

RESEARCH ARTICLE

FUEL MOISTURE DIFFERENCES IN A MIXED NATIVE AND NON-NATIVE GRASSLAND: IMPLICATIONS FOR FIRE REGIMES

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ABSTRACT

Non-native plants have far-reaching effects on many terrestrial ecosystems. There are several examples of non-native species altering fire regimes, either by increasing or decreasing the potential intensity and severity of fires. To investigate this phenomenon, we sampled fuel moisture content of four native grass species (*Festuca californica* Vasey, *Danthonia californica* Bol., *Elymus glaucus* Buckley, and *Bromus carinatus* Hook. & Arn.) and four non-native grass species (*Phalaris aquatica* L., *Cynosurus echinatus* L., *Arrhenatherum elatius* [L.] J. Presl & C. Presl, and *Anthoxanthum odoratum* L.) in northern California grasslands across the 2012 growing season. No significant differences in moisture content were found between native and non-native groups ($P = 0.337$). Across all dates, moisture content of the eight

RESUMEN

Las plantas no-nativas tienen efectos de gran alcance en muchos ecosistemas terrestres. Hay varios ejemplos de especies de plantas no-nativas que alteran los regímenes de fuego, tanto por aumentar o disminuir la intensidad potencial y la severidad de los fuegos. Para investigar este fenómeno, nosotros muestreamos el contenido de humedad del combustible de cuatro especies de gramíneas nativas (*Festuca californica* Vasey, *Danthonia californica* Bol., *Elymus glaucus* Buckley, y *Bromus carinatus* Hook. & Arn.) y cuatro especies de gramíneas no-nativas (*Phalaris aquatica* L., *Cynosurus echinatus* L., *Arrhenatherum elatius* [L.] J. Presl & C. Presl, y *Anthoxanthum odoratum* L.) en pastizales del norte de California en la temporada de crecimiento de 2012. Diferencias no significativas en el contenido de humedad fueron encontradas entre grupos de nativas y no-nativas. ($P = 0.337$). A través de todas las fechas, los contenidos de humedad de las ocho especies de gramíneas difirieron significativa-

grass species differed ($P < 0.001$). The non-native annual *Cynosurus echinatus* had the lowest moisture content in August (21%), and fell well below ignition thresholds before the other grasses. *Phalaris aquatica*, an aggressive perennial non-native, had the highest moisture content for all months and differed significantly from all species for all dates ($P < 0.05$). Our results suggest that some non-native species have the capacity to alter fire behavior by either increasing or decreasing fire intensity and rate of spread. These findings reveal another way non-native species complicate restoration and management of fire-dependent ecosystems.

mente ($P < 0.001$). La especie no-nativa anual *Cynosurus echinatus* tuvo el contenido de humedad más bajo en agosto (21%), que fue por debajo del límite de ignición de otras gramíneas. *Phalaris aquatica*, una especie no-nativa perenne y agresiva, tuvo el contenido más alto de humedad en todos los meses y se diferenció significativamente de todas las especies en todas las fechas ($P < 0.05$). Nuestros resultados sugieren que algunas especies no-nativas tienen la capacidad de alterar el comportamiento del fuego incrementando o disminuyendo la intensidad del fuego y la velocidad de propagación. Estos hallazgos revelan otra forma en que las especies no-nativas complican la restauración y el manejo de ecosistemas dependientes del fuego.

Keywords: California, ecological restoration, *Festuca californica*, flammability, grasslands, invasive grasses, *Phalaris aquatica*, prescribed fire

Citation: Livingston, A.C., and J.M. Varner. 2016. Fuel moisture differences in a mixed native and non-native grassland: implications for fire regimes. *Fire Ecology* 12(1): 73–87. doi: 10.4996/fireecology.1201073

INTRODUCTION

Non-native plant invasions are responsible for a broad range of ecological effects, including the alteration of fire regimes (Brooks 1999, Davies and Nafus 2012, McDonald and McPherson 2013). In extreme cases, non-native plant invasions may cause community level changes, or even complete transformations of ecosystems by either increasing or decreasing the prevalence of fire (Mack and D'Antonio 1998, Brooks *et al.* 2004). For example, where non-native grasses invade desert shrubland, they create a novel fuel source that has dramatic consequences for these ecosystems (Brooks 1999, D'Antonio 2000, Davies and Nafus 2012). In cases in which non-native species differ only subtly from native species in the communities that they invade, they may have small effects on biomass, moisture content, or other fuel properties, causing sub-

tle changes to fire regimes (Mack and D'Antonio 1998, D'Antonio 2000, Brooks 2008, McGranahan *et al.* 2013).

