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ORIGINAL ARTICLE

Radial growth responses of singleleaf pinyon (*Pinus monophylla*) to wildfire

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Abstract

Dendroecological methods for quantifying and dating historical canopy disturbance events have been widely applied for temperate forests, but may not be useful for semi-arid woodlands, where growth is more strongly influenced by drought cycles. Our study focuses on the potential utility of dendroecological methods for reconstructing historical fire in woodlands of the Nevada Great Basin, USA, which are dominated by singleleaf pinyon pine (*Pinus monophylla* Torr. and Frem.). We assess growth responses to a historical fire of known date, and compare different analytical methods involving radial-growth averaging approaches.

Despite the strong influence of climate on radial growth of trees growing in semi-arid woodlands, most pinyon pines sampled in this study exhibited profound growth releases in response to fire. The growth releases could be detected using radial-growth averaging criteria, even given thresholds of percent growth change that effectively eliminated responses to climatic variability. The most conservative dendroecological method was radial-growth averaging with a 10 yr moving window and a percent growth change (PGC) threshold of at least 125%. This method detected the known fire for nearly one in three surviving trees, with very minimal occurrence of false positives in control trees or in the historical record. Results suggest that such approaches may be useful for identifying and approximately dating historical fires that burned adjacent to living pinyon trees. However, these methods will likely not be able to separate historical wildfire from other disturbance types, such as pinyon ips (*Ips confusus*) or root rot fungi, which could be expected to cause growth releases in surviving trees. Also, the year of growth release following the known burn was delayed until years of good precipitation, resulting in a lagged response that can confound the ability of growth release methods to accurately pinpoint the year of disturbance.

Keywords: Growth release; Canopy disturbance; Radial-growth averaging; Great Basin; Fire effects

Introduction

For many forest types, canopy disturbance is associated with abrupt radial growth releases among surviving trees (Henry and Swan, 1974; Lorimer and Frelich, 1989). Such responses have been used to detect

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historical canopy disturbances including windthrow, forest pathogens, insects, and non-lethal wildfires (Payette et al., 1990; Ziegler, 2002). Use of growth releases to indicate past disturbance events is especially important where tree age distribution is only weakly linked to disturbance history. This is the case for shade-tolerant tree species in mesic systems, which may not require canopy gaps for establishment (Lorimer and Frelich, 1989). This is also the case for shade-intolerant tree species in arid systems which may establish over protracted periods of decades to centuries following disturbance, resulting in uneven-aged stand structures. However, it has been questioned whether trees in arid and semi-arid woodlands exhibit consistent growth release responses to canopy disturbance (Nowacki and Abrams, 1997).

Radial growth of trees can be highly sensitive to climatic influences such as precipitation and temperature, forming the basis for the science of dendroclimatology. It is critical to account for the effects of climatic variability prior to the use of growth releases for detecting canopy disturbance events. Methods often involve comparing growth over a certain period following a given year to growth rates of the prior period, using an arbitrary growth change threshold to distinguish growth release (Foster, 1988). Releases that are sufficiently intense (e.g. ⩾100%), sustained (e.g. ⩾15 yr), and abrupt are likely to be caused by canopy disturbance and not by climatic variability (Lorimer and Frelich, 1989). Recent studies characterize growth releases by calculating the percentage of growth change (i.e. PGC) using a differenced moving average with a time window of 5 or 10 yr (Nowacki and Abrams, 1997; Piovesan et al., 2005). Recognition of a disturbance event requires the PGC to exceed a threshold level, which may be fixed or allowed to vary as a function of prior growth rates (Black and Abrams, 2003, 2004).

