Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest

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Abstract: The view that subalpine forest vegetation dynamics in western North America are “driven” by a particular disturbance type (i.e., fire) has shaped our understanding of their disturbance regimes. In the wake of a recent (1990s) landscape-extent spruce beetle (*Dendroctonus rufipennis* Kirby) outbreak in the southern Rocky Mountains, we re-examined the temporal continuity in disturbance types and interactions and the possible role of drought on their occurrence by reconstructing antecedent disturbances for 11 sites across the Markagunt Plateau, southern Utah, USA. Multiple consistent lines of evidence suggested that historic fires were the primary antecedent disturbance, while relatively minor, stand-specific spruce beetle activity occurred later in stand development but prior to the recent outbreak. Unlike the recent outbreak, antecedent fires were spatially and temporally asynchronous over the period examined (~1600–2000). Reconstructed fire events primarily occurred during periods of prolonged drought. Similarly, historic spruce beetle activity, indicated by species-specific tree-ring release, and timing of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) death dates from the recent outbreak were related to drought conditions. Vegetation dynamics on this landscape were strongly driven by historic fires and the recent spruce beetle outbreak, and drought conditions likely influenced the occurrence of both disturbance types.

Résumé : L’idée que la dynamique de la végétation forestière subalpine dans l’ouest de l’Amérique du Nord soit déterminée par un type particulier de perturbations (c.-à-d. le feu) a façonné notre compréhension de ces régimes de perturbation. À la suite de l’épidémie récente (années 1990) du dendroctone de l’épinette (*Dendroctonus rufipennis* Kirby) à l’échelle du paysage dans la partie sud des montagnes Rocheuses, nous avons réexaminé la continuité temporelle et les interactions dans le type de perturbations, ainsi que le rôle potentiel de la sécheresse sur leur occurrence, en reconstituant les perturbations antérieures dans 11 stations réparties sur le plateau de Markagunt dans le sud de l’État de l’Utah, aux États-Unis. Des sources de données multiples et concordantes indiquent que les feux étaient dans le passé la principale perturbation tandis que l’activité du dendroctone, relativement mineure et spécifique à certains peuplements, est apparue plus tard dans le développement du peuplement mais avant l’épidémie récente. Contrairement à la vague récente, les feux antérieurs étaient asynchrones dans le temps et l’espace pendant la période qui a été étudiée (~1600–2000). Les épisodes de feu reconstitués sont survenus surtout pendant des périodes de sécheresse prolongée. De la même façon, l’activité passée du dendroctone, révélée par l’élargissement des cernes annuels, spécifique à certaines essences, et le moment où est survenue la mortalité chez l’épicéa d’Engelmann (*Picea engelmannii* Parry ex Engelm.) à la suite de l’épidémie récente, étaient reliés aux conditions de sécheresse. La dynamique de la végétation dans ce paysage était fortement déterminée par les feux passés et l’épidémie récente du dendroctone; et les conditions de sécheresse ont probablement influencé l’occurrence des deux types de perturbations.

[Traduit par la Rédaction]

Introduction

In the subalpine forests of the Rocky Mountains, stand-replacing fire and bark beetle (*Dendroctonus* spp.) outbreaks are two primary stand-replacing disturbances (Peet 2000). By fundamentally altering forest structures and compositions, these disturbances directly affect stand dynamics (Veblen et al. 1991*a*) and shape larger scale forest landscape patterns (Turner et al. 1994), which in turn influence the probability, severity, and extent of subsequent disturbances (White and Jentsch 2001; Kulakowski et al. 2003; DeRose and Long 2009). Fire is often cited as the driving disturbance in subalpine systems, purportedly exhibiting a multicentury recurrence. However, the recent occurrence of large-scale bark beetle outbreaks, likely influenced by changing climate conditions, has called into question the temporal continuity of disturbance regimes.

The occurrence of large-scale disturbance in subalpine forests is strongly influenced by climate, both directly and indirectly (as cited in Swetnam and Anderson 2008). Regional drought, for example, influences the occurrence of disturbance, e.g., spruce beetle (*Dendroctonus rufipennis* Kirby)

Received 16 December 2011. Accepted 20 June 2012. Published at www.nrcresearchpress.com/cjfr on 17 August 2012.

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outbreaks in Colorado and Utah (Hebertson and Jenkins 2008) and stand-replacing fire in the southwestern United States (Margolis et al. 2007). Drought is commonly characterized using Palmer's drought severity index (PDSI), which algorithmically combines the influence from mean temperature and moisture availability (precipitation) to describe drought (Alley 1984). In subalpine forests of the Rocky Mountains, a negative departure of PDSI (i.e., drought) can be associated with water stress of individual trees (Bréda et al. 2006) and increasing mortality of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and, to a lesser extent, Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) (Bigler et al. 2007). Drought has also been shown to predispose spruce-dominated forests to high-severity fires (Bigler et al. 2005; Sibold and Veblen 2006; Margolis and Balmat 2009) and spruce beetle outbreaks (Berg et al. 2006; Hebertson and Jenkins 2008). Low-frequency variation in PDSI is thought to influence long-term (decades to centuries) differential growth rates in subalpine tree species (Villalba et al. 1994). These potential influences of drought are not surprising given that prolonged drought periods are a characteristic of the climate of the western United States (Mock 1996; MacDonald and Tingstad 2007).

To determine potential interactions between disturbances and the possible role of drought on their occurrence, disturbance history must be reconstructed. Some forested systems are characterized by frequent disturbance, with fire-tolerant species and historic records providing direct evidence of past disturbance events (e.g., fire-scarred trees). However, many subalpine forests have long disturbance return intervals and therefore can have a paucity of direct evidence for historical disturbance agents, e.g., a paucity of fire-tolerant trees, so that indirect methods of disturbance reconstruction are required. Demographic reconstructions of patterns of tree establishment and subsequent patterns of species-specific growth or death can help elucidate the type of disturbance that initiated and shaped the development of subalpine forest stands (Kipfmueller and Baker 2000; Antos and Parish 2002; Margolis and Balmat 2009). Dendroecological methods, which explore differences in tree ages, radial growth increment, stand structure, and species composition, allow the retrospective detection of vegetation responses to wildfire or spruce beetle outbreaks (Veblen et al. 1994; Eisenhart and Veblen 2000; Kulakowski and Veblen 2006).

In subalpine forests of the southern Rocky Mountains, mortality due to stand-replacing fires is not particularly species-specific (Peet 2000). As a result of newly opened growing space and reduced competition from overstory remnants, forest response to fire is characterized by (*i*) pulses in establishment of shade-intolerant pioneers or species that establish in mineral soil (Veblen 1986), (*ii*) rapid initial radial growth of new recruits (Parish et al. 1999), and (*iii*) radial growth release of remnant trees (Kulakowski and Veblen 2006). In contrast, mortality as a result of spruce beetle outbreaks is disproportionate among larger trees and is species-specific, with large-diameter Engelmann spruce (>10 cm; Schmid and Frye 1977) particularly susceptible. After an outbreak, the previously established understory and subcanopy trees, when present, are released (DeRose and Long 2010). Forest response to a spruce beetle outbreak is characterized by the potential establishment of nonhost shade-intolerant species, radial growth release of nonhost species (Eisenhart and Veblen 2000), and surviving (if any) spruce. The relative spatial and temporal synchrony of forest response across multiple sites can provide evidence for the scale of disturbances.

