CSIRO PUBLISHING

International Journal of Wildland Fire, 2007, **16**, 96–106 www.publish.csiro.au/journals/ijwf

Impact of prescribed fire and other factors on cheatgrass persistence in a Sierra Nevada ponderosa pine forest*

Jon E. Keeley[A,B,C] *and Thomas W. McGinnis*[A]

[A]USGS Western Ecological Research Center, Sequoia and Kings Canyon Field Station, 47050 Generals Highway, Three Rivers, CA 93271, USA.
[B]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA.
[C]Corresponding author. Email: jon_keeley@usgs.gov

Abstract. Following the reintroduction of fire *Bromus tectorum* has invaded the low elevation ponderosa pine forests in parts of Kings Canyon National Park, California. We used prescribed burns, other field manipulations, germination studies, and structural equation modelling, to investigate how fire and other factors affect the persistence of cheatgrass in these forests. Our studies show that altering burning season to coincide with seed maturation is not likely to control cheatgrass because sparse fuel loads generate low fire intensity. Increasing time between prescribed fires may inhibit cheatgrass by increasing surface fuels (both herbaceous and litter), which directly inhibit cheatgrass establishment, and by creating higher intensity fires capable of killing a much greater fraction of the seed bank. Using structural equation modelling, postfire cheatgrass dominance was shown to be most strongly controlled by the prefire cheatgrass seedbank; other factors include soil moisture, fire intensity, soil N, and duration of direct sunlight. Current fire management goals in western conifer forests are focused on restoring historical fire regimes; however, these frequent fire regimes may enhance alien plant invasion in some forest types. Where feasible, fire managers should consider the option of an appropriate compromise between reducing serious fire hazards and exacerbating alien plant invasions.

Additional keywords: aliens, *Bromus tectorum*, Downy brome, fire intensity, non-native, structural equation modelling.

Introduction

Cheatgrass (*Bromus tectorum*) is an annual alien species from Eurasia and the Middle East that has become invasive throughout interior parts of the western United States. It is particularly widespread in the Colombia and Great basins, which were invaded over a century ago (Mack 1981), and today is increasingly evident in California on the western slopes of the Sierra Nevada (Keeley 2006). In all plant communities, disturbance from livestock grazing and fire seem to be a prerequisite for cheatgrass colonisation (Warg 1938; Stewart and Young 1939; Young and Evans 1978; Knapp 1996). In part this is because it competes weakly with established plants, but is successful in competition with seedlings of most native species (Harris 1967; Melgoza *et al*. 1990; Melgoza and Nowak 1991; Rafferty and Young 2002; Humphrey and Schupp 2004). Its rapid growth rate (Hulbert 1955), ability to photosynthesise at cold temperatures (Harris 1967; Rice *et al*. 1992; Chatterton *et al*. 1993), and its competitive ability under drought stress (Melgoza *et al*. 1990), are additional factors that contribute to cheatgrass dominance in many communities.

Contributing to cheatgrass success is the fact that it increases the probability of further disturbances (D'Antonio and Vitousek 1992), as these fine and highly combustible fuels dry early in the season, and greatly increase the length of the fire season in some ecosystems. Aggressive establishment has altered some sagebrush landscapes from natural patchy fuels to more continuous fuel cover that produces larger less patchy burning, often with negative impacts on native flora (Stewart and Young 1939; Billings 1994). Substantial cheatgrass invasion has happened in sagebrush ecosystems, particularly where they have been managed as rangelands through repeated burning, which was necessary in order to open these closed-canopy shrublands (Baker 2006).

Some lower elevation forests dominated by ponderosa pine (*Pinus ponderosa*) have reported cheatgrass establishment (Warg 1938; Hulbert 1955), but these communities are generally considered to be less vulnerable to invasion than shrubland and grassland ecosystems (Pierson and Mack 1990*a*, 1990*b*; Pierson *et al.* 1990). This is particularly true for forests where fire suppression has effectively excluded fire for much of the 20th century (Keeley 2006). However, following disturbance, cheatgrass is capable of invading drier forests, and logging, burning, and herbicide treatments are known to encourage cheatgrass invasion (McDonald and Everest 1996; Pierson and Mack 1990*a*, 1990*b*; Crawford *et al*. 2001; Keeley *et al*. 2003).

Approximately a decade ago, following the reintroduction of fire through prescription burning, cheatgrass invasion was recognised as a problem in ponderosa pine forests in Kings Canyon National Park, in the Sierra Nevada Range of California (Caprio *et al*. 1998). The National Park Service, concerned that additional

*This article was written and prepared by US Government employees on official time and is therefore in the public domain and not subject to copyright.

 10.1071/WF06052 1049-8001/07/010096

disturbance could increase cheatgrass, voluntarily halted further burning in forests along the South Fork of the Kings River, until the problem could be evaluated.

Here, we investigate how fire and other factors affect the persistence of cheatgrass in these previously burned cheatgrass infested ponderosa pine forests of Kings Canyon National Park. Experimental prescribed burns were used to assess the effect of burning season and fire intensity on cheatgrass success. We examined several measures of fire intensity and how they related to cheatgrass persistence following burning. Fireline intensity was determined as it is often a good indicator of aboveground fire effects, such as scorching height of conifer crowns and other biological impacts (Albini 1976; Borchert and Odion 1995). However, other measures of fire intensity such as maximum temperature and duration of heating were included because they sometimes have greater effects on ecological components such as seed banks (Beadle 1940; Armour *et al*. 1984; Bradstock and Auld 1995; Brooks 2002). Other field experiments investigated the effect of changes in soil nutrients, as both elevated and reduced nutrients can affect success of cheatgrass and other alien species (Yoder and Caldwell 2002; Blumenthal *et al*. 2003; Belnap *et al*. 2003; Beckstead and Augspurger 2004). We also considered the role of propagule limitations (e.g. D'Antonio *et al.* 2001) and included plots enhanced with either cheatgrass seeds or native bunchgrass seeds. As cheatgrass invasion was tied to fire restoration in these forests we investigated the effect of increased shade and surface litter that would be characteristic of long-unburned forests. To understand how fire affects cheatgrass regeneration, in the laboratory we examined the effect of moist and dry heat on cheatgrass seed germination, and used these temperature-responses to make estimates of how our experimental burns might affect cheatgrass seedbanks. Finally, we conclude by modelling the response of cheatgrass to fire and other environmental factors with multivariate structural equation models (Grace 2002, 2006).

Methods

Study sites

Field experiments were conducted in the valley along the South Fork of the Kings River, from Cedar Grove to Zumwaldt Meadow in Kings Canyon National Park. The park was established in 1940; however, this canyon was withheld from National Park status as a potential reservoir site until 1965 (Strong 2000). The study areas were selected with the criteria that they were on relatively flat terrain, had been burned by prescription in the 1990s, and contained abundant cheatgrass. Precipitation as rain and snow is concentrated between October and April and for the 5-year record (2000–2004) from the Cedar Grove Remote Automated Weather Station averaged 485 mm per year. A 74-year record for the Sierra Nevada (http://www.ncdc.noaa.gov/oa/climate, accessed April 2005) showed 2000 and 2003 to be near average for the region and 2001, 2002 and 2004, to be 20, 17 and 26% below average, respectively.

The dominant tree species are ponderosa pine, incense-cedar (*Calocedrus decurrens*), black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*). Native understorey species include three perennial bunchgrasses, needlegrass (*Achnantherum occidentalis*), one-sided bluegrass (*Poa secunda*), squirreltail (*Elymus elymoides*), annual fescue (*Vulpia microstachys*), lupine (*Lupinus* spp.), *Eriogonum wrightii*, and scattered shrubs of manzanita (*Arctostaphylos patula*).