Such methods, reviewed in Rubino and McCarthy (2004), have been applied to retrospective investigations of canopy disturbance primarily in mesic forests of the eastern U.S. and Canada (e.g. Payette et al., 1990), less frequently in more xeric coniferous forests of the western US (e.g. Heyerdahl et al., 2001), and apparently never in the rather xeric juniper and pinyon–juniper woodlands, which occupy 24 million ha of the western United States (Miller and Wigand, 1994). Dendroecological methods for detecting and dating historical canopy disturbance events in temperate deciduous forests may not work well for semi-arid woodlands, where growth is more strongly influenced by climatic variability (Nowacki and Abrams, 1997). However, belowground competition among trees for water and nutrients in arid woodlands may be equally significant as competition for light in denser, mesic forests. Competition for limiting resources would provide a mechanism for increased growth rates following mortality of neighboring trees.

Our study focuses on the potential utility of dendroecological methods for detecting and dating historical fire in singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) woodlands. Little is known concerning the historical fire regime of the widespread and diverse pinyon–juniper vegetation type (reviewed in Baker and Shinneman, 2004). This debate is difficult to resolve because pinyon seldom forms fire scars, and is a poor recorder of fire. Our main objective is to examine *P. monophylla* growth responses to a historical fire of known date, in order to ascertain:

(1) Whether surviving pinyon exhibit a consistent growth response to wildfire, and whether any such response is manifested as growth suppression or release;
(2) Whether the occurrence of a particular wildfire event can be reliably detected and dated according to the growth response of surviving (but un-scarred) trees in unburned island patches, or at the edge of the burn; and
(3) Which of several dendroecological methods for objectively defining significant growth variations associated with canopy disturbance is best suited for *P. monophylla* in semi-arid woodlands.

Methods

Field and laboratory methods

We analyzed *P. monophylla* growth response to the Crow Canyon fire, which burned approximately 650 ha of sagebrush and pinyon–juniper woodland in August 1981. This fire was located in central Nevada, USA near the town of Austin (117°05′W, 39°28′N). This burn was selected because the fire event was old enough to have sufficient post-fire radial growth to study growth releases, yet recent enough to easily find the fire boundary. The study area (Fig. 1) is near the geographic center of the Great Basin in the western United States, and is broadly representative of many Great Basin sites of similar elevation (1890–1980 m above sea level). This portion of the Great Basin can be considered a "cold desert," with most precipitation accumulating as Winter snowfall. Mean annual precipitation values range from 20 to 35 cm, depending on elevation and varying considerably among years.

We sampled 45 trees within 10 m of the fire edge (i.e. edge trees) and 30 control trees at least 20 m distant from the edge (Fig. 1). Among the first group, eleven trees had a possible fire scar and three scars were dated from 1981 (trees CC07, CC29, and CC30). For each

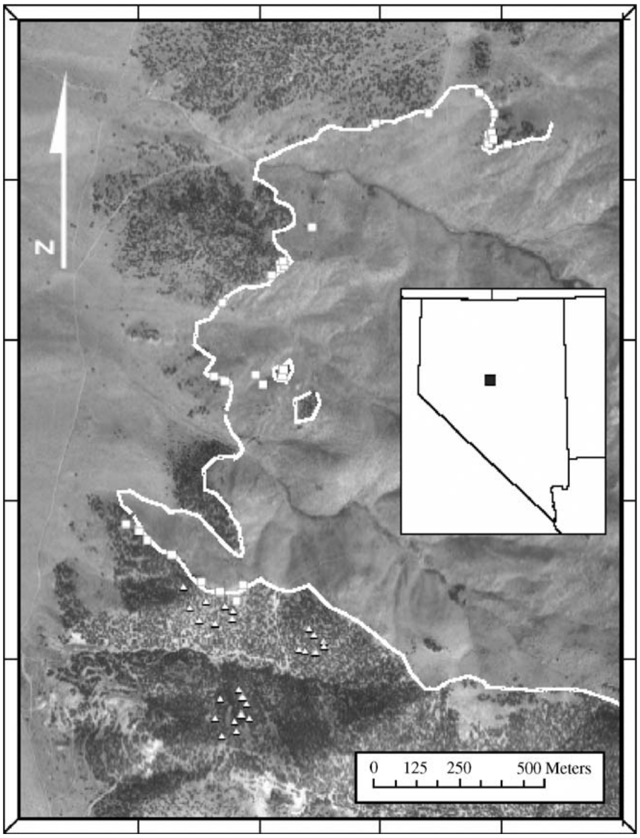

Fig. 1. Aerial photograph of Crow Canyon in 1995. The image is a United States Geological Survey (USGS) digital orthophotoquad (DOQ) at 1 m pixel resolution. The 1984 burn boundary is shown as a thick white line. Square symbols show sampled "edge trees" within 10 m of the burn boundary, while triangular symbols show "control trees" at least 20 m distant from the burn.

