

Effects of fire radiative energy density dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality

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Abstract. Climate change is projected to exacerbate the intensity of heat waves and drought, leading to a greater incidence of large and high-intensity wildfires in forested ecosystems. Predicting responses of seedlings to such fires requires a process-based understanding of how the energy released during fires affects plant physiology and mortality. Understanding what fire ‘doses’ cause seedling mortality is important for maintaining grasslands or promoting establishment of desirable plant species. We conducted controlled laboratory combustion experiments on replicates of well-watered nursery-grown seedlings. We evaluated the growth, mortality and physiological response of *Larix occidentalis* and *Pinus contorta* seedlings to increasing fire radiative energy density (FRED) doses created using natural fuels with known combustion properties. We observed a general decline in the size and physiological performance of both species that scaled with increasing FRED dose, including decreases in leaf-level photosynthesis, seedling leaf area and diameter at root collar. Greater FRED dose increased the recovery time of chlorophyll fluorescence in the remaining needles. This study provides preliminary data on what level of FRED causes mortality in these two species, which can aid land managers in identifying strategies to maintain (or eliminate) woody seedlings of interest.

Additional keywords: carbon, FRED, intensity, photosynthesis, recovery, severity.

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Introduction

Anthropogenic climate change is projected to increase the incidence of heat waves, drought and fire danger (Allan and Soden 2008; Pechony and Shindell 2010; Dai 2013). These changes are broadly associated with projected increases in wildfire in many of the already fire-prone regions of the world, particularly at mid and high latitudes (Moritz *et al.* 2012; Knorr *et al.* 2016). A significant increase in fire activity over the western United States since the mid-1980s has been associated with anthropogenic climate change (Abatzoglou and Williams 2016). Projected changes in climate in this region will produce

conditions conducive to more lightning ignitions, greater area burned and an increasing occurrence of very large fires (Lutz *et al.* 2009a; Spracklen *et al.* 2009; Barbero *et al.* 2015; Sheehan *et al.* 2015), leading to ever more complex effects on firescapes (Smith *et al.* 2016a). These higher fire frequencies and higher severities associated with very large fires will likely cause a shift in forest demographics towards younger populations (Thompson *et al.* 2007; Lutz *et al.* 2009b; Chmura *et al.* 2011; Larson *et al.* 2013; Lutz 2015), a trend that will be exacerbated by higher non-fire mortality rates for trees (van Mantgem *et al.* 2009). This may lead to increased ecosystem vulnerability to

wildfire (Vaillant *et al.* 2016), including unexpected effects on seedlings and saplings that otherwise would have developed fire-resistant features, such as greater canopy height, increased bark thickness and deeper root systems (Bradstock and Myerscough 1988; Wade 1993; Smith *et al.* 2014). In many grassland and savanna systems, fire exclusion and in some cases the adaptation of fire-resistant woody plants has led to an increase in abundance of those species (Ansley *et al.* 2015). Consequently, small and frequent prescribed fires are often conducted to kill undesirable woody plants and thus promote the maintenance of grasslands and savanna ecosystems (Bachelet *et al.* 2000; Joubert *et al.* 2012). Equally, forests are often managed to promote the survival of desirable timber species. However, knowledge of the maximum heat dose that seedlings and saplings of various species can endure in wild or prescribed fires is not well understood (Battaglia *et al.* 2009).

It is widely accepted that plant mortality from fires will occur if critical plant components are sufficiently affected (Whelan 1995). Fires can consume live plant tissues and it is clear that extreme heat directly causes necrosis in plant tissues, phloem, roots, and foliage (Ducrey *et al.* 1996; Jones *et al.* 2006; Michaletz and Johnson 2007; Butler and Dickinson 2010). Likewise, it is well understood that as seedlings age, their canopy height, bark thickness and other structural elements often provide greater resistance to fire, decreasing their mortality (Bradstock and Myerscough 1988; Wade 1993; Ansley *et al.* 2015). Although a discussion of different approaches to predict tree mortality from fires is provided in the literature (Thies and Westlind 2012; Woolley *et al.* 2012), the majority of previous studies can be broadly described as observational and probabilistic. Some observational seedling studies assume a simplistic live/dead binary mortality response; namely, that the occurrence of fire or noticeable charring is assumed to cause mortality (Edwards and Krockenberger 2006). In contrast, observational studies in tropical forests have observed a range of mortality percentages across a wide variety of seedling species in response to low-intensity surface fires (Otterstrom and Schwartz 2006). Probabilistic approaches through the use of correlations or logistic regressions provide a likelihood of mortality but are mainly focused on mature trees and do not generally provide any information on fire-damaged living plants (Ryan and Reinhardt 1988; Battaglia *et al.* 2009; Joubert *et al.* 2012; Thies and Westlind 2012; Woolley *et al.* 2012). In some cases, these predictions are based on pre-fire data (Joubert *et al.* 2012).

More recently adopted mechanistic approaches to understand fire-related mortality through heat transfer and physiological processes provide likelihood of mortality and additional information on plant vigour (Michaletz and Johnson 2007; Kavanagh *et al.* 2010; Michaletz *et al.* 2012; Smith *et al.* 2016b; Sparks *et al.* 2016). The position of the individual plants in this unaffected–mortality continuum effectively represents a descriptor of severity for that individual organism. As proposed by Smith *et al.* (2016b) the units of such a severity metric could consist of carbon or water physiology metrics (e.g. net photosynthesis or change in water potential) that are sensitive to this range of conditions. The applications of such mechanistic severity metrics can help overcome the limitations frequently highlighted with commonly applied methodologies (Roy *et al.* 2006; Lentile *et al.* 2009; Kolden *et al.* 2015b; Smith *et al.*

2016b). Recent studies have proposed the metric of fire radiative energy density (FRED, MJ m⁻²) as one pathway to characterise heat transfer ‘doses’ on seedlings and larger trees (Sparks *et al.* 2016; Smith *et al.* 2016b). As described in detail by Kremens *et al.* (2012) and Hudak *et al.* (2016), FRED is the integral of fire radiative flux density (FRFD, W m⁻²) that is time integrated from ignition to cessation of the fire. Maximum values of FRFD have been shown to relate to Byram’s fireline intensity and a wide array of studies have related total fire radiative energy to biomass consumed on a unit area basis (e.g. Wooster *et al.* 2005; Kremens *et al.* 2012; Smith *et al.* 2013). FRFD, FRED and related fire radiative power metrics are readily measurable using laboratory radiometers as well as from experimental towers (Kremens *et al.* 2010; Sparks *et al.* 2017), airborne sensors (Hudak *et al.* 2016) and satellite remote sensing data (Heward *et al.* 2013). Usage of maximum FRFD may lead to improved metrics to predict plant physiology response, especially given that maximum FRFD may relate to the degree of convective heat flux in mature tree canopies (Sparks *et al.* 2017). However, maximum FRFD relates to a single moment in time that is difficult to reproduce on demand, whereas exact FRED ‘doses’ can be easily replicated using fuelbeds with known combustion properties (Smith *et al.* 2013). In addition, the maximum FRFD signal can be obscured by canopy vegetation, leading to an underestimate or missed event (Mathews *et al.* 2016). FRED is also thought to be well correlated with the other heat transfer modes given that the fraction of the total energy that is released in the form of radiation is relatively constant, with most studies reporting proportions between 11.7 ± 2.4% and 17 ± 3% (Wooster *et al.* 2005; Freeborn *et al.* 2008; Kremens *et al.* 2012; Smith *et al.* 2013).