Prior to Euro-American settlement, these forests had a relatively short fire return interval of ~11 years (Warner 1980). Some of this burning may have been due to Native Americans, although permanent Indian settlements apparently were not made in the valley, and this source of fire was eliminated by the mid-nineteenth century (Sellers 1970; Kilgore and Taylor 1979). Fire records show that no fires greater than 900 m^2 occurred in the area until the National Park Service began a program of prescription burning in 1979. Over the past century there has been some increase in tree density but compared to similar valleys such as Yosemite Valley further north, forest structure has not changed markedly over the past century (Bueno *et al*. 2000). All of our study sites were prescribed burned once or twice between 1979 and 1998 (Table 1).

Livestock grazing began in the late 1890s, mostly from sheep that were herded through the valley to higher pastures (Muir 1891; Stillman 1897). Until the highway was completed in 1939 pack trains were the primary conveyance for visitors (Dilsaver and Tweed 1990) as well as for alien propagules (Gerlach *et al*. 2003). Herbarium specimens at THRI (Sequoia National Park) document that cheatgrass has been present in patches along the trails and roads of Kings Canyon for at least 50 years. Expansion

Table 1. Mean preburn fuel load (and standard error) in the six study sites west to east in Cedar Grove
$n = 52$. All plots had been prescribed burned once in the past couple decades and some were burned twice (Sequoia and Kings Canyon National Parks fire database)

Study site	Burn history (% plots burned twice)	Fine fuels (kg oven-dry mass m^{-2}): Understorey herbs[A]		1 h surface		10 h surface		100 h surface		Down woody fuel (% ground surface cover)	
		$\bar{X}$	s.e.	$\bar{X}$	s.e.	$\bar{X}$	s.e.	$\bar{X}$	s.e.	$\bar{X}$	s.e.
Concession	49	0.057	0.004	0.423	0.083	0.047	0.010	0.096	0.031	0.281	0.134
Motor Nature Trail West	0	0.055	0.003	0.272	0.055	0.079	0.015	0.273	0.075	3.828	0.852
Motor Nature Trail East	0	0.060	0.003	0.145	0.035	0.048	0.012	0.134	0.053	3.406	0.852
Roaring River	43	0.055	0.003	0.248	0.059	0.094	0.020	0.308	0.086	5.672	0.912
Kings River Bridge	100	0.056	0.003	0.201	0.044	0.041	0.011	0.166	0.093	1.500	0.390
Zumwaldt	0	0.043	0.003	0.205	0.039	0.055	0.010	0.143	0.050	1.969	0.527

[A]Mostly cheatgrass with some forbs and an occasional subshrub.

into surrounding forests was first noticed in the early 1990s by National Park Service staff and appeared to be associated with sites that had been prescribed burned. Prescription burning was halted in these forests in the late 1990s.

Field experiments

Six experimental sites (~3 ha each) were selected across a distance of 6 km in the valley floor, and seventy 5 × 5 m cheatgrass dominated plots, separated by a minimum of 1 m buffers, marked off within each site. Prior to the burns the following environmental data were collected in 2001 for each of the experimental plots: canopy gap size, daily duration of sunlight, litter cover and depth, soil texture, nutrients, and pH. Canopy gap size was estimated from the middle of each plot with a convex spherical densitometer. Sunlight duration at the soil surface was estimated with a Solar Pathfinder (Solar Pathways, Pleasantville, TN, USA), in each plot in May and November. Soil was collected from five locations (plot centre and four other mid-plot locations) and combined into one sample per plot. As there was a weak and irregular horizon development all samples were taken from a standard depth of 10 cm, which in most cases was in mineral soil. Soil texture was determined with the hydrometer method according to Cox (1995). A pH meter was used to determine pH, using an equal mixture of soil and distilled water incubated overnight at room temperature. Soil nutrients were determined on a soil sample from each plot as follows: ammonium and nitrate were from a 2 M potassium chloride extraction, and soil exchangeable potassium was from a 1 N ammonium acetate extraction. In order to investigate fire effects on nutrients, samples were collected at 2 cm depth immediately before and after the autumn 2002 burns. Precipitation was measured at the Cedar Grove Remote Automated Weather Station (RAWS) over the period of the study.

Both before and after each burn treatment cheatgrass and other understorey cover were estimated in each 5 × 5 m plot, categorising them into cover values of 0, 1, 5 and 10%, and 10% increments up to 100%. Biomass of cheatgrass and other understorey was estimated by clipping all plants within a 26 cm diameter area in each plot during the growing season after fire. These were oven-dried and weighed and the ratio of mass to area was used to estimate biomass of understorey cover.

Dead surface fuel categories of 1 h (litter plus branches 0.1–6.4 mm diameter), 10 h (6.5–25 mm), and 100 h (25.1–76 mm) were calculated using line transects of 2 m (1 h and 10 h fuels) or 4 m (100 h fuel), based on the methodology and calculations in Brown (1974). Larger (1000 h) fuels >76 mm were rare and generally not recorded by our Brown's transects so we made a visual estimate of the ground surface cover for this coarse woody debris. Following each fire these transects and coarse woody fuel estimates were repeated and amount of fuel consumed calculated as the difference between before and after estimates. In some plots partially consumed fuels fell into the plot and thus the postfire fuel levels were higher than prefire estimates. These plots were eliminated from the fireline intensity analysis.

Experimental burns

At each site we randomly assigned one of four burn treatments to each of the 5 × 5 m plots: (1) no burn, (2) autumn 2001 burn, (3) summer 2002 burn, or (4) autumn 2002 burn ($n = 18$ plots per site, except 2001 burn $n = 16$). Burning prescriptions were for air temperatures of −1 to 32°C, relative humidity between 20 and 60%, and wind speeds between 0 and 2.75 m s^{-1} at the lower humidity, and up 4.6 m s^{-1} at the higher humidity levels (determined with Cedar Grove RAWS data). Plots were ignited around the perimeter with a drip torch and flames allowed to carry to the centre. In cases where patches of dry grass remained these were burned off with a propane torch.

Fire temperatures were measured along a profile that included: (i) 15 cm above the soil surface; (ii) at the soil surface; and (iii) 2–5 cm belowground. Two profiles were place 1.6 m apart and 1.6 m from the edge. Thermocouples were 0.16–0.32 diachromel-alumel attached via aboveground wires insulated with aluminum foil to either a Campbell CR10X, CR10WP or 21X data logger, that scanned 6–12 times per minute and recorded the maximum temperature each minute and continued until soil surface temperature returned to ambient. Flame length was estimated by peering through the flames to a meter stick outside the plot. Flame speed was determined from the ignition line to the thermocouples, 1.6 m from the edge.

Other manipulations

After each of the three burns, controls and burned plots from each of the six sites (two replicates at each site, $n = 12$) received the following treatments: no treatment control, nitrogen addition, nitrogen reduction, phosphorous addition, phosphorous reduction, pine needle litter addition (this treatment added after 2001), shading with shade cloth, cheatgrass seed addition, and native bunchgrass seed addition. The nutrient manipulations were nitrogen as NH_4NO_3 (ammonium nitrate, 10 g m^{-2}), and phosphorus as $K_4PO_2O_7$ (tetra-potassium pyrophosphate anhydrous, 10 g m^{-2}). These treatments were given immediately after burning and four months later. The nitrogen addition treatment increased ammonium from 4.1 to 22.7 mg kg^{-1} of soil and nitrate from 0.7 to 10.6 mg kg^{-1} during the subsequent growing season. Nitrogen reduction by addition of sawdust (400 g m^{-2}, applied only once due to concerns it would greatly alter soil water holding properties), and phosphorous reduction by addition of $CaCO_3$ (calcium carbonate, 50 g m^{-2}, added after the burns and 4 months later). Needles from adjacent forests were added to ~5 cm depth. Shade tents were erected over shade addition plots during the first growing season after burning, when cheatgrass seedlings were ~3 cm tall. Shading was with black 51% shade cloth suspended ~1 m above the soil surface. Locally collected cheatgrass and native bunchgrass seeds were added immediately after burns at a density of ~11 500 cheatgrass, ~600 squirreltail and ~100 needlegrass seeds per 25 m^2 plot, or was a rough estimate (based on plant density and seed production) of the density of seeds dispersed by each of these species in these forests.

