

Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest

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Summary

1. Although it is recognized that plant species vary in their flammability, we currently lack a mechanistic understanding of how plant traits influence fire and how litter mixtures behave in a fire. As modified fire regimes and climate change shift the species composition of communities, a mechanistic perspective is especially important to understand and predict fire in potentially novel plant communities. This work addresses three questions: (i) How do eight species common in Sierra Nevada mixed-conifer forest differ in their litter flammability? (ii) What leaf traits are associated with various flammability components? and (iii) Do individual species measurements predict multi-species combinations, or are there non-additive effects?
2. Leaf litter was collected in Sequoia and Kings Canyon National Parks, California, from eight dominant tree species in mixed-conifer forest. Controlled flammability tests were performed on reconstructed monospecific litter beds and on mixed litter beds, using litter from three species. We tested for non-additive effects in multi-species mixtures using the weighted mean of single-species measures for each flammability component as a null expectation for each mixture; departures from this null indicated non-additive effects.
3. Most flammability components fell within two major axes of variation, one relating to total heat release and another to fire intensity. The eight species differed significantly in all flammability components, with large-leaved species creating litter that burned with higher intensity.
4. Non-additive species mixture effects are common in this system. Flammability tends to be driven by the most flammable component of the mixture.
5. *Synthesis.* We have demonstrated positive non-additive effects in mixtures of leaf litter. The most flammable constituent species of a mixture has disproportionate effects on the fire environment faced by the entire community. This could potentially influence community assembly and alter the selective environment faced by co-occurring species.

Key-words: determinants of plant community diversity and structure, flammability, leaf litter, mixed-conifer forest, non-additivity, plant traits, species interactions

Introduction

Fire is a powerful ecological phenomenon shaping vegetation distribution and structure across many biomes. Plants may influence the nature of fire and can vary widely in their flammability, even within the same climate. Different vegetation types will differ in their contribution to fuel continuity and to total fuel load (Van Wilgen, Higgins & Bellstedt 1990; Scarff & Westoby 2006), and this diversity in vegetation composition substantially modifies fire regimes (D'Antonio & Vitousek 1992; Beaty & Taylor 2001; Bekker & Taylor 2001; Brooks *et al.* 2004). Although work has begun to characterize the flammability of particular species (Trabaud 1976; Scarff & Westoby 2006; Kane, Morgan Varner & Hiers 2008; Pausas

et al. 2012), fuels in natural systems often comprise material from many species. The effect of species composition on fire behaviour and how potential interactions among species traits might influence flammability have only recently begun to be examined (Schwilk & Caprio 2011).

Flammability has been suggested as a 'niche constructing' trait (Laland, Odling-Smee & Feldman 1999) that would increase the risk of mortality of neighbouring plants and thus clear gaps that would favour fire-prone species (Mutch 1970; Bond & Midgley 1995). Whether plant traits influence flammability and, in turn, evolutionary processes is controversial (Snyder 1984; Troumbis & Trabaud 1989; Schwilk & Kerr 2002; Gagnon *et al.* 2010). Despite such controversy, there is increasing evidence that trait differences can influence local fire behaviour (Schwilk 2003; Schwilk & Caprio 2011). The flammability of a plant depends on the composition and

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architecture of its tissues (Cornelissen *et al.* 2003). Fires can burn through plant canopies (crown fires) or through litter on the surface (surface fires) – although surface fire can include fires in forests that consume both litter and small stature plants. Traits that have been linked to the flammability of plant canopies include the retention of dead branches (Bond & Midgley 1995; Schwilk & Ackerly 2001; Schwilk 2003), the retention of dead leaves (He, Lamont & Downes 2011), small leaves and branches (Bond & Midgley 1995; Schwilk & Ackerly 2001), leaf chemical composition (Mutch & Philpot 1970; Philpot 1970, Philpot 1977; Alessio *et al.* 2008a,b) and leaf moisture content (Mutch & Philpot 1970; Alessio *et al.* 2008a,b). Traits thought to influence the flammability of leaf litter include leaf size and shape, which affect litter packing and therefore oxygen availability for combustion (Rundel 1981; Scarff & Westoby 2006; Kane, Morgan Varner & Hiers 2008; Schwilk & Caprio 2011), as well as leaf chemical composition (Ormeño *et al.* 2009). Leaf traits vary greatly across species, and they are an indication of a species' ecological and 'economic' growth strategy (Wright *et al.* 2004). In some cases, these structural traits are carried through to the senescence phase, having an afterlife effect in the leaf litter (Cornwell *et al.* 2008) and possibly on flammability as well.

Litter is an important surface fuel in many seasonally dry forest systems (van Wagtenonk & Moore 2010). Past research has demonstrated that litter bulk density is an important factor driving differences in flammability in such systems (van Wagtenonk, Benedict & Sydoriak 1998; Stephens, Finney & Schantz 2004). A trait that influences bulk density and therefore fire behaviour is leaf size: larger leaves result in a less dense fuel bed, which in turn increases oxygen availability and heat diffusion (Scarff & Westoby 2006; Kane, Morgan Varner & Hiers 2008; Schwilk & Caprio 2011). Of course, litter density is influenced not only by leaf size, but also by leaf shape and, importantly, by decomposition rate. Decomposition rates vary both according to site characteristics such as temperature and moisture and according to the physical and chemical characteristics of the leaf litter (Swift, Heal & Anderson 1979; Cornelissen 1996; Cornwell *et al.* 2008), but the trait effect is stronger than the environmental one and leaf economic traits are the primary predictor of decomposition rate (Cornwell *et al.* 2008).