In a simplified prescribed fire experiment using two levels of litter fuel load as treatments, Huddle and Pallardy (1999) illustrated that increases in fuel load led to apparent decreased survival percentages in seedlings of three species (*Acer rubrum*, *Quercus rubra*, *Q. alba*). Ansley *et al.* (2015) showed that increasing fireline intensity (derived from flame length) led to general increases in mortality of *Prosopis glandulosa* seedlings within grass fires. However, Ansley *et al.* (2015) acknowledge that a challenge with flame-length-derived fireline intensity is that this measure is difficult to replicate as it varies with fuel bed structure, microclimate and topography (Alexander and Cruz 2012). A detailed review of logistic regression models to predict tree mortality is provided by Woolley *et al.* (2012). Early work by Ryan and Reinhardt (1988) and subsequently expanded by Hood *et al.* (2007) on large mature trees developed logistic regressions outlining how the probability of fire mortality increases as a function of crown damage, bark thickness and fireline intensity. Similar logistic regression approaches have also been applied to seedlings and saplings (e.g. Battaglia *et al.* 2009) but remain limited in their utility to evaluate post-fire plant conditions as they only provide a live/dead binary result through setting a mortality probability threshold value (usually 50%).

In terms of a mechanistic understanding, a detailed review of how fire affects and kills trees is presented in Michaletz and Johnson (2007). However, it is clear that fire can have variable effects on the survival and growth of individual plant species (Pearson *et al.* 1972; Dieterich and Swetnam 1984; Glitzenstein

et al. 1995; Rieske 2002; Sala *et al.* 2005), and that this alters population dynamics and community composition (Reich *et al.* 1990; Huddle and Pallardy 1996; Bond and Keeley 2005; Green *et al.* 2010; Wait and Aubrey 2014). Likewise, some broad patterns have emerged regarding the effects of fire on ecosystem processes such as soil biogeochemical cycling (Nave *et al.* 2011; Dijkstra and Adams 2015). However, many of the effects of fire on the processes that directly influence carbon cycling are completely (e.g. gross primary productivity) or partially (e.g. nitrogen cycling) a product of fire damage to plants, ranging from the combustion of foliage and fine roots to decreases in physiological function and plant mortality. Equally, the mechanistic understanding of seedling mortality and physiological function is not well understood. A review of young seedling physiology is presented in Johnson *et al.* (2011). Although we have improved our understanding of climate, vegetation dynamics and fire physics to better predict how climate change will affect the likelihood of fire and the resultant fire behaviour, we do not yet have the mechanistic understanding of fire effects on plant physiology needed to develop process models capable of predicting plant mortality or recovery following fire (Michaletz and Johnson 2007; Varner *et al.* 2009; Kavanagh *et al.* 2010; Michaletz *et al.* 2012).

In this study we seek to further the work conducted by Huddle and Pallardy (1999), Michaletz *et al.* (2012), and others by using repeatable doses of FRED to assess the effect of fire on seedling mortality and post-fire physiology of surviving seedlings. We evaluate two physiologically different conifer species as a first step to assess a general methodology.

Methods

Plant materials

A total of 72 seedlings – 36 western larch (*Larix occidentalis* Nutt.) and 36 lodgepole pine (*Pinus contorta* Douglas) were grown in an open-sided greenhouse at the University of Idaho's Center for Forest Nursery and Seedling Research in Moscow, Idaho. *L. occidentalis* is a deciduous conifer and *P. contorta* is an evergreen conifer. Seedlings were grown in 3.8-L pots through two and a half growing seasons under natural light conditions. The seedlings were cultivated using an adaptation of the Dumroese *et al.* (2009) protocol. Water and fertiliser solutions were acidified to a pH of 6.0 using phosphoric acid for the duration of nursery culture. Depending on the seedling growing phase, nutrient solutions of Peters® Professional Conifer Starter™, Grower™ or Finisher™ (The Scotts Co.) along with calcium nitrate and Soluble Trace Element Mix (STEM) were applied to seedlings. For both species, the seedlings at the time of the fire experiments averaged a height of ~0.6 m. Seedlings from each species were randomly divided into four groups of nine, tagged and kept in the greenhouse until the experimental burns were conducted. All seedlings were watered to field capacity 24 h before the experiment and every 48 h post-fire during the duration of the experiment to eliminate any influence of water availability on post-burn seedling recovery. Seedlings were returned to the greenhouse following the experiment. The experiment was a completely randomised design and pots were rearranged each week to minimise environmental variation associated with greenhouse bench position.

Replicated FRED doses

The burn experiments used four FRED dose treatments (unburned control, 0.40 MJ m⁻², 0.80 MJ m⁻² and 1.20 MJ m⁻²) designed to capture a range of surface fire behaviour. FRED doses were determined following the methods described in Smith *et al.* (2016b). These FRED doses were selected following an analysis of literature where we estimated a range of 0.14–1.5 MJ m⁻² for typical surface fires in grasslands, woodlands and pine savannas (Table 1) (Shea *et al.* 1996; Hély *et al.* 2003; Law *et al.* 2003; Wooster *et al.* 2005; Kremens *et al.* 2012; Hudak *et al.* 2016; Sparks *et al.* 2016). FRED doses were created by varying the fuel load of western white pine (*P. monticola*) needles (Smith *et al.* 2013) that had been pure oven dried to ~0% moisture content. Specifically, as described in Smith *et al.* (2016b) the combustion of such western white pine fuelbeds produces a mean consumption of 84 ± 6%, yielding a regression of FRED = 2.679 × pre-fire fuel load (kg).