In the laboratory dry or moist (soaked 1 h) cheatgrass seeds were heated at temperatures from 80 to 120°C for durations from 1 min to 4 h. These were then incubated in seed incubators at diurnally alternating 15°C and 25°C in Petri dishes.

Analysis

Three measures of fire intensity were used to characterise fire behaviour: (1) the maximum temperature at the three vertical profile levels, (2) total duration of elevated temperature at these three levels, and (3) fireline intensity. Temperature measurements were averaged for both sensors at a particular level in each plot. Elevated temperature duration was determined by summing the areas under the curves above the pre-ignition ambient temperature at the thermocouple.

We calculated fireline intensity as defined by Byram (1959):

$$I = HWR,$$

where H equals heat of combustion (kJ kg^{-1} of fuel), W is consumed fuel (kg m^{-2}), and R is the rate of fire spread (m s^{-1}), giving a fireline intensity (I) in kW m^{-1}. We used the average total heat of combustion of 18 700 kJ kg^{-1}, given by Johnson (1992) for a wide representation of plant fuels. Fireline intensity as defined by Byram represents the active front of a fire or the rate of energy release per unit time per unit length of the fire front due to flaming combustion. However, it is difficult if not impossible under field conditions to measure this quantity precisely, because most measures of fuel consumption include the loss of fuels due to both flaming combustion and glowing combustion that continues after the fire front has passed (Alexander 1982).

Least-squares regression was used to evaluate the relationship between different measures of fire intensity, including fireline intensity, maximum temperatures at different points in the profile and elevated temperature durations. Fireline intensity calculated as described above was compared using least-squares regression with the value estimated from the widely used eqn $I = 258F^{2.17}$, where F equals observed flame length (Andrews 1986). In all regression analysis three models were compared, the arithmetic, exponential and power models and the one with the highest r^2 was presented. These were done with SYSTAT 11 software (San Jose, CA, USA).

Field experiments were evaluated with one-way ANOVA and two-sample t-tests were used to analyse treatment effects and natural variations. We assessed treatment effects by comparing treated plots to controls in the same season because of significant seasonal variation in cheatgrass cover. Paired t-tests were used when analysing the effect of microsite variations in needle depth in needle-treated plots and changes in nitrogen availability over a 1-week period before burning. Least significant difference (l.s.d.) pair-wise comparisons were made between treatments and controls where ANOVA results were significant. The Kruskal–Wallis ANOVA (KW) was used to analyse mean peak fire-related temperatures.

Multivariate models

Structural equation modeling, or s.e.m. (Grace 2002, 2006), was used to analyse a multivariate path model. Structural equation modeling is designed to statistically evaluate complex hypotheses involving multiple causal pathways. It provides a means for assessing relationships between inter-correlated variables and evaluating whether data are consistent with the model. Structural equation modeling analyses the covariation matrix from the observed variables and provides a statistical evaluation of the correspondence between the hypothesised path model and the data. Several models were tested that differed in the hypothesised variables and paths and the final model selected was the one with only significant variables and with the best model fit. Model fit was determined with the Chi-square statistic, where significant effects indicated a departure between the model and the data. All analyses were conducted with LISREL 8.54 software created by K. Jöreskog and D. Sörbom (SSI Scientific Software International, Lincolnwood, IL, USA).

Structural equation modeling permits the incorporation of estimates of measurement error for individual indicators of latent variables, thus allowing for reduced bias in path coefficients. An assessment was made of the reliability of individual indicators selected for inclusion in the model. It was judged that several concepts were represented by indicators with little measurement error, but two variables that we believed were particularly susceptible to measurement error were prefire and postfire cheatgrass. For these two measurement variables we estimated reliability through a bootstrap estimate of variation. The average correlation among bootstrap samples gave a measure of reliability and this was used to specify error variances. This reliability value was specified as a fixed parameter in the structural equation model, along with the estimated error variances (error variance = [1 − reliability squared] times the variance).

Results

Fuels and prescription burns

Table 1 shows the fuel conditions at the six study sites. Understorey herbaceous fuels comprised a minor part of the fuel load. The dominant fuels were pine needles and small dead branches (1 h fuels) and the larger 25–75 mm branches (100 h fuels). Large down coarse woody fuels were generally uncommon, amounting to only a few percent of the ground surface cover. Across the six sites understorey biomass was quite similar but for surface fuels there was on average about a twofold difference between the lowest and the highest sites. By inspection of Table 1 it appears that sites with high fuel loads in one category bore little relationship to fuel loads in another category. None the less there were some significant positive relationships between fuel types on a plot basis when all sites were combined (1 h *v.* 10 h fuels, $r^2 = 0.06$, $P < 0.001$; 10 h *v.* 100 h, $r^2 = 0.18$, $P < 0.001$, $n = 237$).

The three prescribed burns exhibited some variation in fire behaviour and the fuels consumed (Table 2). Lowest flame lengths were observed in the autumn 2001 burn and for most fuel categories there was less fuel consumption during this burn. For all burns, temperature profiles followed a common pattern in that aerial temperatures rose quickly and reached the highest peak, surface temperatures lagged behind but had longer heating duration and belowground temperatures remained above the starting ambient temperature longest (Fig. 1).

Fireline intensity was modest in these fires and was a two to several fold difference between sites (Table 2). Average fireline intensity was twice as high in the summer 2002 fire than the autumn 2001 fire. Fireline intensity was significantly related to maximum flame length recorded for each plot and the highest r^2 value was with the power model (Fig. 2), although this relationship only explained ~18% of the variation. This calculated fireline intensity was compared with estimates based just on flame length ($I = 258F^{2.17}$). Approximately one-third of the estimates were greatly under the calculated value, one-third relatively close and one-third greatly over the calculated value.

Table 2. Weather conditions and other characteristics of the three prescribed burns
Min., lowest mean of the six sites; max., highest mean of six sites; $\overline{X}$, mean of all plots from all sites

Variable	Fall 2001			Spring 2002			Fall 2002		
	Min.	Max.	$\overline{X} \pm$ s.e.	Min.	Max.	$\overline{X} \pm$ s.e.	Min.	Max.	$\overline{X} \pm$ s.e.
Air temperature (°C)	14.55	20.6	17.9 ± 0.3	25.0	27.7	26.4 ± 0.1	21.1	26.3	23.7 ± 0.2
Relative humidity (%)	21.8	35.8	29.8 ± 0.8	30.4	37.4	33.4 ± 0.3	21.5	29.0	24.0 ± 0.3
Maximum wind speed ($m\,s^{-1}$)	4.1	8.6	6.8 ± 0.2	2.3	9.9	7.1 ± 0.3	3.4	9.4	7.6 ± 0.3
Fuel moisture (%)	5.1	6.5	5.7 ± 0.05	1.6	4.0	2.5 ± 0.1	1.1	3.0	1.8 ± 0.1
Flame length (m)	0.36	0.71	0.50 ± 0.04	0.63	1.08	0.77 ± 0.08	0.39	1.10	0.72 ± 6.9
Flame speed ($m\,s^{-1}$)	0.02	0.05	0.03 ± 0.003	0.03	0.05	0.04 ± 0.002	0.03	0.05	0.04 ± 0.002
Fireline intensity ($kW\,m^{-1}$)	64	331	178 ± 33	153	822	352 ± 67	196	359	269 ± 37
Fuels consumed (%)									
1 h	6.3	47.7	26.3 ± 4.1	14.7	47.8	35.4 ± 4.3	28.0	51.8	45.2 ± 4.6
10 h	0	19.4	10.4 ± 2.7	8.6	27.4	21.0 ± 3.6	14.2	45.4	27.0 ± 3.8
100 h	6.7	22.9	11.3 ± 3.1	5.6	33.3	19.8 ± 3.8	0	25.0	9.8 ± 2.9
Wood	0	4.3	1.3 ± 0.4	0.7	3.2	1.9 ± 0.5	0.5	4.6	1.8 ± 0.5