Starting in ~1990, a massive spruce beetle outbreak (>250 km^2) began on the Markagunt Plateau in southern Utah and did not subside until essentially all available host trees were killed. Prior to the beetle outbreak, extensive tracts of mature, dense Engelmann spruce forest dominated the landscape, which allowed the recent beetle outbreak to spread across the entire plateau in two decades (DeRose and Long 2012). The primary objective of this study was to reconstruct the disturbance history of multiple stands across the plateau to determine whether the antecedent disturbance history was (*i*) a landscape-extent spruce beetle outbreak such as what might be expected after the recent 1990s event, (*ii*) dominated by wild fire, or (*iii*) some combination of these. Our secondary objective was to ascertain whether the occurrence of reconstructed disturbance events and the recent outbreak were associated with drought. We began this study with two specific hypotheses: first, a landscape-wide spruce beetle outbreak was the antecedent disturbance on the Markagunt Plateau; and second, drought conditions coincided with disturbance events.

Study area

The Markagunt Plateau is located in the Cedar City Ranger District of the Dixie National Forest in southwestern Utah (Fig. 1). Topography of the plateau (average site elevation >3000 m; Table 1) is generally flat, with a gentle slope to the east. Forest vegetation on the high-elevation plateau was dominated by subalpine spruce–fir forests prior to the recent outbreak. Species associated with Engelmann spruce and subalpine fir in these southern Rocky Mountain forests include, in order of abundance in this study, aspen (*Populus tremuloides* Michx.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), limber pine (*Pinus flexilis* James), white fir (*Abies concolor* (Gord. and Glend.)), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws). Prior to the recent outbreak, Engelmann spruce was the oldest tree on every site except for the Bristlecone Pine Trail and Navajo Lake, where overstory Douglas-fir were similar in age (Table 1). The geologic substrate varies widely across the plateau owing to large intrusions of relatively young (Holocene) basalt lava flows, which occur within a matrix of much older (upper Cretaceous) formations composed primarily of sedimentary material, i.e., sandstones, mudstones, and limestones (Moore et al. 2004).

Precipitation on the Markagunt Plateau comes as winter snow augmented by North American Monsoon rainfall during the summer (Mock 1996), and annual averages vary between 368 and 1709 mm (Utah State University 2006). The PDSI effectively characterizes long-term drought periods (months to years) wherein 0 is average, negative numbers are dryer periods, and positive numbers are wetter periods. Strong historical drought–pluvial periods are evident in the PDSI reconstruction for the region, which have fluctuated by as much as –6.1 to +4.6 since ~1600 (grid point 87; Cook and Krusic 2004). The period of this study (~1600–2000) included many large droughts and the largest pluvial period (1905–1917) of the last 500–700 years (Stahle et al. 2007).

Fig. 1. Map of the Markagunt Plateau showing study locations (11 from this study and three (Lava Flow, South Face, Midway Face) from DeRose and Long (2007)).

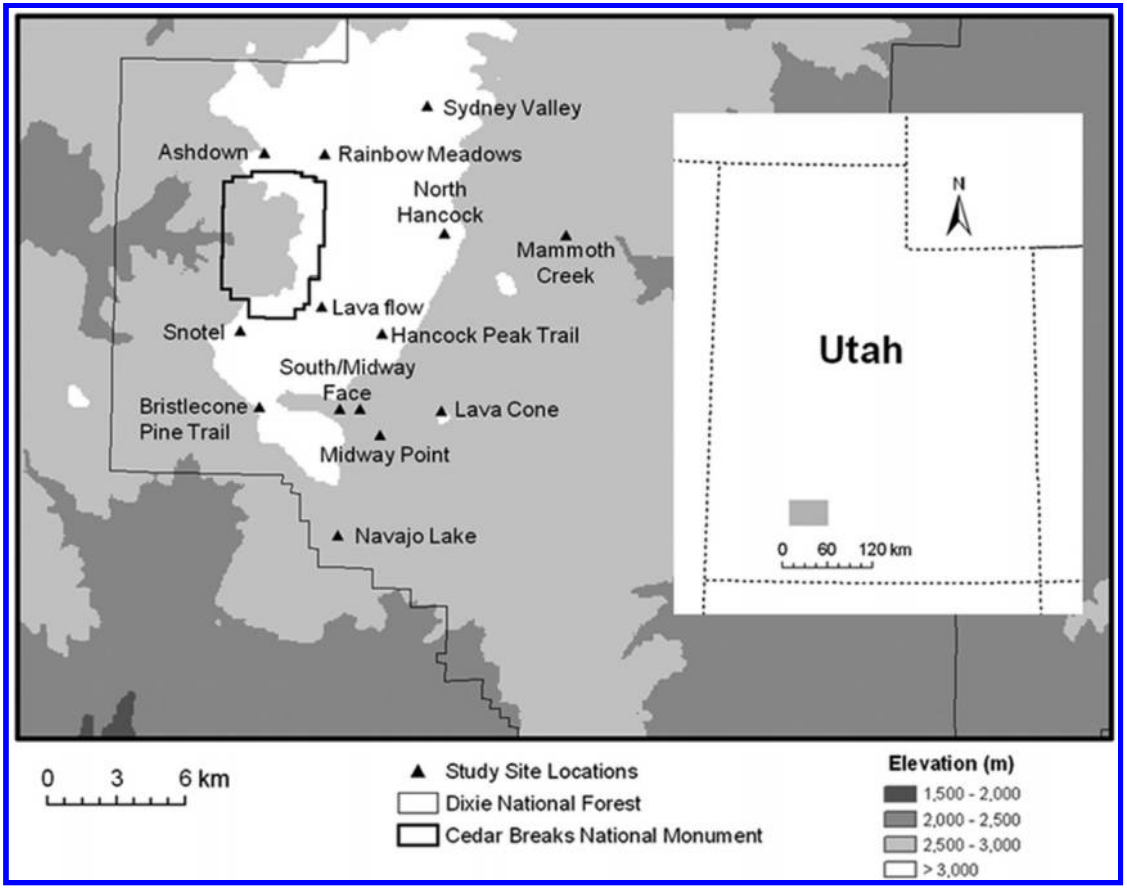

Table 1. Site attributes for the study area by site on the Markagunt Plateau.

Site	Elevation (m)	Aspect	Slope (%)	Age (years)	No. of increment cores	No. of plots
Ashdown	3197	North	0–5	425	86	9
Bristlecone Pine Trail	3006	Northwest	15–40	437	29	4
North Hancock	3090	North	3–30	323	67	10
Hancock Peak Trail	3081	Southeast	0–5	465	99	10
Lava Cone	2979	Variable	0–20	421	93	10
Midway Point	2959	North	0–3	276	136	10
Mammoth Creek	2670	North	15–40	491	58	10
Navajo Lake	2879	Northeast	10–30	470	86	10
Rainbow Meadow	3206	South	2–10	282	51	5
Snotel	3202	North	5–45	492	89	10
Sydney Valley	3095	Southwest	3–15	309	94	10
Average	3033	—	—	399	888	9

Note: Age is from the oldest crossdated individual on each site.

Methods

Field methods

Using restricted random sampling, we selected 11 sites across the Markagunt Plateau (Fig. 1) to characterize the high-elevation spruce–fir forest (Tables 1 and 2). Sites were chosen from aerial photos based on the apparent homogeneity of stand conditions. Site visits were made to verify stand homogeneity and to ensure that no logging had occurred in the stands. The sites varied in size from ~8 to ~30 ha. At each site, four to 10 variable radius prism plots were established on a 100 m systematic grid with a random starting point. The number of plots established on each site varied by the overall stand size. Variable radius plots do not have a

Table 2. Pre-outbreak stand structural and compositional attributes by site for all trees > 5 cm DBH.

