

# Dendroecological reconstruction of 1980s mountain pine beetle outbreak in lodgepole pine forests in northwestern Colorado<sup>1</sup>

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**Abstract:** The mountain pine beetle (MPB) infested 1.6 million ha of forest in Colorado and southern Wyoming from 1996 to 2010, causing extensive tree mortality, especially in lodgepole pine forests. Identifying the extent to which MPB outbreaks have occurred in the past will further our understanding of the current outbreak's causes and consequences. We explore the use of dendroecological methods to reconstruct a prior MPB outbreak event, which occurred in northwestern Colorado in the early 1980s. We used coarse-scale maps of MPB and GIS layers of suitable MPB habitat based on stand attributes to identify 15 stands of probable MPB activity in the 1980s. At 9 sites where field observations indicated probable past MPB activity, we collected tree cores from canopy host trees and subcanopy non-host (Engelmann spruce and subalpine fir) and host trees. The relatively synchronous dates of death of host trees determined by crossdating against live or recently killed trees (*i.e.*, after 1996) confirmed that host trees had died in the 1980s period of reported MPB activity. Tree cores from subcanopy trees of both host and non-host species were used to detect accelerated radial growth (*i.e.*, growth releases) of surviving trees following the death of canopy trees. Over 90% of subcanopy host and non-host trees sampled showed increased radial growth following the 1980s outbreak when evaluated 1) through visual inspection of ring-width series and 2) using a mathematical kernel to identify a period of  $\geq 150\%$  growth increase maintained for at least 5 y. Over half of the canopy-size lodgepole pines that survived the 1980s outbreak also accelerated their growth rates following the 1980s outbreak, although less sharply and for a shorter duration than the subcanopy trees. These results demonstrate the feasibility of using dendroecological methods to detect previous MPB outbreaks in lodgepole pine forests in Colorado over the past several decades and also identify limitations for extending reconstruction efforts back in time beyond the documentary record.

**Keywords:** *Dendroctonus ponderosae*, dendroecology, disturbance, *Pinus contorta*, Rocky Mountains.

**Résumé:** Au Colorado et au sud du Wyoming, 1,6 million d'hectares de forêt ont été affectés par le dendroctone du pin ponderosa entre 1996 et 2010 causant une mortalité considérable des arbres, en particulier dans les forêts de pin tordu latifolié. Déterminer l'importance des épidémies passées de ce dendroctone nous permettra d'améliorer notre compréhension des causes et des conséquences de la présente épidémie. Nous explorons ici l'utilisation de méthodes dendroécologiques pour reconstruire une épidémie passée du dendroctone du pin ponderosa qui s'est produite dans le nord-ouest du Colorado au début des années 1980. Nous avons utilisé des cartes à échelle grossière de la présence du dendroctone et des couches SIG d'habitats adéquats pour cet insecte selon les attributs des peuplements afin de trouver 15 peuplements ayant probablement été affectés dans les années 1980. Dans 9 sites où des observations sur le terrain indiquaient une probable activité passée du dendroctone, nous avons carotté des arbres hôtes du couvert forestier et du sous-couvert ainsi que des arbres non hôtes (épinette d'Engelmann et sapin subalpin) du sous-couvert. Les dates relativement synchrones de la mort d'arbres hôtes obtenues par interdatation avec des arbres vivants ou morts récemment (c'est-à-dire après 1996) ont confirmé que ces arbres hôtes étaient morts durant la période d'activité du dendroctone dans les années 1980. Les carottes des arbres du sous-couvert des espèces hôtes et non hôtes ont été utilisées pour détecter une croissance radiale accélérée (c'est-à-dire une reprise de croissance) des arbres survivants après la mort des arbres du couvert. Plus de 90 % des arbres hôtes et non hôtes échantillonnés dans le sous-couvert montraient une augmentation de la croissance radiale après l'épidémie des années 1980 lorsqu'évalués par : 1) inspection visuelle des séries de largeurs de cernes et 2) identification mathématique de périodes où une augmentation de la croissance de  $> 150\%$  était maintenue durant au moins 5 ans. Plus de la moitié des pins tordus latifoliés du couvert forestier ayant survécu à l'épidémie des années 1980 avaient aussi accéléré leurs taux de croissance, bien que moins abruptement et pour une plus courte durée que les arbres du sous-couvert. Ces résultats démontrent la faisabilité d'utiliser des méthodes dendroécologiques pour détecter des épidémies passées de plusieurs décennies du dendroctone du pin ponderosa dans des forêts de pin tordu latifolié du Colorado. Les résultats ont aussi permis de connaître certaines limites des efforts de reconstruction du passé au-delà du registre documentaire.

**Mots-clés:** *Dendroctonus ponderosae*, dendroécologie, montagnes Rocheuses, perturbation, *Pinus contorta*.

**Nomenclature:** Hopkins, 1909; Weber, 1990.

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## Introduction

Coniferous forests of western North America have experienced a profound increase in bark beetle activity over the past 2 decades that is believed to be driven primarily by a warming climate (Raffa *et al.*, 2008; Bentz *et al.* 2009; 2010). The primary insect responsible for widespread tree mortality since the late 1990s is the mountain pine beetle (MPB; *Dendroctonus ponderosae*). Though this beetle attacks several species of pine (Hopkins, 1909; Furniss & Carolin, 1977), the most extensive tree mortality due to recent MPB activity in the southern Rocky Mountain region of Colorado and southern Wyoming has been in lodgepole pine (*Pinus contorta* var. *latifolia*). In Colorado and southern Wyoming MPB infested 1.6 million ha of forest from 1996 to 2010, causing extensive tree mortality in over 750 000 ha of lodgepole pine forests (USDA Forest Service, online). Warmer temperatures accelerate the life cycle of MPB and decrease cold-related mortality of the larvae, while also reducing host tree resistance by increasing moisture stress (Bentz, Logan & Amman, 1991; Raffa *et al.*, 2008). Natural and anthropogenic disturbances such as widespread fire events, suppression of fires, and a history of logging may affect landscape-level susceptibility to MPB infestation by altering stand structures and stand age-class distributions (Taylor *et al.*, 2006; Chapman *et al.*, forthcoming). In Colorado, the primary sources of historical documentation of previous MPB outbreaks are USDA Forest Service reports (*e.g.*, Lessard, Hildebrand & Haneman, 1987) and maps of insect infestations based on aerial observations (*e.g.*, USDA Forest Service, online). While useful, both of these sources are inadequate in their spatial coverage and time depth, and are of only limited accuracy in depicting stand conditions during an outbreak (Johnson & Ross, 2008; Chapman, 2009). Consequently, in the current study we explore tree-ring based methods of detecting past MPB outbreaks in lodgepole pine forests in Colorado.

The mountain pine beetle is a native insect of North America and has co-evolved over millennia with its pine hosts (Furniss & Carolin, 1977). However, uncertainty remains regarding the history of past MPB outbreaks and how they may compare with the current (post-1996) outbreak in lodgepole pine forests in the southern Rockies. For example, a number of attributes of individual trees (size, vigour) and stands (species composition, density, previous disturbance) have been associated with varying degrees of susceptibility to MPB infestation (Safranyik, Shrimpton & Whitney, 1974). Mature, large trees in denser stands are preferentially attacked in lodgepole pine stands (Safranyik, Shrimpton, Whitney, 1974). The preference for larger-diameter trees relates to the benefits of thicker phloem, which provides more nutrition and winter insulation (Amman, 1972). The preference for dense stands reflects the decreased tree vigour in stands with high competition for resources (Raffa & Berryman, 1983). However, as MPB populations grow from endemic to epidemic levels, these tree- and stand-level constraints appear to have little or no influence on the subsequent spread of the outbreak (Raffa *et al.*, 2008; Boone *et al.*, 2011). Furthermore, there are few systematic long-term observations of how tree- or

stand-level attributes affect the pattern and severity of beetle infestation under changing conditions of MPB population levels as well as climate. It is important to develop long-term tree-ring-based records of past MPB activity that can be linked to specific stand and climate conditions.

Available information about past outbreaks in Colorado allows for only general comparison of current MPB damage to previous outbreaks. A report by Lessard, Hildebrand, and Haneman (1987) indicates roughly 557 km<sup>2</sup> of lodgepole pine forest in the Arapaho-Roosevelt, Routt, and White River National Forests were affected by MPB in 1985 and estimates that lodgepole mortality at that time exceeded 300 000 individuals. A comparative look at MPB activity in the same forest areas for the year 2005, based on USFS aerial detection survey data, indicates damage extent at nearly 1500 km<sup>2</sup> and estimates tree mortality of over 1 000 000 individuals (USDA Forest Service, online).