Research on plant traits that may influence litter flammability has taken two different approaches. Many studies have investigated species-specific flammability measurements on multiple species from a community and linked individual species' flammability to plant traits (Trabaud 1976; Fonda, Belanger & Burley 1998; Scarff & Westoby 2006; Kane, Morgan Varner & Hiers 2008). Other studies have measured field-collected multi-species mixtures (Ganteaume *et al.* 2009; Curt *et al.* 2011). The possibility of flammability interactions in species mixtures, however, has yet to be examined. It is possible that multi-species mixtures may exhibit non-additive effects: the flammability of mixtures may not be predicted by the average effects of the mixture's constituent species. Such non-additive effects have been reported for plant litter decomposition (Hättenschwiler, Tiunov & Scheu 2005). Non-additive effects

have implications for our understanding of community composition and community-scale processes. There may be flammability thresholds in non-additivity: for example, if the flammability of a mixture is driven by the most flammable species, then less flammable species face an environment constructed by potential competitors even when those competitors are relatively rare. Positive non-additivity in flammability would make feedback effects of flammability on community assembly and on evolutionary trajectories more likely (Kerr *et al.* 1999; Schwilk & Kerr 2002).

Understanding the flammability of multi-species mixtures and exploring possible non-additive effects is especially important as species composition continues to change in many fire-prone plant communities. Changing management and changing fire regimes are shifting species composition in some communities, and such shifts may have implications for future fire behaviour (Barbour *et al.* 2002; Schwilk & Caprio 2011). Furthermore, the potential for climate change to produce future novel species assemblages is strong (Williams & Jackson 2007). A better mechanistic understanding of mixture effects on flammability may improve our ability to manage fire in such novel communities beyond our current understanding, which is based on broad categorizations of static vegetation types as fuel.

Although most flammability evaluation has focused on spread rate and flame length as proxies for fireline intensity (Rothermel & Deeming 1980; Agee 1996), other parameters, such as fire duration and total heat release, are important in predicting biological effects of fire (Gagnon *et al.* 2010). Spread rate, maximum flame height (combustibility), time to ignition (ignitability), sustainability, percentage mass loss (consumability), duration of combustion and heat release are standard flammability measures found in the literature (Anderson 1970). It is important to measure multiple components of flammability, as not all of these measures are positively correlated. For example, although fast flame spread and long combustion duration might both be considered high flammability, these parameters are often negatively correlated – a fast moving fire may have high intensity and consume above-ground material but cause little soil heating (Gagnon *et al.* 2010). Plant tissue mortality is largely attributed to high heat killing cambium and perhaps destroying xylem tissue as well (Bond & van Wilgen 1996) and tissue temperatures depend upon the temperature the fire reached and its duration (Wright & Bailey 1982).

The mixed-conifer forests of California historically experienced frequent, low-severity surface fires fuelled by leaf and wood litter (Swetnam & Baisan 2003) and such fires were essential to the maintenance of community structure (Knapp *et al.* 2007). These forests include species that produce very different litter, and bulk density measurements suggest that these species should have different flammabilities (van Wagtenonk, Benedict & Sydoriak 1998). Fire exclusion beginning in the late 19th century, however, drastically altered species composition of these forests by favouring shade-tolerant species over fire-dependent shade-intolerant species. Recent work has shown that such changes in species composition at fairly small scales

within this landscape can influence local fire behaviour by changing the distribution of short- vs. long-leaved species (Schwilk & Caprio 2011). As managers re-introduce fire to this system, they shift species composition back towards longer-leaved species and may create more flammable litter fuels. Understanding how species mixtures influence the flammability of these forests can provide an insight into the structure and assembly of these communities, and how their constituent species interact. This information can then be applied in modelling for future conditions and assist in future forest management.

We examined the litter flammability of the eight dominant tree species of a temperate forest in the Sierra Nevada Mountains of California, USA, and investigated how leaf traits influence different flammability characteristics. By measuring flammability parameters both in single-species litter beds and in litter beds comprised of all possible three-species combinations of the eight species, we were able to characterize how those mixtures burn and examine possible non-additive mixture effects. Given the influence bulk density has on flammability, we expect that leaf size will be a factor determining the flammability of litter beds, with larger or longer-leaved species having higher flammability. We asked whether the flammability of mixtures is disproportionately influenced by the most flammable constituent species: in other words, is the flammability of multi-species mixtures higher than that predicted by a simple average of the species comprising the mixture?

Materials and methods

The study was conducted in the mixed-conifer forests of Sequoia and Kings Canyon National Parks, California, USA (36°36'N, 118°42'W), between 1600 and 2400 m elevation. Leaf litter material was collected during summer (mid-June to mid-July) 2010 from eight tree species: *Pinus jeffreyi* Grev. & Balf., *P. lambertiana* Dougl., *P. ponderosa* Dougl. ex Laws., *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., *A. magnifica* A. Murr., *Calocedrus decurrens* (Torr.) Florin, *Quercus kelloggii* Newb. and *Sequoiadendron giganteum* (Lindl.) J. Buchholz. These species were chosen because they are representative of the mixed-conifer forest in the parks and constitute the dominant overstorey species found across the elevational range of the study area. In this study, leaf litter refers to the superficial layer of the forest floor composed of mostly undecomposed leaves from this year's and the previous year's leaf fall, and small twigs < 0.625 cm (1-h fuels, Pyne, Andrews & Laven 1996). We collected from 21 different sites across the parks, with a minimum of four sites (=populations) per species, to capture potential spatial variation in litter traits within a species (see Table S1 in Supporting information). Due to logistical constraints and occurrence, *A. magnifica* litter was collected from only one location but collection still included variation across 10 individuals. At each site, litter was collected from 2–4 individual trees at least 10 m apart. To obtain more uniform fuel samples representative of the forest floor, we gathered litter at *c.* 2 m from the individual tree chosen to avoid sampling bark and twigs, which tend to fall closer to the trunk. This was performed because we were interested in assessing the flammability of uniform 1-h fuels. Bark and twigs are denser and have higher residence time, which changes flammability. After being brought back to the lab, the material was dried for 48 h at

60 °C to bring the relative humidity to levels < 5% for all samples. This allows us to control for different moisture retention capabilities of the different species, which would become a confounding factor in the analysis.

TRAIT DATA

The leaf trait data for all the species in this study were collected in the summer of 2009 across the natural elevation range for each species in the study area and included all the sites we collected samples from in 2010. This was performed by sampling 8–20 individuals per species (using three leaves or needles per individual) across 43 plots stratified across elevations and aspects. We measured leaf length and area using a flatbed scanner and calculated specific leaf area (SLA). For detailed methodology, see Schwilk & Caprio (2011).

