Patterns of flammability of the California oaks: the role of leaf traits

Eamon A. Engber and J. Morgan Varner, III

Abstract: Fire is one of the most important processes driving plant community composition and structure. Fire regimes are largely governed by climate, vegetation structure, and individual plant traits that influence flammability. We assessed the mechanistic drivers of flammability for a diverse group of 18 California *Quercus* and allied *Chrysolepis* and *Notholithocarpus* species, addressing variation in leaf physical traits, growth form (tree or shrub), phylogeny (*Quercus* subgenera), and fire regime (low, mixed, or high severity). Differences in flammability were not strongly driven by leaf habit, leaf margin type, or surface area to volume ratio; simple measures of leaf size accounted for most of the observed variation. Further, leaf size was tightly linked to fuelbed depth, a known driver of fire behavior. Litter from trees was generally more flammable than litter from shrubs, primarily a function of differences in leaf size. A hierarchical clustering analysis on the flammability data set divided the oaks into three clusters of low, intermediate, and high flammability, corresponding closely to high-, mixed-, and low-severity fire regimes, respectively. The link between plant flammability traits and fire regime provides further evidence that individual species affect ecosystem processes.

Résumé : Le feu est un des plus importants processus qui déterminent la structure et la composition des communautés végétales. Les régimes de feu sont largement gouvernés par le climat, la structure de la végétation et les caractéristiques individuelles des plantes qui influencent l'inflammabilité. Nous avons évalué les mécanismes responsables de l'inflammabilité pour un groupe varié de 18 espèces californiennes de *Quercus*, ainsi que d'espèces apparentées de *Chrysolepis* et de *Notholithocarpus*, en s'intéressant à la variation des caractéristiques physiques des feuilles, à la forme de croissance (arborescente ou arbustive), à la phylogénie (sous-genres de *Quercus*) et au régime de feu (sévérité faible mixte ou élevée). Les différences d'inflammabilité n'étaient pas étroitement déterminées par le type de feuillage, le type de marge des feuilles, ni par le rapport de la surface sur le volume du feuillage; de simples mesures des feuilles expliquaient la plus grande partie de la variation observée. De plus, la dimension des feuilles était étroitement reliée à l'épaisseur du lit de combustible, un déterminant connu du comportement du feu. La litière des arbres était généralement plus inflammable que celle des arbustes, principalement en raison des différences dans la dimension des feuilles. Une classification hiérarchique à partir d'un jeu de données d'inflammabilité a permis de diviser les chênes en trois groupes dont l'inflammabilité est faible, intermédiaire ou élevée et qui correspondent étroitement à des régimes de feu dont la sévérité est respectivement élevée, mixte ou faible. Le lien entre les caractéristiques d'inflammabilité des plantes et le régime de feu fournit une preuve supplémentaire que chaque espèce végétale a un effet sur les processus écosystémiques.

[Traduit par la Rédaction]

Introduction

Fire is a major disturbance process affecting the composition and structure of terrestrial ecosystems around the globe (Bond and Keeley 2005). Throughout many fire-prone ecosystems, plant flammability is a fundamental link in understanding patterns in species coexistence, plant succession, and the mechanisms driving fire behavior and effects (Gagnon et al. 2010). Flammable plants can injure or kill proximal competitors (Bond and Midgley 1995), maintain or generate growing space (Gagnon et al. 2010), or otherwise maintain favorable environments for self-perpetuation. Fuels surrounding individuals influence local fire behavior; the aggregate of these modify the frequency and severity of fires (Schwilk 2003). Few studies have provided empirical evidence linking plant traits, flammability, and ecosystem processes; the diversity of fire-prone landscapes and taxa in California, USA, presents an ideal opportunity to clarify the mechanisms of differential plant flammability and relate these to fire regimes.

Due to a juxtaposition of climates, physiography, and disturbances, the Californian Floristic Province is a globally significant center of biodiversity (Myers et al. 2000). The region's terrestrial ecosystems have a well-recognized relationship with fire (Sugihara et al. 2006), supporting a variety of ecosystems characterized by a diversity of fire regimes. Among its varied flora, California boasts at least 20 species of

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Quercus, approximately 22% of the total number of oaks in the United States (Nixon 2002; all nomenclature follows Hickman (1993) except for *Notholithocarpus densiflorus* (Hook. and Arn.) Manos, C.H. Cannon, and S. Oh). In addition, two related members of the Fagaceae, *N. densiflorus* and *Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmq., represent an additional two allied species in the region. Oak diversity in California extends not only to the richness of species and subgenera (red, white, and golden oaks represented), but also to growth forms, with approximately 10 trees and 10 shrubs, including a number that vacillate between the forms. These species also vary in their leaf habit, or deciduousness: six are deciduous (or tardily so) and 14 are evergreen. California's oaks span a variety of ecosystems, with a similar variability in their local fire regimes. In northwestern California *Quercus garryana* Douglas ex Hook. savannas and woodlands, surface fires are frequent (one or more per decade), are low severity, and occur in late summer – fall (Engber et al. 2011). In southern California *Quercus dumosa* Nutt. chaparral, fire return intervals are variable and often infrequent (less than two or three per century), burn with high intensity, and are concentrated around foehn winds that occur in late fall and early winter (Keeley 1992). *Quercus* species persist in these fire-prone environments supported by different fire-adaptive traits; understanding the linkages between flammability and other adaptive traits is of growing interest to ecologists.

Over the past decade, there has been a resurgence of interest in plant flammability. Research in North America (Fonda 2001; Schwilk and Ackerly 2001; Behm et al. 2004; Kane et al. 2008; Gagnon et al. 2010; Schwilk and Caprio 2011) and in Europe (Ganteaume et al. 2009, 2011; Saura-Mas et al. 2010; Curt et al. 2011) points to high variability in plant flammability among species and ecosystems. Little work has delved into the underlying mechanisms of the observed variability in flammability, an important next step in flammability research. Chemical variability, especially concentrations of volatile terpenes, has been linked to flammability in Mediterranean species (Ormeño et al. 2009). Leaf size (one-sided surface area) was positively related to heat release rates via fuelbed bulk density in semi-arid Australian woodlands (Scarff and Westoby 2006). In Sierra Nevada conifers, variation in leaf length was positively linked with community flammability (Schwilk and Caprio 2011). This study builds on previous works by addressing multiple potential fire-facilitating foliar characteristics, phylogenetic relationships, and flammability × fire regime interactions.