	Quadratic mean diameter		Basal area (BA), m^2 (as a percent)				
Site	All species	Engelmann spruce	Aspen	Engelmann spruce	Subalpine fir	Other	Total BA
Ashdown	49.5	54.2	—	27.5 (85.9)	4.5 (14.1)	—	32
Bristlecone Pine Trail	52.6	43.0	—	41 (68.3)	5 (8.3)	14 (23.3)	46
North Hancock	33.2	37.1	—	31.5 (72.4)	12 (27.6)	—	43.5
Hancock Peak Trail	41.9	48.5	0.8 (1.9)	32 (74.8)	10 (23.4)	—	42.8
Lava Cone	37.9	45.9	2.4 (5.3)	30.4 (67.3)	11.2 (24.8)	1.2 (2.7)	45.2
Midway Point	36.3	41.4	11.4 (24.1)	30.9 (65.2)	5.1 (10.8)	—	47.4
Mammoth Creek	34.9	35.9	4 (13.5)	19.6 (66.2)	2 (6.8)	4 (13.5)	29.6
Navajo Lake	47.6	46.8	0.17 (0.4)	24.7 (55.5)	8.67 (19.5)	11 (24.7)	44.5
Rainbow Meadow	35.9	49.7	13.5 (34.9)	9.9 (25.6)	15.3 (39.5)	—	38.7
Snotel	54.7	57.5	—	47.4 (91.3)	4.5 (8.7)	—	51.9
Sydney Valley	28.6	39.3	12.6 (32.8)	6.9 (18.0)	18.6 (48.4)	0.3 (0.8)	38.4
Average	41.2	45.4	6.4	27.4	8.8	6.1	41.8

Note: Other species includes, in order of abundance, Douglas-fir, limber pine, white fir, and ponderosa pine.

fixed size: instead a prism with a particular basal area factor (3–8 m^2 held constant in each site) is chosen to select which trees would be measured. We had a target of including 10 trees per plot (mean number of trees actually measured = 12.8). For each selected tree, representation on a per-hectare basis was calculated by dividing the prism basal area factor by the basal area of the tree and averaging across plots. In each plot, all live and dead standing trees > 5 cm diameter at breast height (DBH, 1.3 m) were assessed for species, status (alive, dead, cause of mortality), DBH, and tree height. The recent beetle outbreak, which began in the early 1990s, killed most large spruce by ~2005, but nearly every beetle-killed tree was still standing (~99.2%; DeRose and Long 2010). To determine whether the spruce beetle was the cause of mortality, we noted the presence of emergence holes and recent beetle galleries.

To determine tree ages, radial growth patterns, and the year of tree death for Engelmann spruce, increment cores were taken from each tree > 5 cm DBH in each site. Cores were removed as low as possible on the tree bole and were repeatedly cored until the pith or a near-pith sample was attained, evident by curvature of the inner rings. No adjustments were made to tree ages to reflect the height of sampling; therefore, tree ages are interpreted as age at coring height. Because nearly all of the spruce in study area were dead, in addition to increment cores taken within each plot, we opportunistically cored any large, living spruce that we encountered so that we could accurately crossdate increment cores from the spruce killed by the spruce beetle and also determine the year in which they died.

Tree-ring measurement

Standard dendrochronological methods were employed for the increment cores. Species-specific tree-ring chronologies from the largest, living trees were constructed. Because most Engelmann spruce were killed as a result of the recent beetle outbreak, we combined an existing local spruce tree-ring chronology (Briffa et al. 1992) with spruce tree-ring series from opportunistically cored trees. The marker year approach (Yamaguchi 1991) was used to visually date each core before ring widths were measured to the nearest 0.001 mm using a stereo microscope. We relied on the program COFECHA (Holmes 1983) to verify our visually crossdated tree-ring series, especially the numerous dead spruce. For rare tree species, tree-ring dates were checked against the Engelmann spruce chronology. For cores that did not intersect the pith, Duncan's (1989) method was used to estimate the number of rings (up to 25) to the center. Some of the trees had rotten cores, would not crossdate, or had >25 rings to the center and were not included in the age structure or early growth analyses. Of the 1171 trees cored in the field, 888 were successfully crossdated (62% spruce, 26% fir, 8% aspen, 4% other), within 25 years of the pith, used to build age structures, and used to determine initial growing conditions (Table 3).

Reconstructing antecedent disturbances

To reconstruct antecedent disturbances, multiple lines of tree-ring evidence were used (e.g., age structures, tree-ring release dates, initial growing conditions). For this study, "current" stand conditions were reconstructed to represent the for-

Table 3. The time period during which a pulse of establishment occurred, the percentage of trees that established during the 40-year period, the percentage of trees exhibiting rapid early growth during the 40-year period, periods of spruce beetle caused tree-ring release, previous disturbance type, strength of reconstruction, and secondary disturbance history for sites on the Markagunt Plateau.

Site	Beginning decade of establishment pulse	% established over initial 40-year period	% rapid growth during initial 40-year period	Periods of spruce beetle caused tree-ring release	Antecedent disturbance, strength of data / secondary disturbance
Ashdown	1760	32.6	27.6	—	Fire, moderate
Bristlecone Pine Trail	1780	37.8*	45.5	—	Fire, strong
North Hancock	1780	32.9	33.3	1992–1997	Fire, strong / recent spruce beetle
Hancock Peak Trail	1740	37.7	45.0	1867–1876	Fire, strong / spruce beetle
Lava Cone	1700	34.9	30.8	—	Fire, strong
Midway Point	1820	31.0	14.3	1873–1902, 1993–1996	Fire, moderate / spruce beetle and recent spruce beetle
Mammoth Creek	1780	30.5	11.1	—	Fire,mModerate
Navajo Lake	1760	61.1	55.6	1880–1887	Fire, strong / spruce beetle
Rainbow Meadow	1820	34.4	36.4	1958–1966	Fire, strong / spruce beetle
Snotel	1640	37.3	64.0	—	Fire, strong
Sydney Valley	1820	42.5	31.3	1903–1913, 1944–1957	Fire, strong / spruce beetle

Note: Spruce beetle caused tree-ring release defined as >30% trees releasing in a moving 20-year window (Kulakowski and Veblen 2006). An asterisk (*) indicates that the Bristlecone Pine Trail meets the criterion only when the subalpine fir regeneration 1880–1900 is not considered in the analysis.

est immediately prior to the recent spruce beetle outbreak (1990s). Therefore, stand structure, composition, age structures, and tree-ring increment reflect what was present on the landscape when the spruce beetle outbreak of the 1990s began.

Distributions of age structure are a common way to infer stand history. Although criticized for the potential “loss of evidence over time” (Johnson et al. 1994), in some systems (e.g., moist spruce–fir), careful interpretation of age structures is perhaps the only way that demographic histories can be reconstructed due to a paucity of fire-scarred trees (Kulakowski and Veblen 2006; Margolis et al. 2007, 2011). We assembled site-specific age structures for canopy trees (>25 cm DBH) by grouping the number of trees of a given age (represented on a per-hectare basis because of variable radius sampling) from each plot into bidecadal bins and compositing by site. Plot-by-plot age structures within each site were scrutinized to ensure that the establishment signal was not driven by a few plots rather than the site as a whole. We then used a running 40-year window (criterion from Kulakowski and Veblen 2006) to calculate the percentage of trees establishing over the contiguous establishment period in each stand. The beginning date of any 40-year period with >30% trees establishing was considered a stand-replacing wildfire event. Trees that established prior to reconstructed fire events were interpreted as remnants that survived the antecedent disturbance.