Identification of stands affected by past MPB outbreak and documentation of their composition and structure is important for evaluating habitat and other factors that may be conducive to MPB outbreaks. Comparison of coarse-scale mapping of the 1980s MPB outbreak with the post-1996 outbreak shows substantial overlap between the 2; the epicentre of the current outbreak overlaps greatly with the 1980s outbreak (Chapman *et al.*, forthcoming). This overlap may reflect an underlying habitat that is favourable to growth of MPB populations, or a location where host trees are more likely to be drought-stressed (Chapman *et al.*, forthcoming). Given the propensity of MPB to attack mature trees, it is logical to expect that the 1980s outbreak would have reduced subsequent stand-level susceptibility to infestation by reducing the number of mature trees. It is important to determine the precise locations of the 1980s infestation and the attributes of the stands attacked to evaluate possible explanations for the overlap of the 2 outbreaks.

Although tree rings have been used to detect past outbreaks of other forest insect pests in the southern Rockies, sometimes over periods of many centuries (Swetnam & Lynch, 1989; Veblen *et al.*, 1991), reconstructions of MPB outbreaks are rare. Existing tree-ring reconstructions of MPB activity are primarily limited to British Columbia, where they were conducted in Interior Douglas-fir and Sub-boreal Pine Spruce biogeoclimatic zones (Alfaro *et al.*, 2003; Axelson, Alfaro & Hawkes, 2009; 2010), but to our knowledge few have been conducted in the southern Rocky Mountain region (Kulakowski & Jarvis, 2011). There is a long history of using tree rings to detect previous outbreaks of insects that defoliate trees, such as tussock moths (*Orgyia pseudotsugata*) and western spruce budworm (*Choristoneura occidentalis*), based on comparison of the narrow rings of attacked trees with the ring width of a non-host species (Brubaker & Greene, 1979; Swetnam, Thompson & Sutherland, 1985). In contrast, tree-ring detection of past bark beetle outbreaks has been based primarily on identifying past episodes of accelerated radial growth rates on non-host trees (either non-host species or unattacked individuals of host species) that could be distinguished from growth accelerations induced by climate variability or by other types of disturbances such as windstorms (Heath & Alfaro, 1990; Veblen *et al.*, 1991).

Specifically in coniferous forests in Colorado, tree-ring techniques have been applied to the detection of past outbreaks of spruce beetle (*Dendroctonus rufipennis*) and Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) (Veblen *et al.*, 1991; Hadley & Veblen, 1993). Development of tree-ring methods of detecting previously unknown bark beetle outbreaks is typically based on calibration of tree growth patterns and other dendroecological types of evidence against known outbreaks for which stand-level documentary information is available on the severity of outbreak. For example, a widespread and severe outbreak of spruce beetle in northwestern Colorado in the 1940s (Schmid & Frye, 1977) was used to evaluate tree-ring evidence of the outbreak 40 y later (Veblen *et al.*, 1991). Key to developing a tree-ring-based protocol for detecting previous spruce beetle outbreaks in Engelmann spruce and subalpine fir forests in northwestern Colorado was the observation that following the beetle-caused mortality of canopy spruce trees, growth rates of unattacked subcanopy spruce and subalpine fir increase several fold and remain high for many decades. Thus, simple inspection of a spatially dispersed sample of host *versus* non-host tree-ring series, either as individual ring-width series or as standardized mean chronologies, can detect a previous outbreak (Veblen *et al.*, 1991). Disturbance by spruce beetle is distinguished from severe fire disturbance by the presence of a significant range in tree ages and initially slow growth in spruce beetle-affected stands in comparison with relatively even-aged populations and an abrupt truncation of maximum tree ages associated with post-fire cohorts (Veblen *et al.*, 1991). Identification of a synchronous episode of mortality in spruce but not in fir by dating time of death of standing dead trees was also useful in attributing the changes in tree-growth patterns to spruce beetle outbreak rather than other canopy disturbance such as blowdown. Discrimination of disturbance by spruce beetle from windstorm damage is usually possible by evidence such as uniform orientation of fallen logs, multiple species of fallen logs, and a high incidence of uprooting expected in the case of a severe blowdown (Veblen *et al.*, 1991; 2001).

Development of a tree-ring-based protocol for detecting past MPB outbreaks in southern Rocky Mountain lodgepole pine forests that is similar to that developed for spruce beetle detection is challenging for 2 key reasons. First, in contrast to spruce-fir stands, which nearly always have an abundance of subcanopy spruce and fir that can be expected to release when canopy trees are killed, lodgepole pine stands sometimes lack abundant subcanopy trees. At sites where lodgepole pine is seral to spruce and fir there typically will be numerous more shade-tolerant subcanopy spruce and fir individuals, particularly in older stands. In some post-fire stands of pure lodgepole pine there may be few subcanopy trees of any species. Second, the wood of Engelmann spruce is more decay resistant, and the mature canopy trees attacked by spruce beetle are typically larger in diameter and therefore decay more slowly than the lodgepole pine trees attacked by MPB. Decay and disappearance of beetle-killed lodgepole pine occur more rapidly than Engelmann spruce, which remains standing and of suitable

wood quality for taking core samples for many decades after tree death (Veblen *et al.*, 1991; Mast & Veblen, 1994).

The objective of this paper is to evaluate the types of tree-ring evidence and other field observations that are potentially useful in identifying previously undocumented MPB outbreaks in lodgepole pine forests in Colorado. Our focus is primarily on the use of crossdated death dates of beetle-killed trees and related growth releases in surviving host species or non-host species. We pay particular attention to limitations imposed by the decay of evidence over time.

## Methods

### STUDY AREA

The study was conducted in subalpine forests in northwestern Colorado in Arapaho-Roosevelt, Routt, and White River National Forests and in Rocky Mountain National Park (Figure 1). Subalpine forests extend from ~2500 to 3800 m in elevation in this region, and the most important forest types are monotypic lodgepole pine and mixtures of lodgepole pine with Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and aspen (*Populus tremuloides*). Limber pine (*Pinus flexilis*) is frequently dominant in dry subalpine forests, though it also occupies xeric sites across the elevational gradient from lower- to upper-treeline (Peet, 2000). In a small portion of the lower elevations of its range, lodgepole pine can be mixed with Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) where stand-replacing fire is also the dominant fire type.

In our study area, the key disturbance that has shaped the age, structure, and composition of subalpine forests is high-severity fire. Most modern lodgepole pine stands are dominated by even-aged populations that originated after widespread fires that occurred during the second half of the 19<sup>th</sup> century in conjunction with regionally extensive severe droughts (Kulakowski & Veblen, 2002; Sibold & Veblen, 2006; Schoennagel *et al.*, 2007). These 150- to 130-y-old stands of either pure lodgepole pine or mixtures with Engelmann spruce and subalpine fir contain abundant trees in large diameter classes considered susceptible to MPB attack (Amman, 1972). High tree densities in these stands in combination with drought further increase their susceptibility to MPB infestation (Safranyik, Shrimpton, Whitney, 1974; Shore *et al.*, 2006), and the progression of the post-1996 MPB outbreak correlates in time and space with both annual climate variability and presence of these MPB-susceptible stand structures (Chapman *et al.*, forthcoming).

### SAMPLING

ArcGIS was used to identify forest polygons in the USFS R2 Vegetation Database (R2Veg; USDA Forest Service, online) with attributes expected to contribute to stand-level susceptibility to MPB infestation over a large area in northwestern Colorado, which included the Arapaho-Roosevelt, Routt, and White River National Forests and Rocky Mountain National Park (Figure 1). The R2Veg layer delineates homogeneous units of vegetation as interpreted from 1-m resolution, true-colour aerial images (*ca* 2002) at a scale of 1:24 000 and is continually