The objectives of this research were to link leaf traits to flammability across a diverse suite of species and examine whether the variation in flammability is related to fire regime, plant form (tree or shrub), phylogeny, leaf habit, or a combination of factors. We also investigated if flammability is influenced by a number of foliar characteristics including leaf length, width, perimeter, surface area to volume ratio, blade thickness, and curling as well as variation in fuel arrangement (fuelbed depth).

Methods

Fuel collections

Oak foliar litter was collected from wild populations of 18 species across California and southern Oregon, USA (Table S1).[1] Litter samples for each species were skimmed from the forest floor surface (Oi horizon) beneath individual trees or clumps, with eight separate approximately 25 g (dry weight) replicates collected for each species. Collected litter was transported to the laboratory and sorted to remove debris or litter from other species, thereby isolating species-level flammability effects and removing a potentially large source of sample variability (e.g., Ganteaume et al. 2011). After sorting, each sample was oven-dried at 40 °C for 24 h, resulting in an average fuel moisture at the time of burning of 4.0% (SD = 1.1%) on a dry weight basis (subsamples of litter were removed from each sample at time of burn and dried further to calculate time of burn moisture content). Air temperature in the burn facility averaged 20.8 °C (±1.2 °C), while relative humidity averaged 40.8% (±5.1%). Following drying, 15 g (±0.2 g) samples were removed from seven randomly selected bags for burning experiments. Residual litter was subsampled for subsequent leaf measurements.

Leaf measurements

Leaves were measured by randomly selecting 35 leaves (five from each of the seven burn replicates) from each of the 18 species. Leaf length (including petiole), width (at the widest point), and degree of curling (height above the flat surface) were measured to the nearest millimetre with a standard ruler. Leaves were flattened to measure total length. Leaf thickness was measured with an electronic caliper on the edge of all leaves, between primary leaf veins. Leaf outlines were traced to obtain measurements of perimeter (using a mechanical measuring wheel) and surface area (using a digital planimeter). Leaf volume was calculated by multiplying the one-sided surface area by leaf thickness; surface area to volume ratio was then calculated by summing two-sided surface area and perimeter edge thickness and then dividing by volume.

Burning methods

Experimental burning was conducted under laboratory conditions following standard methods (see Kane et al. 2008). Litter samples were constructed within the interior 400 cm^2 of a 35 cm × 35 cm lattice of xylene-soaked cotton strings. The litter was distributed evenly on the surface of the strings on a stainless steel platform situated below a 2.75 m × 2.75 m fume hood. The hood fan generated a constant draw of 15–20 $\mathrm{cm \cdot s^{-1}}$, although no airflow was detected at the fuelbed. Prior to ignition, fuelbed depth was measured in four locations, 7 cm from each corner of the fuelbed. Fuelbed depth was included because it relates to fuelbed bulk density, a consistently strong driver of fire behavior (Rothermel 1972). The fuels were ignited following methods in Fonda (2001). Briefly, strings were ignited from all sides and a timer started when the litter ignited. Maximum flame height was estimated visually to

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-138.

the nearest centimetre by two trained observers using a vertical ruler mounted behind the fuelbed. The duration of flaming (seconds) and smoldering (seconds) combustion was recorded. Following extinction of smoldering, the residual ash was collected, unburned string removed, and the sample weighed to estimate mass loss (percent). The four flammability metrics observed (flame height, flaming duration, smoldering duration, and mass loss) relate to standard flammability characteristics (Anderson 1970).

Data analyses

Since the response variables used in flammability analyses tend to be highly correlated (Kane et al. 2008; here, all $r > 0.50$ excluding smoldering duration), we combined the four flammability metrics for each species using principal components analysis (PCA). PCA scores were generated using standardized (mean = 0 and SD = 1) values for each of the flammability metrics. Given the inherent multicollinearity of foliar characteristics (e.g., long leaves have long perimeters), all foliar metrics were similarly analyzed using PCA. The number of principal components retained for both flammability and foliar metrics was based on a cutoff level of 80% of the total variance in each data set (Afifi et al. 2004). Species-level means for the first two principal components of flammability (hereafter “PCF1” and “PCF2”) and the first two principal components of foliar characteristics (hereafter “PCL1” and “PCL2”) were plotted separately. Factor loadings (correlations) between each retained principal component and the original variables are reported and discussed. Following the PCA, regression (ratio of polynomials) was employed to analyze the relationships between the principal components of flammability (PCF1) and foliar characteristics (PCL1) as well as fuelbed depth (standardized) and leaf perimeter (standardized) using species-level means ($N = 18$).

In addition to leaf and fuelbed physical measurements, we also evaluated the effects of a number of categorical variables on flammability, including growth form (tree or shrub), leaf habit (deciduous or evergreen), leaf margin (lobed or unlobed), fire regime (low, mixed, or high severity), and phylogeny (subgenus: Red, or *Erythrobalanus*; White, or *Lepidobalanus*; and Golden, or *Protobalanus*) using a hierarchical clustering procedure (the two oak allies, *N. densiflorus* and *C. chrysophylla*, were excluded from the phylogenetic analyses). Fire regime comparisons were made using generalized categories that reflect the hypothesized historic fire regime of each species, considering fire severity (low, mixed, or high). The understanding of historic fire regimes for many of the studied species is quite limited, and some species may persist under multiple fire regimes. Further, the California oaks differ markedly from most conifers in that the entire flora is capable of resprouting following top-kill, enabling these species to simultaneously fit into “resister” and “endurer” life history strategies (Fonda et al. 1998). For the purposes of this study, species were grouped into the following fire regime categories: (*i*) “low-severity” group: tree-form oaks were grouped in these categories, as most can resist surface fire injury, with the large deciduous oaks (e.g., *Q. garryana*, *Quercus lobata* Née, and *Quercus kelloggii* Newberry) comprising a low-severity group, (*ii*) “mixed-severity” group: evergreen, live oaks along with *Quercus douglasii* Hook. & Arn. and *Quercus engelmannii* Greene comprise this group, given the variability in reported fire regimes for these species, and (*iii*) “high-severity” group: the shrub oaks are vigorous resprouters, occur in relatively extreme (hot and dry) environments within California, and often burn in crown fires and were therefore categorized in the high-severity group (Sugihara et al. 2006).

Data used for the cluster analysis included species-level mean values for the standardized flammability metrics (flame height, flaming duration, smoldering duration, and mass loss). The clusters were determined using a group average linkage method, where the Euclidian distance (or dissimilarity) between groups was defined as the average distance between each of their members. We employed a goodness-of-fit test for the chosen clusters defined by the cophenetic correlation coefficient, where values above 0.75 are considered a good fit. All analyses were performed using the statistical package NCSS (Hintze 2007).