Several examples of changes to fuelbed properties resulting from non-native species invasions have been described (Brooks *et al.* 2004, Brooks 2008). By increasing horizontal fuel continuity and biomass, cheatgrass (*Bromus tectorum* L.) has increased the spread rate and frequency of fire in sparsely vegetated areas of western North America, creating a feedback between the invasive grass and fire (D'Antonio and Vitousek 1992, D'Antonio 2000, Brooks *et al.* 2004). This grass-fire cycle has resulted in the loss of native shrubsteppe vegetation over vast areas of the western United States, and has shortened the fire return interval from 50 to 100 years, to only three to five years between fires (D'Antonio 2000, Davies and Nafus 2012). The invasive red brome (*Bromus madritensis* ssp. *rubens*

Husn.) has caused similar changes to fire regimes in the Mojave Desert, USA, threatening native plants and altering habitat and food plants of the endangered desert tortoise (*Gopherus agassizii* Cooper; Brooks and Esque 2002). Two invasive grasses in south Florida slash pine (*Pinus elliottii* Engelm. var. *densa* Little & K.W. Dorman) savannas, cogongrass (*Imperata cylindrica* [L.] P. Beauv.) and silk reed (*Neyraudia reynaudiana* [Kunth.] Keng), alter fuelbed properties due to their large biomass relative to native species, resulting in increased fire intensity harmful to native species (Platt and Gottschalk 2001). Similarly, in arid and semi-arid parts of the world, buffelgrass (*Pennisetum ciliare* [L.] Link) dramatically increases fuel loads leading to greater fire intensity, also to the detriment of native species (McDonald and McPherson 2013). The invasion of gamba grass (*Andropogon gayanus* Kunth.), in northern Australia, increased fuel loads resulting in a six-week extension of severe fire season (Setterfield *et al.* 2013). In other cases, non-natives diminish aspects of fire regimes including spread or intensity. The Brazilian pepper tree (*Schinus terebinthifolius* Raddi) invades fire-maintained Florida prairies at such high densities that it suppresses understory fuels necessary to maintain fire (Mack and D'Antonio 1998), as has Chinese tallow (*Triadica sebifera* [L.] Small) in temperate grasslands of North America (Bruce *et al.* 1997).

Fire behavior in grasslands is affected by particle properties of live fuels including foliar moisture content, surface area-to-volume ratio, and heat content (Brooks *et al.* 2004, Dibble *et al.* 2007, Davies and Nafus 2012, McGranahan *et al.* 2013). The moisture content of the species composing a fuelbed determines whether it functions as a heat sink or a heat source influencing the ignitability and combustibility of fuels, and the spread rate and intensity of fire (Chuvienco *et al.* 2004, Dimitrakopoulos *et al.* 2010). By decreasing the moisture content of the fuelbed it has invaded,

cheatgrass has expanded the fire season by approximately 30 days in southeastern Oregon, USA (Davies and Nafus 2012). Conversely, the invasion of the cool season (C3) grass tall fescue (*Festuca arundinacea* Schreb.) into tallgrass prairie composed of native warm season (C4) species decreases fire intensity and spread (McGranahan *et al.* 2013). This dampening effect is due to the asynchronous phenology of tall fescue compared to the native species, which results in its higher moisture content during the fire season (McGranahan *et al.* 2013). Similarly, the high moisture content of invasive iceplant (*Carpobrotus edulis* [L.] L. Bolus) decreases the ignitability of the native, fire-dependent chaparral (D'Antonio 2000, Brooks *et al.* 2004).

Several non-native grass species have successfully invaded the coastal grasslands and neighboring oak savannas and woodlands of the Bald Hills in Redwood National Park, California, USA (Sugihara and Reed 1987, Arguello 1994). Frequent, low intensity fires are necessary for the persistence of these fire-dependent ecosystems that are otherwise susceptible to encroachment from native conifers and potential shift to conifer forest (Sugihara and Reed 1987, Agee 1993, Fritschle 2008, Engber *et al.* 2011). In the Bald Hills and elsewhere in the Pacific Northwest (Tveten and Fonda 1999, Hosten *et al.* 2006, Engber and Varner 2012), managers rely on prescribed fires for the maintenance of these communities, adding to the importance of understanding the effects that non-native species may have on these fire regimes.

To add to the collective understanding of the ways non-native grass species may influence fire regimes, we measured grass fuel properties in a California grassland heavily invaded by a diversity of non-native grasses. We sampled the moisture content and stature of eight dominant native and non-native grass species. We compared moisture content between native and non-native groups, among species, and across collection periods for four

native and four non-native grasses during the 2012 growing season. Our findings have implications for California grasslands and perhaps more broadly, where mixtures of native and non-native grasses occur.

METHODS

Study Site

We collected fuels in the grasslands of the Bald Hills of Redwood National Park, in northwestern California, USA (41° 12' N, 123° 54' W; Figure 1). The Bald Hills span a broad, five-kilometer long ridge dividing the Klamath River and Redwood Creek watersheds. The Bald Hills contain 1700 ha of grasslands and oak (primarily *Quercus garryana* Hook.) savannas and woodlands composed of a mix of native and non-native herbaceous species. The climate is mediterranean, with approximately 90% of the approximately 200 cm of precipitation falling as rain between October and May. A strong Pacific Ocean influence causes summer fog that usually clears by late morning. The mean daily high temperature in July



Figure 1. Moisture content of native and non-native grasses were sampled at Williams Ridge in the Bald Hills of Redwood National Park, California, USA. The grasslands in the foreground are a mixture of native and non-native grass species, including several of the study species.

is 25°C, with temperatures rarely exceeding 38°C (USDI Redwood National Park 1992).