tree, we extracted one or two increment cores at 20 to 50 cm height, which were processed using standard dendrochronological techniques (Stokes and Smiley, 1996). Ring widths were measured to 1 µm precision using a Unislide "TA" Velmex measuring system. Crossdating was first conducted visually using marker years from a regional master tree-ring chronology (F. Biondi, unpublished data), and then verified against the same reference chronology using the software COFECHA (Grissino-Mayer, 2001). Tree-ring series from six edge and control trees, respectively, could not be crossdated and were excluded from the analyses. Raw ring widths were used for growth release analysis, excluding the first 50 yr of tree growth.

Analysis methods

We compared three dendroecological methods with respect to their ability to detect disturbance-induced growth ring variations (i.e. sharp release or suppression).

Method 1

A variant of radial-growth averaging (Lorimer and Frelich, 1989) was first elaborated by Nowacki and Abrams (1997). This method uses a differenced moving average to detect abrupt variations in growth rate. To quantify the growth variation for a given year, one calculates the PGC between the mean growth of the five previous years (including the year of interest), called the "previous growth," and the mean growth of the five following years (excluding the year of interest), called the "next growth," as follows:

$$\mathrm{PGC} = \left[(M2 - M1)/M1\right]\,100, \tag{1}$$

where $M1$ is the previous growth and $M2$ the next growth.

Greater negative or positive PGC values are more likely to indicate a suppression or release that is associated with a canopy disturbance event. The year of the disturbance is considered to be the year of maximum PGC. In practice, it is necessary to define a threshold PGC value which indicates high likelihood of a canopy disturbance. The other arbitrary parameter requiring specification is the length of the time interval over which the moving averages are calculated. This time window must be wide enough to remove annual growth variations, but narrow enough to detect high-frequency growth variations due to episodic disturbance. In this study, we used two time windows: 5 and 10 yr (PGC5 and PGC10) and three threshold PGC values (100%, 125%, and 150%). The method is illustrated in Fig. 2 for three representative tree-ring series.

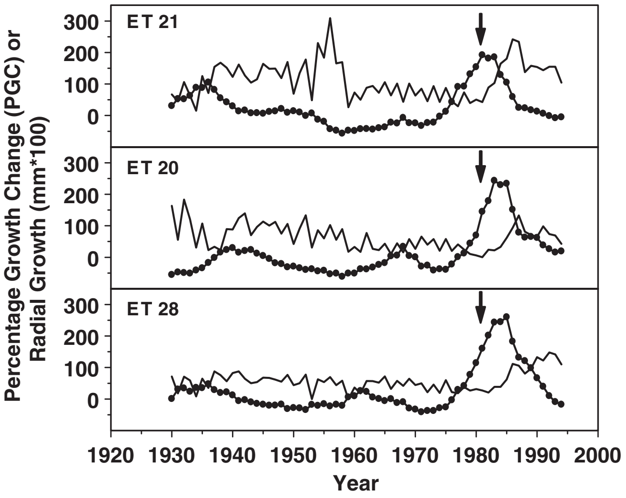

Fig. 2. Ring-width (line) and percentage growth change (circles) chronologies for three *Pinus monophylla* trees from the edge of the Crow Canyon burn in central Nevada. The percentage growth change series is calculated using a moving average of 10 yr. Arrows indicate the year of the 1981 burn.