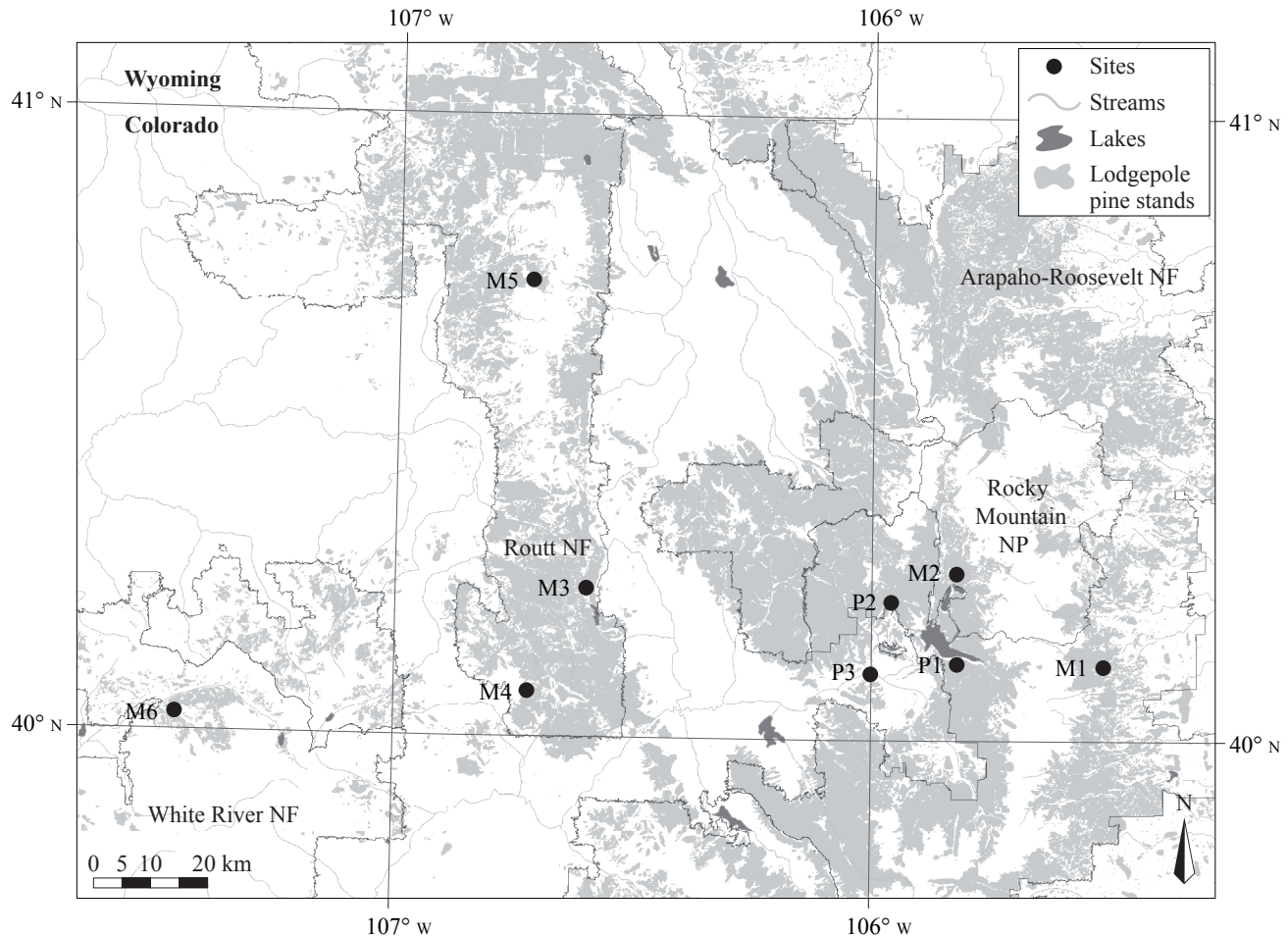


FIGURE 1. Map of sites sampled in the summer of 2008 in northern Colorado. The extent of lodgepole pine is a composite of USFS forest vegetation and aerial detection survey polygons. The composite approximates the total distribution of lodgepole pine in this region from pure to mixed stands.

maintained. We derived a subset of polygons in the R2Veg database containing relevant host species with large or very large diameter at breast height (dbh;  $\geq 23$  cm) and classified as mature habitat structure stages with at least 50% total forest cover. This GIS approach was complemented by historic USFS aerial detection survey (ADS) maps, which indicated the presence of MPB in northern Colorado during the period 1982–1985. These coarse-scale 1982–1985 ADS maps display hand-drawn perimeters of MPB activity and report locations of past occurrence on 1:500 000 scale maps (USDA Forest Service, online). Thus, the scale differences in the mapping of the 1980s MPB infestation and the R2Veg layers precluded any GIS analyses of the relationship of stand attributes and the 1980s MPB infestation, yet allowed us to identify a subset of sites with relatively good probability of MPB activity in the 1980s.

For field sampling in 2008, we randomly selected 15 sites from the GIS subset described above that were at least 50 ha in size and within 2 km of a road. Among the 15 randomly selected sites initial field observations indicated that 9 sites exhibited sufficient field evidence of past MPB infestation to warrant tree-core sampling (Table 1). Four sites were located outside the perimeter of the 1980s MPB infestation on the ADS maps (sites M1, M4, M5, M6), and 4 sites (M2, M3, P1, P2) were located within the

perimeter of the 1980s MPB infestation. A ninth site (P3) was selected for sampling that was within the perimeter of the 1980s infestation but did not meet the other stand attribute criteria in the GIS subset because it was dominated by limber pine. Sites were organized into 2 groups: 1) mixed stands containing host pine and non-host spruce and sub-alpine fir, and 2) pure stands of pine host trees.

All sampled stands had been affected to some degree by the current MPB outbreak, and it was not uncommon to encounter stands greater than *ca* 10 ha in extent exhibiting  $> 90\%$  canopy tree mortality caused by MPB activity in *ca* 2002–2006. The severity of previous outbreak (*i.e.*, 1980s) was typically much lower and was classified on the basis of percentage of canopy trees killed using classes defined as low ( $< 30\%$ ), medium (30–70%), and high ( $> 70\%$ ). Each potential sample site was initially searched for evidence of prior MPB activity that would justify collecting dendroecological evidence. Search areas ranged in size from 10 to over 100 ha and were delineated by the polygon perimeters of the forest stand structure derived from the R2Veg layers as described above. Field evidence of prior MPB activity used to confirm if a site should be sampled included the presence of several large diameter (*e.g.*,  $\geq 25$  cm dbh) fallen logs or snags exhibiting characteristic MPB galleries (vertical, J-shaped; Figure 2a).

TABLE I. Summary table of sampled sites organized by stand composition where M indicates a mixed-species stand and P indicates a pure-pine stand, showing minimum stand age estimate, elevation (m), aspect class, slope (degrees), latitude, longitude, and status as located within the 1980s aerial detection survey maps outbreak perimeter.

Site	Stand composition	Min stand age (y)	Elev. (m)	Aspect	Slope (deg)	Lat.	Long.	ADS map
M1	Lodgepole and Douglas fir	275	2758	SE	5	40.128	-105.507	no
M2	Lodgepole, successional spruce/fir	275	2764	SW	5	40.271	-105.823	yes
M3	Lodgepole, early succession spruce/fir	200	2834	NW	5	40.243	-106.599	yes
M4	Subalpine fir, successional from lodgepole	175	2712	N	5	40.082	-106.718	no
M5	Lodgepole, early succession spruce/fir	300	2912	NE	10	40.739	-106.720	no
M6	Lodgepole, some subalpine fir	125	2641	NW	15	40.038	-107.457	no
P1	Lodgepole	150	2605	NW	10	40.130	-105.821	yes
P2	Lodgepole	125	2838	NE	5	40.217	-105.945	yes
P3	Limber pine	125	2487	SE	15	40.113	-105.997	yes

In addition, sample cores were taken to check for discolouration of sapwood by the blue stain fungus (*Grosmannia clavigera*), which is transmitted between attacked hosts by MPB and helps reduce tree defence against attack by inhibiting vascular transport (Ballard, Walsh & Cole, 1984) (Figure 2b). Once these preliminary observations led to the decision to sample a site, we targeted 20 dead trees for coring (2 cores per tree) per site. These cores were used to determine death dates for trees potentially killed by MPB. At some sites, however, dead trees probably killed in the 1980s were either rare or so decayed that fewer than 20 were sampled. The dbh of each dead tree sampled was measured and the condition of each was noted as standing or fallen. In addition, dead trees were classified into 4 decay classes following Mast and Veblen (1994) (Table II). The occurrence of characteristic galleries and blue stain was recorded when present in sampled individuals.

To identify growth releases, we collected tree cores from subcanopy trees located as close as possible to trees that appeared to have been killed in the 1980s outbreaks. These “release” trees included non-host subalpine fir and Engelmann spruce as well as host lodgepole pine and limber pine. Distance away from the associated MPB-killed canopy tree averaged less than 2 m.

In addition to collecting tree cores for the purpose of dating the death year of trees that potentially were killed in the 1980s MPB outbreak, we also collected tree cores to determine the approximate origin date of each post-fire stand. In addition to using some of the samples taken from the dead trees, we cored living trees to achieve a sample of up to 10 subjectively chosen large-diameter trees per site to estimate date of stand origin (Kipfmüller & Baker, 1998). Whenever possible we chose living lodgepole pine to facilitate the construction of local (*i.e.*, site-based) chronologies; however, post-1996 MPB outbreak conditions hindered this effort as the majority of canopy lodgepole that survived the 1980s outbreak had been recently killed by MPB.