Further evidence for fire as an antecedent disturbance was sought by separately analyzing increment cores for rapid early ring width growth rates. Rapid initial growth indicates that light availability was not limiting immediately following establishment as would be expected after a fire. Following Parish et al. (1999), we defined rapid initial growth of individual trees as >1 mm·year^{-1} for a continuous period of at least 10 years occurring during the first 25 years after tree establishment. We calculated the percentage of trees that exhibited rapid early growth from increment cores that clearly reached the pith. Trees with estimated rings to the pith (up to 25 rings, see above) were not included. For each site recording a fire event (see above), we assumed that rapid early growth of >30% of the trees during the same 40-year period that exhibited pulses in establishment was corroborating evidence for response to a stand-replacing fire that created the necessary growing space for tree establishment. Therefore, fulfilling the 30% establishment criterion was considered evidence of fire, and fulfilling both the establishment and 30% criterion in rapid early growth was considered strong evidence of fire.

To determine whether tree-ring release was due to spruce beetle canopy disturbance or climate, we applied the methodology of Sherriff et al. (2011). We assumed that open-grown Engelmann spruce exhibit tree-ring release purely in response to climatic variability, i.e., they would not respond to mortality of their neighbors. We tested this by subjecting the local Cedar Breaks chronology (Briffa et al. 1992) to the same release analysis as the study trees (see below). Results showed virtually no tree-ring release over the 400-year chronology, corroborating our assumption. Therefore, we inferred that tree-ring release found in our forest-grown trees could not be due to climate but rather must be due to localized events such as spruce beetle caused mortality that killed some trees and resulted in increased growing space for the remaining trees.

Tree-ring release events were reconstructed using mean standardization to emphasize the variation in tree-ring increment over time. This was necessary to detect increases in ring width associated with recently improved growing conditions, e.g., loss of nearby canopy trees as a result of disturbance. This method has been found to be highly effective in the detection of canopy disturbance for trees with complacent ring growth, e.g., spruce (Veblen et al. 1991*b*; Sherriff et al. 2011). For the three species examined in detail in this study (Engelmann spruce, subalpine fir, and aspen), we defined a release as a 250% increase in average ring width over 10 years compared with the 10 years immediately prior. A 10-year time lag was used to reduce temporal autocorrelation, i.e., a recording tree could not record a second release for 10 years. To ensure that tree-ring releases were not indicating pulses of trees ascending to the canopy in response to small-scale disturbance events, we compared sample depth to growth releases on a site-by-site basis. We examined only tree-ring releases for the portions of the tree-ring chronologies with >10 trees per species per site. Using the criterion of Kulakowski and Veblen (2006), we assumed that >30% of trees releasing during a running 20-year window indicated historical spruce beetle activity (but not necessarily an outbreak) that resulted in some canopy tree mortality.

Using the same release criteria as above, we also quantified the response to the recent spruce beetle outbreak. However, because of the large percentage of mortality, we examined any releases that were indicated after the start of the outbreak. Releases were tabulated by site, species, and timing relative to the start of the outbreak at a given site (Table 4).

Drought–disturbance interactions

To test for the influence of drought on spruce beetle occurrence, a plateau-wide composite of tree-ring release data was created by combining the three dominant species. In addition to the 11 sites sampled for this study, tree-ring data from three previously measured sites (DeRose and Long 2007), which had nearly identical sampling protocols, were included in these composites. Due to a large amount of background noise in the tree-ring release data, we defined a release event as any year in which more than two trees recorded a release. We used superposed epoch analysis (SEA; Grissino-Mayer 1995) to examine the interannual relationships between PDSI and independent years of reconstructed spruce beetle activity across the plateau. SEA determined if there were significant differences between the mean PDSI values and the occurrence of spruce beetle activity during the year of the event (year 0) and up to 10 years prior to the event (–10). Monte Carlo simulations (1000) were performed to derive 95%, 99%, and 99.9% confidence intervals. We determined that there was no significant autocorrelation in the tree-ring reconstructed PDSI for up to a 5-year lag. This ensured that the results of SEA were appropriate for describing the interannual relationship between drought and disturbances.

To determine whether the recent spruce beetle outbreak was influenced by drought, we tabulated the primary year of occurrence of spruce beetle caused Engelmann spruce mortality from each site on the Markagunt Plateau (dates from DeRose and Long (2012)) with that year's associated drought value (Table 4). The first year of beetle-caused spruce mortality on each site was used because later dates of death during a spatiotemporally synchronous spruce beetle outbreak with rapidly building beetle populations (DeRose and Long 2012) would almost certainly mask the influence of potentially inciting factors.

Because fire events reconstructed from age structures lacked annual resolution, we tested the relationship between drought and these fire events using smoothed PDSI. To match our bidecadal resolution establishment groups, we filtered the annual PDSI using a 20-year spline with a 0.5 frequency cutoff, which accentuated multidecadal variation in the time series. The chi-square goodness-of-fit statistic was then used to test whether the reconstructed beginning decade of establishment pulse (i.e., fire event; Table 3) occurred more commonly during drought (PDSI < 0) or pluvial (PDSI > 0) periods of the 20-year smoothed PDSI for the time period ~1630–1830. The expected number of drought and pluvial events was determined by counting the number of times that the smoothed PDSI completed one cycle (trough to trough) that crossed average PDSI conditions over the same period.

Results

Antecedent disturbance

Establishment pulses evident in site-specific age structures exceeded the >30% threshold for all sites, indicating that fire was likely the dominant stand-replacing disturbance on the Markagunt Plateau (Fig. 2; Table 3; site-specific age structures and associated species-specific tree-ring release data are available in Supplementary Figs. S1–S10).[1] Stand structural data indicated that all sites had homogeneous structure, were primarily dominated by Engelmann spruce, and were relatively old (Table 2), which provided further evidence for a history of stand-replacing fire. In addition, eight of the 11 sites also had >30% of trees that exhibited rapid initial growth during the initial 40-year postfire period, which we considered strong evidence for stand-replacing fire (Table 3). Temporal synchrony in postfire establishment periods was evident between some sites, primarily in the 1780s and 1820s. However, large spatial distances between the sites suggested that they were likely separate stand-replacing events, although it is possible that the fire events could have occurred during the same fire complex (Table 3; Fig. 1).

Six of the 11 sites had tree-ring release suggestive of spruce beetle activity; however, in all cases, releases postdated the much stronger fire signal by many decades to centuries (Table 3). In addition, reconstructed periods of spruce beetle activity were both spatially and temporally disparate (Table 3). Therefore, although some sites had evidence of non-stand-replacing spruce beetle activity, this was interpreted as endemic beetle populations (Table 3; see Supplementary Figs. S1–S10).[1] As a result, we failed to accept the first hypothesis that the antecedent disturbance was a spruce beetle outbreak.

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-102.

Table 4. The first year that an Engelmann spruce was killed by the spruce beetle during the recent outbreak, associated drought (PDSI) conditions, and species-specific timing of subsequent tree-ring release by site.

Site	First year	PDSI	Release timing (years) / species*
North Hancock	1987	–0.287	1–5 / subalpine fir
Navajo Lake	1987	–0.287	5 / Engelmann spruce
Ashdown	1988	–0.057	—
Snotel	1988	–0.057	—
Hancock Peak Trail	1990	–2.807	1–7 / subalpine fir
Lava Cone	1990	–2.807	—
Bristlecone Pine Trail	1991	–2.180	—
Midway Point	1991	–2.180	2–6 / aspen 5 / Engelmann spruce
Mammoth Creek	1991	–2.180	3 / Engelmann spruce
Rainbow Meadow	1994	–1.399	5 / aspen
Sydney Valley	1994	–1.399	1 / aspen 3 / subalpine fir
Average		–1.422	

Note: The first year that an Engelmann spruce was killed by the spruce beetle on a particular site is from DeRose and Long (2012).

