Annually resolved impacts of fire management on carbon stocks in Yosemite and Sequoia & Kings Canyon National Parks

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Introduction

Fire is a seasonal disturbance in montane forests of the Sierra Nevada that directly impacts tree species composition, vertical and horizontal forest structure, and forests' ecological functions, including carbon storage and accumulation, hydrologic regulation, and provision of wildlife habitat. Historically, a mean fire return interval of 2 to 20 years characterized the lower montane zone (van Wagtendonk and Fites-Kaufman 2006). Frequent fire maintained species composition and structure that perpetuated a low-severity regime. Nearly a century of fire suppression, however, has resulted in a threefold increase in tree density and ladder fuel abundance driven by fire-sensitive, shade-tolerant *Abies concolor* (white fir) and *Calocedrus decurrens* (incense-cedar; Scholl and Taylor 2010; Parsons and DeBenedetti 1979). The greater fuel load has increased the likelihood of high-severity fire, precipitating a shift in the fire regime of Yosemite National Park from generally low severity to mixed severity (Thode et al. 2011). Large-diameter trees, particularly large *Pinus* individuals, have concurrently decreased in abundance, potentially due to increased susceptibility to pathogens (e.g., *Heterobasidium annosum*), bark beetles (e.g., *Dendroctonus* spp.), and resource limitation induced by high tree density (Lutz et al. 2009a; Sherman and Warren 1988).

Maintaining forests with drought-tolerant and fire-resistant constituents is an important management objective, particularly considering projections of warmer temperatures and more variable precipitation patterns that may reduce tree establishment and survivorship and increase fire size, frequency, and severity (Littell et al. 2009; Lutz et al. 2009b; IPCC 2007; Kolb et al. 2007; Westerling et al. 2006). Over the past four decades land managers in the Sierra Nevada have used prescribed fire and lightning ignitions to restore historic species composition, reduce tree density, and remove surface and ladder fuels that facilitate high-severity fire (van Wagtendonk 2007). Effects of these management actions on the diameter distributions of individual species and on basic structural metrics, such as tree density and basal area, have been well documented (Collins et al. 2011; North et al. 2007), but the impacts of fire reintroduction on forest functions, such as carbon accumulation, remain unquantified in many lower montane Sierra Nevada forest systems.

Fire effects in upper montane forests have received even less attention. Historically, upper montane forests were characterized by median fire return intervals between 12 and 69 years (van Wagtendonk and Fites-Kaufman 2006). Some upper montane areas, therefore, still exhibit fire and forest interactions that lie within the historic range of variability (Fulé and Laughlin 2007). Quantifying the effects of fire on carbon accumulation of surviving trees is necessary to inform management decisions in lower montane forests, where fire is used as a restoration tool; the same study of carbon accumulation in upper montane forests is of great ecological interest because it provides an opportunity to quantify the impact of fire in systems less affected by the legacy of fire suppression.

The objective of this study was to examine the effects of lower-severity fire on carbon allocation to tree boles by analyzing the tree-ring widths of seven mixed-conifer tree species that vary in tolerance to drought and fire: *A. concolor*, *Abies magnifica* (red fir), *C. decurrens*, *Pinus contorta* (lodgepole pine), *Pinus jeffreyi* (Jeffrey pine), *Pinus lambertiana* (sugar pine), and *Pinus ponderosa* (ponderosa pine; Table 1). We assessed differences in growth patterns at nearby burned and unburned sites to remove climate-related trends and partitioned variability in growth response by (1) species, (2) tree diameter, and (3) local environment.

Table 1. Relative tolerances and adaptations to fire of seven mixed-conifer species in lower and upper montane forests (Fites-Kaufman et al. 2007; van Wagtendonk and Fites-Kaufman 2006).

Tree species	Drought tolerance	Shade tolerance	Fire resistance	Fire adaptations
Abies concolor	low	high	low (young) moderate (mature)	thick bark (mature)
Abies magnifica	high	high (seedling) moderate (sapling)	low (young) moderate (mature)	thick bark (mature)
Calocedrus decurrens	high	high	low (young) moderate (mature)	thick bark (mature)
Pinus contorta	high, also high tolerance for poor drainage	--	low/moderate	thin bark (mature)
Pinus jeffreyi	high	low	high	thick bark (young); elevated crown (mature); protected buds
Pinus lambertiana	moderate	low (dense shade) high (moderate shade)	low (young) moderate (mature)	thick bark (mature); elevated crown
Pinus ponderosa	high	low	high	thick bark (young); elevated crown (mature); protected buds

Study area

Yosemite and Sequoia & Kings Canyon National Parks are located on the western slope of the central Sierra Nevada (Figures I.1 and I.2). Elevation in Yosemite ranges from 648 m in the foothills to 3,997 m at the crest of Mt. Lyell. Elevation in Sequoia & Kings Canyon ranges from 520 m to 4,418 m at the crest of Mt. Whitney. The Mediterranean climate is reflected in cold, wet winters and warm, dry summers.

Lower montane mixed-conifer stands chiefly occupy an elevational band from 1,500 m to 1,650 m (van Wagtendonk and Fites-Kaufman 2006). Principal tree species include *A. concolor, C. decurrens, P. jeffreyi*, *P. lambertiana, P. ponderosa,* and *Quercus kelloggii* (California black oak). *Pinus ponderosa* and *Q. kelloggii* are common at lower elevations, where reduced water availability limits the abundance of *A. concolor*. *Abies concolor*-mixed-conifer forests generally occupy higher elevation sites with deeper soils. Subdominant *C. decurrens* and *P. lambertiana* are found across the full extent of the lower montane range.

Upper montane mixed-conifer stands are common between 1,950 m and 2,100 m (van Wagtendonk and Fites-Kaufman 2006). *Abies magnifica* intersperses with *A. concolor* at lower elevations and with *P. contorta*, *P. jeffreyi*, *Pinus monticola* (western white pine), and *Tsuga mertensiana* (mountain hemlock) at higher elevations. *Juniperus occidentalis-Pinus jeffreyi* woodlands occupy granitic domes.

Fire suppression in these forests began in 1890 and persisted until 1968 in Sequoia & Kings Canyon and until 1972 in Yosemite, when park managers began to use prescribed fire and lightning ignitions to restore historic fire regimes (van Wagtendonk 2007; Kilgore and Briggs 1972). A network of forest patches has resulted, some that have burned up to five times over the past 40 years and others that may not have burned since before 1890 (van Wagtendonk et al. 2012).