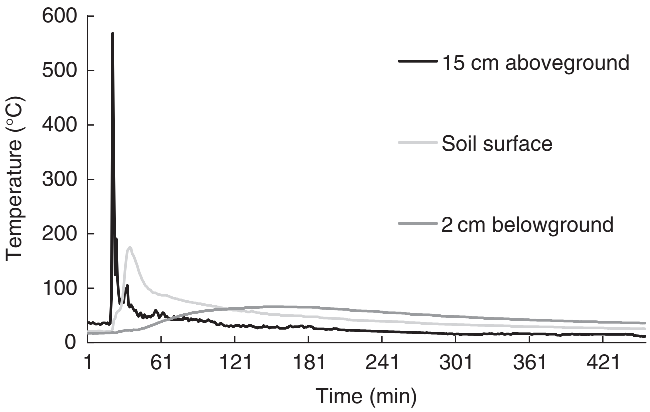

Fig. 1. Temperature profile for a plot during the fall 2002 prescription burn. Maximum flame length was 1.8 m and average flame speed was $0.036\,m\,s^{-1}$. Profile included 15 cm above the soil surface, soil surface, and 2 cm belowground.

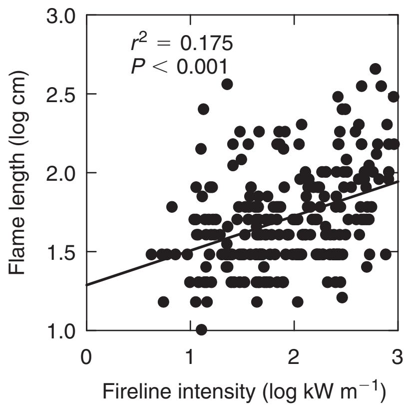

Fig. 2. Relationship between fireline intensity and flame length observed in experimental burns.

Fireline intensity exhibited a highly significant relationship with maximum temperature observed above and belowground (Fig. 3). The highest r^2 values were with the power model but this model explained only ~12–14% of the variation. A similar relationship was observed with the elevated temperature duration along this same vertical profile ($r^2 = 0.15$, 0.16, 0.14 for aboveground, surface and belowground, respectively, $P < 0.001$). The relationship between maximum temperatures observed and total elevated temperature duration were very strongly correlated at all three points along the vertical profile ($r^2 = 0.64$, 0.57, 0.48, $P < 0.001$).

Soil nutrient changes measured before and after the autumn 2002 burns showed slight changes. Nitrate increased significantly ($t_{105} = 2.28$, $P = 0.025$) from a preburn mean of 9.6 to a postburn mean 18.4 $mg\,kg^{-1}$ of soil. Ammonium, however, exhibited no significant change ($t_{105} = 0.61$, $P = 0.55$). Exchangeable soil potassium levels increased significantly after burning, from 137 to 150 ppm ($t_{107} = 7.67$, $P < 0.001$).

Annual cheatgrass cover

In control plots cheatgrass cover exhibited significant annual variation between 2001 and 2004, ranging from a high of 45% in 2001 to a low of ~15% in 2002 and 2004 ($F_{3,15} = 14.47$, $P < 0.001$). Total cover for other understorey species (mostly perennial grasses and forbs) also varied temporally, but in most years was nearly equal to cheatgrass cover, except in 2003 it was approximately twice as high as cheatgrass cover ($t_{15} = 3.75$, $P = 0.004$). Across all years, cheatgrass cover was negatively associated with other understorey cover ($r^2 = 0.04$, $P < 0.001$) and with species richness ($r^2 = 0.03$, $P = 0.002$).

Response to understorey burning

Prescribed burns had relatively few significant effects on the understorey response variables considered in the present study. In the first, and subsequent postfire growing seasons after both fall and summer burns, cheatgrass cover, cheatgrass biomass, other understorey cover and biomass did not change significantly ($P > 0.05$, *t*-test comparison with unburned control plots;

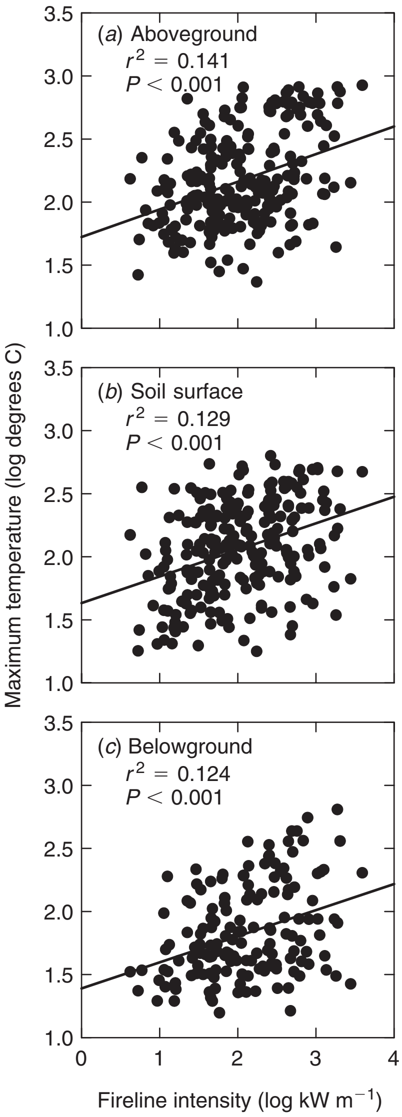

Fig. 3. Relationship between fireline intensity and maximum temperature recorded on the vertical profile at (*a*) 15 cm aboveground, (*b*) soil surface and (*c*) 10 cm belowground, in experimental burns.

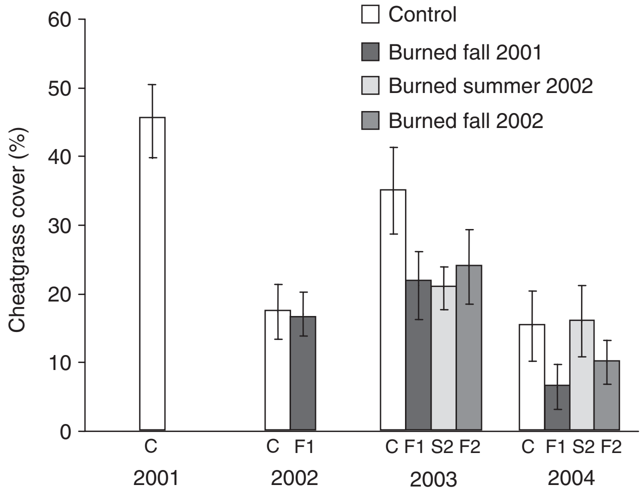

Fig. 4. Cheatgrass cover in control and burned plots measures in 2001–2004 (bars are standard error of the mean).

for cheatgrass cover see Fig. 4). Total species richness was significantly higher in the first growing season after the fall 2001 burn ($t_{20} = 4.60$, $P < 0.001$); however, this was not the case after the other two burns.

Bivariate linear regression analysis of postfire cheatgrass cover *v.* environmental and biological factors showed that the strongest predictor of postfire cheatgrass cover was prefire cheatgrass cover, but only ~12% of the variance was explained ($P < 0.001$). Other significant factors explained much less of the variance, between 1 and 4%, and included other understorey cover, percentage sand, hours of May sunlight in the plot and maximum wind speed during the experimental burns with a positive effect. Postfire cheatgrass cover was not significantly correlated with fireline intensity ($P = 0.30$) or most other measures of fire intensity with the exception of a weak negative relationship with maximum aerial temperature ($r^2 = 0.02$, $P = 0.03$).