#### TREE-CORE PROCESSING AND ANALYTICAL METHODS

All cores were mounted and sanded according to standard lab procedures (Stokes & Smiley, 1968). Once processed, ring counts pith to bark were recorded for each core. If a core did not include the pith, the number of missing rings was estimated using Duncan’s (1989) method. Tree-ring series were measured to the nearest 0.01 mm using a Velmex tree-ring measuring system.

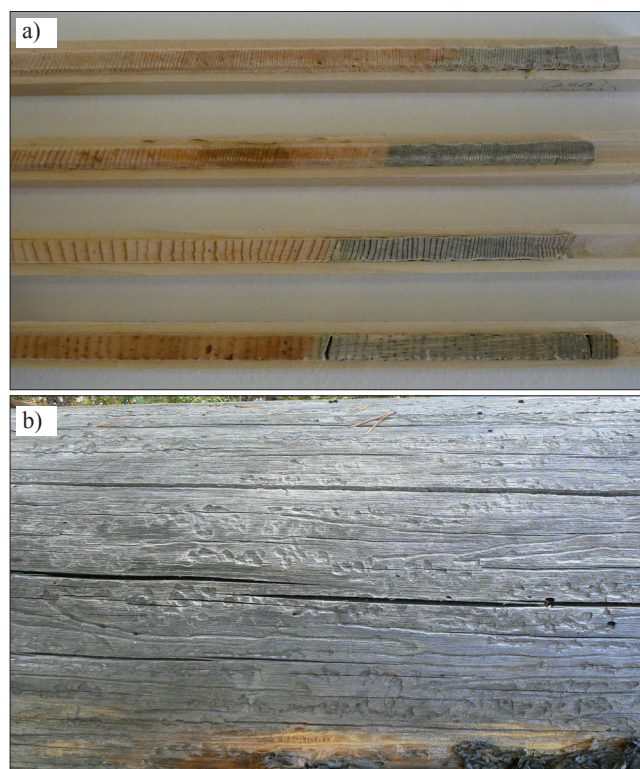


FIGURE 2. Photographs of a) downed log with characteristic J-shaped mountain pine beetle galleries and b) tree cores showing discolouration of sapwood by blue stain fungus.

TABLE II. Decay classes assigned to dead trees sampled for reconstruction of historic mountain pine beetle activity (following Mast and Veblen, 1994).

Decay class	Description
A	Needles, twigs and branches still present.
B	Twigs and branches present. No needles.
C	Branches present. No needles or twigs.
D	No needles, twigs or branches remain.

All tree-core samples were crossdated using a combination of qualitatively identified marker rings and quantitative pattern matching using the computer program COFECHA (Holmes, 1983; Grissino-Mayer, 2001). Visual crossdating of cores sampled from trees killed in the 1980s was attempted by comparing them with regional tree-ring chronologies available from the International Tree Ring Data

Bank (NOAA) as well as unpublished regional chronologies. However, visual crossdating had only limited success because of extremely narrow rings in the outermost 30 to 50 rings on many samples and center rot on many samples from dead trees that resulted in short tree-ring series. Consequently, all samples had to be measured and quantitatively crossdated first with other trees in the same or a nearby sample stand and subsequently with regional chronologies. COFECHA was used to systematically correlate 50-y series segments (with 25-y overlap between segments) from each series in each of the 9 site-level chronologies. These local site chronologies were developed using ring-width series from living canopy lodgepole pine in stands where there were some survivors of the current MPB outbreak. Other than at sites M1 and M6, however, there were few or no living canopy trees that had survived the current outbreak. The death years for trees killed in the current outbreak varied (*e.g.*, from 2003 to 2005 at site M5) as would be expected given that typically MPB disturbance continues over multiple years and rarely affects all trees in a stand in any given year (Taylor *et al.*, 2006). Selection of a subset of tree-ring series at each site that displayed acceptable correlation ( $\geq 0.32$  for segment length of 50 y) to existing regional lodgepole chronologies permitted the positioning of these series in time and allowed for the accurate dating of lodgepole killed in the 1980s outbreak.

To identify growth releases, tree-ring chronologies were created separately for each tree species, including host lodgepole pines (both canopy and subcanopy) as well as the non-host subcanopy Engelmann spruce and subalpine fir. The crossdated ring-width series of all subcanopy trees of all species sampled and canopy lodgepole pine that survived the 1980s outbreak were standardized by dividing each raw ring-width series by the mean series ring width to preserve ring-width variation due to canopy disturbance (Veblen *et al.*, 1991; Eisenhart & Veblen, 2000; Alfaro *et al.*, 2003). Each series was then examined both visually and using a mathematical kernel to detect growth releases that might indicate a mountain pine beetle outbreak. The kernel defines a radial growth release as a period of 5-y growth 150% greater than the preceding 5 y of growth. Release data were then plotted as the number of trees initiating a 5-y 150% release in any given year.

The response of subalpine Rocky Mountain conifers to canopy disturbance has been shown to vary from long sustained periods of increased growth to short periods of dramatic release (Veblen *et al.*, 1991). To account for this variation we qualitatively evaluated each standardized tree-ring series as showing no release, a pulse release, or a sustained release following the 1980s MPB infestation. Sustained releases lasted longer than *ca* 15 y, whereas pulse releases showed initially sharp increases in ring widths but were not sustained for more than 5 to 10 y. In cases where standardized series revealed both a pulse and also sustained increased growth, the more dramatic release type (*i.e.*, the pulse) was used to categorize release behaviour.

## Results

### FIELD EVIDENCE OF PRIOR MPB ACTIVITY AND TREE DECAY

The dead trees sampled in stands that had been initially evaluated in the field as likely affected by prior MPB

outbreak had high percentages of blue stain and beetle galleries (Figure 3a). The exception is site M1, where > 40% of the sampled dead trees recorded blue stain but well-preserved beetle galleries were lacking. Of the 147 dead host trees sampled for dating time of death (128 lodgepole and 18 limber pine), the majority were fallen (65%) rather than standing (35%). Given the preference for sampling standing rather than fallen trees because of the greater likelihood of obtaining sound wood samples from the former, these

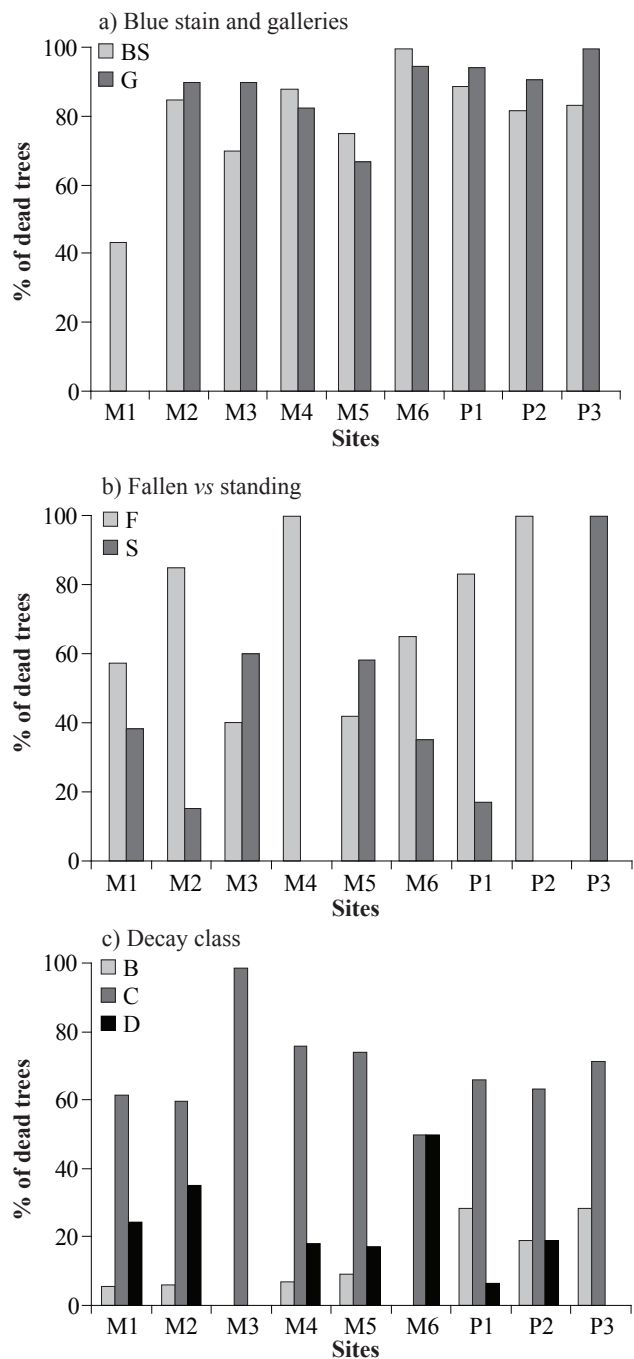


FIGURE 3. Percentages of sampled dead trees targeted to identify the 1980s MPB infestation showing a) MPB galleries (G) and blue stained (BS) sapwood; b) trees fallen (F) versus standing (S); and c) decay class category B–D, where and D is most decayed, as in Table II.