FLAMMABILITY TESTS

The flammability tests were performed both on monospecific litter beds and in litter beds composed of mixtures of litter from three different species at a time (each species accounting for a third of the total mass). The eight species were used in 55 litter arrangements (eight single-species tests and 47 different combinations of three species, see Table S2), replicated 3–5 times, bringing the total number of experimental trials to 219. The number of combinations is lower than the total possible with all 56 possible mixtures. Unfortunately, due to limitations in the amount of material brought from the collection sites, it was impossible to burn five replicates of all mixtures. To encompass as much variability as possible, we decided to include the mixtures that offered the greatest range of leaf sizes in the mixture, balancing naturally existing and non-occurring mixtures.

The burn table was built to approximate a one-dimensional cross-section of a flaming front through a litter bed, with a minimum length that would allow steady-state flame spread and a minimum depth and width that permitted 'natural' fuel arrangement, thus creating a bulk density similar to that observed in the field. If the table was built too narrowly, the larger leaves would arrange themselves along the trough, an arrangement that would not be expected in the field. Nevertheless, these are recreated litter beds, and we did not expect to obtain a replica of a natural litter bed. We conducted a preliminary set of experiments with tables of different widths to determine the minimum width that did not influence the random arrangement of leaf litter by constraining leaf orientation. As a result, the width was set at 15 cm (results not shown). The litter for burn trials was placed in a 15 × 150 cm channel made of 0.3-mm steel sheeting 12 cm high, and it was closed at both ends with 6.5-mm grid wire cloth to hold the material in and still allow for ventilation and access for the ignition source. The thin steel sheeting was backed by 7-mm-thick ceramic insulation (McMaster-Carr, Los Angeles, CA, USA) surrounded by a wood frame. Ignition was provided by a propane torch, which can achieve a maximum adiabatic flame temperature of 1899 °C (<http://www.bernzomatic.com/products/fuel.aspx>). We visually assessed maximum flame height using two rulers positioned at 50 and 100 cm from the ignition end of the table. Temperature (in °C) was measured with K-type thermocouples connected to HOBO U12 dataloggers (Onset Corporation, Cape Cod, MA, USA) and placed at 50, 100 and 150 cm along the table. At each position, we placed three thermocouples, one at the bottom of the litter bed, one on its surface and one at 25 cm above the surface. In the data presented here, we chose to only consider the bottom thermocouple, as is the one that can give a more stable measurement of temperature, as well as being the one that better correlates with soil heating. Given the high correlation of

temperature measurements at 50 and 100 cm, we chose to average the values and use 75 cm as our reference. We established 100 °C as our temperature threshold since at this temperature we have already reached cellular death, and it is the temperature at which water evaporates. Temperature was recorded every second during each trial. For each burn trial, the height of the litter bed was measured at four points along the table and its average taken to calculate bed depth and from that litter bulk density.

We standardized the samples by mass, with each trial set at 450 g of leaf litter, which provides a large range of variation in litter depth, from 3 to 11 cm, mimicking the natural variation in the field. All weight measures were taken using a balance sensitive to 0.1 g (model XS16001L; Mettler Toledo, Columbus, OH, USA).

We determined such flammability parameters as ignitability, calculated as the time from moment of exposure to a heat source to production of flame; combustion time (sustainability), measured as the time flame was visible from ignition until fire extinction; spread rate, calculated as the ratio between the length of the burned surface and the residence time; maximal flame height (combustibility), calculated by means of marks on two stainless steel metre rulers, positioned at 50 and 100 cm along the table, taken as reference; and percentage of mass loss (consumability), calculated as the difference between fuel mass before and after flame extinction (Anderson 1970; Cornelissen *et al.* 2003; Ormeño *et al.* 2009). We measured duration above 100 °C, which is the length of time the fire burned hotter than 100 °C, temperature above 100 °C, which is the average temperature the fire burned at after it reached 100 °C, and temperature integration, which integrates duration of combustion and temperature above 100 °C and serves as a proxy for heat release.

A stopwatch was used to measure (i) time to ignition (ignitability, in s), which is the time it takes for the fuel to catch fire once exposed to the propane torch; (ii) time for the flaming front to reach the end of the table (rate of spread, in cm s⁻¹); and (iii) time until flames are extinguished (which, added to the previous, accounts for sustainability, in s).

The burn trials took place in a cement structure used to simulate house fires at the Fire Department of the City of Lubbock. This eliminated wind and helped regulate temperature and relative humidity. Temperature and relative humidity were measured every two hours using a Kestrel 3000 (Nielsen-Kellerman, Boothwyn, PA, USA) to examine possible covariates of flammability measures. The trials were conducted from 2 October 2010 to 9 December 2010, and 15–22 trials were conducted each day. No more than one replicate of a mixture type was burned on any day.

ANALYSES

We measured eight flammability parameters that were likely to co-vary, and therefore, flammability parameters were first studied using principal components analysis (PCA) to explore such covariance and to guide selection of key flammability parameters for further analyses (Mardia, Kent & Bibby 1979; 'prcomp' function, R Development Core Team 2011). We used analysis of variance (ANOVA) to test for species differences in each flammability parameter (using only the monoculture trials). We tested whether three leaf traits (leaf area, leaf length, SLA) predicted litter flammability and which had the strongest effects. To accomplish this, we explored three linear models for each flammability parameter with leaf traits as the explanatory variables with species as a random nesting factor. We then determined the strength of the effect based on the *P*-values.

We assessed non-additivity in mixtures by comparing the flammability parameters to a null model based on the average of the mono-

culture flammability values of the three individual species that made up a mixture. Under the null model, the expected difference between the measured parameter and the predicted one is zero. We tested for a significant departure from zero using a mixed effects linear model ('lme' function, from the 'nlme' package in R, Pinheiro *et al.* 2011). Such a departure was indicated by a significant intercept term in a model with the flammability parameter as the response variable and with mixture type as a random factor and with no fixed effects (Pinheiro *et al.* 2011). Spread rate, time to ignition and percentage mass loss were log-transformed to meet the assumption of normality of the linear models. We conducted an additional analysis of non-additivity in which the null expectation was the average flammability parameters weighted by volume rather than by mass to explore effects of weighting method on our results. We also used an additional method to predict expected litter density: the expected density of a mixture was calculated as the total mixture mass divided by the sum of the volumes of the constituent species – this null expectation assumes no physical mixing of particles.