Fires in the Bald Hills were historically caused by both lightning ignitions and by Native American burning (Agee 1993). Native Americans routinely burned the prairies and woodlands of the Bald Hills to favor plants for human consumption, sustain basketry materials, and attract wildlife (Underwood *et al.* 2003, Hosten *et al.* 2006). European settlers arrived in the late 1860s and began grazing sheep and cattle (Underwood *et al.* 2003). A study from the early twentieth century indicates that, prior to European settlement, the prairies in the Bald Hills were likely dominated by native bunchgrasses, including species of *Danthonia* DC., *Stipa* L., *Melica* L., *Poa* L., and *Festuca* L., mixed with annual and perennial clovers (*Trifolium* L. spp.) (Davy 1902). Livestock grazing in the Bald Hills continued until 1978 and had a dramatic influence on vegetation. Many non-native grass and forb species were introduced as a result of grazing and have since become widespread (Saenz and Sawyer 1986, Sugihara *et al.* 1987, Grenier 1989). Fire suppression, which began after European settlement, also contributed to a shift in species composition (Underwood *et al.* 2003).

By the early 1990s, tall oatgrass (*Arrhenatherum elatius* [L.] J. Presl & C. Presl), sweet vernal grass (*Anthoxanthum odoratum* L.), and dogtail (*Cynosurus echinatus* L.), were among the most dominant non-native species in the grasslands of the Bald Hills (Saenz 1983, Grenier 1989, Arguello 1994). Harding grass (*Phalaris aquatica* L.) was first detected in the park at this time, and quickly spread throughout the grasslands. Due to its tendency to form dense monocultures, Harding grass is currently the most problematic non-native grass in the park (S. Samuels, National Park Service, Orick, California, USA, personal communication). A prescribed fire program was initiated in the early 1990s to control invasion of the native conifer Douglas-fir (*Pseudotsuga men-*

ziesii [Mirb] Franco var. *menziesii*) and to maintain native herbaceous species richness (Underwood *et al.* 2003). The fire season for the area spans early summer to late fall; prescribed fires typically occur between September and early November each year.

To compare fuel moisture of native and non-native grasses, we sampled eight grass species during the 2012 growing season. We concentrated sampling over 131 days from 6 June through 14 October 2012 within in a 150 m × 150 m area within the East and West Williams Ridge burn units. The study site is representative of a typical grassland in the Bald Hills, based on the species composition (Figure 1). Away from edges of oak woodlands and conifer forest, grasslands in the Bald Hills are largely devoid of woody fuels (Engber *et al.* 2011). The burn units were 22.5 km inland from the Pacific Ocean at an elevation of 730 m. Both units were located within 1 km of a remote automated weather station (RAWS) located at Schoolhouse Peak (SHUC1). Williams Ridge West was burned in 1992, and both units were burned in 1995, 1997, 2005, and on 19 October 2012. One study species, Harding grass, was not abundant in the Williams Ridge burn units so a population was selected in a separate burn unit within 1 km of the other species. Following sampling in June, the initial patch of Harding grass selected for our study was accidentally sprayed with herbicide. For all other months, sampling occurred approximately 10 m downslope of the original population.

Field Data Collection

The grasslands in the Bald Hills are dominated by perennials, though several annual grasses are also present, the majority of which are non-native (Livingston 2014). The eight species chosen for this study were selected based on their prevalence. The native species studied were California brome (*Bromus californica* Hook. & Arn.), blue wildrye (*Elymus*

glaucus Buckley), California oatgrass (*Danthonia californica* Bol.), and California fescue (*Festuca californica* Vasey) (Figure 2). The non-native species studied were Harding grass, dogtail, tall oatgrass, and sweet vernal grass (Figure 2). All study species are perennial with the exception of dogtail, a small-statured annual, and all are physiologically similar, cool season (C3) species. All of the species have a generally cespitose, or at least tufted, growth form, and several are sometimes also rhizomatous. Harding grass is rhizomatous, and sweet vernal grass and tall oatgrass are sometimes rhizomatous. Blue wildrye sometimes has rhizomes or short stolons. California fescue is an exceptionally robust native grass, with a clump-like growth form that retains abundant dead thatch. It is considered important in regional fire regimes because it is a highly flammable native species (Hastings *et al.* 1997, Engber *et al.* 2011).

Grass fuel moisture sampling occurred throughout the growing season, once each month during June to August of 2012, and at two week intervals during the peak of the prescribed fire season starting in September. Sampling ended one week prior to the prescribed burning of Williams Ridge East and West on 19 October 2012. We sampled fuel moisture via clipping stalks and leaves approximately 1 cm from the ground surface. We placed collected biomass in pre-weighed 15 cm × 23 cm polyethylene bags. Seven samples were collected for each species on each sampling date. Samples ranged from 20 g to 60 g (oven-dry weight), depending on the size of the species. With the exception of California fescue, samples included live and, as the season progressed, cured material of the current year's growth. Due to its unique habit, the large bunchgrass California fescue was sampled by cutting a section from the outside edge of the bunch toward the center, which included dead thatch connected to the plant and live plant material. We also recorded heights for each species on each sampling date to track