Multiple regression analysis for predictors of postfire cheatgrass cover gave an adjusted $r^2 = 0.24$ ($P < 0.001$) with four significant independent variables: prefire cheatgrass cover, precipitation during the growing season, soil NH_4 levels all had positive effects and sunlight hours in the plot during May had a negative effect. With prefire cheatgrass cover removed this relationship was still significant (adjusted $r^2 = 0.15$, $P < 0.001$).

Effect of other treatments

Experimental manipulations included added nitrogen, reduced nitrogen, added phosphorous, reduced phosphorous, additional cheatgrass seeds, additional native grass seeds, increased shade, and (after 2001) additional needle litter. Following the 2001 burn, cheatgrass cover in 2002 was significantly affected by these treatments ($F_{7,88} = 3.78$, $P < 0.001$), with shade being the only treatment significantly different (greater) than controls. Other understorey cover showed no significant effects ($F_{7,88} = 0.92$, $P = 0.49$). Following the 2002 burns, cheatgrass cover and other understorey cover in 2003 (Fig. 5) were significantly affected by treatments ($F_{7,88} = 3.78$ and $F_{8,99} = 5.27$, respectively, $P < 0.001$). Unlike the previous year's experiment, the 2003 sampling included an additional treatment of needle addition, and the least significant difference test indicated this was the only significant manipulation for both cheatgrass and other understorey cover.

Cheatgrass germination

Seed survival during fires is affected by the maximum temperatures and duration of heating they experience during fire, as well as the moisture status of the seeds. Cheatgrass seed germination experiments indicate that when dry, these seeds were tolerant of a 1 h heating at temperatures up to 110°C (Fig. 6*a*). Moist seeds experienced highly reduced germination at 80°C and no germination above 100°C. Within the temperature range of 80–100°C, substantial increases in duration of heating had negligible effects: 98–100% germination occurred with 4 h at 80, 90 or 100°C, and 84% germination for 2 h at 110°C.

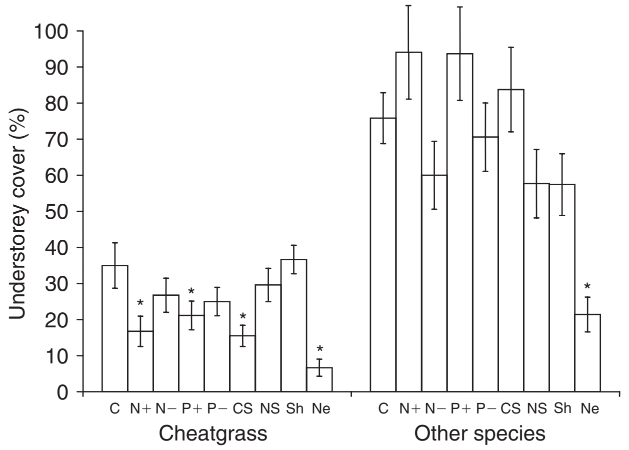

Fig. 5. Understorey cover of cheatgrass and other species recorded in 2003 following 2002 burns (bars indicate standard error of the means). CS, addition of cheatgrass seeds; N+, nitrogen addition; N−, nitrogen subtraction with sawdust addition; Ne, addition of surface needles; NS, addition of native bunchgrass seeds; P+, phosphorous addition; P−, phosphorous subtraction with addition of calcium carbonate; Sh, shade ($P < 0.05$).

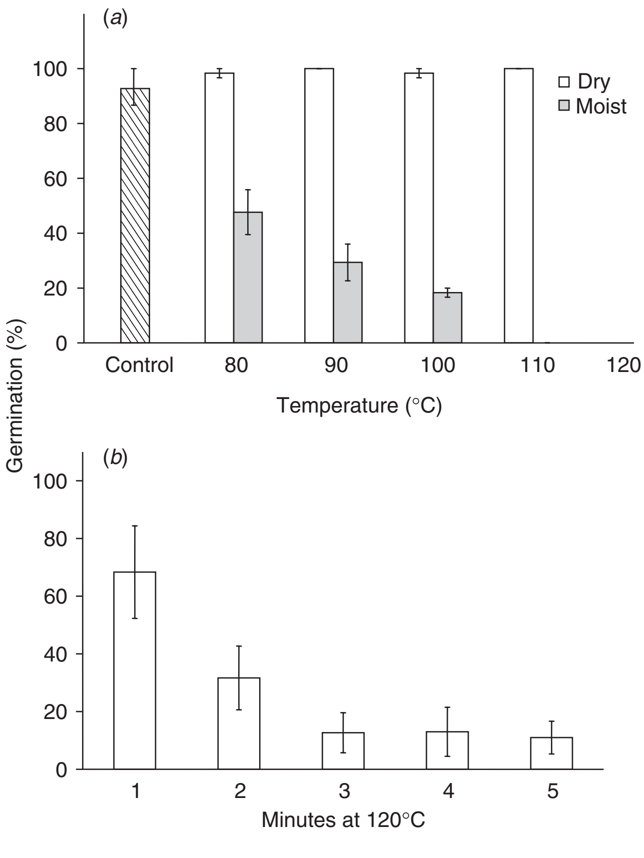

Fig. 6. Germination of cheatgrass seeds after (*a*) different temperature treatments for 1 h on dry and moist seeds, and (*b*) for different durations of heating dry seeds at 120°C.

Cheatgrass seeds survived brief exposures to 120°C, but germination dropped off rapidly beyond 1 min (Fig. 6*b*). Generally, heat-treated seeds that did not germinate rotted in the dishes, suggesting these treatments were lethal.

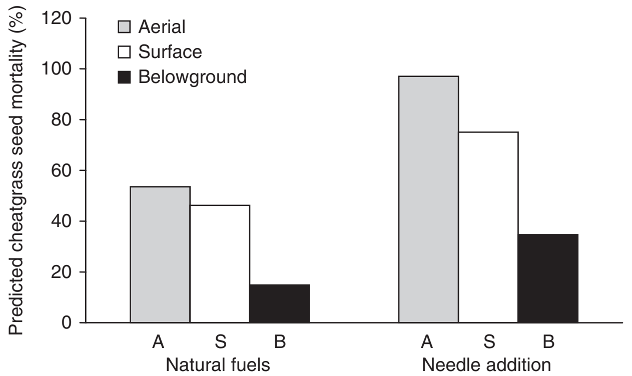

Fig. 7. Predicted cheatgrass seed mortality based on percentage of thermocouples with peak temperatures greater than 120°C. Shaded bars represent areas with natural fuel loads. White bars represent areas with 5 cm of pine needles added as fuel. A, 15 cm above ground measured with 'rapid-response' 0.16 cm diameter probes; S, surface level measured with rapid-response probes; B, 2 cm belowground.

Combining the relationship in Fig. 6 and the field thermocouple measurements, and assuming seeds are evenly distributed across the plots, predictions were made of mortality for seeds held aboveground on the plant, or on the soil surface, or buried at 2 cm (Fig. 7). With the natural fuel loads on these sites (Table 1), and burning conditions during these fires (Table 2), it is apparent that aerial seeds are the most likely to be killed, but based on the values reported in Fig. 7 over 40% are predicted to survive these burning conditions. If we narrow our predictions to include only those experimental plots where additional pine needles were added we find a much greater reduction in seed survival (Fig. 7).