percentages reflect the difficulty of finding abundant standing dead trees 25 y or more following a MPB outbreak. The exception was the limber pine site (site P3), where all the samples taken from dead trees were from standing dead trees (Figure 3b). However, most sites (except M4 and P2) had at least a few standing dead snags potentially dating from the 1980s MPB event (Figure 3b). Among the fallen dead trees ( $n = 95$ ), 65% had been uprooted and 35% were wind snapped (*i.e.*, had broken boles). The average diameter at breast height of the lodgepole pine apparently killed by prior MPB outbreak was 33 cm.

Among the 147 sampled dead trees, 69% were in decay class C (*i.e.*, with branches remaining), implying this was the most common decay condition *ca* 25 y after MPB-caused tree mortality. Eleven percent of trees presumably killed by the 1980s MPB outbreak were in decay class B (with twigs), and 20% were in decay class D (lacking branches) (Figure 3c). The majority of lodgepole pine apparently killed in the 1980s MPB outbreak retained branches. In most cases all or a large portion of bark was missing from the dead trees, though the clear visibility of insect galleries suggests weathering was confined to a few mm in depth or less. There was no occurrence of decay class A in trees apparently killed in the 1980s, but the majority of standing dead lodgepole pine that had been killed by recent (mostly 2003–2006) MPB attack retained some needles and consequently were in decay class A. These recently killed trees were clearly distinguishable from the older MPB signal due to the presence of fresh pitch tubes, full covering of bark, and red or fading-to-red needle colour.

While canopy mortality from the current outbreak was high at most sites (*i.e.*, > 90% of host canopy trees), the 1980s MPB mortality was much lower and was estimated to never exceed 50% of the canopy trees. Severity estimates were subjectively assigned as medium at sites M2, P1, and P3 and low at sites M3, M5, M6, and P2 (Table III). Estimates of 1980s severity for sites M1 and M4 are not reported given the crossdating results described below, which indicate non-synchronous canopy host mortality at those sites.

#### DENDROECOLOGICAL EVIDENCE OF MOUNTAIN PINE BEETLE INFESTATION

Crossdating to detect year of death was accomplished successfully for 124 out of 147 dead trees sampled at 9 sites

that exhibited evidence of previous MPB activity. Death dates ranged from 1949 to 2003, with a mode of 1984. The frequency distribution approximates a normal curve centred on the time period of known MPB outbreak from *ca* 1979 to 1986. Sites M1 and M4 account for the majority of dates outside the interquartile range (IQR = 1980 to 1985, standard deviation = 8.5 y) (Figure 4a).

Dates from site M1 show the most variability, with no clear pulse of mortality associated to any single time period consistent with background mortality and low-density endemic bark beetle activity. Conversely, trees from site M2 all date to the 1980s outbreak, with a high concentration around 1983. Tree death dates from site M4 are also variable, with mortality increasing in recent years, starting in 1988 and then continuing through the late 1990s and early 2000s. The remaining sites show a predominance of death dates during the 1980s and in the case of sites M5, M6, and P3 some mortality in the 1970s and 2 outliers: mortality in 1995 and in 2002 at sites M6 and P3, respectively (Figure 4b).

Crossdating was most confident at sites M1, M2, M4, and M6, where average segment correlations were greater than 0.5 (Table III). This is likely due to the availability of live canopy lodgepole pines for local chronology construction at sites M1 and M6 and the high correlation of series from sites M2 and M4 with existing regional lodgepole chronologies. Death years from sites M5, P1, and P2 are derived with less confidence, yet average segment correlations are still within the 95% confidence level for segments of 50 y (Pearson's product-moment correlation). Sites P3 and M3 were dated with the least confidence, displaying average segment correlations below 0.32. Site P3 was dominated by sparsely spaced limber pine. This open site appeared to be more xeric than the other sample sites. This may have resulted in a somewhat different sensitivity of tree growth to regional climatic variation and poor crossdating with other sites. Furthermore, all large-diameter limber pines were killed in the 1980s outbreak, thus precluding the sampling of live trees to include in the local chronology at that site. At site M3 the 1980s outbreak was low severity and trees exhibiting characteristic signs of previous attack were few. When encountered, these dead trees were often rotten, and we were unable to meet our target sample of 20 double-cored trees.

TABLE III. Results of dating dead trees showing the number of individuals dated, mortality date range, chronology length, and average maximum segment correlation for crossdated tree death years at 9 sites sampled for 1980s mountain pine beetle activity. Major pulses of mortality are indicated by decade and estimated severity of the 1980s outbreak is noted where applicable. The average segment correlation is based on comparing all series at a site among themselves.

Site	# of trees dated	Mortality date range	Chronology length (y)	Average segment correlation	Mortality pulse	1980s severity estimate
M1	18	1949–2003	273	0.611	variable, endemic ?	n/a
M2	20	1979–1987	267	0.539	1980s	medium
M3	8	1981–1985	209	0.308	1980s	low
M4	17	1954–2002	181	0.716	late 1990s–2000s	n/a
M5	10	1976–1986	246	0.357	1980s	low
M6	18	1975–1994	105	0.508	1980s	low
P1	12	1979–1986	156	0.427	1980s	medium
P2	8	1978–1986	123	0.399	1980s	low
P3	14	1975–2002	126	0.319	1980s	medium