Method 2

We started from the assumption that tree growth in xeric ecosystems is strongly dependent upon climatic variability. Although the first method is robust to most high-frequency variations in climate (Nowacki and Abrams, 1997), it is possible that detected mean growth variations might be the consequences of abrupt climate fluctuations. We therefore attempted to standardize for climate-induced growth variation. For each series, the annual growth was relativized to a standard normal distribution by subtracting the mean and then dividing by the standard deviation. To obtain tree-ring indices expressing interannual deviations from each tree's base level of radial growth, we subtracted the standardized tree-ring series for each core from that of the composite chronology for control trees, which had been similarly standardized. This difference was then rescaled from 0 to 100 in order to represent the percentage of variation. PGC was then calculated according to Eq. (1), using the rescaled difference values instead of raw radial growth measurements. We used the same time windows as for Method 1 (5 or 10 yr), but used three different threshold values to indicate disturbance (75%, 100%, and 125%).

Method 3

A modification of that developed by Black and Abrams (2003), who observed that the potential for growth release is dependent upon prior growth rate, and so adjusted growth-change thresholds for establishing growth releases accordingly. They compared the observed variation in growth rate to a maximum potential growth rate (PGC_{max}), developed across pooled measurements for numerous sampled trees, for each broad level (0.5 mm segment) of prior growth. Maximum potential growth rate was determined by plotting the PGC of each year against the previous growth (i.e. average of prior moving window) for that year. They then fit a negative exponential boundary line to the highest PGC values, thus approximating the PGC_{max} as a function of prior growth rate.

We followed the same general approach, except that we developed PGC_{max} separately for each tree instead of first pooling all radial growth data. Trees with the slowest growth rate, perhaps growing as suppressed individuals in the understory, or on poor sites, intrinsically have the highest potential for rapid growth change response to improved growing conditions. Instead of estimating the boundary line statistically, we estimated PGC_{max} mathematically for each value of mean growth within the previous time window ($M1$), simply by setting the $M2$ parameter in Eq. (1) to the maximum value observed for all "next growth" observations in the data set. We then defined thresholds for identifying historical disturbances according to the ratio of PGC to PGC_{max}, expressed in units of percent (i.e. 50%, 75%, and 90%).

To determine if any of the three methods allowed us to detect the fire of 1981, we allowed for a delay of up to 5 yr to account for fire-induced trauma to tree cambial tissue or other ecophysiological factors (Sutherland et al., 1991). We summarized our results according to the growth anomaly detection method employed, as the percentage of edge and control trees classified as having experienced a disturbance over that 5 yr period. We also calculated the frequency of apparent disturbances arising from these methods which did not reflect the 1981 fire, for the period between 1940 and 2004. This provided an indication of the level of risk for obtaining a false positive result in the absence of known fire disturbance.

Results

Growth releases were observed for all samples where an abrupt growth variation was detected using any of the methods, without any instances of growth suppression. The degree to which the 1981 fire was detected as a growth release for edge trees and control trees varied according to the dendroecological method, the threshold level of abrupt growth increase, and the length of the time window used for averaging (Table 1). Regardless of method, the longer (10 yr) time window resulted in few false positives. Method 2, using standardized tree-ring series differenced from the reference chronology, was the most conservative when compared to the other methods using 5 yr time windows. However, the radial growth averaging method (Method 1) was most conservative at high growth thresholds and long time windows, not recording growth releases for any of the control trees while recording releases for nearly 1/3 of

Table 1. Percentage of trees where a disturbance was detected between 1982 and 1986 for each method, over the two moving window lengths

	Threshold (%)	5 yr Window		10 yr Window	
		% ET	% CT	% ET	% CT
Method 1	100	66.67	25.00	38.46	4.17
	125	56.41	16.67	30.77	0.00
	150	56.41	8.33	30.77	0.00
Method 2	75	33.33	4.17	33.33	4.17
	100	25.64	4.17	25.64	4.17
	125	23.08	4.17	15.38	4.17
Method 3	50	69.23	41.67	46.15	4.35
	75	56.41	20.83	15.38	0.00
	90	35.90	20.83	0.00	0.00

% ET – percentage of edge trees ($n = 39$), % CT – percentage of control trees ($n = 24$).

trees at the edge of the fire (Table 1). When used with a 5 yr window, this method showed the greatest difference between edge trees detecting the fire (56% true positives) and control trees falsely detecting the fire (8%). Method 3, or the radial growth averaging method modified from Black and Abrams (2003), was also effective in separating control and edge trees when the lowest growth threshold (50%) was used with the longer (10 yr) period.