To further explore which species drove the mixture effects studied above, we investigated the contribution of each individual species to the behaviour of a mixture. The average flammability contribution for each species in a mixture represents how close the behaviour of a mixture is to the behaviour of the species individually. To do this, we calculated an 'average effect in mixture' for each species across all mixtures. We averaged the differences between the observed value of a mixture and that of each of the three species contributing to it, for all species and all parameters under investigation. This provided us with an average value for each species for each parameter, which indicates the contribution of each species to a mixture. Values of low magnitude indicated that the species' flammability in monoculture was similar to that of mixtures in which it occurred.

The building eliminated wind, but air temperature and relative humidity were measured every two hours. Average temperature for the trials was 18.8 °C (±4.8), and average relative humidity 31.3% (±8.9). For each flammability parameter, we compared the main model to two additional models (one that included relative humidity and one that included temperature in addition to the main predictor of interest). We used Akaike's information criterion (Burnham & Anderson 2002) to determine whether including these climate covariates improved model fit (reduced AICc).

Results

Our reconstructed litter beds, despite using only upper layer undecomposed leaf litter, had bulk densities not too different than that reported for natural litter beds of many of these species. In general, our densities were about half the average (of a wide range) reported in the literature (See Table S3), but our values tended to be very close to those reported by Miller & Urban (1999). There was no effect of trial date, relative humidity or temperature on any results (model without climate covariates was always the highest ranked); therefore, we have reported further results ignoring these climate covariates and our random blocking eliminates bias.

SINGLE-SPECIES TRIALS

The eight species behaved differently in terms of flammability, but not consistently across all parameters (Table 1). The species with the shortest time to ignition were

Table 1. Average values of flammability parameters for the single-species tests (mean \pm standard deviation, $N = 5$)

Species	Time to ignition (s)	Sustainability (s)	Spread rate (cm s ⁻¹)	Percentage mass loss (%)	Maximum flame height (mm)	Temperature integration > 100 °C (°C min)
<i>Abies concolor</i>	1.9 ^c \pm 0.7	830.7 ^{cd} \pm 229.7	0.208 ^c \pm 0.066	94 ^a \pm 4.4	773.3 ^{bcd} \pm 161.6	2884.3 \pm 1375.4
<i>Abies magnifica</i>	3.1 ^{bc} \pm 0.8	1257.7 ^{bc} \pm 55.0	0.129 ^d \pm 0.006	96.7 ^a \pm 0.4	744 ^{cd} \pm 53.2	3810.7 \pm 284.0
<i>Calocedrus decurrens</i>	3.3 ^{bc} \pm 1.2	1532.6 ^{ab} \pm 383.2	0.109 ^d \pm 0.028	75 ^b \pm 12.9	516.7 ^e \pm 123.6	2948.8 \pm 1412.4
<i>Pinus jeffreyi</i>	2.7 ^{bc} \pm 0.9	487.5 ^d \pm 26.4	0.321 ^{ab} \pm 0.018	95.4 ^a \pm 0.5	1060 ^a \pm 48.5	2923 \pm 544.1
<i>Pinus lambertiana</i>	2.1 ^c \pm 1.1	690.3 ^d \pm 158.8	0.277 ^{bc} \pm 0.032	85.6 ^{ab} \pm 14.5	854 ^{abc} \pm 101.6	2783.7 \pm 660.7
<i>Pinus ponderosa</i>	7.1 ^a \pm 1.5	765.8 ^{cd} \pm 58.1	0.202 ^c \pm 0.015	96.8 ^a \pm 1.7	974 ^{ab} \pm 50.7	2893.7 \pm 972.3
<i>Quercus kelloggii</i>	1.2 ^c \pm 0.5	595.5 ^d \pm 288.1	0.438 ^a \pm 0.014	89.2 ^{ab} \pm 6.4	959 ^{abc} \pm 113.6	3612 \pm 314.8
<i>Sequoiadendron giganteum</i>	5.1 ^a \pm 3.5	1880.1 ^a \pm 558.7	0.091 ^d \pm 0.028	88.5 ^{ab} \pm 5.2	586 ^{de} \pm 127.8	3302.4 \pm 672.0
P-value	< 0.0001	< 0.0001	< 0.0001	0.0005	< 0.0001	0.5219
F-statistic, d.f.	8.2, 7	16.07, 7	43.55, 7	5.11, 7	16.69, 7	0.89, 7

Differences across species were tested using ANOVA, and the statistics for the full model are listed in the final two rows. Mean values sharing a superscript do not show a significant difference ($P < 0.05$) under Tukey's HSD test for all possible pairs of species (28). Spread rate was log-transformed to meet the assumptions of the model.

Q. kelloggii, *A. concolor*, *A. magnifica*, *C. decurrens*, *P. jeffreyi*, *P. lambertiana*, and the least were *P. ponderosa* and *S. giganteum*. Conversely, *S. giganteum* and *C. decurrens* had the highest sustainability (longest time of flaming combustion) and *Q. kelloggii*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa* and *A. concolor* were the fastest to burn. *Q. kelloggii* and *P. jeffreyi* were the species that showed fastest spread rate, in line with the result for sustainability, and *A. magnifica*, *S. giganteum* and *C. decurrens* took longer to burn. The tallest flames were produced by *P. jeffreyi*, *P. lambertiana*, *P. ponderosa* and *Q. kelloggii*. Highest mass loss was observed in *P. jeffreyi*, *P. ponderosa*, *A. magnifica*, and *A. concolor*. For temperature integration (°C min), which acts as a proxy for total energy release, the highest values belonged to *A. magnifica*, *Q. kelloggii* and *S. giganteum*.