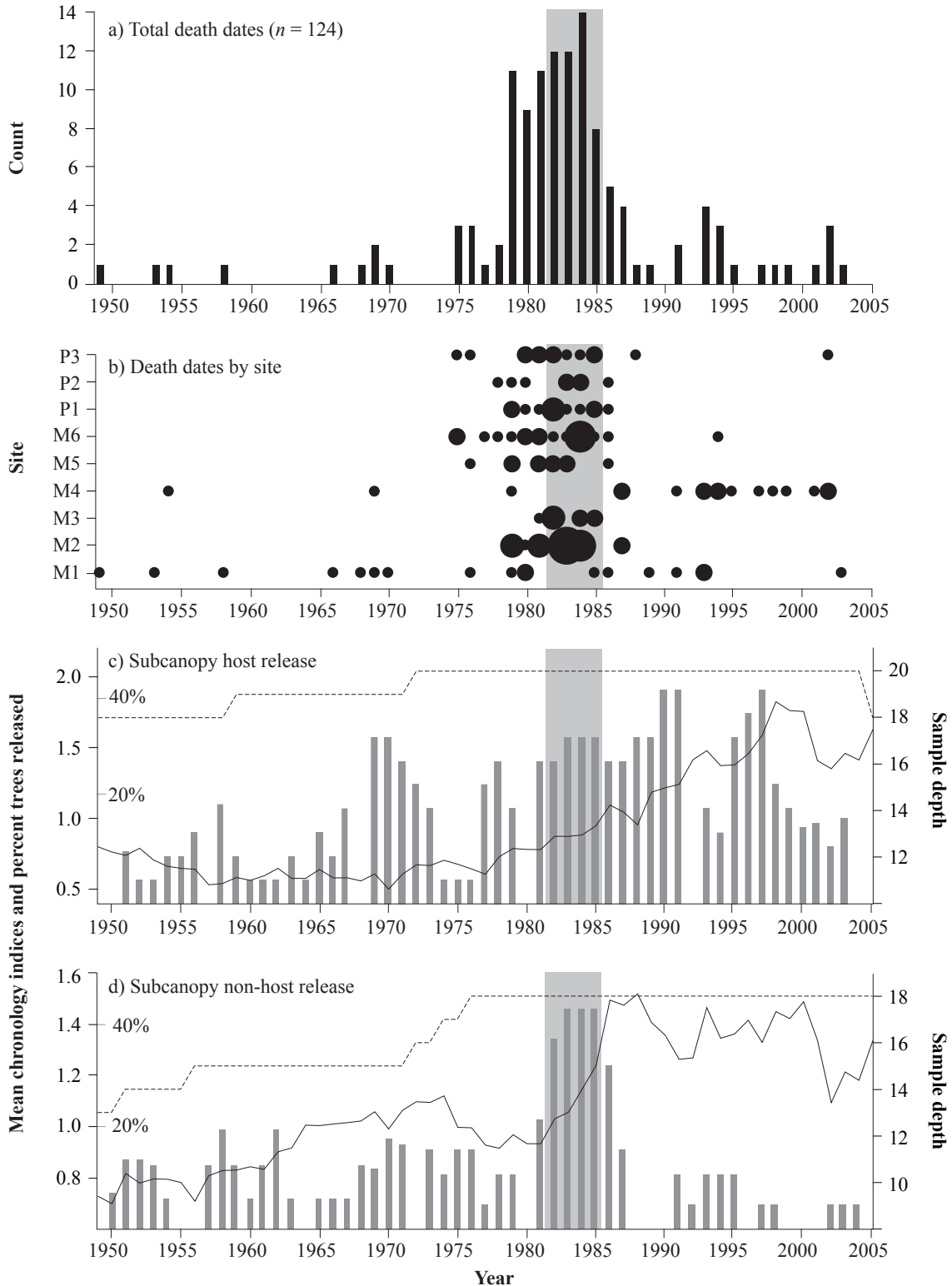


FIGURE 4. a) Frequency distribution of all crossdated death dates for dead trees exhibiting evidence of MPB attack ( $n = 124$ ); b) graduated dots display the number of crossdated death dates for each site, where the smallest dot size indicates 1 date, the next larger dot size indicates 2 dates, and so forth to a maximum of 5; c) mean standardized ring-width chronology for subcanopy host species (includes lodgepole and limber pine,  $n = 20$ ; solid line) and histogram showing the percent of trees expressing a 150% or greater increase in radial growth detected by using the mathematical kernel described in the text for subcanopy host trees (grey bars); d) mean standardized ring-width chronology for subcanopy non-host species (includes Engelmann spruce and subalpine fir,  $n = 18$ ; solid line) and histogram showing the percent of trees expressing a 150% or greater increase in radial growth detected by using the mathematical kernel described in the text for subcanopy non-host trees (grey bars). Grey shading behind bars on panes a–d indicate the period of coarse-scale mapping of the 1980s outbreak by aerial detection survey (1982–1985). Dashed lines indicate sample depth on panes c–d (*i.e.*, the changing number of living trees over time). Data from sites M1 and M4 excluded.



## IDENTIFYING GROWTH RELEASES

Synchronous radial growth increases (releases) following tree mortality in the 1980s were apparent at 7 of the 9 sites (M2, M3, M5, M6, P1, P2, P3) when ring-width series were examined individually (Table IV; Figure 5). Subjective assessment indicated that high percentages of subcanopy lodgepole pine as well as subcanopy non-host species (Engelmann spruce and subalpine fir) exhibited sustained releases lasting at least 15 y (Table IV), most notably in subcanopy host individuals, where 65% of sampled trees show a sustained release. Subcanopy non-host species exhibited both pulse and sustained releases at a nearly equal rate, 50% and 44% respectively. Of the 38 subcanopy individuals examined here, only 2 showed no release following the early 1980s. The high percentage of subcanopy trees that showed evidence of release indicates the effectiveness of our sampling procedure, which targeted trees likely to release because of their proximity to trees apparently killed by prior MPB activity.

Mean standardized chronologies (Figure 4c,d) and histograms of the percent of trees showing a  $\geq 150\%$  growth release (Figure 4c,d) showed upward trends in radial growth rates following the 1980s MPB activity for subcanopy lodgepole pine as well as subcanopy non-host Engelmann spruce and subalpine fir. Based on departure from mean growth rate, subcanopy lodgepole pine tended to show a more gradual release *versus* the sharp increase in growth rates for the other 2 species (Figure 4c,d; solid lines). This is consistent with differences in the annual synchrony of release for non-host and host subcanopy species as detected by the mathematical kernel. The percentage of subcanopy host trees showing synchronous release generally increased from the late 1970s and early 1980s to dual peaks in the early and middle 1990s (Figure 4c; grey bars). In contrast, subcanopy spruce and fir exhibited higher percentages (*ca* 40%) of trees initiating a  $\geq 150\%$  growth release for a few years directly following the onset of MPB activity in 1979 and 1980, but then the percentage drops off after 1986 (Figure 4d; grey bars).

Approximately half of the canopy lodgepole pine that survived the 1980s outbreak also recorded a growth release (Table IV). These trees predominantly displayed shorter

pulses of dramatic radial growth (47%), and only 6% showed a sustained growth release (Table IV). This is not unexpected given that these trees were not sampled in direct spatial association to trees killed during the 1980s outbreak and that canopy trees benefit less from enhanced resource allocation following fine-scale disturbance.

The mean standardized growth of canopy trees that were killed by MPB infestation in the 1980s differs from that of trees that survived (Figure 6). Mean growth rate was similar for both groups of trees until the 1950s, when the growth rate of the trees that were killed in the 1980s began to decline. Annual variability in growth is highly correlated for both groups of trees, probably reflecting their similar responses to regional climatic variation. However, growth decline from the 1950s onward was much greater for the trees that died in the 1980s (Figure 6). Trees that survived the 1980s MPB outbreak showed a pulse of increased growth in the mid- to late-1980s, but most of these survivors were subsequently killed by MPB activity in the early 2000s.

## Discussion

Approximately 25 y following an outbreak of MPB in lodgepole pine-dominated forests, dendroecological samples in combination with field observations were effective for detecting the precise location at a stand scale of the tree mortality caused by MPB. Coarse-scale (1:500 000) maps based on aerial observations of the 1980s MPB outbreak in northwestern Colorado were useful in directing our field search for stand-scale evidence of past MPB activity. Fine-scale (1:24 000) GIS vegetation layers filtered to include stand types known to be most susceptible to MPB attack were useful in identifying stands of *ca* 10 to 100 ha in extent that were searched for field evidence of past probable MPB infestation. This procedure identified sites of 1980s MPB activity in stands both within the perimeter of the 1980s outbreak as drawn on the ADS maps and also in stands many tens of km distant from the documented location of the 1980s outbreak. This result suggests that historical (pre-1990s) ADS maps are useful in directing field searches for tree-ring evidence of past MPB activity, but they should not be relied upon solely. Instead, a finer-scale and more extensive database of cover types and forest stand attributes is necessary for locating areas of probable past MPB activity. This conclusion applies to areas outside documented perimeters of mapped MPB activity that may not have been included in the aerial detection of insect outbreaks in the 1980s and earlier. It also applies to areas within the perimeters of the mapped 1980s MPB outbreak, because fine-scale heterogeneity of the outbreak (*e.g.*, unaffected forest within the outbreak perimeter) was not included on the ADS maps.

Once guided to stands of high susceptibility to MPB outbreak based on stand attributes (pine dominance, large tree size, mature habitat structural stage), field observations were required to justify the collection of tree-ring samples for confirmation of past MPB activity. In order to obtain our target number of samples, tree cores were extracted from dead trees throughout the identified R2Veg forest polygons. The relatively low density of MPB-caused mortality in the

TABLE IV. Presence or absence and type (pulse *versus* sustained) of releases based on visual inspection of ring-width series from individual ring-width series of trees that survived the 1980s MPB outbreak. Includes subcanopy host species (lodgepole and limber pine), subcanopy non-host species (Engelmann spruce and subalpine fir), and surviving canopy host species (lodgepole). The percentage of each release type for each class of surviving trees is given in parentheses. Data from sites M1 and M4 excluded. Examples of release classifications are shown in Figure 5.