*Release timing was calculated as the time from the first year to the year of release, and species indicating release are provided.

Fig. 2. Example age structure from the Navajo Lake site showing the 1760–1800 pulse of establishment used to indicate a stand-replacing fire event. The broken vertical line in the top panel indicates the decade assigned to the fire event (Table 3). Species-specific tree-ring releases are plotted in the bottom three panels, and the hatched area indicates reconstructed periods of endemic spruce beetle activity (see Table 3).

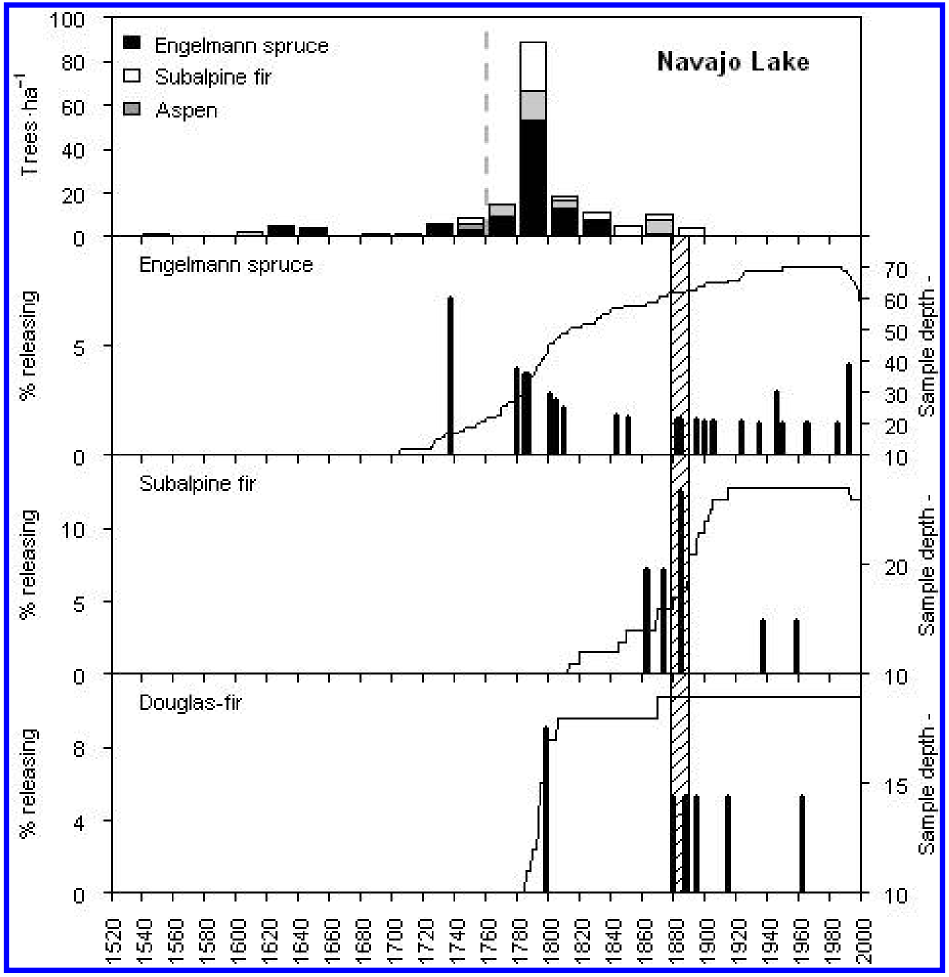
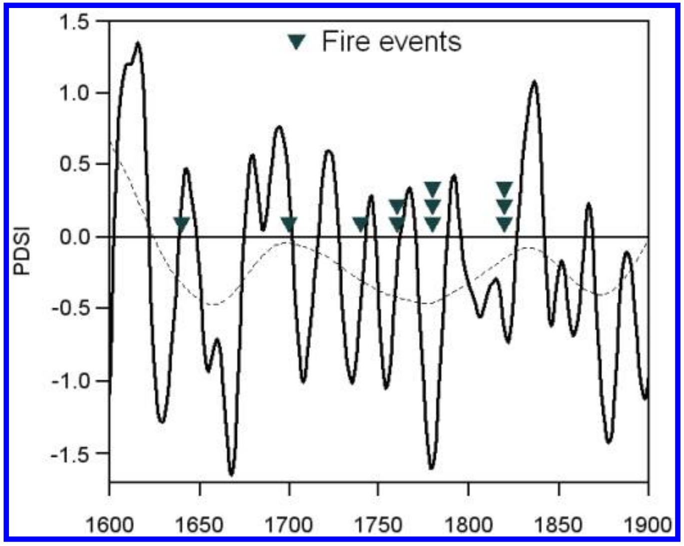


Fig. 3. Reconstructed fire events (n = 11 events; Table 3) plotted with tree-ring reconstructed PDSI smoothed using a 20-year spline with a 0.5 frequency cutoff showing that fires occurred significantly more often ($\chi^2 = 4.17$, $P < 0.05$) during drought conditions. The dotted line is the 100-year smoothed PDSI indicating that long-term dry conditions were prevalent during most fires. Stacked triangles indicate multiple fire events in a given decade.



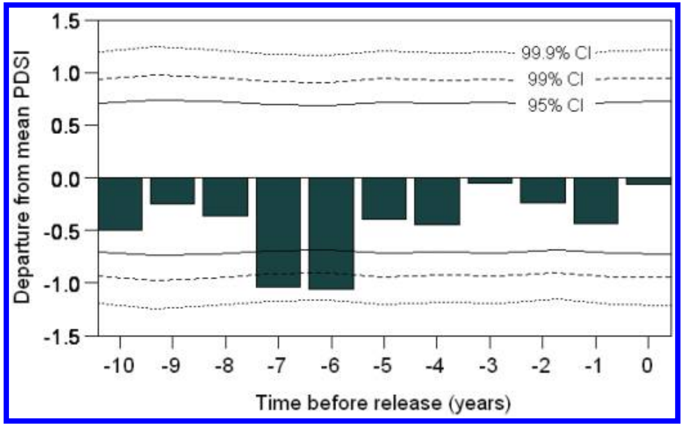
Drought–disturbance interactions

The beginning decade of establishment periods, initiated by putative fire events, occurred significantly more often than expected during periods of drought, indicated by the smoothed PDSI ($\chi^2 = 4.17$, $P < 0.05$; Fig. 3). Because reconstructed fire dates were not determined to annual resolution, this result merely suggested that drought conditions existed during, or at some point immediately prior to, the fire event. Regardless, drought was implicated as a possible factor influencing the occurrence of reconstructed fire disturbances.

Years in which more than two trees recorded tree-ring release, i.e., reconstructed spruce beetle activity, were significantly related to drought (negative PDSI). For all species combined (i.e., aspen, Engelmann spruce, and subalpine fir) across the plateau, the relationship was significant 6–7 years prior to release (Fig. 4). This suggested that antecedent drought conditions inciting past spruce beetle activity were recorded 6–7 years later as increased tree-ring increment. In comparison, the timing of tree-ring release in response to known dates of within-stand mortality during the recent outbreak varied from 3 to 5 years for Engelmann spruce, from 1 to 7 years for subalpine fir, and from 1 to 6 years for aspen (Table 4).

