et al. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. – Ecology 84: 362–371.

Bigler, C. and Bugmann, H. 2004. Predicting the time of tree death using dendrochronological data. – Ecol. Appl. 14: 902–914.

Bigler, C. et al. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. – Ecology 86: 3018–3029.

Bigler, C. et al. 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. – Ecosystems 9: 330–343.

Bréda, N. et al. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. – Ann. For. Sci. 63: 625–644.

Breshears, D. D. and Allen, C. D. 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. – Global Ecol. Biogeogr. 11: 1–5.

Breshears, D. D. et al. 2005. Regional vegetation die-off in response to global-change-type drought. – Proc. Natl Acad. Sci. USA 102: 15144–15148.

Cherubini, P. et al. 2002. Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently. – J. Ecol. 90: 839–850.

Clinton, B. D. et al. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta basin. – Ecology 74: 1551–1558.

Diffenbaugh, N. S. et al. 2005. Fine-scale processes regulate the response of extreme events to global climate change. – Proc. Natl Acad. Sci. USA 102: 15774–15778.

Diggle, P. J. 2003. Statistical analysis of spatial point patterns. – Arnold.

Diggle, P. J. et al. 1995. Second-order analysis of space-time clustering. – Stat. Meth. Med. Res. 4: 124–136.

Dobbertin, M. 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. – Eur. J. For. Res. 124: 319–333.

Donnegan, J. A. and Rebertus, A. J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. – Ecology 80: 1370–1384.

Duncan, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). – N. Z. Nat. Sci. 16: 31–37.

Elliott, K. J. and Swank, W. T. 1994. Impacts of drought on tree mortality and growth in a mixed hardwood forest. – J. Veg. Sci. 5: 229–236.

Gavin, D. G. et al. 2006. Weak climatic control of stand-scale fire history during the late Holocene in southeastern British Columbia. – Ecology 87: 1722–1732.

Hanson, P. J. and Weltzin, J. F. 2000. Drought disturbance from climate change: response of United States forests. – Sci. Total Environ. 262: 205–220.

Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measuring. – Tree-Ring Bull. 43: 69–78.

Innes, J. L. 1998. The impact of climatic extremes on forests: an introduction. – In: Beniston, M. and Innes, J. L. (eds), The impacts of climate variability on forests. Springer, pp. 1–18.

Irvine, J. et al. 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. – Tree Physiol. 18: 393–402.

Knapp, A. K. and Smith, W. K. 1981. Water relations and succession in subalpine conifers in southeastern Wyoming. – Bot. Gaz. 142: 502–511.

Kueppers, L. M. and Harte, J. 2005. Subalpine forest carbon cycling: short- and long-term influence of climate and species. – Ecol. Appl. 15: 1984–1999.

Kueppers, L. M. et al. 2004. Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. – Oecologia 141: 641–651.

Kulakowski, D. and Veblen, T. T. 2002. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. – J. Ecol. 90: 806–819.

Leuzinger, S. et al. 2005. Responses of deciduous forest trees to severe drought in Central Europe. – Tree Physiol. 25: 641–650.

Lloyd, A. H. and Graumlich, L. J. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. – Ecology 78: 1199–1210.

Manion, P. D. 1981. Tree disease concepts. – Prentice-Hall.

Martínez-Vilalta, J. et al. 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. – Ecol. Model. 155: 127–147.

Mast, J. N. and Veblen, T. T. 1994. A dendrochronological method of studying tree mortality patterns. – Phys. Geogr. 15: 529–542.

Mielke, J. L. 1950. Rate of deterioration of beetle-killed Engelmann spruce. – J. For. 48: 882–888.

Mueller, R. C. et al. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. – J. Ecol. 93: 1085–1093.

Ogle, K. et al. 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. – Ecology 81: 3237–3243.

Pataki, D. E. et al. 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. – Ecology 81: 2557–2566.

Pedersen, B. S. 1998. The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. – Ecology 79: 79–93.

Peet, R. K. 2000. Forests of the Rocky Mountains. – In: Barbour, M. G. and Billings, W. D. (eds), North American terrestrial vegetation. Cambridge Univ. Press, pp. 63–102.

Peterken, G. F. and Mountford, E. P. 1996. Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. – Forestry 69: 125–136.

Ripley, B. D. 1976. The second-order analysis of stationary point processes. – J. Appl. Probab. 13: 255–266.

Romme, W. H. and Despain, D. G. 1989. Historical perspective on the Yellowstone fires of 1988. – BioScience 39: 695–699.

Schmid, J. M. and Hinds, T. E. 1974. Development of spruce-fir stands following spruce beetle outbreaks. USDA For. Serv. Res. Paper RM-131. – Rocky Mountain For. Range Exp. Stn, Fort Collins, CO, USA.

Sibold, J. S. and Veblen, T. T. 2006. Relationships of subalpine forest fires in the Colorado Front Range with interannual and multi-decadal scale climatic variation. – J. Biogeogr. 33: 833–842.

Stohlgren, T. J. et al. 2004. Global change impacts in the Colorado Rockies biogeographical area: final report, 1999–2003. p. 39.

Suarez, M. L. et al. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. – J. Ecol. 92: 954–966.

Tyree, M. T. and Sperry, J. S. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? – Plant Physiol. 88: 574–580.

Tyree, M. T. and Ewers, F. W. 1991. The hydraulic architecture of trees and other woody plants. – New Phytol. 119: 345–360.

Veblen, T. T. et al. 1989. Blowdown and stand development in a Colorado subalpine forest. – Can. J. For. Res. 19: 1218–1225.

Veblen, T. T. et al. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. – Ecology 72: 213–231.

Veblen, T. T. et al. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. – J. Ecol. 82: 125–135.

Villalba, R. and Veblen, T. T. 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. – Ecology 79: 2624–2640.

Villalba, R. et al. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. – Ecology 75: 1450–1462.

Wiegand, T. and Moloney, K. A. 2004. Rings, circles, and null-models for point pattern analysis in ecology. – Oikos 104: 209–229.

Willmott, C. J. et al. 1985. Climatology of the terrestrial seasonal water cycle. – J. Climatol. 5: 589–606.

Worrall, J. J. et al. 2004. Incidence, host relations and population structure of *Armillaria ostoyae* in Colorado campgrounds. – For. Ecol. Manage. 192: 191–206.

Zar, J. H. 1999. Biostatistical analysis. – Prentice-Hall.

Appendix A1–A3

Can be found as On Line appendix O16034 at www.oikos.ekol.lu.se/Appendix