Species	Release type		
	Pulse	Sustained	None
Subcanopy host species ( <i>n</i> = 20)	6 (30%)	13 (65%)	1 (5%)
Subcanopy non-host species ( <i>n</i> = 18)	9 (50%)	8 (44%)	1 (6%)
1980s surviving canopy host trees ( <i>n</i> = 51)	24 (47%)	3 (6%)	24 (47%)

1980s made a plot-based sampling strategy unattractive, and thus our results for a given site can be related to the spatial extent of the underlying forest vegetation polygon, which, like the search areas, ranged from *ca* 10 to 100 ha in size. Characteristic J-shaped galleries on large-diameter (*ca* 30 cm) fallen and standing logs in conjunction with the occurrence of blue-stained sapwood were the key observations used in tentatively ascribing tree mortality to MPB activity. Other causes of mortality, such as fire or blow-down, were fairly easy to determine by noting charcoal on the ground surface, char on standing trees, and directions of fallen logs. Even though blue-stained sapwood and/or J-shaped galleries are positive indicators of past MPB

activity, dendroecological evidence is required to distinguish between tree mortality due to endemic MPB activity and a strong pulse of coincident tree mortality associated with a stand-level or regional-scale MPB outbreak. For example, at site M1 50% of sampled dead trees displayed blue stain; dating of the death years of trees in this stand revealed a relatively continuous record of tree mortality spanning 1949 to 2003 (Figure 4a). It is probable that the occurrence of blue stain at site M1 can be attributed to some past endemic MPB activity; however, the absence of characteristic J-shaped galleries at M1 suggests that any such activity was limited and/or that surface erosion of dead tree boles obscured clear evidence of J-shaped galleries at this

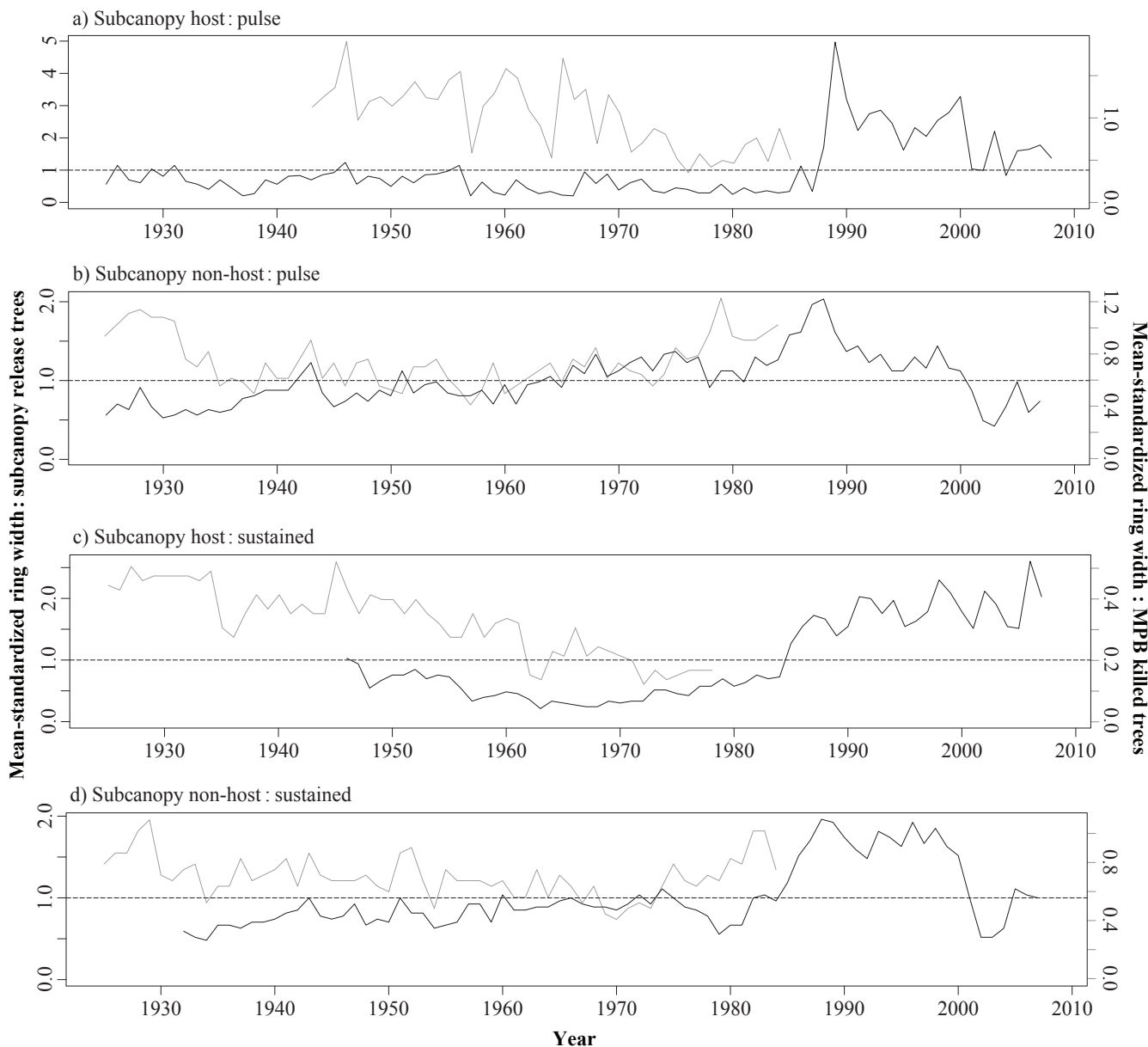


FIGURE 5. Examples of individual tree-ring series (standardized by a horizontal line passing through the mean) for a) a subcanopy host limber pine showing a pulse release; b) a subcanopy non-host subalpine fir showing a pulse release; c) a subcanopy host lodgepole pine showing a sustained release; and d) a subcanopy non-host subalpine fir showing a sustained release. Black lines display the mean-standardized index values for individual trees exemplifying each release pattern, straight horizontal dashed lines display the mean value for each released tree, and grey lines display the tree-ring series for the neighbouring pine killed by MPB.

site. These factors, coupled with the lack of synchronous tree mortality, did not support the initial field assessment of potential MPB infestation in the 1980s, suggesting instead background mortality due to multiple causes over the past 50 y.

The majority of trees killed by MPB in the 1980s were recorded as decay class C (branches remaining), but the speed of decay was variable at each site, rendering it impossible to use decay to make a precise assessment of time since death. For example, the distribution of decay classes at sites M2, M4, and M5 is quite similar (Figure 3c); however, only sites M2 and M5 experienced the 1980s outbreak. Site M4 shows a wide range of death years and an obvious increase of mortality in the 1990s and through the early 2000s. Thus, we conclude that the decay class of dead trees is not a reliable method of estimating actual date of tree death in the time spans represented by these stands (*i.e.*, 1980s *versus* 1990s).

Standing dead trees dating from the 1980s MPB outbreak were present at most but not all sites, and local site factors appeared to influence treefall as well as decay rates. At site M4, despite the fact that most dead trees had died

recently (1990s), most were fallen trees. This site was located adjacent to a wet meadow where saturated soils as well as lack of wind protection would be expected to make trees less wind-firm. Given that our field protocol called for targeting standing trees for sampling because of the better likelihood of obtaining sound samples, the absence of standing trees at some sites (*e.g.*, P2 and M4) reflects a true scarcity of dead standing trees rather than sample bias. The scarcity of dead standing lodgepole pine in some areas affected by the 1980s MPB infestation contrasts strongly with the slow treefall rates for Engelmann spruce killed by spruce beetle in nearby areas in Colorado. For example, 20 y following the 1940s spruce beetle epidemic in north-western Colorado less than 30% of the dead spruce had fallen (Hinds, Logan & Amman, 1965), and even 40 y after the epidemic standing dead spruce were abundant in these stands (Veblen *et al.*, 1991). In the current study, despite the sampling bias favouring standing dead trees, approximately two-thirds of the sampled dead trees were fallen logs. The tendency for dead lodgepole to fall relatively quickly after death renders the species less robust for increment core sampling since decay is hastened once dead wood is on the ground (Mast & Veblen, 1994). As a result, the probability