Following Smith *et al.* (2016b), FRED was selected as the dose metric because (i) unlike maximum FRFD, conductive heat flux or convective heat flux, FRED doses are readily replicated by combusting fuel matrices of known properties (Smith *et al.* 2013), (ii) conduction measurements require thermal witness devices embedded both within the stem (at a set distance *L*) and on the surface, which for these small-stemmed seedlings (diameter ~1 cm) was considered too destructive, (iii) we assume that the proportion of FRED incident on the entire plant is constant (due to average branch geometries across the nine replicates), and (iv) that surface fires in similar fuel types occur over similar durations (Smith *et al.* 2016b). Further, use of heat transfer metrics like FRED is a considerable improvement over traditional fire behaviour metrics like fireline intensity, which can exhibit high variability within similar fuel treatments (Alexander and Cruz 2012). We acknowledge that other metrics, such as maximum FRFD or conductive heat flux actually incident on the plant stems or roots could provide a metric more directly related to the plant physiology effects. However, due to multiple factors including diameter of the seedling stems, occlusion of incoming energy by branches and foliage, convective drafts moving branches, and uncertainty due to the vertical placement of thermal witness devices (with respect to present canopy and branches), such measures are difficult to pre-plan, replicate and accurately measure.

Physiological response to FRED doses

Measurements of diameter at root collar (DRC) were taken on all seedlings from 2 h pre-burn to 4 weeks post-burn at 6-h intervals through the first two weeks and then subsequently at 12-h intervals. DRC is commonly used in lieu of diameter at breast height in small or multi-stemmed plants, or in plants where canopy foliage is near ground level. Percentage change from 2 h pre-fire was calculated to remove variation associated with each pre-fire seedling size. Water potential (fascicle for *P. contorta* and small branches for *L. occidentalis*) was measured at midday and predawn before the experiment and at 1, 4, 7, 14 and 28 days post-fire, as well as 3, 6 and 12 h post-fire using a Model 600 Pressure Chamber (PMS Instruments Co.). Water potential is a measure of the transpiration-induced negative pressure that exists inside the plant and is a metric of plant water

Table 1. Typical fire radiative energy density (FRED) values from surface fires derived using inverse modelling and direct measures using *in situ* towers

FRED is estimated as product of fuel load per square metre, percentage fuel consumed, high heat of combustion (H) and fraction of energy released as radiation (fr). For grass sites¹, fr = 0.180 and H = 18.03 MJ Kg⁻¹; pine sites⁵, fr = 0.147, H = 22.60 MJ Kg⁻¹; and for oak litter sites³, fr = 0.13–0.22 and H = 17.10 MJ Kg⁻¹

Site description	Fuel load (g m ⁻²)	Fuel consumed (%)	Estimated FRED dose (MJ m ⁻²)
<i>Typical surface fire characteristics</i>			
Various southern African grass sites ^{A,B}	44–242	100	0.14–0.79
Dambo grassland ^B	209	100	0.68
North-eastern United States Oak litter ^C	150–400	FRED directly measured	0.30–1.50
Regional southern African grass ^D	351	69.4	0.79
South-western United States pine needles ^E	224	65	0.48
<i>Surface fire upper limits (total surface, litter and duff consumption)</i>			
North-western United States (complete forest floor consumption – no wood) ^F	2000	65 (estimated)	8.60
North-western United States slash (masticated woody fuels, litter and duff) ^G	3100–21,900	FRED directly measured	1–10

^AWooster *et al.* (2005).

^BShea *et al.* (1996).

^CKremens *et al.* (2012).

^DHély *et al.* (2003).

^ESmith *et al.* (2013).

^FLaw *et al.* (2003).

^GSparks *et al.* (2017).

stress. Leaf photochemical efficiency was expressed as leaf chlorophyll fluorescence (F_v/F_m), measured using an LI-6400–40-leaf chamber fluorometer (LI-COR, Inc.). Chlorophyll fluorescence is an indicator of the degree of photosynthetic energy conversion in plants, often referred to as the photosystem II status. In this context, F_o is the initial peak of fluorescence immediately after exposure to weak white light and it is when Q_A (plastoquinone-A) – an integral component of the electron chain in photosynthesis – is fully chemically reduced (Jones 2014). F_m is the maximal fluorescence, which is the peak fluorescence obtained after exposure of the leaf to bright white light; this occurs when Q_A is fully oxidised. F_v , which is called the variable fluorescence, is then the difference between F_m and F_o . F_v/F_m is calculated as the maximum fluorescence minus the fluorescence yield in the absence of photosynthetic light divided by the maximum fluorescence (Maxwell and Johnson 2000). In general a F_v/F_m value of around 0.8 is considered healthy, and values less than 0.8 are indicative of plant stress (Jones 2014).

The terminal shoots were allowed to dark adapt by covering them with foil for 20 min before taking chlorophyll fluorescence measurements. Needles were placed across the cuvette, and minimum fluorescence (F_o) was measured using a weak measurement beam ($<1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). Maximum fluorescence (F_m) was determined following a red light saturating pulse ($>7000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) centred at 630 nm. Light-saturated ($1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density) gas exchange measurements (photosynthesis, stomatal conductance) were performed after chlorophyll fluorescence measurements using a LI-6400XT and 6400–05 conifer chamber (LI-COR, Inc.). Stomatal conductance is a measure of how open the plant stomata are. Gas exchange and chlorophyll fluorescence were measured 1 day before the burns and then at 1, 4, 7, 14 and 28 days following the burns. Fluorescence was

also measured at 3 and 12 h following the burns. At each period, physiological measurements were collected from five random seedlings per group. Prior to the flush of new foliage during the following growing season, we counted all live *P. contorta* needles ($n = 24$; *L. occidentalis* is deciduous) and subsampled 20 needles from each seedling to assess leaf area (processed with ImageJ v1.49). In these experiments, we define seedling mortality as the death of all foliage, the inability of meristems to regenerate shoots and the cessation of respiration. Statistical analyses were performed using ANOVA (SPSS version 22) with a *post hoc* Dunnett's two-sided multiple comparisons test and a Tukey's honest significant difference ($\alpha = 0.1$).

Results

Seedling diameter at root collar dose – response

In each species, DRC decreased with increasing FRED dose (Fig. 1). After 28 days, the DRC curves (across the control and three dose levels) exhibited similar trajectories and degrees of spread, which is striking given these are two distinctly different conifer species (Lotan and Critchfield 1990; Schmidt and Shearer 1990), likely indicating a similar underlying physiological response. During the experiment, the control groups experienced a steady increase in DRC. The medium (0.80 MJ m^{-2}) and high (1.20 MJ m^{-2}) FRED doses resulted in proportional reductions in DRC, with the high dose producing an immediate decline, followed by a slight recovery ($\sim 30\%$) within the first day following the experimental burns. The low (0.40 MJ m^{-2}) dose caused a reduction in DRC throughout the evaluation period (28 days) that was not significantly different from the control. Fig. 1 also demonstrates the general differences in seedling crown condition following the respective FRED doses.