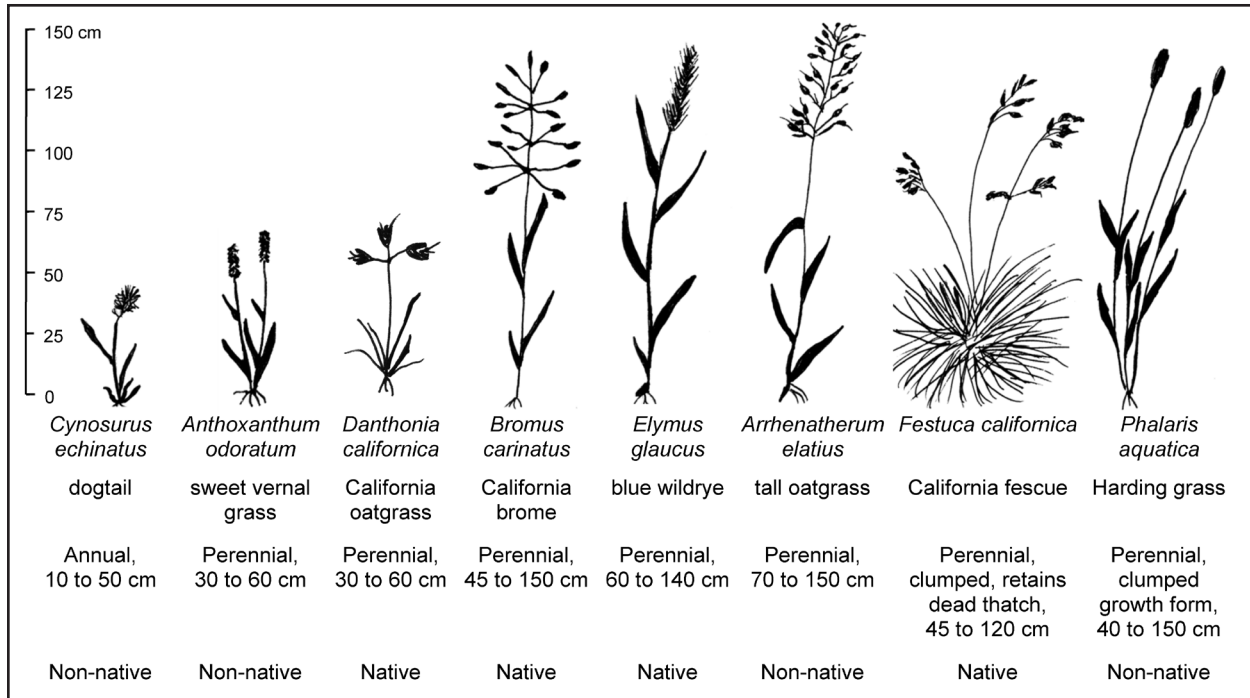


Figure 2. Grass species sampled for foliar moisture content during the 2012 fire season in the Bald Hills of Redwood National Park. We selected four native and four non-native grass species to study their effects on the fuelbed.

relative differences in stature throughout the growing season. After collection, we transported all grass samples directly to the laboratory. With the exception of 14 October, when the weather was partly cloudy, sampling occurred on clear days between 1130 hr and 1700 hr. Our sampling window was slightly longer than what others have considered ideal for minimizing variation in environmental conditions (Countryman 1974, Rice 1989, Agee *et al.* 2002); however, the large amount of sampling necessitated expanding the window. To determine wet weight, we weighed each specimen inside the pre-weighed polyethylene bag, and then subtracted the bag weight to determine actual wet weight. After weighing, we dried grasses in a convection oven at 70°C for 48 h until dry weight stabilized. We weighed all dry samples to determine dry weight (gravimetric basis).

The grass populations sampled, for all species except Harding grass, were spread throughout a 150 m × 150 m area; the Harding

grass population was less than 1 km away. Species were sampled in the same order on each date to maximize efficiency and maintain consistency. To evaluate the effect that time of collection had on fuel moisture values, we sampled from a subset of four species every two hours over an eight-hour period, on a single day on 10 October 2012. Two native species, California fescue and blue wildrye, and two non-native species, Harding grass and sweet vernal grass, were sampled. We sampled these species at two-hour intervals between 0900 hr and 1700 hr. Due to the small amount of Harding grass remaining at our study site, only two to three samples of this species were collected at each interval. The number of samples collected for the other species depended upon the abundance of easily accessible material; three samples were collected for blue wildrye, four for California fescue, and five for sweet vernal grass. Throughout the eight-hour sampling period, the air temperature ranged from 12.8°C to 16.7°C,

relative humidity ranged from 62% to 80%, and wind speeds ranged from 3.2 km h⁻¹ to 9.7 km h⁻¹.

Data Analysis

To evaluate differences in grass moisture content (%) among the eight grass species, across the six sampling dates, and for the species and date interaction, we used a two-way analysis of variance (ANOVA). A two-way ANOVA was used instead of a time series analysis because of the small number of sampling dates, and due to the fact that the dates increased in frequency during peak fire season. Residual plots were evaluated and assumptions for normality and homogeneity of variance were met (Zar 1999). When differences were detected, we used the conservative Tukey HSD (Honest Significant Difference) multiple comparison test to compare all pairwise differences. Significance for all statistical analyses was determined using $\alpha = 0.05$.

A hierarchical, linear mixed effects model with binomial error structure and logit link was used to evaluate differences among the mean moisture content of the native species and non-native species across all sampling dates, with the eight species nested into a native or non-native group type. Our model included a single fixed effect categorical variable for native or non-native species. Moisture content was the response variable. Sampling date and species were designated as random effects (Crawley 2013). Residual plots were assessed, revealing that the model met the assumptions for normality and homogeneity of variance (Zar 1999). Diurnal sampling results were evaluated by comparing mean and standard error of moisture content of each species at each interval over the eight-hour sampling period.