Data

Site selection and sampling design

Plot locations were determined by geographic information system based on forest type (Keeler-Wolf et al. 2012**;** Sequoia and Kings Canyon National Parks Photo Interpretation Report 2007), burn status, fire severity, slope, and distance from streams, roads, and trails. Plots were at least 50 m within the intended forest type and fire perimeter, varied in slope from 0° to 35°, and were >100 m from streams, roads, and trails. We assessed forest type and burn status in the field and repositioned plots to better meet specifications if necessary. Balanced representation of burned and unburned forests dominated by *P. ponderosa, A. concolor, P. jeffreyi,* and *A. magnifica* was a key objective. Burned sites were prioritized over unburned sites in *P. contorta* forests due to the availability of similar data collected in 2010 from unburned stands of *P. contorta* in Sequoia & Kings Canyon.

Data acquisition

Between June and September of 2011 we established 105 0.1 ha circular plots, 46 that had not burned since at least 1930 (hereafter, unburned; Yosemite: 35 plots; Sequoia & Kings Canyon: 11 plots) and 59 that had burned one to five times since 1930 (hereafter, burned;

Yosemite: 32 plots; Sequoia & Kings Canyon: 27 plots; Figures 1.1 and I.2). The burned plots were located within the perimeters of 47 fires (Table 2; Lutz et al. 2011; Eidenshink et al. 2007). A GPS set to the datum NAD83 determined the UTM coordinates at plot center. Species and diameter at breast height (1.37 m; dbh) were recorded for stems ≥2.5 cm dbh. Two increment cores were extracted at dbh from 10 trees ≥8 cm dbh that represented the species and diameter complement of conifers at each plot. Cores were taken parallel to contour lines and oriented 180° from one another. Only cores from *A. concolor*, *A. magnifica*, *C. decurrens*, *P. contorta*, *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*, the most thoroughly sampled species, were included in this analysis. Diameter distributions of each plot are available in the appendices of Becker (2014).

We used the Relative differenced Normalized Burn Ratio (RdNBR), a satellite-derived metric developed by Miller and Thode (2007), to characterize fire severity (Table 3). Each plot was enclosed within a 1 ha circular buffer and RdNBR values from all 30 m × 30 m pixels with centers that fell within the buffer were extracted. The pixel values associated with each plot were averaged to obtain RdNBR values with minimal georectification error (Key and Benson 2006).

Increment core preparation

Increment cores were air-dried, glued to wood mounts, and sanded to a high polish with increasingly smooth sandpaper (220 - 400 grit). Each core was examined under a microscope, and dots were penciled on the cores to mark each decade. All cores were scanned at 1200 dots per inch, and ring-widths were measured manually in WinDENDRO (version 2012a). Unusual rings were checked under a microscope to ensure correct measurement. Lists of marker years were manually generated for each core based on inspection of the scanned image. Core series from the same tree were crossdated and then compared with crossdated tree-ring series from the same site. Seventy-eight trees from burned plots and 69 trees from unburned plots were excluded from further analysis because neither increment core from the tree crossdated well (Table 4). Of the trees retained, 391 trees from burned plots and 340 trees from unburned plots were represented by two cores; 115 trees from burned plots and 42 trees from unburned plots were represented by single cores. Missing rings were identified and inserted in one core of 24 trees from burned plots and in one core of 5 trees from unburned plots. Missing rings were identified and inserted in both cores of 13 trees from burned plots (Table 4).

Table 2. Fire attributes and sample depth for 29 fires in Yosemite National Park and 18 fires in Sequoia & Kings Canyon National Park (Lutz et al. 2011; Eidenshink et al. 2007).

Fire name	Start date	Cause	Size (ha)	Species sampled	No. of plots	No. of trees
Yosemite National Park						
Wawona	1970	MI	178.9	CADE, PIPO	2	14
Wawona	1971	MI	61.2	CADE, PIPO	1	7
Wawona	1973	MI	36.1	CADE, PIPO	1	7
Wawona	1975	MI	18.7	CADE, PIPO	1	7
PW27	9/27/1978	MI	2074.3	CADE, PIJE, PIPO	2	17
PW09	1979	MI	1932.5	ABCO, PILA	1	9
YNP-111	1980	MI	830.4	ABCO, PILA	1	9
So. Wawona 3/4	4/15/1985	MI	36.9	CADE, PIPO	1	7
Eleanor	1986	LTG	583.6	ABCO, CADE, PIPO	1	8
Elbow	8/10/1988	LTG	182.3	ABMA, PICO	4	37
Pw3	10/16/1989	MI	688.4	ABCO, ABMA, PIJE, PILA	4	38
M Grove	1990	MI	9.4	ABCO, PILA	1	10
South Fork	10/15/1992	MI	209.6	ABCO, CADE, PILA, PIPO	3	23
YNP-0065	9/14/1993	MI	37.4	ABCO, CADE	1	6
Studhorse	6/7/1994	MI	56.5	CADE, PIPO	1	7
Ackerson	8/14/1996	LTG	23938.7	ABCO, CADE, PIJE, PILA, PIPO	5	46
Mg #9	9/17/1997	MI	17.3	ABCO, PILA	1	10
Kibbie Relight	9/18/1997	MI	993.4	ABCO, ABMA, PIJE, PILA	2	19
Eleanor	8/10/1999	LTG	1042.3	ABCO, CADE, PIPO	1	8
Studhorse 4	5/13/2002	MI	21.3	CADE, PIPO	1	7
YI Burn	9/27/2002	MI	31.4	ABCO, CADE	1	6
PW-3 Gin Flat	10/3/2002	MI	1360.3	ABCO, ABMA, PIJE, PILA	4	38
Soupbowl	6/1/2005	MI	57.4	CADE, PIPO	1	7
PW5-AD	6/27/2005	MI	104.3	ABCO, CADE, PILA	1	9
PW3-23	8/28/2005	MI	699.0	ABCO, CADE, PILA	2	19
Jack WF	11/8/2007	LTG	447.9	ABCO, CADE, PILA	1	9
Mariposa Grove	9/30/2008	MI	53.5	ABCO, PILA	1	10
Wawona NW	10/14/2008	MI	249.5	ABCO, CADE, PILA	2	15
Big Meadow	8/26/2009	MI	3058.7	ABCO, CADE, PILA, PIPO	3	24
Sequoia & Kings Canyon National Park						
Atwell Mil	6/20/1946	MI	90.0	ABCO, ABMA	1	10
Castle Gro	9/15/1947	MI	149.6	ABMA	1	7
Comanche	7/22/1974	LTG	1218.4	ABCO, ABMA, PICO, PIJE	8	70
Ferguson	6/26/1977	LTG	4216.3	ABMA, PICO, PIJE	1	10
Lewis Crk	9/30/1980	MI	3368.8	PIJE, PIPO	3	16
Sugarloaf	7/28/1985	LTG	1152.2	ABCO, ABMA, PICO, PIJE	8	70
Paradise	1/14/1994	MI	55.7	ABCO, CADE, PILA	1	5
Mineral I	10/11/1995	MI	843.1	ABCO, CADE, PILA	1	5
Shee Cree	10/27/1997	MI	149.7	ABCO, PIPO	1	7
Lewis Cree	10/13/1998	MI	645.2	PIJE, PIPO	3	16
Tar Gap	8/17/1999	MI	248.3	ABMA	1	9
Tar Gap RX	10/10/2002	MI	489.4	ABCO, ABMA	2	19
Atwood	6/25/2003	MI	1098.4	ABCO, ABMA, CADE, PILA	3	24
Williams	7/28/2003	LTG	1404.8	ABCO, ABMA, PICO, PIJE	5	49
Comb	7/22/2005	LTG	3947.3	ABMA, PIJE	4	30
Highbrid E	10/24/2005	MI	344.6	PIJE	1	10
Horse	7/19/2009	LTG	268.7	PICO	1	7
Sheep Complex	7/16/2010	LTG	3650.1	ABCO, PIPO	1	7