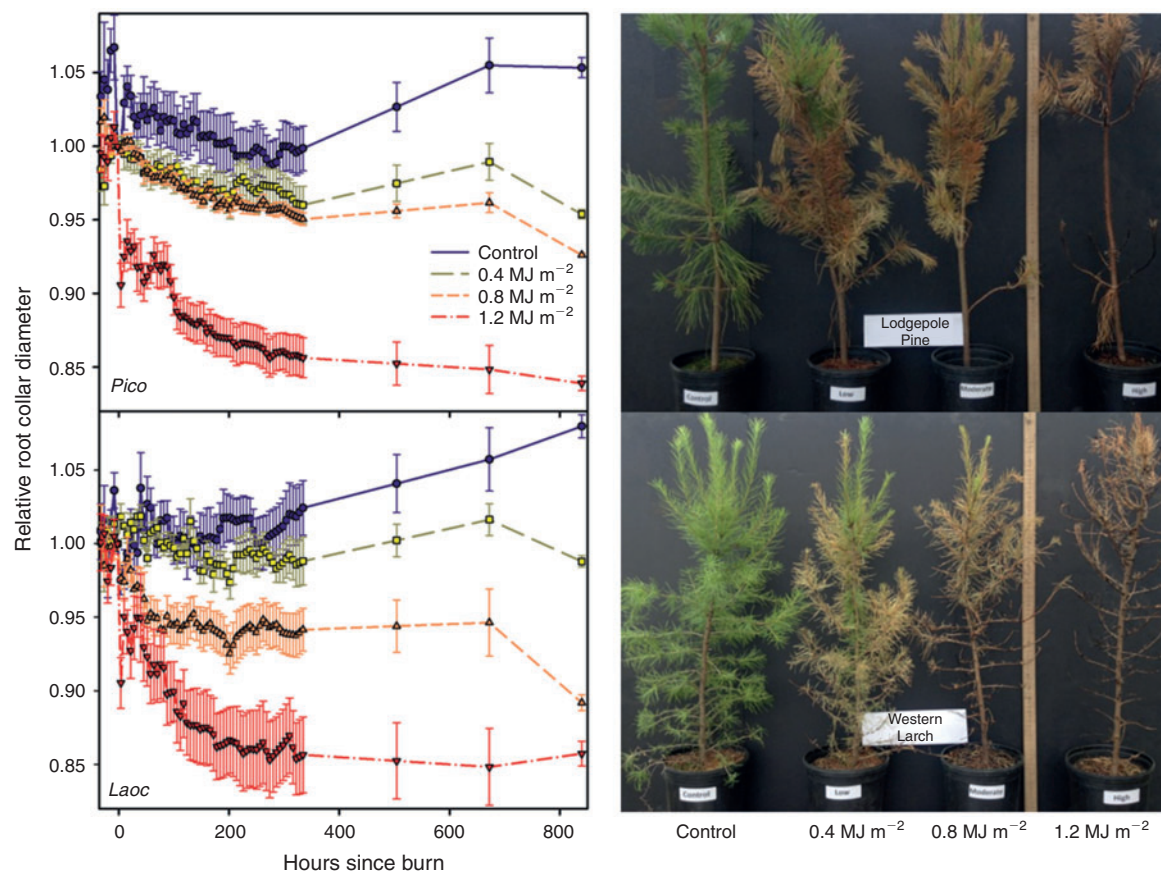


Fig. 1. Diameter at root collar and visible changes. Relative changes in diameter at root collar in lodgepole pine (*Pico*) and western larch (*Laoc*) for up to 800 h post-fire. Photographs show the relative change in foliage immediately post-fire: control, 0.4 MJ m⁻², 0.8 MJ m⁻² and 1.2 MJ m⁻² doses (left to right).

Seedling gas exchange dose – response

In general, increasing FRED dose resulted in decreases in both leaf-level photosynthesis (Fig. 2a, b) and seedling leaf area (Fig. 3a). In the 2 weeks initially following fire, stomatal conductance and photosynthesis were highly variable among FRED doses in both species. However, there was a clear decrease in these gas exchange metrics compared with the control after 28 days. At 1 month following the experimental burns, increase in FRED dose in both species led to similar linear decreases in the net leaf-level photosynthesis (Fig. 3b, *L. occidentalis*: $r^2 = 0.79$, $P < 0.001$, s.e. = 1.4; *P. contorta*: $r^2 = 0.83$, $P < 0.001$, s.e. = 1.91). In addition, the combustion treatments caused decreases in chlorophyll fluorescence – an indicator of photosystem II status – that were more severe and longer lasting with increasing FRED dose (Fig. 2). However, these decreases in chlorophyll fluorescence were not the apparent cause of the reduction in photosynthesis at 4 weeks because fluorescence had recovered in all except the 1.2 MJ m⁻² dose treatment for *P. contorta* (Fig. 2c, d).

We posit that photosynthesis at 4 weeks may instead have been limited by stomatal conductance (Fig. 2e, f). The FRED treatments caused differences ($P = 0.001$) in intercellular CO₂ concentrations (Ci), with lower Ci under higher FRED doses and a positive relationship between photosynthesis and Ci in each

species (*L. occidentalis*: $P = 0.058$, *P. contorta*: $P = 0.004$; data not shown). These changes occurred despite there being little evidence of water stress from the midday water potential measurements following the burns ($-0.67 \text{ MPa} < \psi < -1.43 \text{ MPa}$; Table 2). Although there was some variation among the measurement dates, there was a generally consistent rank order among the control, 0.4 MJ m⁻² and 0.8 MJ m⁻² treatments for midday water potential that was similar for both species (Table 2): the most negative values were found in the control seedling (average across measurement period: *P. contorta*: $-1.17 \pm 0.03 \text{ MPa}$; *L. occidentalis*: $-1.04 \pm 0.03 \text{ MPa}$), then the 0.4 MJ m⁻² treatment ($-0.72 \pm 0.02 \text{ MPa}$; $-0.79 \pm 0.02 \text{ MPa}$) and the 0.8 MJ m⁻² treatment ($-0.63 \pm 0.02 \text{ MPa}$; $-0.64 \pm 0.03 \text{ MPa}$). Notably, these rankings mirrored the changes in leaf area (Fig. 3a) and stomatal conductance, consistent with decreased whole plant water demand. Given that these water potentials do not indicate water stress, we speculate that the changes in stomatal conductance could be due to changes in leaf structure. There were no water potential data in the 1.2 MJ m⁻² treatments for *L. occidentalis* because of the complete loss of live foliage, whereas 1.2 MJ m⁻² treatments for *P. contorta* responded inconsistently (measurement interval means from -1.3 MPa to -2.3 MPa). In *P. contorta*, there was a strong relationship between surviving leaf area per seedling and

the 4-week change in DRC ($r^2 = 0.47$, $P < 0.001$), highlighting that fire caused decreases in photosynthetic area and photosynthesis per unit area (Table 3).