For the recent spruce beetle outbreak, dry conditions existed during the first year that an Engelmann spruce was killed by the spruce beetle at every site on the plateau (Table 4). Although the dry conditions varied from –0.057 in 1988 to –2.807 in 1990, the 6-year drought period from 1987 to 1992 represents one of only three extensive (6+ years) drought periods in the last 400 years, implicating the role of drought in inciting the recent outbreak. Ultimately, the evidence supported hypothesis two — that drought conditions were associated with disturbance events — for reconstructed fire events, reconstructed spruce beetle activity, and the contemporary spruce beetle outbreak.

Fig. 4. Superposed epoch analysis of tree-ring release years (indicating response to spruce beetle caused mortality, n = 46 events) with PDSI for all species combined (aspen, Engelmann spruce, and subalpine fir) showing significant negative interannual departure from mean PDSI over the period 1737–1997 for time lags of 6–7 years prior to the release.



Discussion

Antecedent disturbance

Overall, the tree-ring evidence was consistent with well-known patterns of establishment and stand dynamics following stand-replacing fires in subalpine systems (Antos and Parish 2002; Kulakowski and Veblen 2006; Margolis et al. 2007; Margolis and Balmat 2009). High-severity, stand-replacing fires typically create a mineral soil seedbed for the successful and rapid establishment of spruce, recorded as pulses for all sites in this study. What constitutes rapid establishment for shade-tolerant Engelmann spruce is relative because it continues to establish over a protracted period, oftentimes extending well over a century, making its full occupation of the site a "gradual" process (Stahelin 1943; Fiedler et al. 1985; Aplet et al. 1988; Kulakowski and Veblen 2006; DeRose and Long 2010). Our data suggest that "stand-replacing" fires on the Markagunt Plateau actually leave large numbers of surviving trees. A similar observation was made by Kulakowski and Veblen (2006) for forests on the Grand Mesa in Colorado. It is possible that by sampling multiple plots per site, we potentially introduced more spatial variability into age structures within a given "stand", which may have decreased our ability to detect details of site-specific fire histories. Regardless, we positively identified past stand-replacing fire using an independent criterion (Kulakowski and Veblen 2006).

In addition to establishment pulses, tree-ring analysis provided insight into the postfire growing environment. Because fires remove a majority of the previously existing vegetation, establishing trees should exhibit rapid growth early in stand development. Eight of the 11 sites exhibited rapid early growth, and of the three that did not, two occurred on extremely low vigor sites where establishment and early growth may proceed much slower due to relatively poor growing conditions (Fiedler et al. 1985). On the other hand, the sites with steep slopes (Navajo Lake and Snotel), where fires are expected to be more intense, had the clearest establishment pulses and rapid initial growth indicative of fire (Table 3; Figs. 2; Supplementary Fig. S9).[1]

Although we initially sought fire-scarred trees to corroborate fire dates, we found no spruce or subalpine fir with fire scars. The only fire-scarred individuals that we found included one limber pine (reported in DeRose and Long (2007)) that was not precisely dateable but had a ring count placing the fire scar in the 1880s and a few fire-scarred Douglas-fir on Bristlecone Pine Trail and Navajo Lake that had characteristically rotten fire scars and were therefore not dateable. The lack of fire-scarred trees was expected given that the three primary subalpine species, Engelmann spruce, subalpine fir, and aspen, have extremely thin bark and are typically killed when exposed to fire (Sherriff et al. 2001). Ours is not the only attempt to reconstruct stand-replacing fires in southwestern spruce–fir that has met considerable difficulty in finding fire-scarred trees. Margolis et al. (2011) noted the absence of fire scars in spruce–fir above 3100 m elevation, which was similar to the average elevation of our study sites (Table 1).

Had the antecedent disturbance been a large-scale spruce beetle outbreak, we would expect to have seen a release of the shade-tolerant advance regeneration, having established prior to the outbreak, as has been observed after other outbreaks in the Rocky Mountains (Mielke 1950; Schmid and Hinds 1974). The releasing understory would not have exhibited rapid early growth, nor would there be pulses in establishment; rather, the pre-existing seedling bank would have been establishing "chronically" over many decades (DeRose and Long 2010), and surviving individuals would have exhibited a relatively synchronous release in tree-ring increment regardless of age (Veblen 1992). In addition, an historic landscape-wide outbreak would be detected via relative synchrony of releases among spatially disparate sites. If an antecedent outbreak exhibited severity on par with the 1990s outbreak, few if any remnant spruce would remain (DeRose and Long 2010). Mielke (1950) noted the presence of numerous trees generally <10 cm DBH following the ~1920s beetle outbreak on Aquarius Plateau in southern Utah, indicating that the outbreak was not as severe as the 1990s outbreak on the Markagunt Plateau. On the extensive White River, Colorado, outbreak of the 1940s, Cahill (1951) reported that dead spruce made up less than half of total stand volume after the outbreak. The ubiquitous remnant spruce that predate the establishment pulses on the Markagunt Plateau are consistent with the severity of historical non-stand-replacing outbreaks observed elsewhere. The 1990s outbreak, in which beetles successfully reproduced in trees down to 6.5 cm DBH and killed substantially more than 50% of standing volume, appears anomalously severe. In any case, whether or not remnant spruce were the survivors of an antecedent beetle outbreak, the tree-ring release data suggest a fire origin for the stands on the Markagunt Plateau, not a beetle outbreak.

There are several reasons why it is unlikely that the reconstructed fire events were predated by a landscape-extent spruce beetle outbreak similar to the one in the 1990s. First, in our data, there was a lack of synchrony among stand initiation dates between sites that presumably would have been killed by an outbreak (i.e., similar stand conditions). Second, establishment pulses that recorded reconstructed fire events typically included many remnant Engelmann spruce that survived the fire, which does not characterize the response to the recent outbreak. Furthermore, recent modeling suggested that extreme potential fire behavior is not an inevitable consequence of spruce beetle outbreaks (Jenkins et al. 2008; DeRose and Long 2009). More work is needed to determine the possible interplay between spruce beetle outbreaks and subsequent stand-replacing fire.

Non-stand-replacing spruce beetle activity was detected using tree-ring releases in six of the stands (Table 2), but in all cases, the disturbances were relatively minor, i.e., endemic, and occurred well after the stand-replacing disturbance that established the stand. The tree-ring release evidence for endemic spruce beetle activity was primarily indicated by Engelmann spruce, but also included the tree-ring data for subalpine fir and aspen. Because the only independent tree-ring chronology available for climate sensitivity verification (see Methods) was Engelmann spruce, the interpretation that subalpine fir and aspen tree-ring release was due to spruce beetle caused canopy mortality is tenuous. However, by detecting tree-ring release for all species in response to the recent beetle outbreak, our interpretation that historic tree-ring release was caused by spruce beetle is bolstered.

Drought–disturbance interactions

Previous studies have documented the influence of drought on wildfire (Sibold and Veblen 2006; Margolis et al. 2007; Schoennagel et al. 2007; Margolis and Balmat 2009) and drought on spruce beetle outbreaks (Hebertson and Jenkins 2008) in subalpine forests, although to our knowledge, no one has developed a link between drought and both disturbances on the same site as was demonstrated in this study. The occurrence of large fires in subalpine forests is thought to be limited primarily by climatic factors such as drought (Schoennagel et al. 2004). Drought acts to directly increase fire risk by reducing dead fuel moisture. Drought can also influence fire risk indirectly via stressed plant–water relations (Bréda et al. 2006), which reduces transpiration and live fuel moisture and, in cases of extreme drought, can modify the fuels complex via plant mortality in ways that might influence subsequent fire behavior.