Multivariate models

Examination of bivariate relationships of all relevant parameters indicated that all conceptual variables were best represented by a single observed variable. Our cheatgrass model explained postfire cheatgrass dominance by seven variables, including fire intensity, which was explained by just two variables (Fig. 8). There were 8 degrees of freedom and a chi-square of 6.94, which gave a $P = 0.54$, indicating no significant departure between data and the model. Postfire cheatgrass dominance was affected positively by cheatgrass seedbank, growing season precipitation, soil nitrogen, and number of hours of sunlight during the fall, and negatively by canopy coverage, summer sunlight hours and fire intensity. Fire intensity was slightly affected negatively by fuel moisture and most strongly by the positive effect of fuel load (coarse woody fuels were not included because they comprised a very small portion of the total fuel and often were not part of the available fuel). Hypothesised factors with very weak or no effect and removed from the model were the direct effect of soil texture and the direct effect of competition by other understorey plants.

An alternative model examined the factors determining postfire cheatgrass dominance in the absence of information on prefire cheatgrass seedbank (Fig. 9). This model had 7 degrees of freedom and a chi-square of 3.27 with a $P = 0.86$, indicating no significant departure between our model and our data.

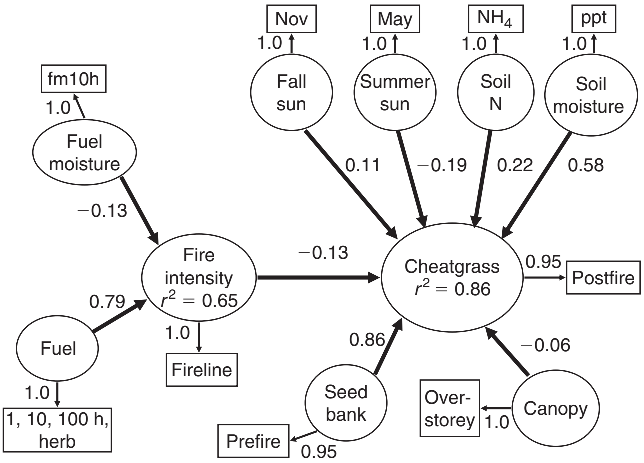

Fig. 8. Structural equation model of factors hypothesised to affect postfire cheatgrass dominance. Conceptual or latent variables (circles) and measurement variables (rectangles) are as follows (bold indicates name in figure): (i) **Cheatgrass** dominance (measured by cover at the end of the first **postfire** growing season), (ii) **Seedbank** of cheatgrass (measured by **prefire** cheatgrass cover, which is closely related to the relative seed production at different sites), (iii) canopy (measured by the inverse of light gap size in the **overstorey**), (iv) **Soil moisture** (measured by precipitation, **ppt**, the postfire growing season), (v) **Soil N** (measured by postfire $\mathbf{NH_4}$; nitrate and ammonium covaried across our sites), (vi) **Summer sun** (sun = hours of sunlight in **May**), (vii) **Fall sun** (sun = hours of sunlight in **Nov**), (viii) **Fire intensity** (measured by calculated **fireline** intensity), (ix) **Fuel moisture** (measured by percentage water in 10 h fuels; **fm10h**), and (x) **Fuel** (measured by total biomass of herbaceous fuels, and 1, 10, and 100 h dead surface fuels; **1, 10, 100 h, herb**). Standardised regression coefficients (standardised by the standard deviations of the variables) are presented adjacent to path arrows. Adjacent to arrows connecting latent variables to measurement variables are the loadings based on error estimates.

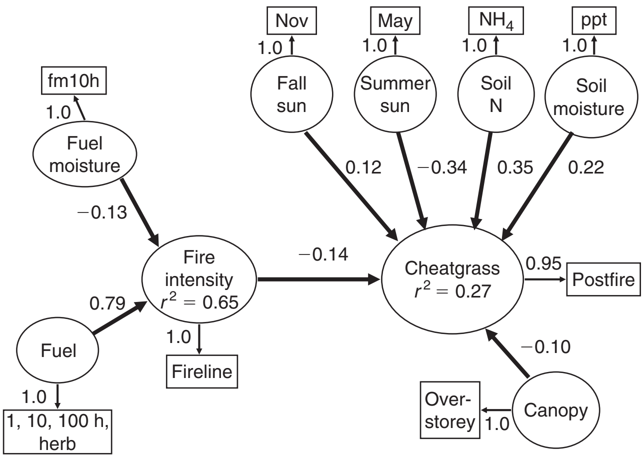

Fig. 9. Structural equation model of factors hypothesised to affect postfire cheatgrass dominance without the cheatgrass seedbank variable. See Fig. 8 legend for definitions of abbreviations.

Without information on prefire cheatgrass seedbanks the model still generated an $r^2 = 0.27$. In this model the positive effects of soil nitrogen and negative effects of summer sun became more important.

Both of these models were run with fireline intensity as the measure of fire intensity. We also tried two other measures of fire intensity: maximum temperature and duration of elevated temperature aboveground, at the surface, and belowground. Using each of these six other measurement variables separately to define fire intensity failed to provide a good model fit.

Discussion

Historically, western United States forests have not been highly threatened by non-native plants (Pierson and Mack 1990*a*, 1990*b*; Schwartz *et al.* 1996), thus the recent cheatgrass invasion in some ponderosa pine forests of Kings Canyon National Park is of considerable concern. The coincidence of this invasion with initiation of prescription burning in the late 1980s suggests that fire has played a role in the success of this alien, and this is consistent with other reports of alien increases following fire in south-western USA ponderosa pine forests. For example, Crawford *et al.* (2001) reported substantial increases in cheatgrass as well as many other alien species following burning in northern Arizona ponderosa pine forests. However, not all burning in ponderosa forests is accompanied by alien invasion (e.g. Laughlin *et al.* 2004), so it is a challenge to understand how burning interacts with site factors and other management practices to favour alien invasion on some landscapes and not others.

Once established in open ponderosa pine forests, our study suggests that relatively low intensity prescribed burning favours the long-term persistence of cheatgrass. Altering the burning season to coincide with growing season seed maturation (early summer on our sites), has been proposed as a means of controlling other annual species that depend on yearly restocking of the seed bank (e.g. DiTomaso *et al.* 1999), and has shown promise for controlling alien annuals in some forest types (Prober *et al.* 2004). However, our comparison of summer and fall burns does not point towards this as a viable option for control of cheatgrass in the southern Sierra Nevada, perhaps because the level of fuels (Table 1) resulted in fire intensities insufficient to decimate the cheatgrass seedbank (e.g. Fig. 7). It should be noted that the fireline intensities (Table 2) were well within the range for low intensity surface fires (Agee 1993), so this response may be generalisable to other semi-arid ponderosa sites. However, relative to the higher elevation mixed conifer forests in the southern Sierra Nevada, which have not experienced fires in more than a century, the fuel loads in the Kings Canyon ponderosa forests (Table 1) are substantially lower. In the former forest types, fuel loads are roughly 100–200 Mg ha^{-1} (Stephens *et al.* 2004; Knapp *et al.* 2005), which is orders of magnitude greater than observed on our sites, and thus cheatgrass response to prescription burning might be expected to differ in those forest types.