We used PCA to explore the pattern of covariance among these variables (Fig. 1). The first two principal components accounted for 63.7% of the total variance: the first axis captures intensity-related measures (sustainability, maximum flame height and spread rate were the three parameters with highest axis loadings); and the second axis captures variables related to total heat release (temperature integration, duration above 100 °C and average temperature above 100 °C had the highest loadings). Only percentage mass loss and ignitability do not fall as clearly on these two-first principal components. In the case of ignitability, we believe this is due to the high variability within the data (CV = 63.5%) and our ignition method of propane torch is not ideal for testing ignitability. Based on the PCA (Fig. 1), we reduced the flammability parameters used in further analyses to spread rate, sustainability, flame height, duration above 100 °C and temperature integration above 100 °C, which represent three parameters from the first axis and two from the second.

Leaf size influenced bulk density and flammability: bulk density decreased with leaf area or leaf length. Leaf area (Fig. 2) was the best explanatory variable in regression analysis, followed by leaf length ($P < 0.0001$ and $P = 0.0007$, respectively). SLA showed no pattern for any of the flammability parameters studied. Spread rate had a positive relationship with leaf area, indicating that bigger leaves generate faster-moving fires ($P < 0.0001$). Sustainability exhibited a negative relationship with leaf area, meaning that larger-leaved species tend to have a lower residency time for the fire. Of the relationships studied, three of the five were significant ($P < 0.05$), including spread rate, sustainability and maximum flame height. Our data were dominated by needle-leaved species, and there-

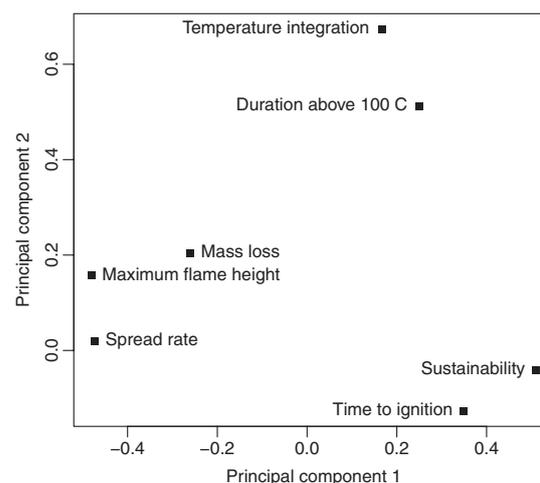


Fig. 1. Principal components analysis biplot of flammability parameters under study. Parameters are average temperature above 100 °C; degree minutes above 100 °C; duration above 100 °C; maximum flame height; percentage mass loss; time to ignition; flame spread rate; and sustainability. The first two principal components accounted for 63.7% of the total variance.

fore, leaf area was tightly correlated with leaf length. When we excluded the one broad-leaved species (*Q. kelloggii*), the results are similar but the significant P -values showed that leaf length rather than leaf area was the best predictor (e.g. for spread rate $P = 0.003$ vs. $P < 0.001$, see Tables S4 and S5).

MULTI-SPECIES MIXTURES

Across all 47 three-species mixtures, non-additive effects were very common. Of the five flammability parameters explored,

four showed significant departures from the null expectation (Table 2, Fig. 3), when mass was used as the weighting factor. In general, mixtures had higher flammability than expected. Only sustainability had a negative value, indicating that the mixtures had a lower duration of flaming combustion than predicted, consistent with the negative relationship between spread rate and sustainability in our data (Fig. 1). When we used volume rather than mass as the weighting factor for prediction, only spread rate lost significance. A positive value for the difference between observed and predicted spread rate, flame height, temperature integration and duration above