Table 3. Fire severity thresholds for the Relative differenced Normalized Burn Ratio (RdNBR; Miller and Thode 2007). Landsat-undifferentiated fire severity refers to areas within fire perimeters with RdNBR values that do not differ from adjacent unburned areas (Kolden et al. 2012).

Fire severity	RdNBR	No. of plots	No. of cores
Undifferentiated	<69	14	125
Low	69-315	30	136
Moderate	316-640	16	274
High	>640	1	5

Table 4. Number of crossdated cores and trees retained for analysis and number of manipulations to those cores based on crossdating inferences. Trees remained in the analysis if at least one core could be crossdated.

Species	Burned						Unburned					
	Collected		Retained		Manipulated		Collected		Retained		Manipulated	
	Cores	Trees	Cores	Trees	Cores	Trees	Cores	Trees	Cores	Trees	Cores	Trees
Abies concolor	214	110	176	100	4	4	195	98	155	80	0	0
Abies magnifica	226	114	208	109	8	6	244	122	225	115	1	1
Calocedrus decurrens	122	63	82	48	8	6	118	60	80	43	3	3
Pinus contorta	164	82	116	71	1	1	33	17	27	15	0	0
Pinus jeffreyi	255	129	199	112	20	15	124	62	103	58	0	0
Pinus lambertiana	74	38	60	33	0	0	69	35	59	31	0	0
Pinus ponderosa	95	48	56	33	9	5	115	57	73	40	1	1
Total	1150	584	897	506	50	37	898	451	722	382	5	5

Analysis

Tree cores were categorized first by species and then by geographic area. We analyzed species separately because we expected species to respond differently to fire. Degree of fire tolerance as well as the adaptations that confer fire resistance differ among species (Table 1). Moreover, we expected fire behavior to differ depending on the species present. Species composition varies with site productivity, which can influence fire severity via the amount and type of accumulated fuel (Kane et al. 2015; Guarín and Taylor 2005). Species, themselves, also generate unique fuel beds. Short fir needles produce a more compact layer that burns less intensely relative to pine needles (van Wagtendonk and Moore 2010; Stephens et al. 2004).

Tree cores of each species were grouped by geographic area so that tree-ring series from burned and unburned plots would share the same climate signal (Figures I.1, I.2, II.1, II.2, III.1, III.2, IV.1, IV.2, V.1, V.2, VI.1, VI.2, VII.1, and VII.2).

Raw ring-width data were used in this analysis. Series from the same tree were averaged together and standardized to enable comparisons of fire effects on growth among trees of different sensitivities. Ring-width indices for each tree were created by subtracting the series mean from the raw ring-width values and dividing by the series standard deviation. The influence of early growth on the ring-width indices was minimized by excluding growth rings that fell within 10 years of pith.

For each species within each geographic area, the effects of climate on ring-width were removed by subtracting an unburned control chronology from growth chronologies associated with the burned sites (Peterson et al. 1994). One unburned control chronology was developed for each geographic area by averaging together the ring-width indices of trees from the unburned plots. Burned plots within each geographic area were categorized by fire history. A burned chronology was developed for each set of plots with a common fire history by averaging together the ring-width indices of trees from the burned plots. The control chronology was subtracted from each burned chronology and the corresponding standard deviation was calculated. These results were graphically displayed over the period of known fire history (1930-2010). To verify that differences in growth could be primarily attributed to fire at the burned sites rather than irregular growth at the control sites, the unburned control indices used to generate the control chronology were categorized by plot and dbh and graphically displayed.

We visually examined growth patterns over the five years following each fire event. The duration of post-fire study was consistent with previous work by van Mantgem et al. (2003), who demonstrated that most fire-related mortality occurs within five years after fire. By examining growth over a five-year period, we included both the immediate and delayed effects of the disturbance.

We explored variability in growth response among trees from burned plots by subtracting the control chronology from individual tree indices that were categorized by dbh and plot and graphing the results. This analysis was repeated on the unburned control indices of each geographic area to establish a control for growth variability within and among series. The unburned chronology was recalculated to exclude a particular control series and was then subtracted from that series. These difference indices were categorized by dbh and plot and graphically displayed.

We quantified incidences of anomalous growth increases and decreases that occurred during the five-year period following each fire event. Growth increases and decreases were considered anomalous if they exceeded a threshold value. The appropriate unburned control chronology (paired by species and geographic area) was subtracted from each burned series, creating difference indices. These indices were categorized by sign. The mean and standard deviation were calculated separately for positive and negative indices values. Threshold values were generated by adding the standard deviation of the positive indices to the mean of the positive indices and by subtracting the standard deviation of the negative indices from the mean of the negative indices. Five iterations of post-fire indices were compared to the threshold values, beginning with the index of the first year after fire and continuing with the mean of the indices of the first and second, first through third, first through fourth, and first through fifth years after fire. Post-fire indices were averaged because tree growth is autocorrelated, and index values associated with later post-fire years should not be regarded as independent of growth during preceding years. Threshold values were computed five times per series, each time excluding the post-fire year or years under examination from the calculation of the mean and standard deviation.

We identified the effects of species, diameter class, RdNBR, fire cause, fire event, and plot on the frequency of different types of anomalous post-fire growth. We grouped difference indices by the categories within each variable and calculated the proportions of series exhibiting anomalous growth increases and decreases in each group.