In terms of understanding fire effects on cheatgrass in ponderosa pine forests we expected measures of fire intensity such as maximum temperature or heating duration may be critical to survival of this annual plant's seed bank (Beadle 1940; Keeley 1991; Brooks 2002). However, fireline intensity showed the strongest relationship to postfire cheatgrass cover (Figs 8 and 9), and fireline intensity was only weakly related to other measures such as maximum temperature ($r^2 = 0.12$–0.14) and duration of heating ($r^2 = 0.14$–0.16). This weak relationship between fireline intensity and maximum temperature has been reported from other studies as well (e.g. Bradstock and Auld 1995). Fireline intensity is a rather time consuming parameter to measure and thus it is often estimated from flame length, based on the documented allometric relationship between flame length and measured fireline intensity (Andrews 1986; Johnson 1992). In our burns there was a statistically significant relationship between these two parameters, but flame length would be of limited predictive value as it explained only ~18% of the variation (Fig. 2). The weak correlation could be attributed to the fact that we only recorded maximum flame length for each 25-m^2 burn plot, rather than an average flame length, whereas fire intensity was based on the total fuel consumption in the plot. Or, the discrepancy could relate to the fact that measures of fireline intensity assume the only fuel consumed is that due to combustion by the flaming front, when in fact 10 h and 100 h fuels continue to combust after the flaming front passes. Neither of these factors seems likely as they both would predict a consistent bias in the predicted value, but instead we found about an equal number of expected values above the observed value as well as below (Fig. 5). Alternatively, the weak relationship between flame length and fireline intensity could be a characteristic of low severity fires generated largely by litter and pine needles. Nelson and Adkins (1986) reported that regardless of fuel load, such fires often produced a constant flame length due to boundary layer effects; a phenomenon apparently of lesser importance in more intense forest fires. These observations suggest that in light of the widespread use of this relationship between fireline intensity and flame length, there is need for greater documentation of the extent of its applicability.

Our models relating fire intensity to postfire cheatgrass success (Figs 8 and 9) apply to forests where cheatgrass has already established. Thus, propagule limitation is not likely to be a major factor (and this is supported by our cheatgrass addition experiment Fig. 5); and these models would not necessarily apply to forests where cheatgrass has not already established. Postfire cheatgrass success is well predicted by the cheatgrass seedbank, which in the present study was estimated by the prefire cheatgrass cover. However, this effect was only weakly evident from bivariate and multiple regression analysis. Thus, cheatgrass seedbanks alone are weak indicators of postfire cheatgrass dominance but very important in the context of other factors included in our models.

As fire intensity increases there is a negative effect on cheatgrass establishment but the overall effect was relatively weak. In this model the most important physical factor determining cheatgrass is the growing season precipitation. If we ignore the cheatgrass seedbank it is possible to explain a significant amount of variation in postfire cheatgrass establishment based on precipitation, soil ammonium levels, and gap characteristics that affect the amount of sunlight observed in late spring and early summer (Fig. 9).

Management implications

In addition to the Kings Canyon National Park invasion, cheatgrass has been reported from many sites in the Sierra Nevada Range. For example, further north it is frequent between 1200 and 2500 m elevation in Yosemite National Park (Gerlach *et al*. 2003). Also, on USFS forests both north and south of these parks, cheatgrass is acknowledged as a potential problem. On the Sequoia National Forest, particularly the Kern River drainage, there has been an increase of cheatgrass in recent years and the association of this alien with fires has raised concerns about management activities (Fletcher Linton, USFS, personal communication, August and November 2003). Farther north on the Eldorado National Forest cheatgrass and other annual bromes have invaded the Cleveland Fire of 1992 and altered the surface fuel structure, contributing to the 2001 St Pauli Fire (Mike Taylor, USFS, personal communication, October 2003). This latter fire re-burned a portion of the replanted Cleveland Fire area, killing ~70 000 trees over an area of ~100 ha for an estimated loss of US$250 000 in silvicultural treatments. The late 20th century increase of cheatgrass in Pacific slope Sierra Nevada ponderosa forests suggests that a new habitat is opening up to this species. With the recent passage of the *Healthy Forests Restoration Act of 2003 (H.R. 1904)* it is expected that in the coming decade western forests will have more thinning and fire restoration, which could enhance cheatgrass in some of these forests.

Current fire management in western conifer forests is focused on restoring structure and function because of perturbations in these forests. Certain national efforts at defining regional needs for such restoration, such as LANDFIRE, are focused on mapping deviations from historical fire regimes. However, historical fire regimes were played out on a landscape free from alien invaders. All of our study sites were burned once or twice during the latter part of the 20th century. Under these conditions cheatgrass thrives and the only treatment that showed potential for inhibiting cheatgrass was needle litter accumulation, which directly affected cheatgrass establishment (Fig. 5), and when burned it reduced cheatgrass seed banks (Fig. 8). Longer fire intervals are expected to naturally play this same role; however, we lack a clear model relating the length of fire intervals to litter accumulation sufficient to inhibit cheatgrass persistence. Until we have adequately studied the problem, fire managers might benefit from a more prudent approach that recognises there are potential negative resource impacts related to restoring historical fire frequencies. Of course returning to an era of total fire exclusion is not a viable solution; however, there is a large range of fire intervals between these two extremes. Where feasible, fire management should consider the option of an appropriate compromise between reducing serious fire hazards and exacerbating alien plant invasions.

Acknowledgements

Funding was from the Joint Fire Science Program (JFSB 00-1-2-04). We would like to thank Sequoia and Kings Canyon National Park staff, especially Bill Kaage, Tony Caprio, Jeff Manley, Dave Bartlett, Ben Jacobs, and Kevin Smith from fire management, who devoted a generous amount of time to the research burns. We thank Nate Wojkic and the Sanford Laboratory at the University of Denver for providing soil nitrogen data for this study. We thank USGS research personnel, Matt Brooks, Jayne Belnap, J. R. Matchett, Bridget Lair, Melissa Trader, Tyler Godin, Andi Heard, Sarah Graber, Tanya Baxter, Dale Ritenour, Joseph Rodriguez, Kim Bollens, Wil Mundy and statistician Julie Yee.

References

Agee JK (1993) 'Fire Ecology of Pacific Northwest Forests.' (Island Press: Covelo, CA)

Albini FA (1976) Estimating wildfire behavior and effects. USDA Forest Service, Intermountain Forest and Range Experiment Station General Technical Report INT-30. (Ogden, UT)

Alexander ME (1982) Calculating and interpreting forest fire intensities. *Canadian Journal of Botany* **60**, 349–357.

Andrews PL (1986) BEHAVE: fire behavior prediction and fuel modeling system: BURN subsystem, Part 1. USDA Forest Service, Intermountain Forest and Range Experiment Station General Technical Report INT-194. (Ogden, UT)

Armour CD, Bunting SC, Neuenschwander LF (1984) Fire intensity effects on the understory in ponderosa pine forests. *Journal of Range Management* **37**, 44–49.

Baker WL (2006) Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* **34**, 177–185. doi:10.2193/0091-7648(2006)34[177:FAROSE]2.0.CO;2

Beadle NCW (1940) Soil temperatures during forest fires and their effect on the survival of vegetation. *Journal of Ecology* **28**, 180–192. doi:10.2307/2256168

Beckstead J, Augspurger CK (2004) An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions* **6**, 417–432. doi:10.1023/B:BINV.0000041557.92285.43

Belnap J, Sherrod SK, Miller ME (2003) Effects of soil amendments on germination and emergence of downy brome (*Bromus tectorum*) and *Hilaria jaamesii. Weed Science* **51**, 371–378. doi:10.1614/0043-1745(2003)051[0371:EOSAOG]2.0.CO;2

Billings WD (1994) Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. In 'Proceedings – Ecology and Management of Annual Rangelands'. (Eds SB Monsen, SG Kitchen) pp. 22–30. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-GTR-313. (Ogden, UT)

Blumenthal DA, Jordan NR, Russelle MP (2003) Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* **13**, 605–615.

Borchert MI, Odion DC (1995) Fire intensity and vegetation recovery in chaparral: a review. In 'Brushfires in California Wildlands: Ecology and Resource Management'. (Eds JE Keeley, T Scott) pp. 91–100. (International Association of Wildland Fire: Fairfield, WA)

Bradstock RA, Auld TD (1995) Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* **32**, 76–84. doi:10.2307/2404417

Brooks ML (2002) Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecological Applications* **12**, 1088–1102.