Results

Primary gradients in flammability and leaf traits

The 18 oak species differed widely across all measured flammability metrics (maximum flame height, flaming duration, smoldering duration, and mass loss) and fuelbed depth (Table 1). Among the most flammable were the deciduous tree oaks (an exception was the evergreen shrub *Quercus sadleriana* R. Br. ter) *Q. kelloggii*, *Q. garryana*, *Q. sadleriana*, and *Q. lobata*, consistently generating tall flames (maximum = 89 cm), brief flaming duration (range 34–47 s), and substantial mass loss (>85%). These species were characterized by deep fuelbeds, ranging from 5.3 to 7.1 cm. Oaks that consistently burned poorly were typified by the evergreen shrub oaks, particularly *Quercus vaccinifolia* Kellogg, *Quercus durata* Jeps., *Q. dumosa*, and *Quercus john-tuckeri* Nixon & C.H. Mull. These low-flammability litters generated short flames (<24 cm), consumed little fuel (<53%), and flamed for long durations (>113 s). Intermediate burners included the evergreen live oaks (e.g., *Quercus agrifolia* Née, *Quercus chrysolepis* Liebm., and *Quercus wislizeni* A. DC.) along with *Q. engelmannii* and *Q. douglasii*. These species had intermediate fuelbed depths (2.9–3.5 cm), mass loss from 59% to 77%, variable smoldering duration, and flame heights ranging from 21 to 42 cm. Within the small-leaved shrub oaks, *Quercus palmeri* Engelm. stood out with substantially taller flames (45.6 cm) and greater mass loss (76.8%) than *Q. durata*, *Q. vaccinifolia*, *Q. dumosa*, and *Q. john-tuckeri* (Table 1).

The 18 species encompassed a wide diversity of leaf morphologies (Table 2). The evergreen shrub oaks had the smallest leaves typified by low curled height (<4.5 mm), intermediate to low surface area to volume ratio ($<120\ \mathrm{cm^2 \cdot cm^{-3}}$), and low, compact fuelbeds (<3 cm). *Quercus sadleriana* was an anomaly within the shrubs with its large leaves and deep fuelbeds. The highly flammable species *Q. kelloggii*, *Q. garryana*, *Q. sadleriana*, *Q. lobata*, *N. densiflorus*, and *C. chrysophylla* had long leaves (60–105 mm), high curl (10–33 mm), long perimeters (>200 mm), and high surface area to volume ratio ($113–197\ \mathrm{cm^2 \cdot cm^{-3}}$). The deeply lobed and highly flammable *Q. kelloggii* had the greatest length, width, perimeter, curl height, and fuelbed depth of all of the oaks studied, while the shrubs *Q. durata* and *Q. vaccinifolia* had the smallest leaves (Table 2).

Table 1. Mean and SE values for laboratory burning characteristics of 18 California oaks and their allies comprising the flammability study.

Burning characteristic																		
Maximum flame height (cm)																		
Species	QUKE	QUGA	QUSA	QULO	NODE	CHCH	QUGABR	QUTO	QUPA	QUAG	QUWI	QUCH	QUJO	QUEN	QUDO	QUDU	QUVA	QUDUR
Mean	83.0	76.0	64.9	63.6	63.6	57.4	50.4	47.9	45.6	41.4	39.9	37.9	24.1	23.3	21.7	20.6	14.6	13.8
SE	3.1	2.3	1.7	1.5	1.2	1.8	2.3	3.7	2.1	2.5	3.4	4.3	3.6	1.6	2.0	3.9	2.3	2.7
Flaming duration (s)																		
Species	QUJO	QUVA	QUPA	QUEN	QUCH	QUDO	QUDU	QUDUR	QUAG	QUTO	QUWI	CHCH	QUGABR	NODE	QUSA	QULO	QUGA	QUKE
Mean	157.9	158.9	133.3	117.7	110.6	113.1	115.9	113.1	107.4	94.4	88.9	78.1	64.7	57.1	47.1	45.4	41.1	34.1
SE	6.5	18.6	9.1	9.3	4.9	11.8	17.9	16.8	9.0	9.3	6.2	2.4	6.8	3.3	2.1	3.4	4.2	1.8
Smoldering duration (s)																		
Species	QUSA	QULO	QUTO	QUDO	QUWI	QUCH	QUGABR	QUEN	CHCH	QUAG	NODE	QUGA	QUKE	QUPA	QUDU	QUJO	QUDUR	QUVA
Mean	386.0	325.1	310.0	296.0	284.6	281.9	278.7	273.4	252.4	249.4	245.6	246.7	233.3	189.1	156.2	100.4	96.0	79.6
SE	55.2	26.4	31.1	18.5	17.7	16.8	32.5	33.3	14.8	15.4	19.2	24.5	16.3	10.0	31.4	11.5	20.2	10.3
Mass loss (%)																		
Species	QUSA	QUKE	NODE	QUGA	QUGABR	CHCH	QULO	QUTO	QUAG	QUPA	QUCH	QUWI	QUEN	QUDO	QUJO	QUDU	QUVA	QUDUR
Mean	92.5	92.3	88.5	87.9	85.5	85.5	85.3	77.8	76.6	76.8	75.7	72.1	60.2	59.6	53.2	43.9	34.9	29.3
SE	0.5	0.2	1.1	0.5	1.5	0.8	0.9	1.4	2.3	0.7	1.4	1.9	4.8	3.6	3.5	7.9	5.4	6.7
Fuelbed depth (cm)																		
Species	QUKE	QUGA	QUSA	QULO	QUGABR	NODE	CHCH	QUTO	QUDO	QUPA	QUAG	QUEN	QUWI	QUCH	QUDU	QUJO	QUDUR	QUVA
Mean	7.10	6.64	5.66	5.30	4.80	4.77	3.81	3.67	3.52	3.23	3.22	3.15	3.14	2.92	2.80	2.7	2.41	1.90
SE	0.21	0.20	0.24	0.20	0.17	0.13	0.11	0.14	0.06	0.14	0.14	0.10	0.21	0.13	0.22	0.06	0.11	0.07