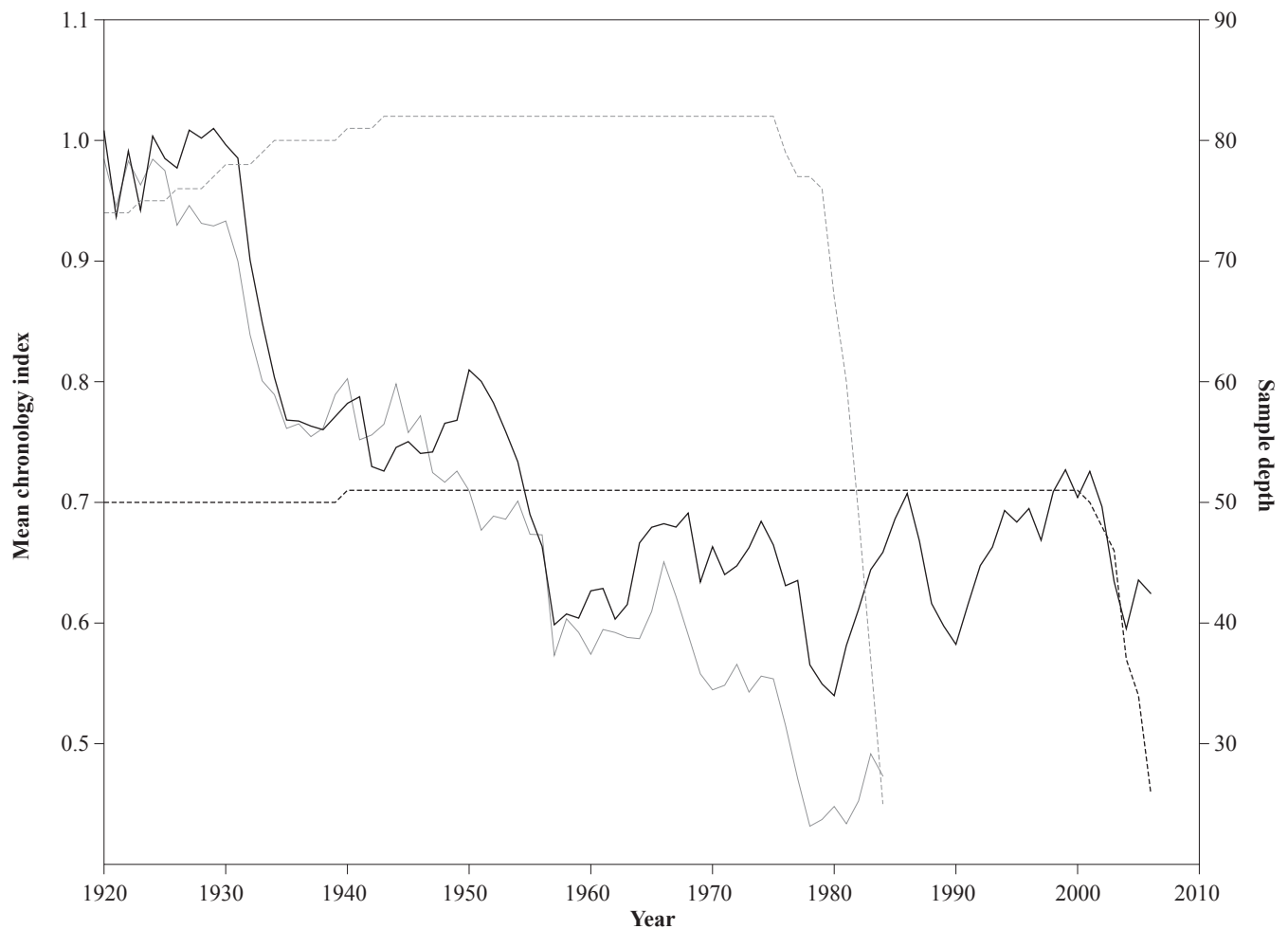


FIGURE 6. Mean standardized ring-width chronology of trees killed by MPB in the 1980s (grey line,  $n = 82$ ) and of canopy lodgepole pine that survived the 1980s outbreak (black line,  $n = 51$ ). The dashed lines are the sample depths for the respective chronology. Data from sites M1 and M4 excluded. The chronologies are not plotted when the sample depth is less than 20.

of accurately crossdating tree-ring series from dead wood is drastically reduced as time since death increases for lodgepole pine as compared to Engelmann spruce.

Given the difficulty of establishing long and robust records of tree mortality for lodgepole pine, growth releases of surviving trees will necessarily be an important component in detecting earlier MPB outbreaks. In the case of the 1980s MPB outbreak examined in the current study, the use of growth releases to detect past MPB activity was effective. Subcanopy individuals of both lodgepole pine and non-host species Engelmann spruce and subalpine fir exhibited strong releases following the mortality of canopy trees killed in the 1980s by MPB. The tendency for lodgepole pine in the subcanopy to exhibit more gradual growth releases compared to the sharp (pulsed) growth releases of the non-host species may be related to interspecific differences in shade tolerance. Subcanopy individuals of lodgepole pine, a shade-intolerant species, usually have quite limited leaf areas and may require several years of higher light levels to increase leaf and root structures fully responding to increases in light and other resources that follow the death of canopy trees. In contrast, as relatively shade-tolerant species, Engelmann spruce and subalpine fir in the understory typically have much larger foliage volumes and are better able to quickly accelerate their height and radial growth in response to increased light levels. For all species, delays of one to several years in the initiation of growth releases following mortality of canopy trees may also reflect gradual increases in light levels as dead needles and tree boles fall over several years. Furthermore, MPB infestation itself occurs over several years, typically beginning with attacks on larger trees and gradually spreading to smaller trees, such that MPB-caused tree mortality within any stand is spread over several years at least.

Approximately 50% of the canopy-sized lodgepole pine sampled in our study showed releases following the 1980s MPB infestation, suggesting that even mature trees can be used to detect past outbreaks. However, higher percentages of subcanopy host and non-host species exhibited sustained releases, making these individuals more useful in detecting past outbreaks. Since our GIS-based protocol for selecting MPB-susceptible stands for sampling excluded young post-fire stands, all our stands had abundant subcanopy trees. For much older (*e.g.*, pre-1900) MPB outbreaks, it is likely that few if any MPB-killed trees will be found that can be sampled for determination of death dates. It is possible that the preservation of dead MPB-killed trees may be extended in certain locales due to microtopographic conditions (*e.g.*, extremely dry) or tree characteristics (*e.g.*, large size); however, these conditions are rare and would not accurately represent the full range of lodgepole stands affected by a prior MPB outbreak. Nevertheless, crossdating of tree death years in these cases would provide a useful reference point with which one could compare the timing of synchronous growth release. Thus, for reconstruction of older outbreaks we recommend the collection of a much larger sample of cores, including samples from canopy trees, to determine if there are periods of synchronous growth releases that could be due to MPB-caused tree mortality. The application of a mathematical kernel may speed

the identification of synchronous release periods. However, given the variability in timing and duration of releases, we recommend visual inspection of measured individual tree-ring series. These can be either standardized or raw ring-widths for individual series, but when pooled to create average growth chronologies they need to be standardized to allow equal weighting of each series. As found in other studies (Veblen *et al.*, 1991; Alfaro *et al.*, 2003), a horizontal line passing through the mean of each series is the most useful standardization procedure.

The objective of our study was not to produce an extensive reconstruction of multiple dates of past MPB outbreaks, but rather to examine the utility of tree-ring methods for characterizing an outbreak that previously had been documented by coarse-scale aerial detection maps and generalized field observations (Lessard, Hildebrand & Haneman, 1987). The results of our calibration of tree-ring methods of detecting the 1980s MPB outbreak imply that these methods are likely to be effective for events that have occurred within 50 y or so of the field sampling date. In Colorado, there are currently ample opportunities to apply these methods more extensively to precisely date and locate episodes of MPB activity over the second half of the 20<sup>th</sup> century for comparison with the current MPB epidemic. Such research could be directed at determining if the tree and stand attributes that contributed to MPB susceptibility in previous outbreaks are continuing to play an important role under the conditions of a warmer climate and more severe regional-scale epidemic. For example, our initial results clearly show that slower-growing trees were more susceptible to MPB attack in the 1980s (Figure 6), which is consistent with past studies relating MPB attack to reduced tree growth rates and vigour, which can in turn be affected by management actions (Safranyik, Shrimpton & Whitney, 1974; Raffa & Berryman, 1983). However, given the high percentages of tree mortality during the current MPB outbreak in Colorado, tree growth rates appear to be a less important influence on tree susceptibility to MPB infestation. The methods examined in the current study can be applied more extensively to determine if tree and stand attributes during past MPB outbreaks have varied over time and if they are associated with different climatic conditions.

Knowledge of past MPB outbreaks in Colorado is limited by the coarse spatial resolution, inaccurate observations, and fragmentary temporal and spatial coverage of aerial detection surveys of forest health conditions (Johnson & Ross, 2008; Chapman, 2009). Consequently, there is a need to develop more spatially precise and longer records of MPB activity to develop a more comprehensive understanding of the historical range of variation of this important disturbance agent. The current study demonstrates the potential of tree-ring based methods for reconstructing MPB outbreaks over at least the past 50 y. Within shorter time periods, crossdating of trees exhibiting clear evidence of being killed by MPB (*e.g.*, J-shaped galleries, blue stain) provides the most unequivocal method for reconstructing past outbreaks; however, the detection of synchronous accelerated growth in neighbouring trees provides important corroborating evidence. Reconstructions of outbreaks over longer time periods, while challenging because of the poor preservation

of MPB-killed lodgepole pine, may also be feasible if based on large samples of trees showing synchronous growth releases following the death of MPB-killed trees.

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