RESULTS

The mean monthly moisture content of the native grass species did not differ significantly

from the non-native grasses across all six sampling dates (fixed-effects ANOVA; $F_{1,6} = 1.088$, $P = 0.337$). There was, however, a significant difference in moisture content among the eight species across the sampling dates ($F_{47} = 179.4$, $P < 0.001$). Harding grass had higher mean moisture content on all sampling dates compared to the other seven species (Tukey HSD $P < 0.05$); it was the only species that differed from all other species across all sampling dates. The mean moisture content of Harding grass was 303% in June while the mean moisture content of all other species ranged from 107% to 266%. As the growing season progressed, the gap between mean moisture content of Harding grass and all other species widened (Figure 3). On 25 September, when Harding grass was driest, its mean moisture content was still more than double that of California fescue (116% compared to 49%). The mean moisture content of Harding grass was several times higher than all the other species, which ranged from only 6% to 19%.

The non-native dogtail had significantly lower mean moisture content than all other species except sweet vernal grass and California oatgrass (Tukey HSD $P < 0.05$). On 6 August, the mean moisture content of dogtail and California oatgrass were 21% and 42%, respectively. They were the only species to fall below an ignition threshold at this date, assuming a conservative moisture of extinction value of 55% (Dimitrakopoulos *et al.* 2010). Mean moisture content of all other species ranged from 57% to 182% in August. By the next sampling date, 5 September, the mean moisture content for all other species except Harding grass and California fescue ranged from 6% to 29% (Figure 3) and fell below a probable threshold for moisture of extinction. On this date, the mean moisture content of California fescue was 59%, while the moisture content of Harding grass remained much higher with a mean of 117%.

The moisture content of the grasses throughout the growing season varied to dif-

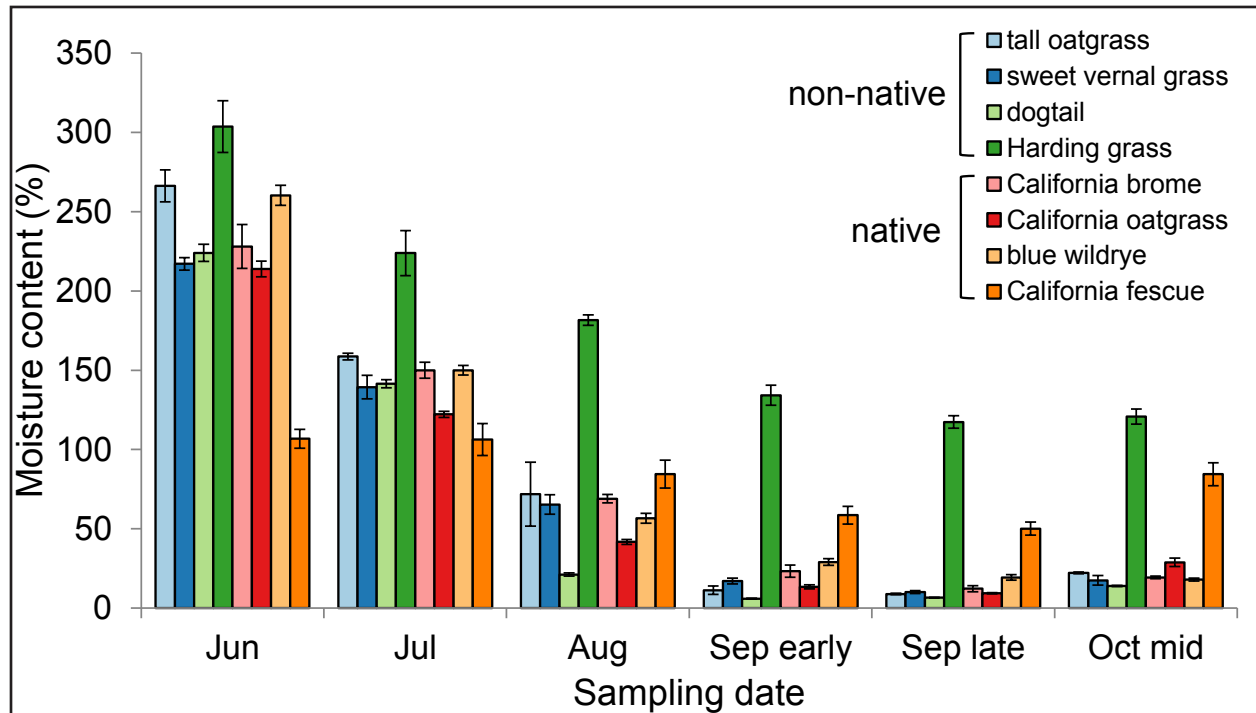


Figure 3. Moisture content of four native (pink through orange) and four non-native (blue through green) grass species across the 2012 fire season in the Bald Hills of Redwood National Park. Error bars represent SE.

ferent extents. The native California fescue’s mean moisture content varied the least across the sampling period. Its mean moisture content was highest in June (107%) and lowest in late September (50%). Harding grass had the next smallest amount of change across the season, from a high average of 304% to a low of 117%. Dogtail had the largest range of mean moisture content values, ranging from a high of 224% in June, to a low of 6% in early September.