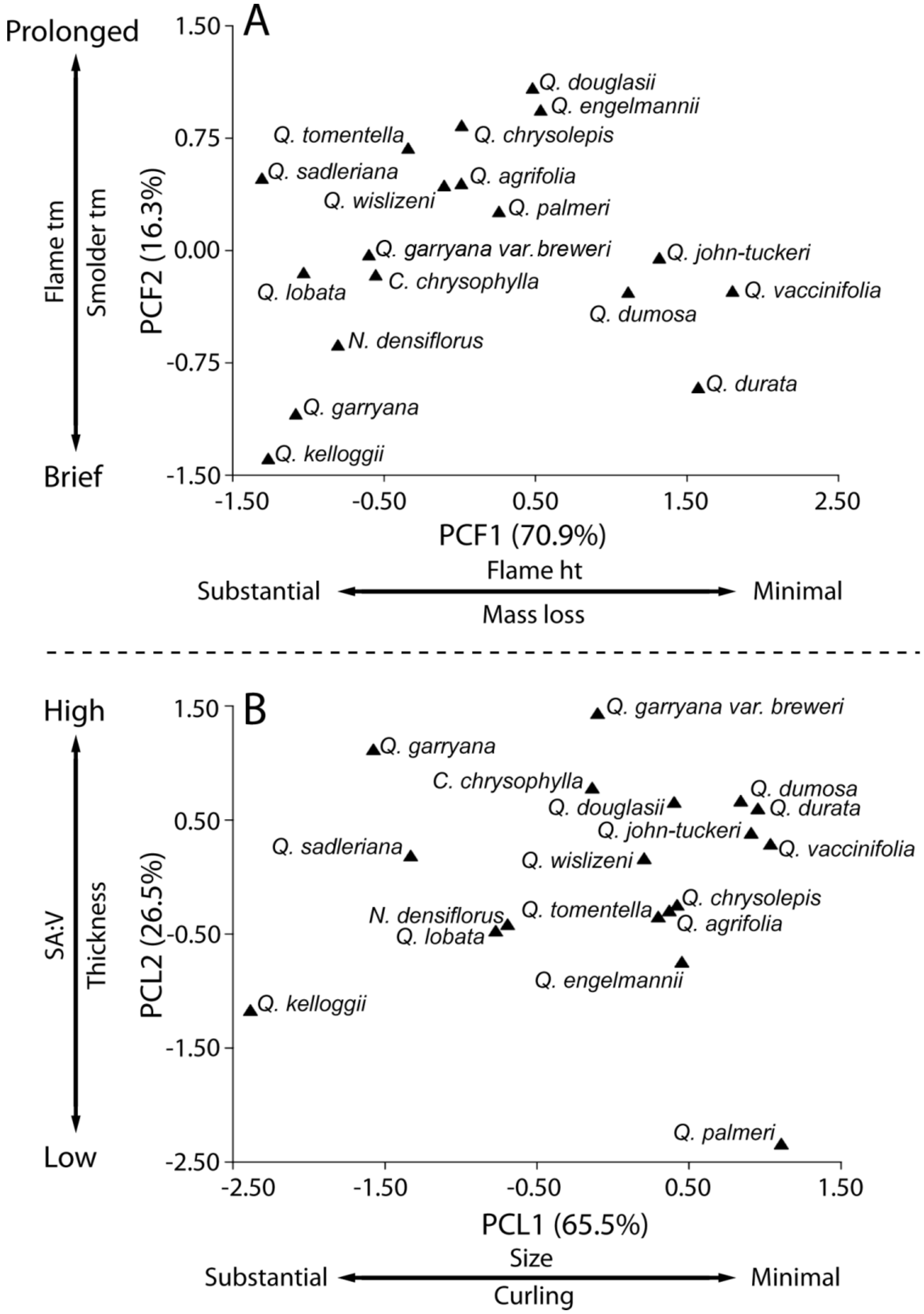
Note: QUAG, *Quercus agrifolia*; QUCH, *Quercus chrysolepis*; QUDO, *Quercus douglasii*; QUDU, *Quercus dumosa*; QUDUR, *Quercus durata*; QUEN, *Quercus engelmannii*; QUGA, *Quercus garryana*; QUGABR, *Quercus garryana* var. *breweri*; QUJO, *Quercus john-tuckeri*; QUKE, *Quercus kelloggii*; QULO, *Quercus lobata*; QUPA, *Quercus palmeri*; QUSA, *Quercus sadleriana*; QUTO, *Quercus tomentella*; QUVA, *Quercus vaccinifolia*; QUWI, *Quercus wislizeni*; CHCH, *Chrysolepis chrysophylla*; NODE, *Notholithocarpus densiflorus*.

Table 2. Mean and SE values for foliar characteristics of 18 oaks and their allies comprising the flammability study.

Foliar characteristic																		
Leaf curl height (mm)																		
Species	QUKE	QULO	QUSA	QUGA	NODE	CHCH	QUEN	QUTO	QUWI	QUGABR	QUAG	QUDO	QUCH	QUPA	QUDUR	QUDU	QUJO	QUVA
Mean	33.83	20.73	19.57	19.09	16.14	10.33	8.98	8.71	8.5	8.43	7.29	7.28	7.33	6.33	4.42	4.67	4.21	3.03
SE	2.26	2.38	1.70	2.25	2.13	1.39	1.20	0.55	0.59	1.29	0.99	0.45	0.45	0.69	0.26	1.18	0.60	0.50
Leaf length (mm)																		
Species	QUKE	QUSA	NODE	QUGA	CHCH	QULO	QUEN	QUTO	QUWI	QUAG	QUGABR	QUCH	QUDO	QUPA	QUVA	QUJO	QUDU	QUDUR
Mean	105.49	101.52	89.91	86.65	70.66	61.45	51.81	50.31	49.33	45.53	45.04	44.88	38.36	31.98	20.18	19.20	18.88	17.12
SE	4.01	5.27	4.88	5.19	5.99	9.79	2.56	3.81	1.92	4.23	2.98	2.09	1.43	0.94	1.15	0.86	3.59	1.51
Leaf width (mm)																		
Species	QUKE	QUGA	QUSA	QULO	NODE	QUAG	QUGABR	QUTO	QUCH	QUWI	QUPA	QUEN	QUDO	CHCH	QUJO	QUDU	QUDUR	QUVA
Mean	78.07	59.34	51.14	48.80	38.29	29.10	26.81	26.70	25.52	25.67	24.59	22.59	19.69	18.56	14.34	13.49	11.79	11.08
SE	3.69	4.65	3.55	4.44	2.12	2.58	1.86	2.10	0.86	1.69	0.83	1.51	0.85	1.39	0.96	2.48	0.85	1.19
Leaf edge thickness (mm)																		
Species	QUPA	QUEN	QUTO	QUCH	QUAG	QUVA	NODE	QUJO	QULO	QUWI	QUDU	QUKE	QUDUR	QUDO	CHCH	QUSA	QUGABR	QUGA
Mean	0.41	0.25	0.22	0.21	0.21	0.20	0.19	0.19	0.19	0.18	0.18	0.18	0.18	0.16	0.15	0.15	0.12	0.11
SE	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Leaf perimeter (mm)																		
Species	QUKE	QUGA	QUSA	QULO	NODE	CHCH	QUGABR	QUWI	QUTO	QUEN	QUCH	QUAG	QUDO	QUPA	QUJO	QUDU	QUVA	QUDUR
Mean	408.07	253.97	239.44	220.29	206.33	139.37	129.86	120.62	118.17	110.08	105.38	107.65	89.45	83.86	55.0	50.57	45.24	40.14
SE	16.13	21.62	16.13	18.48	10.92	11.81	10.30	5.80	9.06	5.98	4.19	10.26	3.58	2.82	3.16	10.92	3.25	2.48
Leaf surface area to volume ratio ($cm^2 \cdot cm^{-3}$)																		
Species	QUGA	QUGABR	QUSA	CHCH	QUDO	QUKE	QUDU	NODE	QULO	QUWI	QUDUR	QUJO	QUVA	QUTO	QUCH	QUAG	QUEN	QUPA
Mean	196.79	167.38	146.61	142.35	126.07	121.64	120.83	113.18	113.21	112.56	110.83	108.09	102.75	99.25	97.29	96.08	83.30	52.01
SE	11.21	11.05	3.34	5.82	11.57	5.82	8.81	4.23	9.52	8.26	6.29	6.98	5.89	7.86	3.00	4.21	3.11	2.00