Results

Seven types of growth responses during the five-year post-fire period were observed in the burned chronology minus control chronology difference indices: (1) Post-fire growth did not deviate noticeably from pre-fire growth, (2) Post-fire growth decreased immediately after fire, followed by an increase, (3) Post-fire growth decreased immediately after fire, followed by a decrease, (4) Post-fire growth decreased immediately after fire, followed by a return to pre-fire levels, (5) Post-fire growth increased immediately after fire, followed by an increase, (6) Post-fire growth increased immediately after fire, followed by a decrease, or (7) Post-fire growth increased immediately after fire, followed by a return to pre-fire levels (Table 5). Growth patterns at unburned sites did not exhibit unusual fluctuations following fire years, supporting the inference that differences between the burned and unburned chronologies reflected responses to fire at the burned sites (see unburned control plots indexed in the List of Figures).

All seven species included instances of (1) no apparent fire response, (2) an initial decrease in growth followed by an increase, and (3) an initial increase in growth followed by a decrease (Table 5). The second of these scenarios manifested more strongly. The difference index of zero fell more than one standard deviation from the difference indices during either the initial or the delayed post-fire response for all species, and during both the initial and delayed response periods for *A. concolor* and *C. decurrens* (Table 5). All species except *P. contorta* demonstrated instances of initial growth decreases followed by a return to pre-fire growth levels (Table 5). The remaining growth patterns of (1) an initial followed by a delayed decrease, (2) an initial followed by a delayed increase, and (3) an initial increase followed by a return to pre-fire levels were less widespread, surfacing in no more than three species each (Table 5).

Neither plot nor diameter class was a reliable indicator of similar growth response among the difference indices of individual burned series minus the control chronology. Although all species included at least one instance in which growth patterns were similar within the same plot, all species also demonstrated the reverse (Table 6). Moreover, the level of within-plot variability was not consistent across plots that shared the same fire history. All species except *P. ponderosa* exhibited similar levels of variation in growth patterns among plots with the same fire history, but all seven species also included one or more instances depicting the opposite (Table 6). Diameter class produced the same set of contradictory trends. All species included some instances where trees in the same diameter class had similar growth patterns and others where growth patterns differed. Similarly, growth patterns differed among diameter classes for all species in some but not all cases (Table 6).

Post-fire growth decreases that fell below the negative threshold value were much more common than growth increases that exceeded the positive threshold value (Tables 7 through 10). Proportions of growth decreases one year after fire categorized by species ranged from 0.24 to 0.43, while the proportions of growth increases ranged from 0 to 0.05 (Table 7). These values differed considerably from 0.16, the expected proportion if post-fire difference indices were randomly distributed, and may indicate a uniform, downward shift in the distribution of post-fire growth. Unsurprisingly, this pattern resurfaced when the same data were split based on diameter class, RdNBR, fire cause, fire event, and plot (Tables 8 through 10; Appendices I and II).

As the post-fire period under scrutiny lengthened, the proportion of series with anomalous growth decreases tended to diminish, evidence of subsequent increases in growth. This pattern held true for all species except *A. magnifica*, all diameter class except 75.1-90.0 cm and 105.1-120.0 cm, low and moderate but not undifferentiated fire severity, and both lightning- and management-ignited fires (Tables 7 through 10). Collinearity among these exceptions was low: Representation in the 75.1-90.0 cm and 105.1-120.0 cm diameter classes of *A. magnifica* (12; 12) was comparable to that of *A. concolor* (17; 5), *P. jeffreyi* (12; 11), and *P. lambertiana* (6; 7), and only 11.2% percent of the tree-ring series burned at undifferentiated severity were *A. magnifica* (Table 11). Species, diameter class, and fire severity may, therefore, have some merit as predictors of post-fire growth, while fire cause does not.

Table 5. Variability in post-fire growth responses across species. The initial response refers to the first or second year after fire. The delayed response is capped at five years. A weak response indicates that the difference index of zero fell within one standard deviation of the difference indices. A moderate response indicates that the difference index of zero fell more than one standard deviation from the difference indices either during the initial response period or the delayed response period. A strong response indicates that the difference index of zero fell more than one standard deviation from the difference indices during both the initial and delayed response periods. An example figure is noted in the table for each species that demonstrated a particular growth response.

Post-fire growth response — Initial	None	Decrease			Decrease			Decrease		Increase			Increase			Increase	
Delayed	None	Increase			Decrease			None		Increase			Decrease			None	
		Weak	Mod	Strong	Weak	Mod	Strong	Weak	Strong	Weak	Mod	Strong	Weak	Mod	Strong	Weak	Strong
Abies concolor	Fig. 13	Fig. 13	Figs. 3, 17	Fig. 5			Fig. 41	Fig. 11		Fig. 9			Fig. 15	Fig. 39			
Abies magnifica	Fig. 21	Fig. 5	Fig. 13		Fig. 3			Fig. 25					Fig. 17			Fig. 7	
Calocedrus decurrens	Fig. 7	Fig. 3	Figs. 11, 17	Fig. 3					Fig. 15					Fig. 25			
Pinus contorta	Fig. 11		Fig. 9										Fig. 3				
Pinus jeffreyi	Fig. 5	Fig. 3	Fig. 3					Fig. 20						Fig. 7			
Pinus lambertiana	Fig. 25	Fig. 15	Fig. 3						Fig. 22	Fig. 23				Fig. 13		Fig. 9	
Pinus ponderosa	Fig. 3	Fig. 3	Fig. 11					Fig. 19		Fig. 7			Fig. 17			Fig. 25	

Table 6. Variability within and among plots and diameter classes by species. An example figure is noted in the table for each species that demonstrated either heterogeneity or homogeneity in growth response.

Species	Plot				Diameter class			
	Differ within	Similar within	Differ among	Similar among	Differ within	Similar within	Differ among	Similar among
Abies concolor	Fig. 10a	Fig. 32a	Fig. 32a	Fig. 10a	Fig. 10b	Fig. 20b	Fig. 12	Fig. 4
Abies magnifica	Fig. 4a	Fig. 16a	Fig. 4a	Fig. 16a	Fig. 4b	Fig. 6	Fig. 4b	Fig. 4b
Calocedrus decurrens	Fig. 12a	Fig. 12a	Fig. 4b	Fig. 3	Fig. 6	Fig. 18b	Fig. 16	Fig. 3
Pinus contorta	Fig. 4a	Fig. 10a	Fig. 10a	Fig. 4a	Fig. 4b	Fig. 14	Fig. 8	Fig. 10b
Pinus jeffreyi	Fig. 6a	Fig. 21a	Fig. 6a	Fig. 19a	Fig. 6b	Fig. 4	Fig. 4	Fig. 6b
Pinus lambertiana	Fig. 12a	Fig. 20a	Fig. 12a	Fig. 8	Fig. 16	Fig. 26	Fig. 10	Fig. 16
Pinus ponderosa	Fig. 12a	Fig. 4	Fig. 12a		Fig. 14	Fig. 4	Fig. 12b	Fig. 4

Table 7. Proportion of tree-ring series by species that demonstrated post-fire growth decreases (-) and increases (+) relative to the unburned control chronology that exceeded one standard deviation below (-) or above (+) the mean value of the negative (-) or positive (+) difference indices generated from subtracting the unburned control chronology from each burned series.