The moisture content of all eight grass species followed the seasonal precipitation trends for 2012, and a significant interaction was found between species and date ($F_{288} = 179.4$, $P < 0.001$). Precipitation in 2012 was higher than the 10-year average, according to data from the Schoolhouse Peak weather station, and the moisture content values likely reflect this. Precipitation during March was double the 10-year average, and April and June had slightly more precipitation than average.

During July, 26 mm of rain fell, nearly twice the 10-year average. Mean moisture content of all species was highest in June and July when precipitation was still occurring (Figure 4), and declined in August after rainfall ended for the season. The moisture content of all species except blue wildrye increased by the 14 October sampling date after a cumulative 10.4 mm of rain had fallen. Mean moisture content of blue wildrye was 19% in late September and 18% on 14 October.

Results from sampling diurnal moisture content confirmed that influence from weather variation was minimal after late morning (1100 hr) and that our fuel sampling window (1130 hr to 1700 hr) was appropriate for these grasses. Three of the four species we sampled showed a large decrease in moisture content between the 0900 hr and 1100 hr morning collection times. Between 1100 hr and 1700 hr, the moisture content of all species sampled were relatively stable. Data from diurnal sam-

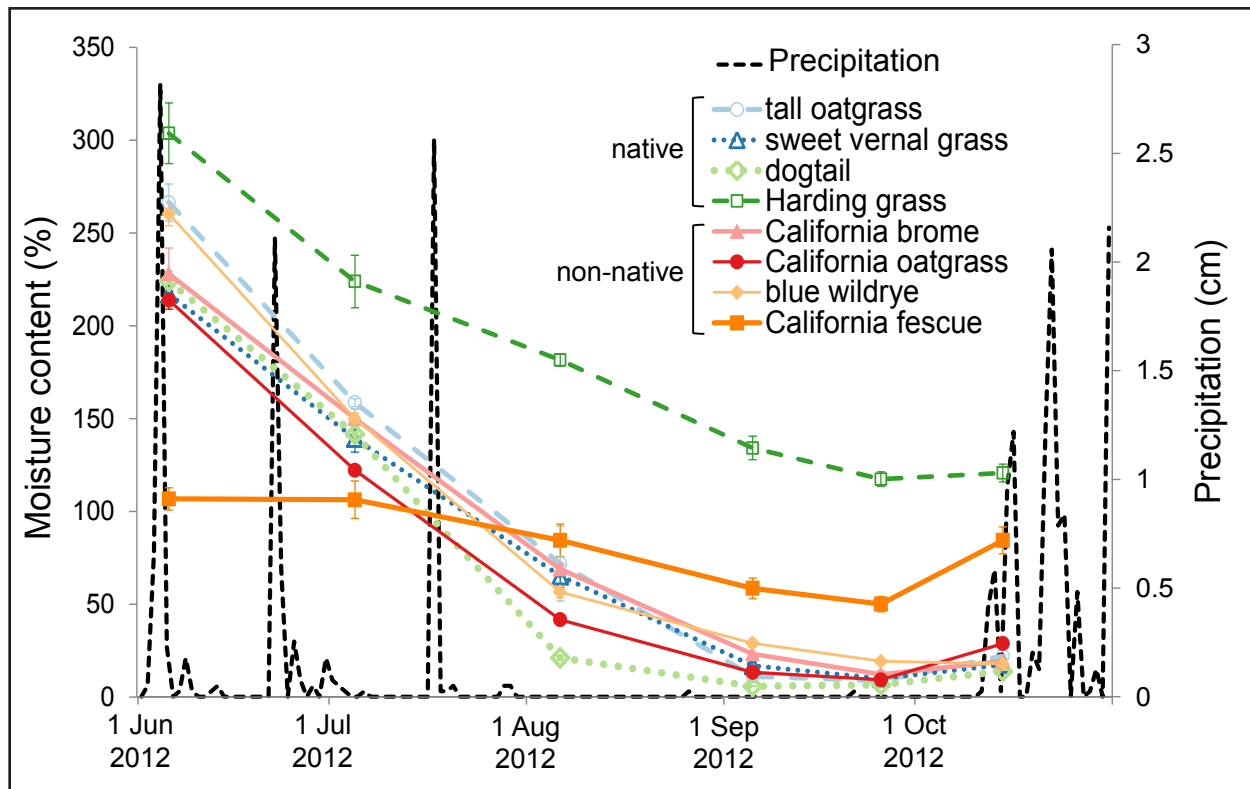


Figure 4. Moisture content of four native (solid symbols and lines) and four non-native (open symbols and broken lines) grass species followed seasonal precipitation trends during the 2012 fire season in the Bald Hills of Redwood National Park. Moisture content was highest in June and July and declined in August when rainfall ended. Moisture contents increased in October after 1 cm of rain. A prescribed burn on 19 October 2012 ended sampling.

pling on 10 October were not analyzed with the data we collected regularly between 1130 hr and 1700 hr throughout the growing season.

DISCUSSION

In many ecosystems, non-native grass species have been implicated in altering fire regimes, particularly where they invade areas with no native analogues (Brooks 1999, D'Antonio 2000, Brooks *et al.* 2004, Brooks 2008). In the Bald Hills, potential effects on the fire regime are complex, depending to a large extent on the degree to which the composition of the fuelbed has shifted with species invasions. Of the four non-native species that we studied, one of these, Harding grass, sustained high moisture content throughout the growing season and may act to delay ignition and dampen

fire spread and intensity. In contrast, the non-native annual dogtail might decrease fuel moisture levels and increase their ignitability earlier in the fire season compared to most native perennial species. Two of the non-native species that we studied, sweet vernal grass and tall oatgrass, did not differ from the native species' moisture contents.