Note: QUAG, *Quercus agrifolia*; QUCH, *Quercus chrysolepis*; QUDO, *Quercus douglasii*; QUDU, *Quercus dumosa*; QUDUR, *Quercus durata*; QUEN, *Quercus engelmannii*; QUGA, *Quercus garryana*; QUGABR, *Quercus garryana* var. *breweri*; QUJO, *Quercus john-tuckeri*; QUKE, *Quercus kelloggii*; QULO, *Quercus lobata*; QUPA, *Quercus palmeri*; QUSA, *Quercus sadleriana*; QUTO, *Quercus tomentella*; QUVA, *Quercus vaccinifolia*; QUWI, *Quercus wislizeni*; CHCH, *Chrysolepis chrysophylla*; NODE, *Notholithocarpus densiflorus*.

Fig. 1. (A) Principal components analysis of the flammability of 16 California oaks and two oak allies. Flammability results are based on four fire behavior metrics including flame height, flame time, smolder time, and fuel consumption. (B) Principal components analysis of the foliar characteristics of 16 California oaks and two oak allies. Foliar characteristics include leaf length, width, perimeter, curling, thickness, and surface area to volume ratio.



Principal components of oak flammability and leaf characteristics

The PCA for flammability across the 18 species explained 87.26% of the variation in the flammability data set with the first two principal components (Fig. 1A). Flaming characteristics (flame height and duration) and mass loss were each closely related to axis 1 (PCF1), explaining 70.9% of the variation in the data set (Table 3). Smoldering duration, and to a lesser extent flaming duration, drove axis 2 (PCF2), accounting for an additional 16.33% of the variation in oak litter flammability. Flammable species had large negative values for PCF1, while less flammable species had large positive values (Fig. 1A).

The PCA for foliar characteristics was also useful, explaining 92.07% of the total variation in the foliar data set in the

Table 3. Factor loadings from the principal components analysis (PCA) of flammability and leaf foliar characteristics of 18 oak species studied.

PCA flammability			PCA leaves		
Variable	Axis 1	Axis 2	Variable	Axis 1	Axis 2
Flame height	–0.92	–0.24	Curled height	–0.92	–0.23
Flame time	0.78	0.47	Length	–0.92	–0.15
Smolder time	–0.74	0.59	Width	–0.93	–0.26
Mass loss	–0.91	0.16	Thickness	0.44	–0.86
			Perimeter	–0.96	–0.22
			Surface area to volume ratio	–0.52	0.81
% variance	70.93	16.33		65.51	26.56

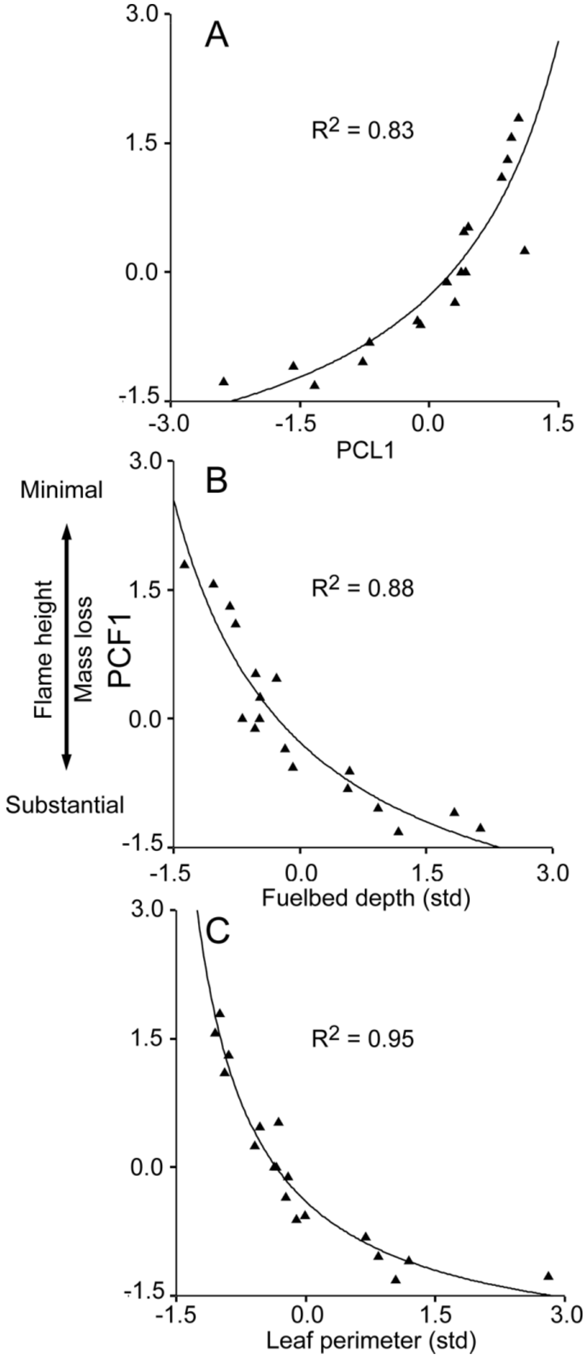
Note: The total amount of variation explained by each axis ("% variance") is reported.

first two principal components (Fig. 1B). Leaf perimeter, width, curled height, and length were aligned with axis 1 (PCL1), explaining 65.51% of the variation in the oak foliar characteristics (Table 3). Leaf thickness and surface area to volume ratio were the only factors strongly related to axis 2 (PCL2), accounting for an additional 26.56% of the variation in the data set. Large, curled leaves had large negative values for PCL1, while small, flat leaves had large positive values (Fig. 1B).