Species	1 year post-fire			1-2 years post-fire			1-3 years post-fire			1-4 years post-fire			1-5 years post-fire		
	-	+	n	-	+	n	-	+	n	-	+	n	-	+	n
Abies concolor	0.27	0.05	165	0.21	0.04	154	0.16	0.02	136	0.15	0.01	131	0.15	0.02	131
Abies magnifica	0.33	0.02	122	0.34	0.02	122	0.38	0.03	122	0.34	0.04	122	0.37	0.04	122
Calocedrus decurrens	0.29	0.04	93	0.21	0.01	89	0.17	0.01	88	0.15	0.03	86	0.10	0.03	86
Pinus contorta	0.29	0.05	93	0.19	0.03	86	0.20	0.05	86	0.20	0.07	86	0.19	0.08	86
Pinus jeffreyi	0.24	0.03	199	0.18	0.04	199	0.08	0.03	199	0.07	0.06	199	0.07	0.05	199
Pinus lambertiana	0.43	0.00	46	0.29	0.02	41	0.29	0.03	35	0.30	0.03	33	0.30	0.06	33
Pinus ponderosa	0.31	0.05	65	0.16	0.02	61	0.21	0.03	61	0.16	0.03	61	0.11	0.02	61

Table 8. Proportion of tree-ring series by diameter class that demonstrated post-fire growth decreases (-) and increases (+) relative to the unburned control chronology that exceeded one standard deviation below (-) or above (+) the mean value of the negative (-) or positive (+) difference indices generated from subtracting the unburned control chronology from each burned series.

Diameter class (cm)	1 year post-fire			1-2 years post-fire			1-3 years post-fire			1-4 years post-fire			1-5 years post-fire		
	-	+	n	-	+	n	-	+	n	-	+	n	-	+	n
8.0-15.0	0.32	0.05	38	0.19	0.00	36	0.14	0.00	36	0.08	0.03	36	0.06	0.03	36
15.1-30.0	0.29	0.02	123	0.24	0.03	116	0.19	0.04	113	0.21	0.02	111	0.18	0.02	111
30.1-45.0	0.28	0.06	172	0.21	0.06	169	0.16	0.04	161	0.15	0.07	160	0.11	0.07	160
45.1-60.0	0.31	0.05	131	0.20	0.03	122	0.16	0.03	117	0.14	0.04	115	0.15	0.04	115
60.1-75.0	0.29	0.03	127	0.20	0.02	124	0.21	0.03	123	0.17	0.06	122	0.18	0.05	122
75.1-90.0	0.18	0.02	49	0.22	0.02	46	0.20	0.02	45	0.20	0.02	45	0.22	0.02	45
90.1-105.0	0.36	0.02	61	0.28	0.00	58	0.23	0.02	56	0.22	0.04	55	0.22	0.04	55
105.1-120.0	0.25	0.03	36	0.33	0.03	36	0.33	0.03	33	0.24	0.03	33	0.30	0.03	33
>120	0.28	0.00	46	0.18	0.00	45	0.19	0.00	43	0.22	0.00	41	0.20	0.00	41

Table 9. Proportion of tree-ring series by RdNBR that demonstrated post-fire growth decreases (-) and increases (+) relative to the unburned control chronology that exceeded one standard deviation below (-) or above (+) the mean value of the negative (-) or positive (+) difference indices generated from subtracting the unburned control chronology from each burned series.

RdNBR	1 year post-fire			1-2 years post-fire			1-3 years post-fire			1-4 years post-fire			1-5 years post-fire		
	-	+	n	-	+	n	-	+	n	-	+	n	-	+	n
Undifferentiated	0.11	0.03	124	0.09	0.02	124	0.09	0.03	124	0.07	0.03	115	0.07	0.04	115
Low	0.30	0.03	267	0.25	0.04	267	0.26	0.04	257	0.23	0.05	257	0.23	0.05	257
Moderate	0.37	0.01	134	0.26	0.03	110	0.18	0.02	100	0.16	0.06	100	0.09	0.04	100
High	0.80	0.00	5	0.80	0.00	5	--	--	0	--	--	0	--	--	0

Table 10. Proportion of tree-ring series by fire cause that demonstrated post-fire growth decreases (-) and increases (+) relative to the unburned control chronology that exceeded one standard deviation below (-) or above (+) the mean value of the negative (-) or positive (+) difference indices generated from subtracting the unburned control chronology from each burned series.

Cause	1 year post-fire			1-2 years post-fire			1-3 years post-fire			1-4 years post-fire			1-5 years post-fire		
	-	+	n	-	+	n	-	+	n	-	+	n	-	+	n
Lightning-ignited	0.30	0.03	337	0.23	0.03	330	0.18	0.02	330	0.15	0.05	321	0.14	0.04	321
Management-ignited	0.28	0.04	446	0.22	0.03	422	0.20	0.03	397	0.19	0.04	397	0.19	0.04	397

Table 11. Examination of collinearity between species and RdNBR and fire cause.

Species	RdNBR				Fire cause	
	Undiff.	Low	Mod.	High	LTG	MI
Abies concolor	32	64	23	2	29	140
Abies magnifica	14	76	6	0	43	85
Calocedrus decurrens	12	18	16	0	17	78
Pinus contorta	14	44	3	0	93	0
Pinus jeffreyi	36	47	64	0	148	58
Pinus lambertiana	11	13	10	3	7	39
Pinus ponderosa	6	12	14	0	14	53

Discussion

The most startling result of this study was the marked lack of strong growth responses to fire relative to the background level of annual variability in growth. This was due, in part, to the high level of background variability. Much dendrochronological research targets trees in environments defined by specific limiting factors, circumstances which homogenize growth responses. This study, in contrast, included forest-grown trees of diverse ages, diameters, and heights, differences likely to coincide with heterogeneous responses to local climate and soil, insects, pathogens, mechanical damage, competitive processes – and fire. Interestingly, however, trees did not often exhibit greater sensitivity to fire than to other drivers of stand dynamics. In cases where growth did demonstrate a fire response, post-fire difference indices generally did not vary more than one standard deviation from the difference index of zero and often fell within the same range as pre-fire growth (Table 5).