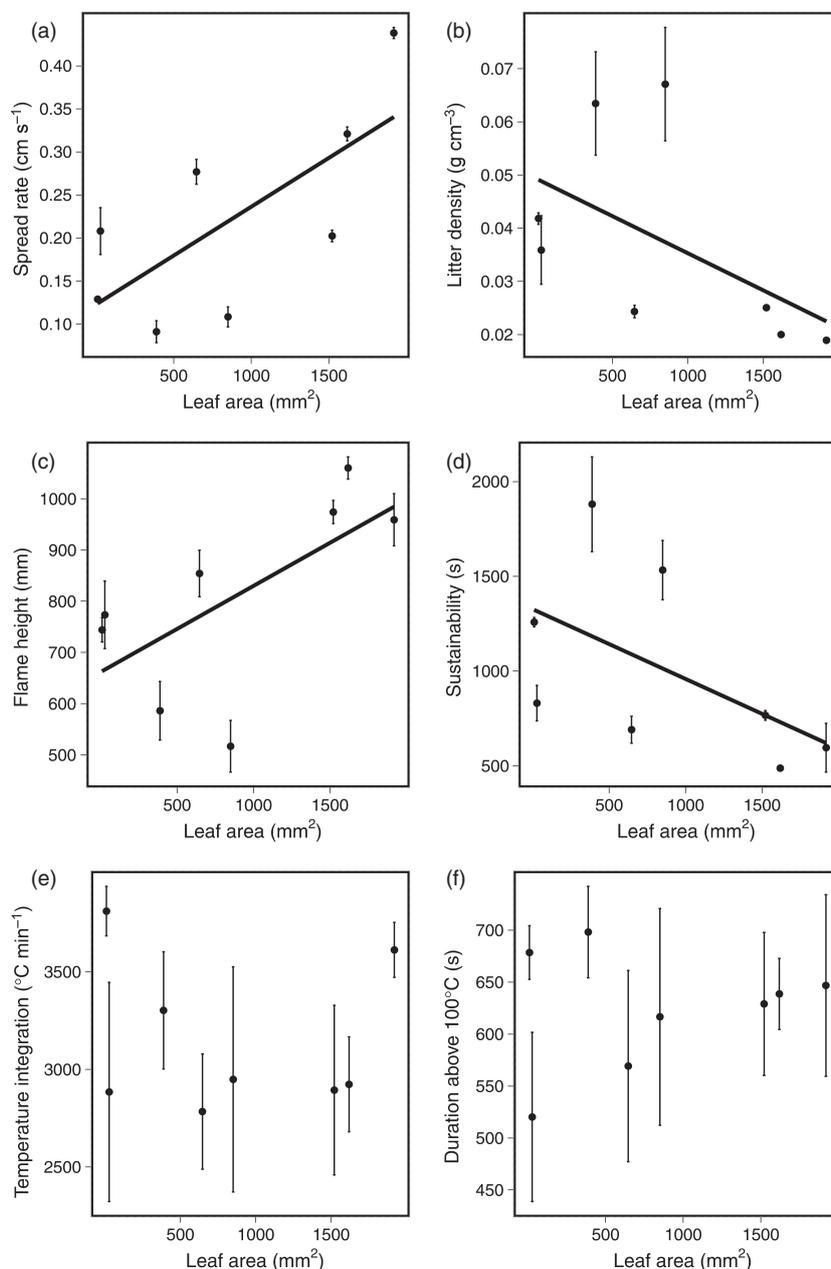


Fig. 2. Relationship between flammability parameters and leaf area across eight tree species. Lines indicate best fit linear models with species as a random nesting factor. a – spread rate ($P < 0.0001$, $r^2 = 0.383$), b – litter density ($P < 0.0001$, $r^2 = 0.266$), c – flame height ($P < 0.0001$, $r^2 = 0.352$), d – sustainability ($P < 0.0001$, $r^2 = 0.255$), e – temperature integration ($P = 0.637$, $r^2 = -0.014$) and f – duration above 100°C ($P = 0.261$, $r^2 = 0.005$). The bars indicate ± 1 standard deviation across trials within each species.

Table 2. Average non-additivity effect (difference between observed and predicted values) of six flammability parameters

Flammability parameter	By mass			By volume		
	Observed-predicted	Standard error	<i>P</i> -value	Observed-predicted	Standard error	<i>P</i> -value
Spread rate (cm s ⁻¹)*	0.387	0.034	<0.001	-0.006	0.005	0.268
Sustainability (s)†	-397.7	25.088	<0.001	-0.309	0.028	<0.001
Flame height (mm)	113.3	10.109	<0.001	-73.3	17.272	<0.001
Temperature integration (°C min)	128.8	69.651	0.067	-486.2	67.825	<0.001
Time above 100 °C (s)†	10.8	12.037	0.373	-0.18	0.024	<0.001
Bulk density (g cm ⁻³)†	-0.012	0.001	<0.001	-0.189	0.023	<0.001

Shown are differences relative to two alternative null models, one in which the predicted effect is based on a mass-weighted average and one in which the prediction is volume weighted. The symbols * and † denote parameters that were log-transformed to meet the assumptions of the model, for mass and volume, respectively. *P*-values are based on departures from the expectation of zero difference and were assessed with linear mixed effects models using mixture identity as a random effect and no fixed effect.

100 °C indicated higher flammability, whereas the negative value for the difference between observed and predicted for sustainability can be viewed both ways, depending on how flammability is approached. The longer a fire sustains itself in a given area, the more likely it is to cause harm to plant tissues. In this case, the negative non-additivity effect for sustainability signifies lower residency time and reduced flammability in mixtures than predicted.

The observed values of spread rate were significantly higher than the prediction of the null model (Fig. 3a, *P* < 0.001). Because litter density influences spread rate ('intensity axis', axis 1 in the PCA), the result shown on Fig. 3 for spread rate could be a result of a non-additive mixture effects on bulk density alone. Mixtures did have lower bulk density than was expected (*P* < 0.001, Table 2, Fig. 3b). However, when the data were separated into monocultures and mixtures, we observe that for any given value of bulk density, the mixtures exhibit higher spread rate than the monocultures (Fig. 4, *P* = 0.031). When non-additivity was assessed by comparing mixture results to a null model in which the prediction was an average weighted by species volume contributions (this effectively assumes no mixture effect on bulk density itself), non-additivity is present for all parameters except spread rate (Table 2).

We investigated the contribution of each individual species to the behaviour of a mixture ('average effect in mixture'). These eight species contribute very differently to the mixtures (Table 3). The smaller the absolute value is for a given species, the more that species dominates the flammability response of the mixtures in which it occurs. *Pinus lambertiana*, *P. jeffreyi*, *P. ponderosa* and *Q. kelloggii* had the smallest values for each flammability parameter, suggesting that these species drive the flammability of the mixtures in which they occur.

Discussion

Our results describing leaf trait effects on litter flammability are generally consistent with other experimental studies (Scarff

& Westoby 2006; Kane, Morgan Varner & Hiers 2008). Larger or longer-leaved species (*Q. kelloggii*, *P. jeffreyi*, *P. ponderosa*) have higher flammability values across most flammability parameters. In general, these species ignite quicker, burn faster, hotter and produce taller flames. To the extent that higher intensity and faster spread are considered 'more flammable', (Rothermel 1972) our results demonstrate that larger leaves create more flammable litter. Interestingly, SLA, an important trait in the leaf economic spectrum (Wright *et al.* 2004), appears unrelated to flammability in our study. Our results suggest that leaf size, rather than leaf economic traits correlated with SLA, influences litter flammability. On the other hand, total heat release and heating duration are important for heat transfer to plant tissue and soil heating (Miller 2000), and these parameters are not well-predicted by the traits we measured. Recently, Gagnon *et al.* (2010) have argued that the negative effects of duration and heating may have driven the evolution of traits that increase spread rate. The heat release parameters such as duration, temperature integration and mass consumed were not correlated with spread rate nor leaf size, and it may be that heat release and consumption is driven by unmeasured chemical differences among species. Recent work in Mediterranean shrubs has demonstrated population level differences in temperature integration/heat release that appear to be chemical in origin (Pausas *et al.* 2012). Spread rate and sustainability, despite both being previously used to describe flammability (Anderson 1970), are inversely related, partially as a mathematical result of their definitions. It is possible in theory, however, for a fuel to have a fast flame spread rate followed by lingering flaming combustion and therefore a high sustainability. In our data, despite some continued flaming combustion following the passage of the flame front, these two measurements were strongly inversely correlated. This issue has been tangentially addressed by Gagnon *et al.* (2010) who, while accepting spread rate as a good definition of flammability, argued that fast spread and therefore low sustainability would be beneficial to plants.