The PCA of flammability revealed strong linkages to individual leaf and aggregate fuelbed characteristics (Fig. 2). The depth of the fuelbeds was tightly related to flammability (Fig. 2B), with fuelbed depth alone explaining 88% of the variation in PCF1. Among leaf characteristics, leaf perimeter was most strongly related to litter flammability (Fig. 2C), with a ratio of polynomials model explaining 95% of the variation in PCF1.

Comparing the principal axes for flammability and leaf characteristics revealed interesting relationships. Oak fuelbeds with long, wide, curled leaves generated tall flames, with brief flaming duration, consuming the vast majority of the fuel. In contrast, small, narrow, flat-laying oak leaves burned with diminutive flames and consumed little fuel. Flaming duration and smoldering duration were relatively less important than flame height and mass loss in the flammability PCA, while leaf surface area to volume ratio and thickness were less important than perimeter, curl, length, and width in the foliar PCA. The relationship between PCF1 and PCL1 was curvilinear, with a ratio of polynomials model explaining 83% of the variation in PCF1 (Fig. 2A).

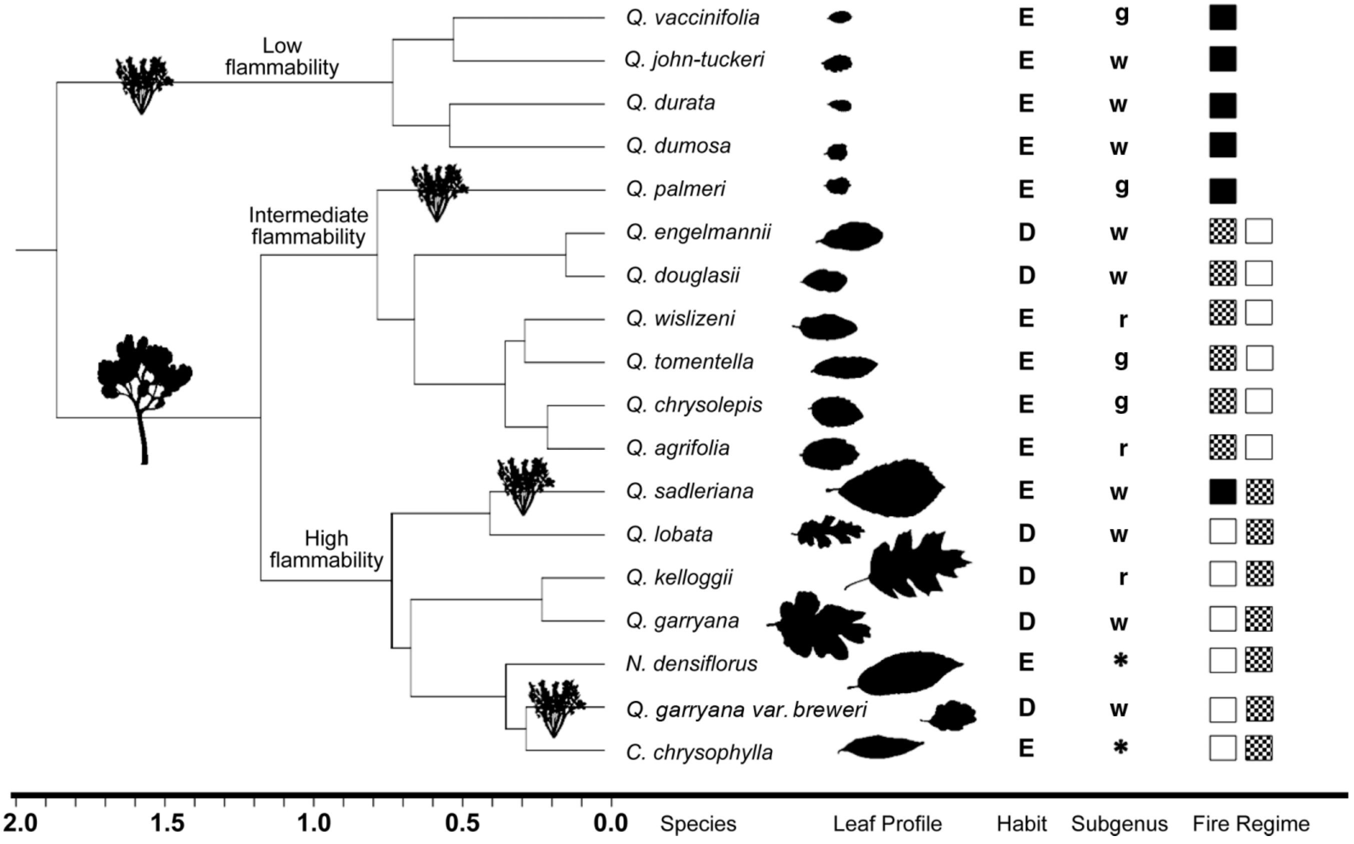
Fig. 2. Relationship between the first principal component of flammability (PCF1) and (A) the first principal component of foliar characteristics, (B) fuelbed depth (standardized), and (C) leaf perimeter (standardized).