Seedling mortality dose – response

The 1.20 MJ m⁻² FRED doses caused complete mortality in both species within 28 days. In each species, the plants subjected to the 1.2 MJ m⁻² FRED dose exhibited new bud formation around 14 days post-fire but ultimately did not survive. The

other two FRED doses did not cause mortality during the 28-day observation period following the experimental burns. However, a companion study that is focused on temporal trajectories of spectral responses and survivability of these seedlings after 1 year did observe that yearly mortality rates increase with the FRED dose that was received (Sparks et al. 2016). Specifically, at 1 year post-fire, the *P. contorta* mortality rates were 0% and 33% for the 0.4 MJ m⁻² and 0.8 MJ m⁻² FRED doses. Similarly, the 1 year post-fire *L. occidentalis* mortality rates were 33% and 50% for the 0.4 MJ m⁻² and 0.8 MJ m⁻² FRED doses.

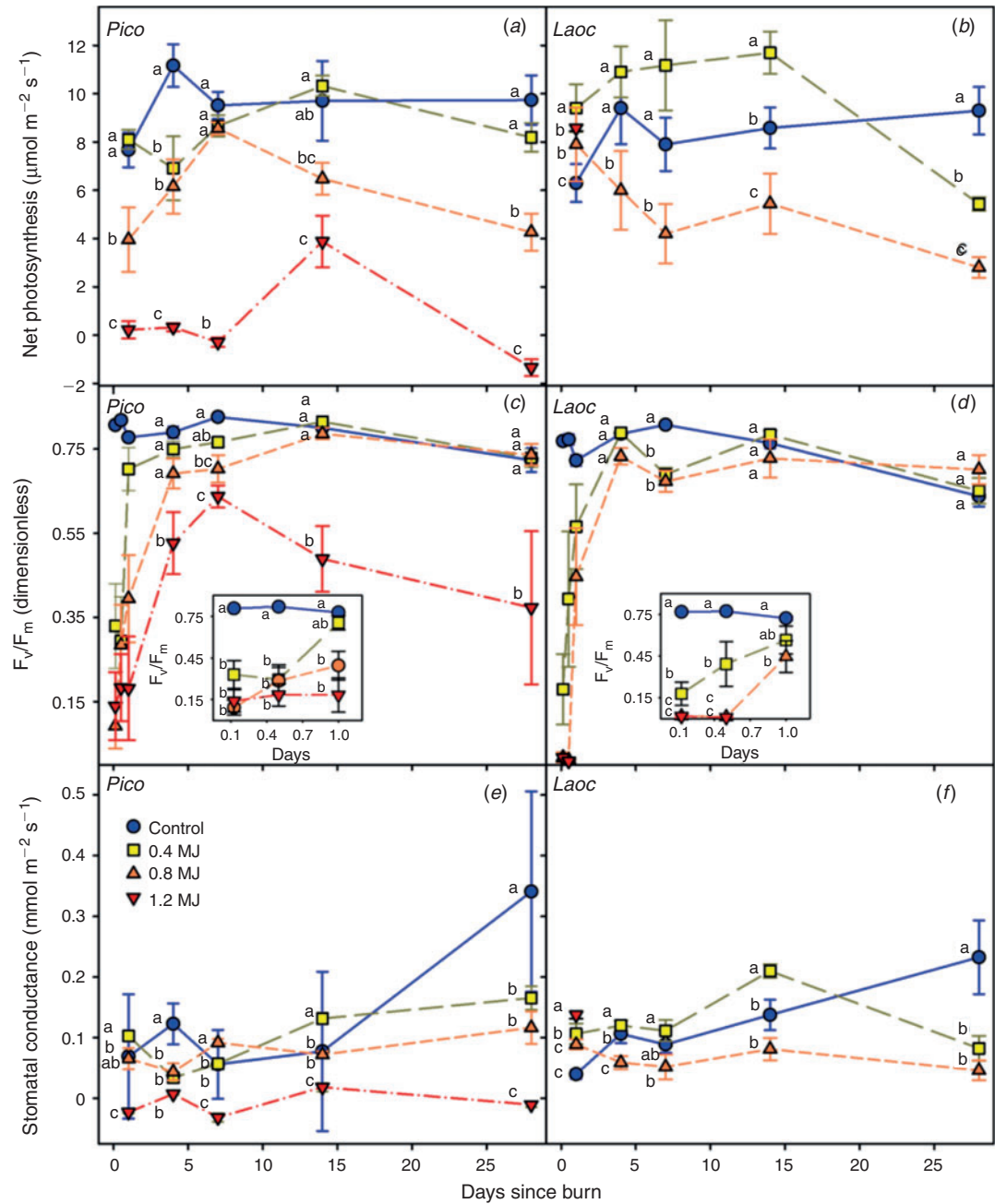


Fig. 2. Plant physiological changes due to increasing fire radiative energy density (FRED) dose. Data are shown for net photosynthesis (a, b), dark-adapted leaf photochemical efficiency expressed as leaf chlorophyll fluorescence (F_v/F_m) (c, d) and stomatal conductance (e, f) of both species. Superscript letters denote statistical differences among treatments within species.

Fig. 4 illustrates the mortality and vigour (from surviving seedlings) data from the study in a toxicological dose–response formalism (Klaassen 2013). The curves are shown for illustrative purposes and do not represent regression lines of best fit.