The subtle growth responses that did surface in this study corroborated previous work on fire and tree growth. Our most prevalent trend was an initial growth depression following a fire event (Table 7). Similarly, Slayton (2010) found that fire suppressed growth of *P. ponderosa* in the Payette National Forest of central Idaho for three years following fire. Varner et al. (2009) detected growth decreases in *Pinus palustris* (longleaf pine) one year after fire. Mutch and Swetnam (1995) found a growth reduction in *Sequoiadendron giganteum* (giant sequoia) for one year following high-severity fire. We demonstrated this trend in six additional species: *A. concolor*, *A. magnifica*, *C. decurrens*, *P. contorta*, *P. jeffreyi*, and *P. lambertiana* (Table 7).

Our study examined growth responses in trees that ranged from 8.0 cm to >120.0 cm dbh. Mutch and Swetnam (1995) found that *S. giganteum* experienced prolonged growth increases following prescribed fire in the Sierra Nevada, suggesting that larger diameter trees, with thicker bark to minimize cambial damage, could be more likely to show growth increases during the post-fire period. Interestingly, our results showed that delayed post-fire growth increases were actually more consistent among diameter classes <75.0 cm dbh, although the trend was also observed among trees 90.1-105.0 cm and >120.0 cm dbh (Table 8). Lack of post-fire growth increases in some large-diameter trees could reflect damage to stem and root systems that can occur when accumulations of bark flakes combust, increase the fire temperature near the tree, and prolong exposure to high temperature by smoldering (Varner et al. 2009; Kolb et al. 2007). In general, post-fire growth trends varied among trees regardless of diameter class, suggesting that (1) fire severity varied within plots and (2) trees varied in their growth responses (Table 6).

Growth responses also varied with fire severity. Growth depressions followed by growth increases were common among series associated with low and moderate severity fire (Table 9).

Series associated with undifferentiated fire, however, less frequently demonstrated reductions in growth immediately after fire and were not characterized by a subsequent growth increase (Table 9). This suggests that fires of undifferentiated severity may exert minimal effect on tree growth. Alternatively, undifferentiated fire severity could, in some cases, delineate unburned patches within a fire perimeter (Kolden et al. 2012). This could explain why a smaller proportion of series associated with undifferentiated fire severity were characterized by growth responses typical of trees actually exposed to flames (Table 9).

Fire cause did not partition variability in post-fire growth response, indicating that effects on tree growth of prescribed versus natural fires may not differ at the 0.1 ha scale (Table 10). This is a surprising result, given that prescribed fires allegedly burn areas more uniformly, leaving behind fewer unburned patches and burning areas more consistently at undifferentiated and low severity. These results may be skewed by the inclusion of the 2009 Big Meadow fire in the management-ignited category. Although this fire was ignited intentionally, it rapidly transitioned into a wildfire that burned a much larger area than expected (3058.7 ha) at higher severity relative to controlled prescribed fires (Table 2). It is unlikely, however, that the inclusion or exclusion of this single fire event would alter the overall result. Only 24 trees in this study, less than 5.6% of the trees representing management-ignited fires, were located within the perimeter of the Big Meadow fire (Table 2). A more probable explanation is that these results are an artifact of our sampling design. Our study only included cores from trees that exhibited post-fire growth and were sufficiently undamaged to enable crossdating. Among this population, cause of ignition may have minimal influence on fire effects because we pre-selected for trees that likely experienced a similar level of exposure to fire.

In general, the scope of inference of this study was limited to fire effects on trees that were (1) long-term fire survivors and (2) sensitive to similar limiting factors and therefore possible to crossdate. The selection of cores included here may consequently represent only a fraction of the possible growth responses to fire. This is a limitation common to all post-fire studies where pre-fire demography data are unavailable.

While our study's scope was limited, our objective was broad – to examine the growth responses in two National Parks of seven species across their full diameter range to undifferentiated, low, moderate, and high severity fire. With data collection limited to a single season, we were unable to conduct a fully balanced study. The burned and unburned series of each species that were differenced to identify fire effects on growth were not always located in comparably-sized geographic areas, nor were the unburned control chronologies always generated from a consistent number of trees representing the full range of diameter classes. Our results, therefore, do not provide an exhaustive list of all post-fire growth possibilities for each species, nor do they necessarily represent the proportions of different fire responses within each species that a more traditional study with a balanced design, random sampling, and large sample sizes could have revealed. Consequently, definitive comparisons among species should be avoided. Within species, instances where the control chronology was based on a large number of trees that (1) occupied areas adjacent to associated burned sites and (2) represented the same diameter classes as trees sampled at the burned sites yield more robust results (e.g., *A. concolor* Crane Flat). Interpretation of this study should be guided by the maps of sample locations for each species and the sample size information that is included in each table and figure caption.

Although sample depth was not consistent across all species and geographic areas, this study did quantify the effect of fire on tree growth, a key step in assessing the impacts of prescribed and natural fires on carbon accumulation in forests of the Sierra Nevada. We catalogued growth responses of seven mixed-conifer species to prescribed and natural fires and examined growth sensitivity across diameter and fire severity classes. Post-fire growth patterns seldom differed noticeably from growth fluctuations that resulted from other natural disturbances. This result suggests that use of fire in Yosemite and Sequoia & Kings Canyon National Parks will not adversely affect the capacity of survivors to attain pre-fire rates of carbon accumulation within five years of a fire event.

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Appendix I. Proportion of tree-ring series by fire event that demonstrated post-fire growth decreases (-) and increases (+) relative to the unburned control chronology that exceeded one standard deviation below (-) or above (+) the mean value of the negative (-) or positive (+) difference indices generated from subtracting the unburned control chronology from each burned series.