The response of *P. monophylla* trees to the 1981 fire was usually delayed (Figs. 2 and 3). For example, the three tree-ring series shown in Fig. 2 indicate canopy disturbances in 1981, 1983, and 1985, as indicated by year of maximum PGC, despite the fact that all trees survived the 1981 burn. Regardless of whether a 5 or 10 yr window was used for radial-growth averaging, the growth release associated with the 1981 fire usually occurred in 1984 (56% of cases), which would suggest a late Summer fire occurring in 1983 (Fig. 3). This is likely due to a lagged effect of reduced tree growth potential following drought and possible fire damage. *P. monophylla* in the vicinity of the study area experienced only average growing conditions in 1982 (Fig. 3), according to the reconstructed Palmer drought severity index (PDSI) of Cook et al. (2004), as well as the radial growth indices from a composite chronology using only trees that were not exposed to wildfire (F. Biondi, unpublished data). This followed moderate drought conditions in 1981, the year of the fire (PDSI = −1.334). Conditions improved in 1983, a relatively wet year, while tree growth reached its maximum in 1984 (Fig. 3), the second consecutive wet year following a dry period.

Another indicator of the robustness of the three methods for detection of historical canopy disturbance is the frequency of false positive "disturbances" not associated with the known 1981 wildfire that were detected over the 60 yr period from 1940–2004 (not including the years 1981–1985). We estimated this "noise" component of the growth release reconstruction as the average number of non-fire disturbances detected per tree (Table 2). This number was very low (<1 falsely detected disturbance per 600 yr) for Methods 1 and 3, using the higher growth release thresholds and longer (10 yr) time window. Most of the false disturbances detected by any of the methods reflected the drought period from 1959 to 1961, which is often marked by missing rings in the tree-ring series. The year 1962 was marked by rapid growth relative to preceding years, resulting in a high PGC. However, this apparent growth release, associated with climate variability and not episodic disturbance, was seldom detected as a release using Methods 1 and 3 with a 10 yr averaging window.

Discussion

Comparison of growth release detection methods

Results suggest that the majority of surviving trees at the edge of the burn experienced growth releases within