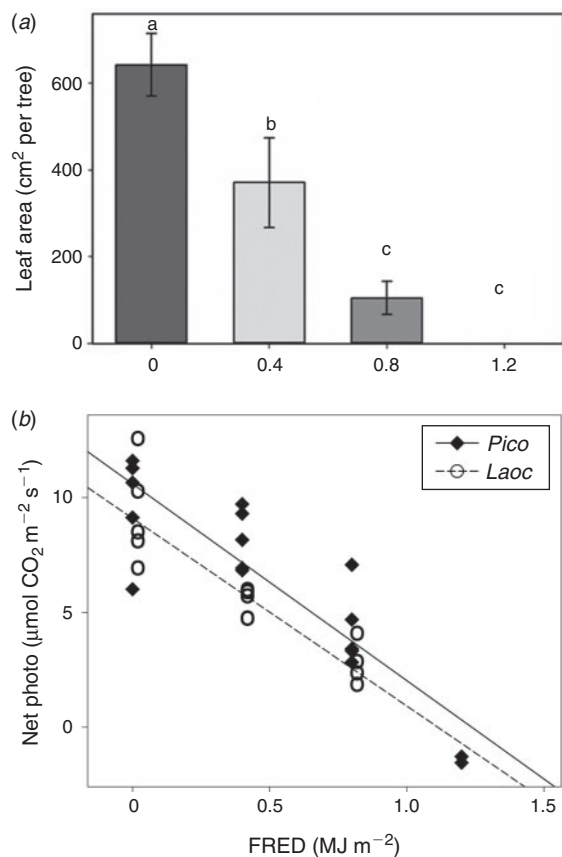


Fig. 3. Changes in leaf area and net photosynthesis: (a) average (\pm s.e.) live leaf area per seedling for lodgepole pine (*Pico*) in each of the four FRED treatments assessed at the end of winter dormancy before new spring growth. Letters represent significant ($P < 0.05$) differences between treatments. Although not quantified, increasing FRED caused greater losses of foliage in western larch (*Laoc*); (b) reductions in net photosynthesis at 28 days following the combustion experiment ($r^2 \sim 0.78$, $P < 0.001$). Adapted from Sparks *et al.* (2016).

Fig. 4a represents the percentages of mortality (of nine replicates per dose) at 1-year post-fire, whereas Fig. 4b shows the relative change in photosynthesis at 28 days and is effectively the inverse of Fig. 3b re-presented as a dose–response curve. Fig. 4a demonstrates that for these experimental results, the FRED dose expected to lead to 50% mortality (i.e. the ‘LD50’) is $\sim 0.8 \text{ MJ m}^{-2}$, which is analogous to the 50% mortality probability threshold used within logistic regression approaches. For *P. contorta*, these and the other data (Fig. 1–3) suggest that at some FRED dose $< 0.8 \text{ MJ m}^{-2}$ but $> 0.4 \text{ MJ m}^{-2}$ a threshold exists where *P. contorta* seedlings are susceptible to mortality following the fire. In dose–response studies this threshold is referred to as the NOAEL (no-observed-adverse-effect level), which is simply the maximum dose that causes no adverse effects; it is then assumed that doses below the NOAEL will also produce no adverse effects. For *L. occidentalis*, insufficient data are available to determine if such a threshold is present and thus this approach currently suggests that this species is susceptible to fire at all doses. The LOAEL (lowest-observed-adverse-effect level) for mortality is 0.4 MJ m^{-2} and 0.8 MJ m^{-2} for *L. occidentalis* and *P. contorta*. The LOAEL is thus the minimum dose that is observed to cause an adverse effect. Fig. 4b demonstrates that the change in seedling vigour, as described by net photosynthesis at 28 days, also can be well described by a characteristic dose–response curve. In Fig. 4b, insufficient data exist to determine if a NOAEL threshold for changes in net photosynthesis exists for either *L. occidentalis* or *P. contorta*, suggesting that both species are susceptible to reductions in photosynthesis following fires at all dose levels.

Discussion

This experiment furthered our mechanistic understanding of how fire affects seedlings by exposing them to increasing FRED doses representing surface fires in a range of fire-prone terrestrial ecosystems (Table 1) and measuring changes in seedling size (Fig. 1), leaf gas exchange (Fig. 2a–f) and leaf area (Fig. 3a). There is an increasing amount of research describing the physiological response of seedlings and trees to fire (Aubrey *et al.* 2012; Clark *et al.* 2012; Renninger *et al.* 2013; Battipaglia *et al.* 2014; Wait and Aubrey 2014; Starr *et al.* 2015). However, previous research has been limited to understanding how plants have responded to a single fire intensity dose (Reich *et al.* 1990;

Table 2. *Larix occidentalis* (*Laoc*) and *Pinus contorta* (*Pico*) leaf water potentials (MPa) before and following the experimental fires. Pre-fire water potential values were only acquired for the control group. Midday except where noted. Mean values shown with standard error in parentheses

FRED dose	Pre-fire –21	3	6 (1700 hours)	Hours since combustion experiment				
				27	99	171	339	675
<i>Laoc</i>								
0	–1.4 (0.05)	–1.4 (0.13)	–1.3 (0.07)	–1.2 (0.05)	–1.0 (0.03)	–0.9 (0.03)	–0.9 (0.03)	–1.2 (0.02)
0.4		–0.9 (0.08)	–0.8 (0.03)	–0.8 (0.02)	–0.7 (0.01)	–1.0 (0.07)	–0.7 (0.03)	–0.7 (0.15)
0.8		–0.6 (0.05)	–0.5 (0.02)	–0.7 (0.03)	–0.4 (0.02)	–0.6 (0.03)	–0.3 (0.04)	–1.1 (0.21)
<i>Pico</i>								
0	–1.6 (0.06)	–1.2 (0.13)	–2.0 (0.04)	–2.0 (0.06)	–1.3 (0.17)	–0.8 (0.03)	–0.8 (0.02)	–0.9 (0.04)
0.4		–0.7 (0.03)	–0.8 (0.10)	–0.7 (0.02)	–0.7 (0.02)	–0.9 (0.08)	–0.6 (0.01)	–0.7 (0.02)
0.8		–0.9 (0.06)	–0.6 (0.07)	–1.0 (0.07)	–0.5 (0.12)	–0.5 (0.03)	–0.4 (0.02)	–0.7 (0.02)
1.2		–1.3 (0.07)	–2.3 (0.32)					

Table 3. *Pinus contorta* needle counts and areas following the experimental fires
Mean values shown with standard error in parentheses. DRC, diameter at root collar; n/a, not applicable

FRED dose	Needle count	Needle area (cm ²)	Needle area per seedling (cm ²)	Associated ΔDRC
0	1595 (224)	0.4 (0.03)	643 (72)	0.4 (0.37)
0.4	781 (192)	0.5 (0.04)	371 (104)	−0.3 (0.20)
0.8	212 (78)	0.5 (0.05)	105 (38)	−0.8 (0.14)
1.2	0	n/a	n/a	−2.5 (0.17)