Fire	1 year post-fire			1-2 years post-fire			1-3 years post-fire			1-4 years post-fire			1-5 years post-fire		
	-	+	n	-	+	n	-	+	n	-	+	n	-	+	n
Wawona1970	0.21	0.07	14	0.14	0.00	14	0.14	0.00	14	0.07	0.00	14	0.07	0.00	14
Wawona1971	0.14	0.00	7	0.14	0.00	7	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7
Wawona1973	0.14	0.14	7	0.00	0.14	7	0.00	0.14	7	0.00	0.14	7	0.00	0.00	7
Wawona1975	0.00	0.14	7	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7
PW27	0.24	0.06	17	0.24	0.00	17	0.18	0.00	17	0.18	0.06	17	0.24	0.06	17
PW09	0.11	0.11	9	0.00	0.11	9	0.11	0.00	9	0.11	0.00	9	0.11	0.11	9
YNP-111	0.11	0.00	9	0.11	0.00	9	0.11	0.11	9	0.11	0.11	9	0.11	0.00	9
So. Wawona 3/4	0.00	0.14	7	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7
Eleanor 1986	0.00	0.00	8	0.00	0.00	8	0.00	0.00	8	0.00	0.00	8	0.00	0.00	8
Elbow	0.00	0.11	37	0.00	0.05	37	0.00	0.08	37	0.00	0.08	37	0.00	0.08	37
Pw3	0.13	0.00	38	0.08	0.03	38	0.05	0.05	38	0.05	0.03	38	0.05	0.05	38
M.Grove	0.00	0.00	10	0.00	0.00	10	0.00	0.00	10	0.00	0.00	10	0.00	0.00	10
South Fork	0.35	0.00	23	0.13	0.00	23	0.09	0.00	23	0.09	0.00	23	0.04	0.00	23
YNP-0065	0.17	0.00	6	0.17	0.00	6	0.17	0.00	6	0.17	0.00	6	0.33	0.00	6
Studhorse	0.43	0.00	7	0.43	0.00	7	0.29	0.14	7	0.29	0.14	7	0.14	0.00	7
Ackerson	0.26	0.04	46	0.17	0.04	46	0.15	0.02	46	0.11	0.07	46	0.07	0.07	46
Mg #9	0.40	0.10	10	0.20	0.10	10	0.20	0.10	10	0.20	0.00	10	0.20	0.00	10
Kibbie Relight	0.11	0.00	19	0.05	0.05	19	0.11	0.16	19	0.16	0.16	19	0.05	0.11	19
Eleanor 1999	0.75	0.00	8	0.63	0.00	8	0.63	0.00	8	0.63	0.00	8	0.25	0.00	8
Studhorse 4	0.57	0.00	7	0.00	0.00	7	0.29	0.00	7	0.14	0.00	7	0.14	0.00	7
YI Burn	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6
PW-3 Gin Flat	0.42	0.00	38	0.32	0.05	38	0.29	0.05	38	0.26	0.03	38	0.26	0.03	38
Soupbowl	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7
PW5-AD	0.89	0.00	9	0.89	0.00	9	0.89	0.00	9	0.78	0.00	9	0.67	0.00	9
PW3-23	0.47	0.05	19	0.58	0.00	19	0.47	0.00	19	0.42	0.00	19	0.37	0.11	19
Jack WF	0.22	0.00	9	0.22	0.00	9	0.22	0.00	9	--	--	0	--	--	0
Mariposa Grove	0.50	0.00	10	0.40	0.00	10	--	--	0	--	--	0	--	--	0
Wawona NW	0.40	0.13	15	0.40	0.20	15	--	--	0	--	--	0	--	--	0
Big Meadow	0.46	0.04	24	--	--	0	--	--	0	--	--	0	--	--	0
Atwell Mil	0.00	0.00	4	0.00	0.00	4	0.00	0.00	4	0.00	0.00	4	0.00	0.25	4
Castle Gro	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7	0.00	0.14	7	0.00	0.14	7
Comanche	0.59	0.02	66	0.45	0.02	66	0.27	0.00	66	0.29	0.00	66	0.26	0.00	66
Ferguson	0.40	0.00	10	0.20	0.00	10	0.10	0.00	10	0.10	0.00	10	0.20	0.00	10
Lewis Crk	0.25	0.13	16	0.25	0.13	16	0.31	0.13	16	0.31	0.13	16	0.31	0.13	16
Sugarloaf	0.16	0.04	68	0.07	0.06	68	0.01	0.04	68	0.01	0.07	68	0.01	0.07	68
Paradise	0.00	0.40	5	0.20	0.00	5	0.00	0.00	5	0.00	0.20	5	0.00	0.20	5
Mineral I	0.00	0.00	5	0.00	0.00	5	0.00	0.00	5	0.00	0.20	5	0.00	0.20	5
Sheep Cree	0.17	0.33	6	0.00	0.00	6	0.17	0.00	6	0.17	0.00	6	0.17	0.00	6
Lewis Cree	0.13	0.00	16	0.00	0.00	16	0.00	0.00	16	0.00	0.00	16	0.00	0.00	16
Tar Gap	0.33	0.00	9	0.44	0.00	9	0.33	0.00	9	0.44	0.00	9	0.44	0.00	9
Tar.Gap RX	0.58	0.00	19	0.32	0.00	19	0.37	0.00	19	0.47	0.00	19	0.53	0.00	19
Atwood	0.25	0.00	24	0.33	0.00	24	0.50	0.00	24	0.50	0.04	24	0.50	0.00	24
Williams	0.29	0.00	48	0.42	0.00	48	0.44	0.00	48	0.29	0.02	48	0.35	0.00	48
Comb	0.30	0.03	30	0.13	0.03	30	0.13	0.03	30	0.10	0.10	30	0.10	0.10	30
Highbrid E	0.60	0.00	10	0.60	0.00	10	0.30	0.00	10	0.20	0.00	10	0.20	0.00	10
Horse	0.57	0.00	7	--	--	0	--	--	0	--	--	0	--	--	0
Sheep Complex	--	--	0	--	--	0	--	--	0	--	--	0	--	--	0

Appendix II. Proportion of tree-ring series by plot that demonstrated post-fire growth decreases (-) and increases (+) relative to the unburned control chronology that exceeded one standard deviation below (-) or above (+) the mean value of the negative (-) or positive (+) difference indices generated from subtracting the unburned control chronology from each burned series.