Relationships between flammability clusters and categorical explanatory variables

The hierarchical clustering generated a dendrogram with three distinct flammability clusters for the 18 species (dissimilarity value of 1.00, cophenetic correlation coefficient of 0.80) (Fig. 3). The low-flammability cluster (four species) was characterized by evergreen shrubs with small, thick leaves that burned with small flames for a short duration and with little fuel consumption. All species in the low-flammability cluster are vigorous resprouters that typically burn in crown fires. The intermediate-flammability cluster (seven species) included a diverse mixture (all three subgenera represented) of six trees and one shrub (*Q. palmeri*). Of the intermediate oak cluster, all are evergreen except the drought-deciduous *Q. engelmannii* and the deciduous *Q. douglasii*. The uniting characteristic of the intermediate cluster is that the leaves are relatively small and thickened and their margins mostly entire, resulting in prolonged flaming and smoldering but intermediate flame height and mass loss. These species are also characterized by variable, mixed-severity fire regimes. The third cluster, repre-

Fig. 3. Hierarchical clustering dendrogram for flammability characteristics of 16 California oaks and two oak allies. Three clusters were identified at a dissimilarity value of 1.0 that are represented by the low-flammability cluster (four species), the intermediate-flammability cluster (seven species), and the high-flammability cluster (seven species). Leaf profiles are black and white images of actual leaves scaled to the mean length for each species. Habit refers to evergreen (E) or deciduous (D). Subgenera are represented by the letters "w" (white oaks), "r" (red oaks), and "g" (golden oaks). Three fire regimes are depicted including infrequent, high-severity (solid squares), mixed frequency and severity (checkered squares), and high-frequency, low-severity (open squares). Where two fire regimes are depicted, the first represents the more common followed by a less common second regime. Tree or shrub forms are denoted on the dendrogram.



senting the most flammable seven oaks, was typified by large, thin-leaved species that resulted in tall flames, substantial fuel consumption, and brief flaming and smoldering duration (an exception was *Q. sadleriana*, which flamed and smoldered longer than the others). This highly flammable cluster was primarily represented by tree-form oaks, with the two shrubs *Quercus garryana* var. *breweri* (Engelm.) Jeps. and *Q. sadleriana* included. The majority of deciduous (all except *Q. engelmannii* and *Q. douglasii*) and lobed (all except the shallowly lobed *Q. douglasii*) leaved oaks were categorized into the high-flammability cluster; these species are characterized for the most part by frequent, low-severity fire regimes. Within clusters, there was tremendous phylogenetic diversity, although several fine-scale clades grouped with like subgenera. Within the intermediate-flammability cluster, the deciduous white oaks *Q. engelmannii* and *Q. douglasii* grouped together, and three of the four golden oaks were also represented. Two white oaks, *Q. sadleriana* and *Q. lobata*, grouped together in the high-flammability cluster.

Litter from tree-form oaks burned with greater intensity (mean flame height: trees = 50.5 cm, shrubs = 33.4 cm) and consumability (mean mass loss: trees = 78.9%, shrubs = 59.4%) than the shrub-form oaks. *Quercus sadleriana*, and to a lesser extent *Q. garryana* var. *breweri*, are notable exceptions to this generalization; litter from these shrubs consistently burned similar to the tree-form oaks, in spite of their stature. In general, deciduous oaks were more flammable than evergreen oaks, except for the poor burning behavior of two deciduous species, *Q. engelmannii* (flame height = 23.3 cm, mass loss = 60.2%) and *Q. douglasii* (flame height = 21.7 cm, mass loss = 59.6%). Lobed leaves burned with marginally greater flammability than entire leaves, but this result was blurred by the substantial inter- and intraspecific variation in oak lobedness (e.g., *Q. douglasii* has a wavy, shallowly lobed margin). The fact that leaf perimeter was such a strong predictor underscores this idiosyncrasy.

Phylogenetic groups were characterized by substantial within-group heterogeneity in both foliar characteristics and subsequent fire behavior metrics and did not differ substantially in their flammability (Fig. 3). For example, the white oaks included the highly flammable deciduous lobed trees *Q. garryana* and *Q. lobata* as well as the poorly burning shrubs *Q. durata* and *Q. dumosa*. The red oaks included only trees (*Q. kelloggii*, *Q. agrifolia*, and *Q. wislizeni*), but these species varied substantially in their fire behavior (e.g., flame height = 83.0 cm for *Q. kelloggii* but only 39.9 cm for the related *Q. wislizeni*). The golden oaks included two shrubs (*Q. vaccinifolia* and *Q. palmeri*) and two trees (*Quercus tomentella* Engelm. and *Q. chrysolepis*), an assemblage characterized by heterogeneity in leaf morphology and burning characteristics.

Discussion

Primary gradients in flammability and leaf traits

The observed patterns of flammability in the California oaks suggest that leaf traits are a driving force of litter flammability, providing further evidence that community composition can affect fire behavior (Hiers et al. 2009). This finding is supported by field-based studies, for example, Schwilk and Caprio (2011) correlated community leaf length with fire severity in mixed-conifer forests of California. Less is understood regarding the mechanisms of plant flammability and how flammable traits relate to ecosystem processes such as fire regimes. Our work helps clarify the linkages among plant traits, flammability, and ecosystem processes by investigating the mechanisms of flammability on a suite of species that spans a diversity of fire regimes.

How flammable are the California oaks?

If we compare the litter flammability of California oaks with other North American species, including oaks (Kane et al. 2008) and conifers (Fonda et al. 1998; Fonda 2001) burned using similar methods, this suite of species spans a larger range in flammability. In comparison with southeastern US oaks, the range of values reported here for all flammability metrics was substantially broader. For example, flame height ranged from 33.6 to 81.4 cm for southeastern US oaks compared with 13.8–83.0 cm here. Similarly, fuelbed depth in the California oaks spanned a wider range (1.9–7.1 cm here but only 2.6–6.4 cm for southeastern species). The most flammable Californian species burned with similar intensity (flame height) as longleaf pine (*Pinus palustris* Mill.) in the southeastern United States and ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) in the western United States, two notably flammable fire-resistant conifers that prosper in low-severity fire regimes (Fonda 2001).

Past research has disaggregated flammability into multiple components (i.e., ignitability, combustibility, sustainability, and consumability; Anderson 1970) and mostly employed univariate statistical procedures to compare species and metrics (but see Curt et al. 2011; Ganteaume et al. 2011). Our results suggest that flammability variables can be combined into one or two principal component axes that retain their uniqueness and explain a large proportion of variation in burning characteristics and can used in subsequent analyses. Ganteaume et al. (2011) employed co-inertia analysis, a multivariate approach, to assess the effect of fuelbed composition on flammability. Their analysis explained only 34% of the variation in their flammability data set but clearly illustrated the multivariate nature of flammability. By examining species-level leaf morphological characteristics and burning single-species fuelbeds, we were able to explain substantial variation in both leaf morphology (92%) and leaf flammability (87%) with PCA. This analysis also identified the strongest drivers of each principal component, underscoring the importance of leaf morphological properties in litter flammability.