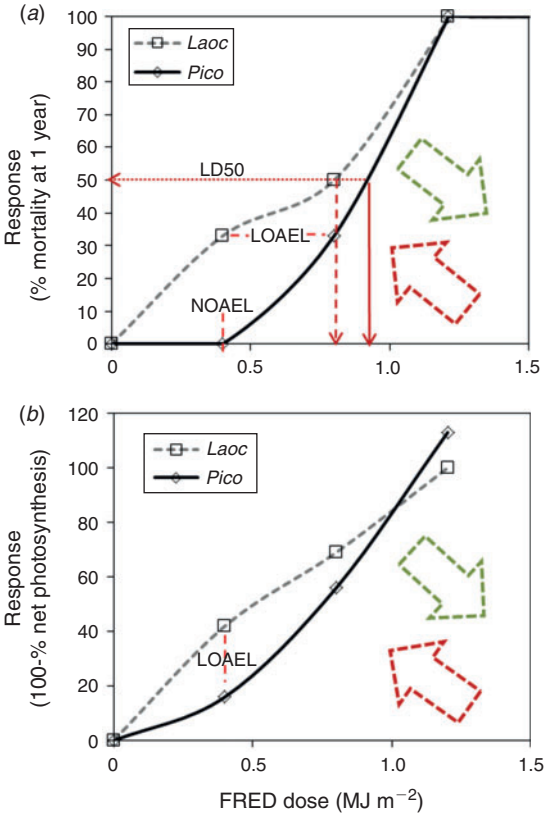


Fig. 4. (a) Dose–response curve of mortality versus FRED dose at 1 year following the experiments. LD50 (lethal dose at 50%) highlights the single dose that would be expected to cause 50% mortality in test species. NOAEL represents the no-observed-adverse-effect level and LOAEL represents the lowest-observed-adverse-effect level. (b) Dose–response curve of vigour versus FRED dose at 28 days following the experiments. In both (a) and (b), the downward and right-pointing arrows indicate a hypothesised shift that would occur if these experiments were translated to prescribed fires within natural settings, whereas the upward and left-pointing arrow indicates a hypothesised shift due to external stressors.

Kruger and Reich 1997; Ryan 2000; Aubrey et al. 2012; Clark et al. 2012; Renninger et al. 2013; Wait and Aubrey 2014; Starr et al. 2015) or treatments conducted using artificial heat sources (Ryan 2000; Michaletz et al. 2012). Thus, our observations that increasing FRED doses created measurable decreases in seedling diameter and photosynthesis (Figs 1 and 2a, b) represent a further step towards developing a mechanistic understanding of fire effects on seedlings.

We believe a likely explanation for the initial decrease in seedling diameter caused by the FRED treatments in the hours following the burn (Fig. 1) was water loss in the phloem and cambium. We have no direct measurements of plant water content to verify this assertion, but it is well known that temperature increases such as those caused by surface fires can cause water loss from plant tissues (Michaletz et al. 2012). The decrease in DRC among the 1.2 MJ m^{−2} treatment seedlings immediately after the burn followed by a short-lived partial recovery would be consistent with a loss of water from the stem. In part, this change in size and loss of water could represent tissue necrosis (Michaletz and Johnson 2007). However, the cause of the continued decrease in seedling diameter in the days to weeks following the burn treatments (Fig. 1) is less certain. It is possible this was due to continued water loss, although water potential trends for the same period do not reflect seedling water stress (Table 2). Continued diameter reduction following FRED treatments could represent a depletion of plant carbon reserves. Decreases in both seedling leaf area (Fig. 3a) and leaf-level photosynthesis (Fig. 3b) would each contribute to lower carbon assimilation and we see evidence of this in the significant ($P < 0.001$) relationship between the amount of surviving leaf area and the relative change in seedling diameter in *P. contorta*. In addition to decreased carbon assimilation, the burned seedlings may also have had to expend carbon to repair damaged tissues and restore water to the phloem and cambium (osmotically driven). Our photosynthesis data demonstrate that seedlings exposed to greater FRED doses captured less carbon and this may have resulted in an unfavourable carbon balance for recovery, growth and survival. However, direct measurement of changes in stored non-structural carbohydrates are needed to confirm this intriguing possibility.

The changes in leaf-level gas exchange (Fig. 2a–f) that we observed in response to fire are not unique to this study; other studies of conifers have found decreases in photosynthetic gas fluxes in the days and weeks following fire. At a pine stand and a mixed oak–pine stand in New Jersey, prescribed fires caused season-long decreases in whole-stand (eddy covariance-based) measurements of evapotranspiration (Clark et al. 2012). Likewise, ecosystem photosynthesis was lower after prescribed fires in two *P. palustris* stands in Georgia (Starr et al. 2015). Notably, these eddy covariance studies lacked an unburned control group. In a *P. rigida* forest, a single prescribed fire decreased sapflux early in the growing season, but increased sapflux later in the season (Renninger et al. 2013). Although leaf-level stomatal conductance and foliar N concentrations were consistently higher in the burned stand, there were no significant differences

in photosynthesis or A/C_i (net CO_2 assimilation rate, A , vs calculated sub stomatal CO_2 concentration, C_i) parameters (Renninger *et al.* 2013). In heat-treated *P. ponderosa* trees, decreases in the amount of live foliage increased leaf-level evapotranspiration and stomatal conductance (Ryan 2000). Our data add to the relatively small amount of previous research intended to understand physiological response of conifers to fire.

Seedlings in natural fires

Our ability to extrapolate the results of this experiment to a natural fire setting is presently limited because we did not allow for potential ecosystem interactions. Our seedlings were well watered following the burns and were supplied with ample light and adequate nutrients to support growth. However, seedlings in natural settings may have access to greater quantities of light, water and nutrients because of decreases in competition for these limiting resources (Reich *et al.* 1990; Kruger and Reich 1997; Dijkstra and Adams 2015). For fires under natural ecosystem conditions – where seedlings may have more established roots, gained some fire-resistant features and survived multiple seasons – we hypothesise that the FRED doses required to produce the same seedling mortality and reductions in vigour would increase as compared with the laboratory fires (Fig. 4, right and down arrow). However, if the seedlings are subjected to additional stressors such as drought we may expect that the same or lower FRED doses would lead to higher mortality and greater physiological responses. The interaction between drought-stressed seedlings and fire may therefore lead to the dose–response curves being ‘shifted’ upwards (Fig. 4, up and left arrow).

Accounting for these ecosystem interactions would make it more difficult to model the complex effects of fire on seedling growth and mortality. We expect that our experimental approach of using varying doses of FRED could be readily applied to seedlings within prescribed fires to generate mechanistic information about how the laboratory results are influenced by ecosystem processes. Further, it remains unclear whether the physiological effects on seedlings are due to radiative heating of the plant stems, convective heating in the canopies or conductive heating on roots through the soil surface (Sparks *et al.* 2017). Future experiments could seek to decouple these energy components (Smith *et al.* 2016b).