This paper's novel contribution is the demonstration of non-additive mixture effects. Although non-additive effects

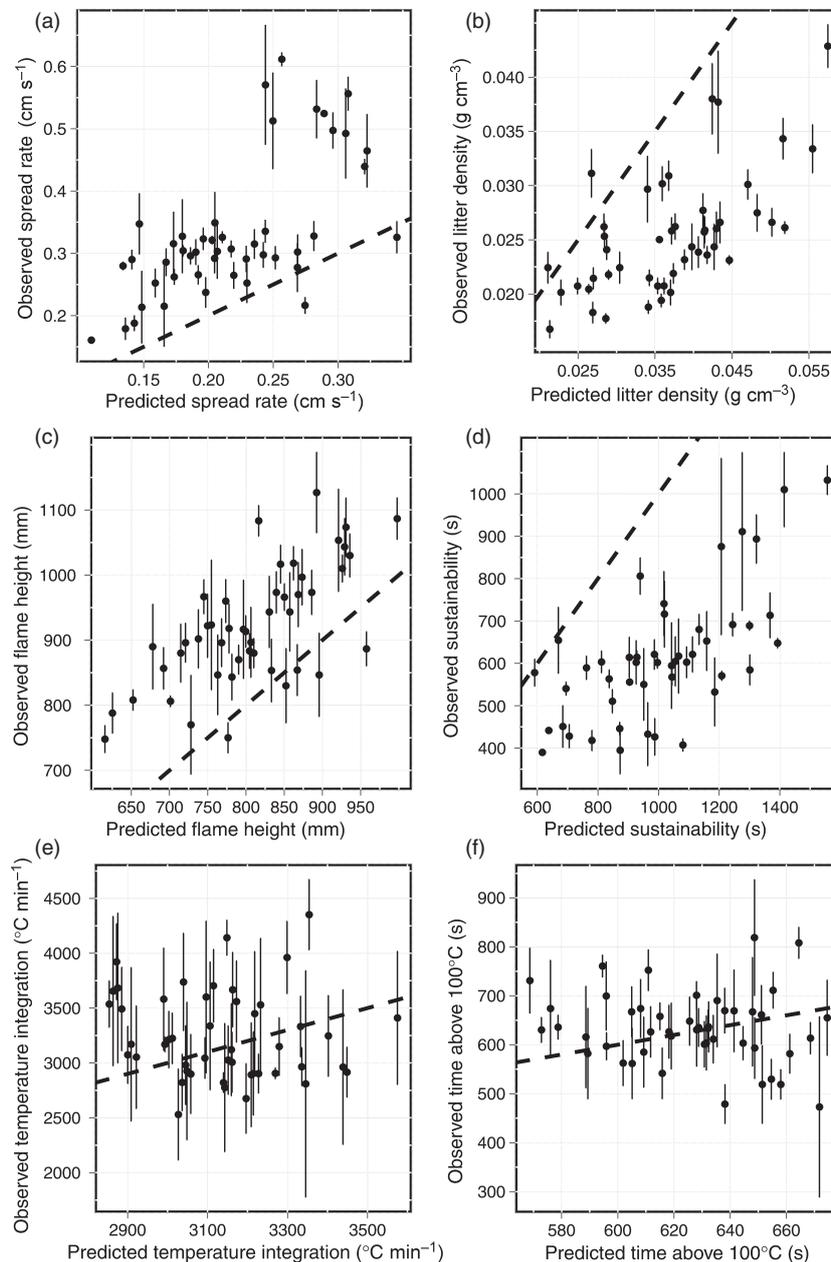


Fig. 3. Observed vs. expected flammability parameters and litter bulk density. The dashed line is the 1:1 line (the null expectation). a – spread rate ($P < 0.0001$), b – litter density ($P < 0.0001$), c – flame height ($P < 0.0001$), d – sustainability ($P < 0.0001$), e – temperature integration ($P = 0.067$) and f – duration above $100\text{ }^{\circ}\text{C}$ ($P = 0.373$). These P -values represent the probability of the data if the null model is correct. Each point represents the average flammability parameter value for all trials of a particular mixture composition ($N = 3\text{--}5$), and bars indicate \pm standard deviation.

have been reported for litter decomposition, to our knowledge, no study has examined possible non-additive mixture effects in litter flammability. Our results demonstrate that non-additive species mixture effects are common in this system (Fig. 3). Unlike reported non-additivity in litter decomposition rates where interactions among species produce idiosyncratic effects in mixtures (Gartner & Cardon 2004; Hättenschwiler, Tiunov & Scheu 2005), interactions in this system were highly consistent across mixtures: flammability was driven by the species with the fastest flame spread rates and tallest flames.

Spread rate was highly correlated with leaf size and litter density. Therefore, one possible explanation for the non-additive effect on spread rate was that litter packing behaves non-additively. Although mixtures were less dense than predicted (Table 2, Fig 3b), this difference did not completely explain the non-additive effect on spread rate because at any given bulk density, the mixtures had faster spread rates than the individual species trials (Fig. 4). This suggests that species-specific differences other than those that affect litter density contribute to flammability and that these effects are also driven primarily by the most flammable species in a mixture. Further