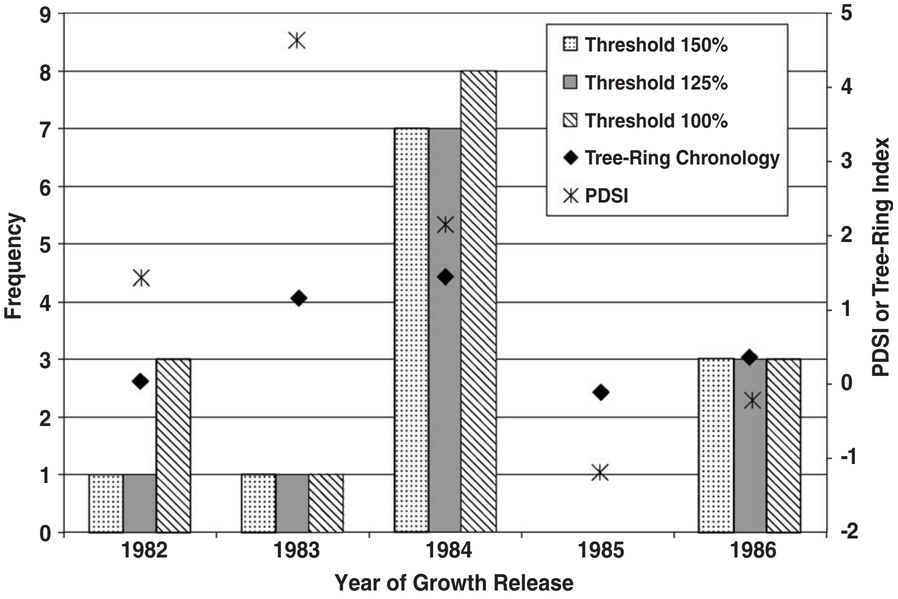

Fig. 3. Distribution of detected growth releases among years for the 1982–1986 period. Shown are the number of edge trees detecting fire according to three percent growth change thresholds (100%, 125% and 150%), for Method 1 (radial-growth averaging) using a moving window of 10 yr. Also shown are values of the regional Palmer drought severity index (PDSI) reconstructed from tree-ring chronologies (Cook et al., 2004), and growth indices from a local master tree-ring chronology (F. Biondi, unpublished data).

Table 2. Mean number of non-fire disturbances recorded per tree, over the 1940–2004 period

	Threshold (%)	5 yr Window		10 yr Window	
		ET	CT	ET	CT
Method 1	100	0.79	0.92	0.21	0.08
	125	0.33	0.63	0.10	0.04
	150	0.21	0.38	0.03	0.08
Method 2	75	1.46	1.42	0.72	0.46
	100	0.95	0.88	0.38	0.25
	125	0.49	0.71	0.21	0.13
Method 3	50	1.31	1.54	0.56	0.83
	75	0.85	0.92	0.18	0.33
	90	0.51	0.71	0.03	0.00

ET – edge trees, CT – control trees.

several years following the fire, when the radial-growth averaging method (Method 1; Nowacki and Abrams, 1997) is applied with rather stringent criteria (i.e. 150% growth change threshold). Method 2, which involved a differencing of *z*-standardized, individual tree-ring series from the composite chronology, was effective in identifying growth releases from the 1981 fire when a lower threshold (75%) was used (Table 1). However, this method was less conservative than the others in that a relatively high frequency of non-fire “false positives” was also identified over the 1940–2004 period (Table 2). Method 3, modified from Black and Abrams (2003), seemed promising at the 50% threshold in that a high number of edge trees but very few control trees recorded the 1981 fire (Table 1). Unfortunately, this method recorded a high frequency of false positives at the 50% threshold (Table 2). At the more conservative threshold of 90%, Method 3 did not detect non-fire events (Table 2), but also failed to detect the 1981 fire (Table 1). Therefore, the radial-growth averaging method of Nowacki and Abrams (1997) appears to be the most suitable for detecting historical canopy disturbance in *P. monophylla*. The use of this method with a time window of 5 yr increases detectability, while resulting in more false positives from control trees or non-fire years. Application of this method with a 10 yr window was quite successful in recording the 1981 fire for nearly 1/3 of edge trees, with very minimal occurrence of false positives in control trees or in the historical record.

Possible causes of growth releases following fire

One clear result of this study is that *P. monophylla* trees which have survived stand-replacing wildfire in the immediate vicinity commonly experience a growth release in the years soon following the fire. Most studies of *P. ponderosa* (Dougl.) responses to fire have observed growth releases (Morris and Mowat, 1958; Pearson et al., 1972; Peterson et al., 1994), although at least one study observed reduced radial growth (Sutherland et al., 1991). This latter study observed growth responses in fire-scarred trees that survived underburning, while our study considers only trees growing at the edge of a stand-replacing fire, which would have been less likely to have been damaged significantly. Giant sequoia has also been observed to respond to fire with increased radial growth (Mutch, 1994). We are not aware of prior studies of *P. monophylla* radial growth response to fire.

The observed growth releases are of a magnitude sufficient to distinguish them from positive responses to favorable climate, despite the strong sensitivity of tree growth to climate in this semi-arid environment. There are at least two general mechanisms for such a strongly positive post-fire response: release from competition and increased availability of plant nutrients.