Drivers of flammability

Individual leaf characteristics and fuelbed depth were tightly linked to flammability in the California oaks. Alone, fuelbed depth explained more variation in the first principal component of flammability than did the first principal component of foliar characteristics. Larger, more curled leaves likely reduce fuelbed bulk density by creating air spaces among fuel particles. Others have found leaf length important (Schwilk and Caprio 2011), and fuelbed bulk density is well recognized as a primary driver of fire spread (Rothermel 1972; Scarff and Westoby 2006; Kane et al. 2008; Ganteaume et al. 2011). Oak leaf thickness and surface area to volume ratio were only weakly related to flammability, but these variables may be more closely related to ignitability (Montgomery and Cheo 1971), which was not measured here. Leaf margin was likewise uninformative, although all of the lobed species were highly flammable. The presence of flammable unlobed species such as *Q. sadleriana*, *N. densiflorus*, and *C. chrysophylla* is evidence that lobing is not the only pathway to flammability. Leaf habit and margin were major determinants of flammability in southeastern US oaks (Kane et al. 2008), a difference likely confounded by the lack of large, curled, but unlobed species in the Kane et al. (2008) study.

Leaf chemical variation was not tested here, although it has been found to be important for other fire-linked genera (e.g., the volatile-rich *Pinus* species; Ormeño et al. 2009). Differences in the cellulose to lignin ratio have been shown to influence flammability (Rundel 1981), and inter- and intraspecific differences in these components have been documented for oaks (e.g., Castro-Díez et al. 1997). The influence of chemical variation on oak litter flammability should be investigated in future works, although we do show that leaf morphology is strongly related to oak litter flammability.

Relationships between flammability clusters and categorical explanatory variables

California's Mediterranean climate, complex topography, and wide range of bioregions result in a diversity of fire regimes where oaks prosper. Results of the hierarchical cluster analysis track these broad fire regime patterns by linking leaf flammability traits to fire regimes, with three clusters that fit within three dominant fire regimes: low severity (highly flammable), mixed severity (moderately flammable), and high severity (low flammability).

The oaks of the high-flammability cluster were dominated by three tree oaks (*Q. kelloggii*, *Q. garryana*, and *Q. lobata*) that fuel fast spreading, low- to moderate-intensity surface fires. These trees also have sparse, deciduous crowns that transmit substantial light to surface herbaceous fuels that sustain surface fires in savannas and woodlands common to the region (Engber et al. 2011). The allied *N. densiflorus* and *C. chrysophylla* also support high-intensity flames, but these species tend to be forest trees, so their high flammability serves to increase local flammability within the region's mixed evergreen forests (*Pseudotsuga menziesii* (Mirb.) Franco, *Umbellularia californica* (Hook. & Arn.) Nutt., *Arbutus menziesii* Pursh, and *Pinus* species; Stuart and Stephens 2006) that burn with considerably less frequency than open oak woodlands and savannas. Trees in the high-flammability cluster dominate in low-severity fire regimes, although portions of each species' range may occupy areas of mixed-severity fire regime (Fig. 3). For example, two oaks within this cluster (*Q. sadleriana* and *Q. garryana* var. *breweri*) are shrubs, but their litter burns in stark contrast with other fire-impeding shrub oaks. *Quercus garryana* var. *breweri* burns as expected; its stature and leaves are diminutive forms of *Q. garryana*, a fire-facilitating tree. *Quercus sadleriana*, on the other hand, is enigmatic: it is variously considered a shade-tolerant understory oak (Stuart and Sawyer 2001), a species that is extirpated in frequent fires (Donato et al. 2009) or a species that thrives following stand-replacing fire (J.M. Varner, personal observation). Aside from these two shrubs, species in the high-flammability cluster maintain flammable leaf litter traits that contribute to low-severity, high-frequency fire regimes in the region.

The intermediate oak cluster was comprised of a taxonomically diverse group, but a group that could be termed the “live oaks” that have characteristic spreading crowns that tolerate surface fires but typically suffer greater top-kill mortality in mixed-severity fires than the fire-facilitating high-flammability cluster. For example, the widely distributed *Q. chrysolepis* has been reported to be easily top-killed by fire (Plumb and Gomez 1983) and also to survive low-intensity prescribed fires (Paysen and Narog 1993). The live oaks typically dominate in woodland environments, cast greater shade than the deciduous oaks, thereby suppressing understory herbaceous fuels, and impede fire within their vicinity. Notable exceptions to this pattern include the semideciduous *Q. englemannii* and deciduous *Q. douglasii* and the shrub *Q. palmeri*. The two deciduous oaks burn with less intensity than their white oak congeners *Q. lobata* and *Q. garryana* but tend to dominate edges bordering crown-fire-prone chaparral communities (Pavlik et al. 1991). *Quercus palmeri* was marginally grouped with this cluster; its burning characteristics were generally more flammable than the low-flammability shrub cluster, although it shares a similar infrequent, high-severity fire regime.

The low-flammability shrub cluster is the clearest of the groupings generated. All four species in this cluster are evergreen shrubs with small, thick leaves with unlobed margins. Ecosystems where these species grow typically burn with stand-replacing canopy fires, and these shrubs can endure fires via vigorous resprouting (Keeley 2006). Litter from the shrub oaks generally burned poorly, but as a part of a crown or canopy, their flammability would be increased because oxygen limitation would no longer be a factor. As with other fire-impeding species (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg., *Pinus contorta* Douglas ex Loudon, and *Pinus banksiana* Lamb.), these species tend to support low-intensity, low-consumption litter fires under moderate fire weather conditions (Fonda 2001). In extreme fire weather, this impeding litter becomes less important than the high winds, low humidities, and elevated air temperatures that facilitate high-intensity surface fire that can ignite and spread through living crowns or continuous canopy strata. Species with low-flammability litter may in fact have flammable stem and crown structures that facilitate canopy fire spread (Schwilk 2003; Scarff and Westoby 2006), concurrent with these species’ fire regimes.

At the subgeneric level, related species were highly variable in leaf morphology and flammability, suggesting a limited role of phylogeny as a driver of flammability in the California oaks. Phylogenetic trends may have been limited due to the low number of species within subgenera, and future work on a greater diversity of oaks across North America will enable us to test these same factors across a broader phylogenetic spectrum.

The clusters generated here could be further refined to incorporate other fire adaptations. Other trait-based work has evaluated bark thickness (Jackson et al. 1999), bark injury and recovery (Romero et al. 2009), growth rate (Keeley and Zedler 1998), and other physiological traits (Cavender-Bares et al. 2004) as they relate to fire regimes. Flammability data sets should be developed to include these fire-linked traits in a more holistic analysis to increase our understanding of the linkages among plant traits, plant ecological strategies, and ecosystem processes in fire-prone environments.

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