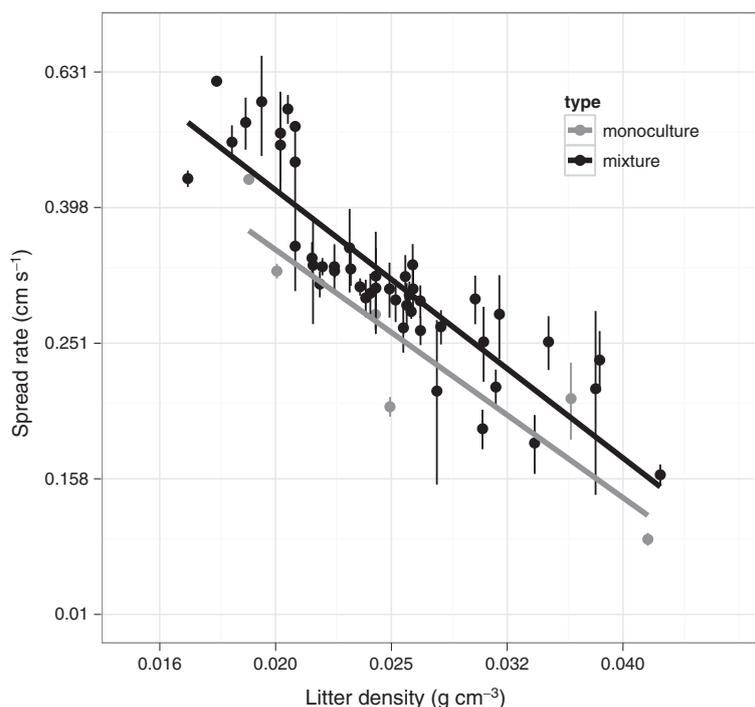


Fig. 4. Spread rate relative to litter density of mixtures vs. single species. The black line is the best fit line for a subset of the data concerning only mixtures, and the grey line is the best fit line for the monocultures. The behaviour of the mixtures is significantly different from that of the monocultures (significant difference in elevation in a mixed effect model with density as covariate, $P = 0.031$).

work is necessary to determine what these other traits might be, but mineral content/silica (Mutch & Philpot 1970; Philpot 1970) and volatile content (Scarff & Westoby 2006; Alessio *et al.* 2008a,b; Ormeño *et al.* 2009) have been suggested as chemical contributors to flammability.

The individual species contribute differently to the mixtures they comprise (Table 3), and the species with the apparently strongest effects on flammability were *P. jeffreyi*, *P. lambertiana*, *P. ponderosa* and *Q. kelloggii*: these were the species that had smaller difference between their flammability alone and in a mixture. These species are all larger-leaved species, which we had hypothesized would be driving the flammability of the mixtures. This effect might be due to the contribution bigger

leaves make to the physical arrangement of the particles, leading to an increased aeration.

Our work examined the mostly undecomposed upper litter layer. Species differ significantly in decomposition rates and therefore original green leaf size does not necessarily predict litter particle size. Our experiment was conducted for dry litter; the extent to which these patterns change with moisture is unknown and deserves further investigation. A remaining question is how moisture of extinction (Rothermel 1972) behaves in mixtures as opposed to monoculture? The role of drying rates and moisture still needs to be examined. Laboratory-based flammability measurements, however, are imperfect. These experiments might not be entirely representa-

Table 3. Average flammability contribution for each species in a mixture. This represents, on average, how close the behaviour of a mixture is to the behaviour of the individual species, and it is calculated as the average difference of a flammability parameter between a species and all the mixtures to which that species contributes.

	<i>Abies concolor</i>	<i>Abies magnifica</i>	<i>Calocedrus decurrens</i>	<i>Pinus jeffreyi</i>	<i>Pinus lambertiana</i>	<i>Pinus ponderosa</i>	<i>Quercus kelloggii</i>	<i>Sequoiadendron giganteum</i>
Sustainability (s)	-174.9	-617.0	-851.8	74.2	-59.7	-224.2	-100.4	-1194.0
Spread rate (cm s ⁻¹)	0.093	0.180	0.189	0.032	0.032	0.167	0.004	0.201
Flame height (mm)	136.7	170.7	376.2	-100.3	27.5	-8.5	19.1	289.7
Temperature integration (°C min)	322.4	-568.1	394.3	248.2	702.9	253.5	-449.9	-65.9
Duration > 100 °C (s)	108.3	-58.9	50.6	-22.2	100.8	-19.6	-46.6	-49.5
Temperature > 100 °C (°C)	-3.9	-21.5	18.8	36.4	-1.6	36.5	-37.4	15.0
Bulk density (g cm ⁻³)	-0.009	-0.016	-0.040	0.003	0.003	-0.003	0.003	-0.036

In bold are the smallest absolute values within each flammability parameter.

tive of ecosystems in which fire is driven by surface litter, yet there remains the possibility of fire spreading to shrubs (Plucinski & Anderson 2008). Furthermore, because we were dealing with manipulated fuel beds, some of these parameters, especially those such as sustainability which might depend upon denser lower, more decomposed, litter layers that we exclude, will not exactly mimic fire behaviour in the field (Fernandes *et al.* 2008). Natural fuel beds are not homogeneous or continuous, (Albini 1976) and reconstructed litter beds sacrifice some realism.

The positive non-additive effects we demonstrate have potentially strong consequences for community assembly. If litter flammability is driven largely by the most flammable constituent species, then those species will have disproportionate effects on the fire environment faced by all members of the community. This may lead to evolutionary pressures as well. Fire is an ancient ecosystem process (Scott 2000; Glasspool, Edwards & Axe 2004), which has been critical in shaping Sierran forests (Millar & Woolfenden 1999), and has been implicated in major past vegetation shifts (e.g. Keeley & Rundel 2005; Bond & Scott 2010). The potential for some species to influence the fire environment even when at relatively low abundances increases the likelihood of feedback effects on community assembly and on evolutionary trajectories (Kerr *et al.* 1999; Schwilk & Kerr 2002). We demonstrate one possible mechanism for species to influence the environment disproportionately to their abundance. If such flammability effects result in positive feedbacks (flammable species favoured by fire, e.g. 'the grass fire cycle,' D'Antonio & Vitousek 1992), then there could be strong consequences for vegetation change. In the Sierra Nevada mixed-conifer forest we studied, for example, increasing prescribed fire is shifting communities to larger-leaved pine species – a management goal. Such shifts, however, may result in faster spread rates and higher fire intensities than assumed under models based on current species composition (Schwilk & Caprio 2011). More generally, these results suggest that our current view of fuels as depending on broadly defined and static vegetation types should be modified to include dynamic communities, especially in view of climate change predictions on species composition and the likelihood of future novel communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Location of the general litter collection sites at Sequoia and Kings Canyon National Parks.

Table S2. Three species litter mixtures examined.

Table S3. Bulk density (g cm^{-3}) comparison between observed in the burn trials and values found in the literature for field measurements.

Table S4. Test of significance of the measured leaf traits in regards to the flammability parameters under study.

Table S5. Test of significance of the measured leaf traits in regards to the flammability parameters under study.

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