Plot	1 year post-fire			1-2 years post-fire			1-3 years post-fire			1-4 years post-fire			1-5 years post-fire		
	-	+	n	-	+	n	-	+	n	-	+	n	-	+	n
P000	0.20	0.10	10	0.10	0.10	10	0.10	0.00	10	0.00	0.00	10	0.00	0.00	10
P002	0.38	0.00	8	0.00	0.00	8	0.13	0.00	8	0.13	0.00	8	0.00	0.00	8
P003	0.33	0.00	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6	0.00	0.00	6
P011	0.43	0.00	14	0.36	0.00	14	0.29	0.00	14	0.21	0.00	14	0.21	0.00	14
P012	0.11	0.00	9	0.11	0.00	9	0.00	0.00	9	0.00	0.11	9	0.00	0.11	9
P017	0.35	0.05	20	0.25	0.00	20	0.25	0.00	20	0.25	0.05	20	0.20	0.05	20
P018	0.50	0.00	10	0.60	0.00	10	0.50	0.00	10	0.40	0.00	10	0.40	0.20	10
P019	0.44	0.11	9	0.56	0.00	9	0.44	0.00	9	0.44	0.00	9	0.33	0.00	9
P020	0.33	0.00	9	0.33	0.00	9	0.11	0.00	9	0.11	0.00	9	0.11	0.00	9
P023	0.80	0.00	10	--	--	0	--	--	0	--	--	0	--	--	0
P024	0.00	0.00	5	--	--	0	--	--	0	--	--	0	--	--	0
P028	0.00	0.20	10	0.00	0.20	10	0.00	0.20	10	0.00	0.20	10	0.00	0.20	10
P029	0.00	0.22	9	0.00	0.00	9	0.00	0.11	9	0.00	0.11	9	0.00	0.11	9
P036	0.22	0.00	9	0.11	0.00	9	0.22	0.00	9	0.33	0.00	9	0.11	0.00	9
P060	0.00	0.00	10	0.00	0.10	10	0.00	0.30	10	0.00	0.30	10	0.00	0.20	10
P061	0.10	0.00	20	0.10	0.10	20	0.05	0.15	20	0.05	0.10	20	0.05	0.15	20
P062	0.33	0.00	18	0.28	0.06	18	0.22	0.06	18	0.22	0.00	18	0.22	0.00	18
P063	0.00	0.10	10	0.00	0.10	10	0.00	0.10	10	0.00	0.20	10	0.00	0.20	10
P065	0.19	0.07	27	0.06	0.06	18	0.11	0.06	18	0.11	0.06	18	0.11	0.06	18
P066	0.20	0.20	10	0.20	0.30	10	--	--	0	--	--	0	--	--	0
P068	0.38	0.00	16	0.31	0.00	16	0.31	0.00	16	0.31	0.00	16	0.13	0.00	16
P073	0.08	0.00	12	0.08	0.00	12	0.08	0.00	12	0.08	0.00	12	0.17	0.00	12
P085	0.89	0.00	9	0.89	0.00	9	0.89	0.00	9	0.78	0.00	9	0.67	0.00	9
P087	0.20	0.00	20	0.20	0.00	20	0.20	0.00	20	0.15	0.00	20	0.15	0.00	20
P088	0.50	0.00	18	0.22	0.00	18	0.22	0.00	18	0.22	0.00	18	0.22	0.00	18
P110	0.22	0.00	9	0.22	0.00	9	0.22	0.00	9	--	--	0	--	--	0
P111	0.07	0.11	28	0.04	0.04	28	0.04	0.04	28	0.04	0.04	28	0.04	0.00	28
P112	0.29	0.03	35	0.14	0.00	35	0.14	0.03	35	0.09	0.03	35	0.06	0.00	35
P113	0.80	0.00	5	0.80	0.00	5	--	--	0	--	--	0	--	--	0
P119	0.30	0.03	30	0.20	0.03	30	0.10	0.05	20	0.10	0.00	20	0.10	0.00	20
P136	0.56	0.00	9	0.22	0.00	9	0.22	0.00	9	0.33	0.00	9	0.33	0.00	9
P137	0.40	0.10	10	0.20	0.10	10	0.20	0.10	10	0.20	0.10	10	0.20	0.10	10
P138	0.22	0.00	9	0.33	0.00	9	0.56	0.00	9	0.56	0.11	9	0.56	0.00	9
P139	0.60	0.00	10	0.80	0.00	10	0.80	0.00	10	0.50	0.00	10	0.60	0.00	10
P140	0.20	0.00	10	0.00	0.00	10	0.00	0.00	10	0.00	0.20	10	0.00	0.20	10
P141	0.00	0.00	7	0.00	0.00	7	0.00	0.00	7	0.00	0.14	7	0.00	0.14	7
P148	0.00	0.13	15	0.07	0.00	15	0.00	0.00	15	0.00	0.13	15	0.00	0.13	15
P149	0.17	0.33	6	0.00	0.00	6	0.17	0.00	6	0.17	0.00	6	0.17	0.00	6
P158	0.38	0.00	8	0.25	0.00	8	0.13	0.00	8	0.13	0.00	8	0.13	0.00	8
P159	0.30	0.00	10	0.50	0.00	10	0.60	0.00	10	0.50	0.00	10	0.60	0.00	10
P160	0.29	0.00	14	0.21	0.00	14	0.00	0.00	14	0.00	0.00	14	0.00	0.00	14
P168	0.17	0.00	18	0.11	0.00	18	0.11	0.06	18	0.06	0.11	18	0.06	0.11	18
P170	0.00	0.08	12	0.00	0.08	12	0.00	0.00	12	0.00	0.00	12	0.00	0.00	12
P186	0.29	0.00	14	0.36	0.00	14	0.50	0.00	14	0.50	0.00	14	0.50	0.07	14
P187	0.33	0.00	9	0.44	0.00	9	0.33	0.00	9	0.44	0.00	9	0.44	0.00	9
P190	0.50	0.08	12	0.33	0.08	12	0.42	0.08	12	0.42	0.00	12	0.42	0.00	12
P192	0.20	0.00	20	0.10	0.00	20	0.10	0.00	20	0.10	0.00	20	0.10	0.00	20
P193	0.50	0.05	20	0.35	0.05	20	0.30	0.05	20	0.30	0.10	20	0.25	0.15	20
P195	0.19	0.04	27	0.15	0.04	27	0.04	0.00	27	0.07	0.04	27	0.07	0.00	27
P196	0.60	0.00	10	0.60	0.00	10	0.30	0.00	10	0.20	0.00	10	0.20	0.00	10
P197	0.45	0.10	20	0.30	0.05	20	0.20	0.00	20	0.20	0.05	20	0.20	0.05	20
P198	0.50	0.00	20	0.40	0.00	20	0.25	0.00	20	0.25	0.00	20	0.20	0.00	20
P251	0.26	0.00	23	0.17	0.09	23	0.00	0.09	23	0.00	0.09	23	0.00	0.04	23
P252	0.40	0.00	10	0.60	0.00	10	0.70	0.00	10	0.40	0.00	10	0.50	0.00	10
P253	0.40	0.00	10	0.20	0.00	10	0.10	0.00	10	0.10	0.00	10	0.20	0.00	10
P255	0.60	0.00	10	0.40	0.00	10	0.50	0.00	10	0.60	0.00	10	0.70	0.00	10
P256	0.57	0.00	7	--	--	0	--	--	0	--	--	0	--	--	0
P263	0.00	0.00	9	0.00	0.00	9	0.00	0.00	9	0.00	0.00	9	0.00	0.00	9
P264	0.00	0.00	9	0.00	0.00	9	0.00	0.00	9	0.00	0.00	9	0.00	0.00	9

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