The only annual species that we studied, the non-native dogtail, had significantly lower moisture content than all other study species across all dates except for the non-native sweet vernal grass and the native California oatgrass, which also had relatively low moisture content. These three grasses are relatively small-statured (Figure 2). Dogtail reached its maximum height early and flowered quickly, fitting with its sharp decline in moisture content early in the growing season. After this

species senesced (at approximately the end of July), samples of this species contained primarily dead material. California oatgrass is unique among the study species because, when its seeds are mature, the dried culms detach from the still-green basal leaves and fall on the ground. This occurred between the 6 August and 5 September sampling dates, when the moisture content for this species decreased sharply (Figure 3). For the remainder of sampling dates, both basal leaves and detached culms were included in samples. With the exception of Harding grass, the moisture content of the four larger perennials (Figure 2; the native California brome, blue wildrye, California fescue, and the non-native tall oatgrass) did not differ significantly from each other.

Due to its substantial mass and the dead fuel it retains, California fescue is considered a highly flammable fuel in oak woodland understories, capable of burning with high intensity where it is dominant (Hastings *et al.* 1997). In the Bald Hills, this species is considered to be an exceptional fuel, contributing to the fast moving, low intensity fires that prohibit young conifers from invading (Engber *et al.* 2011). We did not find a difference in the moisture content for California fescue across all sampling months compared to the other robust perennial species (with the exception of Harding grass, which was significantly higher). California fescue's reputation as an exceptional fuel source is partially dependent on its mass. Oak woodland understory dominated by California fescue in the Bald Hills had more than double the herbaceous mass of mixed grasslands, and a positive correlation was found between herbaceous fuel mass and surface fire temperatures in this ecosystem (Engber *et al.* 2011). Given the large amounts of dead thatch that this species retains, much of which is held close to the ground, it may have responded differently to the wetter than average year compared to the other species, and perhaps it had higher moisture content values than it otherwise would have. Likewise, the low variability in moisture content of this species may also

be related to its growth form and the dead thatch it retains.

In stark contrast to the patterns in moisture content found in the seven other species, the non-native Harding grass had much higher moisture content than all other species throughout the growing season. Even on its driest sampling date, the moisture content of Harding grass was still more than double a probable value for moisture of extinction. One caveat to our findings is that limited pilot sampling on 28 June 2013 confirmed that the new Harding grass location we moved to in July was more mesic than our original Harding grass location. Mean moisture content for Harding grass at our initial location was 239% compared to 290% at the location we moved to (a 18% difference relative to the new location). Harding grass was also sampled from two other locations in the Bald Hills that had mean moisture contents of 201% and 203%, a 31% and 30% difference relative to our new Harding grass location, respectively. On 25 September 2012, however, the relative difference between six of the grass species and Harding grass ranged from 84% to 95% (relative to Harding grass), and the relative difference between Harding grass and California fescue was 58% (relative to Harding grass). It is unlikely that sampling in the more mesic location would negate the general pattern we reported, as the magnitude of difference between Harding grass and the other species was so large. Additionally, at our sampling location, Harding grass culms were noticeably greener late into the fall compared to the other co-occurring species. Although the inferences we are able to make from a single study location are somewhat limited, the patterns that we observed are still noteworthy.

The high moisture content of Harding grass may have implications for prescribed fire. In the Bald Hills, known Harding grass infestations totaled approximately 33 ha in 2012, with infestation densities ranging from scattered individuals to dense monocultures (S. Samuels, personal communication). De-

pending on the density and extent of Harding grass infestations, combined with burn-day weather conditions of wind speed and relative humidity, as well as topographic position, this species may act to dampen fire intensity. Because of the other threats it poses to native species, park managers are currently trying to eradicate this species from the Bald Hills. The potential impediments that this species may pose to prescribed burning may serve as additional motivation for managers to eradicate this species from fire-dependent ecosystems.

The relative dominance of non-native species in a fuelbed will have a significant impact on the overall contribution of the species on the fire regime. A survey of understory vegetation in the oak woodlands of the Bald Hills found that the mean cover of dogtail was 9% (Livingston 2014). Comparatively, mean cover for tall oatgrass, sweet vernal grass, California brome, blue wildrye, and California fescue in oak woodland understories ranged from only 1% to 4%. California oatgrass occurred in woodland understory sampling rarely, and Harding grass was not detected in this survey (Livingston 2014). California oatgrass is one of the more common native grass species in the prairies of the Bald Hills, however, and Harding grass has primarily invaded prairies. Although its overall cover was low in the oak woodland understory survey, California fescue is dominant in several areas of the Bald Hills (Engber *et al.* 2011), and where it does occur, its cover is generally very high. The non-native species that we studied commonly invade other grasslands and woodlands ecosystems in the Pacific Northwest (Dennehy *et al.* 2011, Stanley *et al.* 2011) and elsewhere (Hitchcock 1971), making the results of this study relevant at broader geographic scales.