Surviving trees at the edge of the burn may subsequently experience reduced competition from adjacent trees. There is some evidence that *P. monophylla* and Colorado pinyon (*Pinus edulis* Engelm.) trees growing in denser stands are at higher risk of mortality from severe drought events, suggesting that competition among adjacent trees for water and possibly nutrients is significant (Negrón and Wilson, 2003). As a result of interspecific competition, remnant pinyon trees which survive wildfire are likely to experience increased availability of limiting resources.

Studies of nutrient dynamics in post-fire, pine-dominated forests have shown a rapid pulse of plant-available nutrients, particularly nitrogen and phosphorus, in the years immediately following fire (Harris and Covington, 1983; Covington and Sackett, 1986; Johnson et al., 1997). Although these nutrients typically show post-fire declines, which can be eventually replenished through nitrogen fixation (Johnson et al., 2005), there is often an immediate fertilization effect for surviving trees. The combination of release from competition and short-term increases in available nutrients resulting from combustion of organic matter, provide reasonable explanations for why trees at the edge of a burn might experience dramatic growth increases following the fire event.

Conclusions

Nowacki and Abrams (1997, pp. 242–243) expressed reservations concerning the validity of the radial-growth averaging technique for detecting historical disturbances in arid woodlands, “where competition from neighboring trees is minimal” and “where climate largely dictates tree-ring growth.” As we have discussed, competition among trees is likely significant in *P. monophylla* woodlands, and the radial-growth averaging method successfully detects abrupt growth variations associated with a known, historical wildfire. However, since radial growth is influenced far more by climatic variability than is the case for temperate forests, it is essential that thresholds for PGC used to indicate a disturbance event are much higher. Nowacki and Abrams (1997) reported that a 25% PGC threshold was adequate for oak forests in the Appalachian Mountains (eastern US). The same 25% PGC threshold was employed for detecting disturbance in a *Fagus* forest of the Apennine Mountains (central Italy; Piovesan et al., 2005). For subalpine pine forests in the French Alps, Rathgeber and Roche (2003) used a PGC threshold of only 10%. Our study in a far more xeric system required a PGC threshold of at least 125% (Table 1). Using such stringent criteria, we were able to effectively separate growth responses to the known fire event from climatic influences.

The lagged effects associated with growth dependence upon good climate years can confound the ability of growth release methods to accurately pinpoint the year of disturbance. Trees exhibited growth release responses to the same disturbance event during different years over a 5 yr window (Fig. 3). In such xeric ecosystems, where tree growth during drought years may be only a few tracheids in width, *P. monophylla* trees may not be able to capitalize upon an improved growing environment until environmental conditions permit significant allocation to radial growth. Due to strong dependence of tree growth on precipitation, and high variability of precipitation in the Great Basin and many other semi-arid environments, application of a growth release method is not suitable for precisely dating when historical fires or other canopy disturbances have occurred. Nevertheless, such methods may be suitable for quantifying the overall frequency of such events.

The radial-growth averaging methodology is not likely to discriminate between historical wildfire and non-fire disturbances which also produced distinct mortality patches, such as epidemic beetle kill (pinyon ips), root rot fungi, windstorms, and widespread mortality associated with extreme drought (Shaw et al., 2005). It provides only a generalized index of canopy disturbance (Lorimer and Frelich, 1989; Nowacki and Abrams, 1997). The method needs to be tested for other disturbance types, in other areas, for trees of more diverse ages, and for other known fire events. The utility of this method for reconstructing historical disturbance events in xeric ecosystems may be limited to providing secondary evidence, used to extrapolate from more precise, reliable evidence such as dated fire scars. Multiple lines of evidence are needed to reconstruct fire history in heterogeneous woodlands, including fire scars, growth releases, and other dendroecological proxies such as stand age structure, and reconstructed death dates of snags and logs. However, our results clearly illustrate a positive growth response for *P. monophylla* to canopy disturbance in semi-arid woodlands, which is faithfully recorded in tree rings and distinguishable from growth variations associated with climate.

Acknowledgments

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