Because we used bidecadal stand origin dates to indicate fire events, our results should be interpreted cautiously. Bidecadal binning, necessary due to the lack of fire-scarred trees, removed any interannual variability. Therefore, the drought–fire results are most appropriately interpreted as the presence of long-term dry conditions during, or preceding, fire events. The relative imprecision in dating fire events in spruce–fir forests suggests that the relationship between fire and PDSI for high-elevation spruce–fir forests should be further studied.

In this study, the historic tree-ring release data likely characterized the response of past endemic beetle activity to drought, whereas the contemporary dates of spruce death directly characterized the early response of the recent spruce beetle outbreak to drought. Importantly, however, it is unlikely that drought directly influences spruce beetle populations, which are probably driven by local temperature anomalies (Hansen et al. 2001). Rather, drought more directly influences host vigor by inducing plant moisture stress, which in turn results in less energy for constitutive or induced defenses against attacking beetles (Fettig et al. 2007). In addition, increased solar radiation penetrating the forest canopy, potentially due to a reduction in leaf area during times of drought stress, has been indicated as a predictor of increased spruce beetle (*Ips typographus* L.) brood survival (Jakus et al. 2011). Therefore, the 6- to 7-year period between drier than average conditions and reconstructed spruce beetle activity was likely influenced by (*i*) the time necessary for beetle populations to build before mass attack, (*ii*) the concomitant reduction of tree resistance to beetles induced by drought, and (*iii*) the time necessary for response of surviving trees to be detected with dendroecological methods. Given that the recent spruce beetle outbreak was influenced by drought (Table 4), we can look at tree-ring response to the contemporary outbreak for corroborating evidence of the time lag found for reconstructed spruce beetle activity. We found spruce time lags of 3–5 years, which are close to our reconstructed time lags of 6–7 years. Subalpine fir responded to the recent outbreak on the order of 1–7 years, and aspen responded over 1–6 years, which were also consistent with the reconstructed 6- to 7-year lag. Finally, this is not the first study to associate previous drought conditions with spruce beetle activity. Hebertson and Jenkins (2008) found that PDSI 5 years prior to historic spruce beetle outbreaks in Utah and Colorado was a significant predictor of their occurrence.

Conclusions and summary

Dendroecological data were used to determine that antecedent stand-replacing disturbance in the subalpine spruce–fir forests of the Markagunt Plateau was driven by spatially and temporally disparate wildfire events. Subsequent non-stand-replacing spruce beetle activity was also detected with dendroecological data. In stark contrast, a landscape-wide spruce beetle outbreak was the contemporary (1990s) stand-replacing disturbance on the plateau, affecting all Engelmann spruce forests. For the Markagunt Plateau, multiple stand-replacing disturbances likely drive vegetation dynamics. However, regardless of disturbance type (i.e., stand-replacing or endemic), drought was found to be a factor inciting their occurrence. We found that reconstructed fires occurred significantly more often during times of extended drought. We also found that release in response to the recent outbreak took 1–7 years, and reconstructed spruce beetle activity occurred 6 to 7 years after drier than average (i.e., drought) conditions. Finally, the inception of the contemporary spruce beetle outbreak occurred entirely during dry conditions associated with an extended drought. Drought-induced physiological changes, and their interactions with disturbance agents, have been implicated as potential instigators of large-scale climate change caused forest mortality (Allen et al. 2010). That widespread drought is likely to become more common with changing climate has important implications for subalpine forests of the central and southern Rocky Mountains. Our results indicate that whether disturbance regimes are driven by large fires or beetle outbreaks, increased prevalence of drought could result in more widespread and severe subalpine forest mortality.

Acknowledgements

We acknowledge the Ecology Center and the T.W. Daniel Endowment for support of this study. We thank three anonymous reviewers whose comments substantially improved this manuscript. This research was supported by the Utah Agricultural Experiment Station, Utah State University, Logan, Utah, and is approved as paper no. 8171 of the Utah Agricultural Experiment Station. This article was prepared, in part, by an employee of the USDA Forest Service as part of official duties and is therefore in the public domain.

References

▶Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. **259**(4): 660–684. doi:10.1016/j.foreco.2009.09.001.

▶Alley, W. 1984. The Palmer Drought Severity Index: limitations and assumptions. J. Clim. Appl. Meteorol. **23**(7): 1100–1109. doi:10.1175/1520-0450(1984)023<1100:TPDSIL>2.0.CO;2.

▶Antos, J.A., and Parish, R. 2002. Dynamics of an old-growth, fire-initiated, subalpine forest in southern interior British Columbia: tree size, age, and spatial structure. Can. J. For. Res. **32**(11): 1935–1946. doi:10.1139/x02-116.

▶Aplet, G.H., Laven, R.D., and Smith, F.W. 1988. Patterns of community dynamics in Colorado Engelmann spruce – subalpine fir forests. Ecology, **69**(2): 312–319. doi:10.2307/1940429.

▶Berg, E.E., Henry, D.J., Fastie, C.L., De Volder, A.D., and Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. For. Ecol. Manage. **227**(3): 219–232. doi:10.1016/j.foreco.2006.02.038.

▶Bigler, C., Kulakowski, D., and Veblen, T.T. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology, **86**(11): 3018–3029. doi:10.1890/05-0011.

▶Bigler, C., Gavin, D.G., Gunning, C., and Veblen, T.T. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. Oikos, **116**(12): 1983–1994. doi:10.1111/j.2007.0030-1299.16034.x.

▶Bréda, N., Huc, R., Granier, A., and Dreyer, E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. **63**(6): 625–644. doi:10.1051/forest:2006042.

▶Briffa, K.R., Jones, P.D., and Schweingruber, F.H. 1992. Tree-ring density reconstruction of summer temperature patterns across western North America since 1600. J. Clim. **5**(7): 735–754. doi:10.1175/1520-0442(1992)005<0735:TRDROS>2.0.CO;2.

Cahill, D. 1951. Net impact of spruce beetle outbreak on White River National Forest, 1939–1951. Rocky Mountain Regional Report, US Forest Service, Fort Collins, Colorado, USA.

Cook, E.R., and Krusic, P.J. 2004. The North American Drought Atlas. Lamont-Doherty Earth Observatory and the National Science Foundation. Available from http://www.ncdc.noaa.gov/paleo/pdsi.html [accessed November 2011].

▶DeRose, R.J., and Long, J.N. 2007. Disturbance, structure, and composition: spruce beetle and Engelmann spruce forests on the

Markagunt Plateau, Utah. For. Ecol. Manage. **244**(1–3): 16–23. doi:10.1016/j.foreco.2007.03.065.

DeRose, R.J., and Long, J.N. 2009. Wildfire and spruce beetle outbreak: simulation of interacting disturbances in the central Rocky Mountains. Ecoscience, **16**(1): 28–38. doi:10.2980/16-1-3160.

DeRose, R.J., and Long, J.N. 2010. Regeneration response and seedling bank dynamics of a *Dendoctronus rufipennis*-killed *Picea engelmannii* landscape. J. Veg. Sci. **21**(2): 377–387. doi:10.1111/j.1654-1103.2009.01150.x.

DeRose, R.J., and Long, J.N. 2012. Factors influencing the spatial and temporal dynamics of Engelmann spruce mortality during a spruce beetle outbreak. For. Sci. **58**: 1–14.

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

Eisenhart, K.S., and Veblen, T.T. 2000. Dendroecological detection of spruce bark beetle outbreaks in northwestern Colorado. Can. J. For. Res. **30**(11): 1788–1798. doi:10.1139/x00-104.

Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T. E., Negron, J.F., and Nowak, J.T. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manage. **238**(1–3): 24–53. doi:10.1016/j.foreco.2006.10.011.

Fiedler, C.E., McCaughey, W.W., and Schmidt, W.C. 1985. Natural regeneration in Intermountain spruce–fir forests — a gradual process. USDA Forest Service Research Paper INT-343.

Grissino-Mayer, H.D. 1995. Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico. Dissertation, University of Arizona, Tucson, Arizona.

Hansen, E.M., Bentz, B.J., and Turner, D.L. 2001. Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). Can. Entomol. **133**(6): 805–817. doi:10.4039/Ent133819-6.

Hebertson, E.G., and Jenkins, M.J. 2008. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. Environ. Entomol. **37**(2): 281–292. doi:10.1603/0046-225X(2008)37[281:CFAWHS]2.0.CO;2. PMID:18419898.

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

Jakuš, R., Edwards-Jonášová, M., Cudlín, P., Blaženec, M., Ježík, M., Havlíček, F., and Moravec, I. 2011. Characteristics of Norway spruce trees (*Picea abies*) surviving a spruce bark beetle (*Ips typographus* L.) outbreak. Trees (Berl.), **25**(6): 965–973. doi:10.1007/s00468-011-0571-9.

Jenkins, M.J., Hebertson, E., Page, W., and Jorgensen, C.A. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol. Manage. **254**(1): 16–34. doi:10.1016/j.foreco.2007.09.045.

Johnson, E.A., Miyanishi, K., and Kleb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta – Picea engelmannii* forest. J. Ecol. **82**(4): 923–931. doi:10.2307/2261455.

Kipfmueller, K.F., and Baker, W.L. 2000. A fire history of a subalpine forest in south-eastern Wyoming, USA. J. Biogeogr. **27**(1): 71–85. doi:10.1046/j.1365-2699.2000.00364.x.

Kulakowski, D., and Veblen, T.T. 2006. The effect of fires on susceptibility of subalpine forests to a 19th century spruce beetle outbreak in western Colorado. Can. J. For. Res. **36**(11): 2974–2982. doi:10.1139/x06-182.

Kulakowski, D., Veblen, T.T., and Bebi, P. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. J. Biogeogr. **30**(9): 1445–1456. doi:10.1046/j.1365-2699.2003.00912.x.

MacDonald, G.M., and Tingstad, A.H. 2007. Recent and multi-centennial precipitation variability and drought occurence in the Uinta Mountains region, Utah. Arc. Ant. Alp. Res. **39**(4): 549–555. doi:10.1657/1523-0430(06-070)[MACDONALD]2.0.CO;2.

Margolis, E.Q., and Balmat, J. 2009. Fire history and fire–climate relationships along a fire regime gradient in the Santa Fe municipal watershed, NM, USA. For. Ecol. Manage. **258**(11): 2416–2430. doi:10.1016/j.foreco.2009.08.019.

Margolis, E.Q., Swetnam, T.W., and Allen, C.D. 2007. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. Can. J. For. Res. **37**(11): 2227–2241. doi:10.1139/X07-079.

Margolis, E.Q., Swetnam, T.W., and Allen, C.D. 2011. Historical stand-replacing fire in upper montane forests of the Madrean Sky Islands and Mogollon Plateau, southwestern USA. Fire Ecol. **7**(3): 88–107. doi:10.4996/fireecology.0703088.

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

Mock, C.J. 1996. Climatic controls and spatial variations of precipitation in the western United States. J. Clim. **9**(5): 1111–1125. doi:10.1175/1520-0442(1996)009<1111:CCASVO>2.0.CO;2.

Moore, D.W., Nealey, L.D., Rowley, P.D., Hatfield, S.C., Maxwell, D.J., and Mitchell, E. 2004. Geologic map of the Navajo Lake 7.5′ quadrangle, Kane and Iron counties, Utah. Utah Geological Survey. Available from http://geology.utah.gov/maps/geomap/7_5/pdf/m-199.pdf [accessed November 2011].

Parish, R., Antos, J.A., and Fortin, M.J. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. Can. J. For. Res. **29**(9): 1347–1356. doi:10.1139/x99-080.

Peet, R.K. 2000. Forests and meadows of the Rocky Mountains. *In* North American terrestrial vegetation. Chapter 3. Cambridge University Press, New York.

Schmid, J. M., and R. H. Frye. 1977. Spruce beetle in the Rockies. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, GTR-RM-49.

Schmid, J. M., and T. E. Hinds. 1974. Development of spruce–fir stands following spruce beetle outbreaks. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, RM-131.

Schoennagel, T., Veblen, T.T., and Romme, W.H. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. Bioscience, **54**(7): 661–676. doi:10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2.

Schoennagel, T., Veblen, T.T., Kulakowski, D., and Holz, A. 2007. Multidecadal climate variability and climate interactions affect subalpine fire occurrence, western Colorado, USA. Ecology, **88**(11): 2891–2902. doi:10.1890/06-1860.1. PMID:18051658.

Sherriff, R.L., Veblen, T.T., and Sibold, J.S. 2001. Fire history in high elevation subalpine forests in the Colorado Front Range. Ecoscience, **8**: 369–380.

Sherriff, R.L., Berg, E.E., and Miller, A.E. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. Ecology, **92**(7): 1459–1470. doi:10.1890/10-1118.1. PMID:21870620.

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**(5): 833–842. doi:10.1111/j.1365-2699.2006.01456.x.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology, **24**(1): 19–30. doi:10.2307/1929857.

Stahle, D.W., Fye, F.K., Cook, E.R., and Griffin, R.D. 2007. Tree-ring reconstructed megadroughts over North America since A.D. 1300. Clim. Change, **83**(1–2): 133–149. doi:10.1007/s10584-006-9171-x.

Swetnam, T.W., and Anderson, R.S. 2008. Fire climatology in the western United States: introduction to special issue. Int. J. Wildland Fire, **17**(1): 1–7. doi:10.1071/WF08016.

Turner, M.G., Hargrove, W.W., Gardner, R.H., and Romme, W.H. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J. Veg. Sci. **5**(5): 731–742. doi:10.2307/3235886.

Utah State University. 2006. Climate data. Utah State University, Logan, Utah. Available from http://climate.usurf.usu.edu/products/data.php [accessed November 2011].

Veblen, T.T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. Bull. Torrey Bot. Club, **113**(3): 225–240. doi:10.2307/2996361.

Veblen, T.T. 1992. Regeneration dynamics. *In* Plant succession: theory and prediction. *Edited by* D.C. Glenn-Lewin, R.K. Peet, and T.T. Veblen. Chapman and Hall, London. pp. 152–187.

Veblen, T.T., Hadley, K.S., and Reid, M.S. 1991*a*. Disturbance and stand development of a Colorado sub-alpine forest. J. Biogeogr. **18**(6): 707–716. doi:10.2307/2845552.

Veblen, T.T., Hadley, K.S., Reid, M.S., and Rebertus, A.J. 1991*b*. Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests. Can. J. For. Res. **21**(2): 242–254. doi:10.1139/x91-030.

Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., and Villalba, R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. J. Ecol. **82**(1): 125–135. doi:10.2307/2261392.

Villalba, R., Veblen, T.T., and Ogden, J. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology, **75**(5): 1450–1462. doi:10.2307/1937468.

White, P.S., and Jentsch, A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Prog. Bot. **62**: 399–450.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. **21**(3): 414–416. doi:10.1139/x91-053.