Seedlings under future fire conditions

Given that energy release component (ERC) is a predictive metric used by all US federal land management agencies as part of the National Fire Danger Rating System (NFDRS, Deeming *et al.* 1972; Hardy and Hardy 2007), linking increases in FRED dose to seedling physiological performance and mortality could improve the value of the NFDRS ERC data. ERC reflects the potential total energy release in the flaming front of wildland fires. Therefore, given the general assumption in the literature that the apportionment of total energy to radiative energy is constant, then future research could be focused on developing the form of the relationship between FRED and ERC. A substantial increase in the 90th-percentile ERC is projected by the mid-21st century as a result of anthropogenic climate change

(Fig. 5a) and therefore it is likely that the seedling mortality thresholds will be met more often. Equally, an increase in the frequency of days exceeding ERC values that was historically at the 90th percentile (Fig. 5b) will likely lead to a similar proportional increase in seedlings receiving doses exceeding the LD50 dose. Clearly, the frequency and extent of these increases will depend on species, forest heterogeneity across the landscape (including local tree neighbourhoods) and fire heterogeneity (e.g. Kolden *et al.* 2012, 2015a). However, irrespective of the current heterogeneity, on a dose–response basis, we would expect more seedlings to die in the mid-21st century due to increased ERC during fires (Fig. 5a). This is particularly relevant to understanding the ability of forests to regenerate when one of the manifestations of climate change within the fire regime is more frequent fire (i.e. a higher fire return interval).

Conclusions

The toxicological dose–response curves have high potential utility for fire and land management personnel because they provide a quick reference guide to what level of FRED (or ERC) dose causes no effect or leads to seedling mortality. For instance, prescribed fire practitioners could use this information to guide when and how to conduct treatments to ensure that the heat release remains below the NOAEL threshold. Equally, they could use the information on mortality threshold levels to remove unwanted species. The data could also be useful to managers seeking to conduct rehabilitation treatments following wildfires as the NOAEL, LD50 and complete mortality thresholds could provide valuable information on the degree of reseedling that may be required for a given species. The current data presented in Fig. 4 clearly illustrate the need for further studies with these and other species. Specifically, more data are needed for both *L. occidentalis* and *P. contorta* to identify where the NOAEL mortality threshold occurs and whether such thresholds exist for changes in net photosynthesis and other seedling physiology metrics. Equally more FRED doses are needed for both *L. occidentalis* and *P. contorta* to reduce uncertainty about where total mortality occurs at high FRED doses. Finally, when translating these experiments to a natural fire setting (e.g. prescribed fires), it is likely that a larger range of FRED doses will be needed to fully characterise the dose–response relationships for a range of plant sizes.

In this study, we used FRED, given the ability to pre-plan and replicate the heat doses on the plants. Metrics such as maximum FRFD may prove to be a better correlate when used *in situ* within natural stands with plant physiology responses. However, the inability to accurately predict the magnitude of maximum FRFD, when or where that maximum FRFD occurs, and the added challenges that canopy occlusion may have on the maximum FRFD signal, limits its use within planned dose–response experimental treatments. In the current study, we observed a clear dose–response of FRED on seedling growth, carbon assimilation and mortality. If climate change results in a greater frequency of conditions that have been historically associated with high potential wildfire heat release or simply fire frequency (i.e. leading to insufficient time for new seedlings to acquire fire-resistant properties), then our research suggests there will be proportionally strong effects on seedling

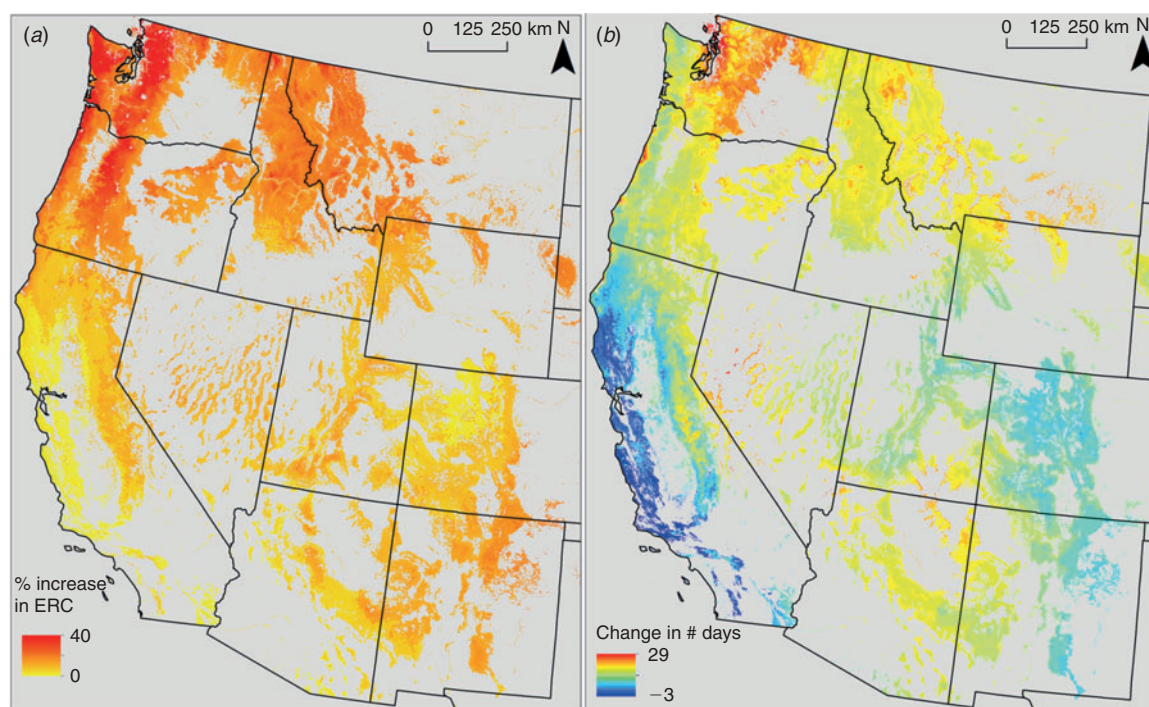


Fig. 5. Projected energy release and fire seasons in the north-western United States. (a) Percentage change between the 90th percentiles of the historic Energy Release Component (ERC) climatology and mid-21st century (2041–2070) ERC climatology. (b) Change in the mean annual number of days per fire season above the historical (1971–2000) 90th percentile ERC for the mid-21st century (2041–2070) for RCP 8.5. Negative numbers (dark blue) indicate a decrease in number of extreme days, whereas red areas indicate up to a 4-week increase in extreme days. As outlined in Abatzoglou and Brown (2012) and Abatzoglou (2013), 90th percentile thresholds were calculated on a per-pixel basis for May–September from 17 downscaled global climate models.

physiology and mortality. These experiments represent further mechanistic information that allows modelling of fire effects on seedlings, addressing a critical knowledge gap in our understanding of the effects of fire on ecosystem function. In closing, although the dose–response approach to fire severity is still relatively new within fire ecology research, this study represents a further step in developing a pyro-ecophysiology understanding of fire effects on vegetation.

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