Brown JK (1974) Handbook for inventorying downed woody material. USDA Forest Service Intermountain Forest and Range Experiment Station, General Technical Report INT-16. (Fort Collins, CO)

Bueno M, Keeley J, Stephenson N (2000) Southern Sierra repeat photography project. Report on file at the USGS research office, Sequoia-Kings Canyon Field Station, Three Rivers, CA.

Byram GM (1959) Combustion of forest fuels. In 'Forest Fire: Control and Use'. (Ed. KP Davis) pp. 61–89. (McGraw-Hill: New York)

Caprio A, Haultain S, Keifer MB, Manley J (1998) Problem evaluation and recommendations: invasive cheatgrass (*Bromus tectorum*) in Cedar Grove, Kings Canyon National Park. National Park Service. Report on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Chatterton NJ, Harrison PA, Thornley WR, Bennett JH (1993) Structures of fructan oligomers in cheatgrass (*Bromus tectorum* L.). *The New Phytologist* **124**, 389–396. doi:10.1111/J.1469-8137.1993.TB03829.X

Cox GW (1995) 'Laboratory Manual of General Ecology.' 5th edn. (WC Brown Publishers, USA: Dubuque, IO)

Crawford JA, Wahren CHA, Kyle S, Mohr WH (2001) Responses of exotic plant species to fires in Pinus ponderosa forests in northern Arizona. *Journal of Vegetation Science* **12**, 261–268.

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**, 63–87.

D'Antonio C, Levine J, Thomsen M (2001) Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *Journal of Mediterranean Ecology* **2**, 233–245.

Dilsaver LM, Tweed WC (1990) 'Challenge of the Big Trees.' (Sequoia Natural History Association: Three Rivers, CA)

DiTomaso JM, Kyser GB, Hastings MS (1999) Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. *Weed Science* **47**, 233–242.

Gerlach JD, Moore PE, Johnson B, Roy DG, Whitmarsh P, Lubin DM, Graber GM, Haultain S, Pfaff A, Keeley JE (2003) Alien plant species threat assessment and management prioritization for Sequoia-Kings Canyon and Yosemite National Parks. US Geological Survey Open-File Report 02-170.

Grace JB (2002) Structural equation modeling. In 'Analysis of Ecological Communities'. (Eds B McCune, JB Grace) pp. 233–256. (MjM Software Design: Gleneden Beach, OR)

Grace JB (2006) 'Exploring Natural Systems Using Multivariate Hypotheses.' (Cambridge University Press: Cambridge, UK)

Harris GA (1967) Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum. Ecological Monographs* **37**, 89–111. doi:10.2307/2937337

Hulbert LC (1955) Ecological studies of *Bromus tectorum* and other annual bromegrasses. *Ecological Monographs* **25**, 181–213. doi:10.2307/1943550

Humphrey LD, Schupp EW (2004) Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* **58**, 405–422. doi:10.1016/J.JARIDENV.2003.11.008

Johnson EA (1992) 'Fire and Vegetation Dynamics: Studies from the North American Boreal Forest.' (Cambridge University Press: Cambridge, UK)

Keeley JE (1991) Seed germination and life history syndromes in the California chaparral. *Botanical Review* **57**, 81–116.

Keeley JE (2006) Fire management impacts on invasive plants in the Western United States. *Conservation Biology* **20**, 375–384. doi:10.1111/J.1523-1739.2006.00339.X

Keeley JE, Lubin D, Fotheringham CJ (2003) Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* **13**, 1355–1374.

Kilgore BM, Taylor D (1979) Fire history of a sequoia-mixed conifer forest. *Ecology* **60**, 129–142. doi:10.2307/1936475

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. History, persistence, and influences of human activities. *Global Environmental Change* **6**, 37–52. doi:10.1016/0959-3780(95)00112-3

Knapp EA, Keeley JE, Ballenger EA, Brennan TJ (2005) Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* **208**, 383–397. doi:10.1016/J.FORECO.2005.01.016

Laughlin DC, Bakker JD, Stoddard MT, Daniels ML, Springer JD, Gilar CN, Green AM, Covington WW (2004) Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management* **199**, 137–152.

Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* **7**, 145–165. doi:10.1016/0304-3746(81)90027-5

McDonald PM, Everest GA (1996) Response of young ponderosa pines, shrubs, and grasses to two release treatments. USDA Forest Service, Research Note, PSW-RN-419-Web.

Melgoza G, Nowak RS (1991) Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distribution. *Journal of Range Management* **44**, 27–33.

Melgoza GR, Nowak S, Tausch RJ (1990) Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* **83**, 7–13. doi:10.1007/BF00324626

Muir J (1891) 'A Rival of the Yosemite: The Canyon of the South Fork of the Kings River, California.' (Outbooks: Golden, CO)

Nelson RM, Jr, Adkins CW (1986) Flame characteristics of wind-driven surface fires. *Canadian Journal of Forest Research* **16**, 1293–1300.

Pierson EA, Mack RN (1990*a*) The population biology of *Bromus tectorum* in forests: distinguishing the opportunity for dispersal from environmental restriction. *Oecologia* **84**, 519–525.

Pierson EA, Mack RN (1990*b*) The population biology of *Bromus tectorum* in forests: effect of disturbance, grazing, and litter on seedling establishment and reproduction. *Oecologia* **84**, 526–533.

Pierson EA, Mack RN, Black RA (1990) The effect of shading on photosynthesis, growth, and regrowth following defoliation for *Bromus tectorum. Oecologia* **84**, 534–543.

Prober SM, Thiele KR, Koen TB (2004) Spring burns control exotic annual grasses in a temperate grassy woodland. *Ecological Management & Restoration* **5**, 131–134.

Rafferty DL, Young JA (2002) Cheatgrass competition and establishment of desert needlegrass seedlings. *Journal of Range Management* **55**, 70–72.

Rice KJ, Black RA, Radamaker G, Evans RD (1992) Photosynthesis, growth, and biomass allocation in habitat ecotypes of cheatgrass (*Bromus tectorum*). *Functional Ecology* **6**, 32–40. doi:10.2307/2389768

Schwartz MW, Porter DJ, Randall JM, Lyons KE (1996) Impact of non-indigenous plants. In 'Sierra Nevada Ecosystem Project: Final Report to Congress. Volume 2. Assessments and Scientific Basis for Management Options'. pp. 1203–1218. (Centers for Water and Wildland Resources, University of California: Davis, CA)

Sellers JA (1970) Mixed conifer forest ecology: a quantitative study in Kings Canyon National Park, Fresno County, California. MA thesis, Fresno State College, Fresno, CA.

Stephens SL, Finney MA, Schantz H (2004) Bulk density and fuel loads of ponderosa pine and white fir forest floors: impacts of leaf morphology. *Northwest Science* **78**, 93–100.

Stewart G, Young AE (1939) The hazard of basing permanent grazing capacity on *Bromus tectorum. Journal of the American Society of Agronomy* **31**, 1002–1015.

Stillman JM (1897) To Tihipite Valley from King's River Grand Canon. *Sierra Club Bulletin* **2**, 44–49.

Strong DH (2000) 'From Pioneers to Preservationists: A Brief Hstory of Sequoia and Kings Canyon National Parks.' (Sequoia Natural History Association: Three Rivers, CA)

Warg SA (1938) Life history and economic studies on *Bromus tectorum*. MSc thesis, State University of Montana, Missoula, MT.

Warner TE (1980) Fire history in the yellow pine forest of Kings Canyon National Park. In 'Proceedings of the Fire History Workshop'. (Eds MA Stokes, JH Dieterich) pp. 89–92. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report GTR-RM-81. (Fort Collins, CO)

Yoder C, Caldwell M (2002) Effects of perennial neighbors and nitrogen pulses on growth an nitrogen uptake by *Bromus tectorum. Plant Ecology* **158**, 77–84. doi:10.1023/A:1014716406271

Young JA, Evans RA (1978) Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* **31**, 283–289.