The non-native dogtail and the native California oatgrass were the first species to fall below a probable threshold for moisture of extinction, and the moisture content of dogtail was much lower than all other study species on 6 August. Depending on the density of

dogtail, it may decrease fuel moisture levels and increase ignitability earlier in the fire season. Although the moisture content of California oatgrass was twice that of dogtail in August (21% and 42% respectively), California oatgrass had possibly cured sufficiently to be ignitable based on the more conservative values for moisture of extinction estimated for grass species (Burrows *et al.* 1991). Although still common in the Bald Hills, California oatgrass is patchily distributed in the prairies, and it is thought to be less dominant now than it was historically (cf. Davy 1902). Potential effects on the fire regime in the prairies of the Bald Hills caused by dogtail may be reduced because of the diminished dominance of California oatgrass. Although the species selected for this study are among the most dominant, there are several other grass species in the Bald Hills, including many other non-native annuals: oats (*Avena* L. spp.), bromes (*Bromus* L. spp.), rattail six-weeks grass (*Festuca myuros* L.), brome fescue (*Festuca bromoides* L.), and silver hair grass (*Aira caryophyllea* L.), and a few native annuals (e.g., *Poa howellii* Vasey & Scribn), that we did not study (Livingston 2014). If other annual species have moisture content values similar to those that we observed for dogtail, they might have an additive effect on the ignition potential of fuel early in the fire season. As our study was not comprehensive, speculation on the net effects of fuel moisture change with invasion is difficult.

The trend we observed in this study for the seasonal curing of grass is consistent with other research from the western United States. In quaking aspen (*Populus tremuloides* Michx.) woodlands, the moisture content of a composite of grass species steadily decreased until fall rains occurred and basal leaves of perennials greened up, and moisture content increased (Brown *et al.* 1989). Composite samples of grass and grass-like plants from the understory of upland Douglas-fir communities showed a similar drying pattern when early and late sea-

son moisture content was compared (Agee *et al.* 2002). Large differences in the moisture content among individual native herbaceous species have been reported from quaking aspen understories in Wyoming (Brown *et al.* 1989) as well as from the Great Lakes region (Loomis *et al.* 1979).

The relative changes in moisture content that we observed at two-hour intervals during our sampling window of 1130 hr and 1700 hr are consistent with relative changes reported for crown foliage and forest floor fuel moisture (Agee *et al.* 2002, Banwell *et al.* 2013). Our diurnal sampling showed that the early morning (between 0900 hr and 1100 hr) changes in fuel moisture were, however, dramatically greater than changes observed for these other fuel types. The moisture content of one-year-old foliage in the Pacific Northwest varied only 4% to 12%, depending on species, when sampled at two-hour intervals from 1000 hr to 1600 hr (Agee *et al.* 2002). Over a twenty-four-hour period in the Lake Tahoe Basin, moisture content of forest floor fuels (1 hr woody fuels, litter, and pine cones) underwent a similar 3% to 11% relative change in moisture content (Banwell *et al.* 2013). The large decrease in moisture content that we observed for three of our four study species (relative change ranged from 40% to 84%) likely resulted from the clearing of coastal fog often present in the morning at our study site, which increases nocturnal moisture content and slows morning drying. Not surprisingly, herbaceous fuels like grasses are much more responsive to ambient moisture.

A definitive value for moisture of extinction—the fuel moisture content at which fire will not spread, or when the probability of ignition is 1%—has not been widely agreed upon for grasses (Dimitrakopoulos *et al.* 2010). Fire ignition and spread was difficult when moisture content approached 35% for spinifex grass fuel in Australia, primarily hard spinifex (*Triodia basedowii* E. Pritz.) and soft spinifex (*Plectrachne schinzii* Henrard) (Burrows *et al.* 1991). Laboratory ignition tests

for grass samples consisting primarily of *Imperata cylindrica* in Indonesia found moisture of extinction to be 40% for dead grass and 44% for live grass (de Groot and Wang 2005). Recent field experiments in Greece estimated the moisture of extinction for slender oat (*Avena barbata* Link.) at 55.5% (Dimitrakopoulos *et al.* 2010). Day of burn weather and topographic conditions also influence moisture of extinction, particularly wind speed, which has been shown to overwhelm ignition potential when fuel moisture is high (Dimitrakopoulos *et al.* 2010). Morphological properties of individual species, including size of culms and leaves, as well as residual dead fuels (not part of our sampling) may also increase the probability of ignition and affect spread, particularly in the robust bunchgrasses (i.e., California fescue).

The potential effects that non-native grass species have on the fire regime in the Bald Hills are complex. The non-native annual dogtail may decrease fuel moisture levels, increasing the ignitability of fuels early in the fire season via its early senescence, as has been observed in other non-native grasses (Brooks 1999, Davies and Nafus 2012). In contrast, where Harding grass invades and occurs at high densities, it may serve as an impediment to fire throughout the fire season via its high, stable moisture content. Only one other invasive grass species, tall fescue, has been shown to have a dampening effect on fire in tallgrass prairies, and this is caused by its asynchronous physiology (McGranahan *et al.* 2013). Our results may be the first that identify a large magnitude difference in moisture content between cool season native and non-native grass species in a fuelbed. Although the effects of individual non-native species may be moderated by the characteristics and density of other species in the fuelbed, our study demonstrates their capacity for altering ecosystem processes and potentially complicating the restoration of fire-dependent ecosystems.

ACKNOWLEDGEMENTS

Funding for this research was provided by the USDA McIntire-Stennis Forestry Research Program and the University of California Agriculture and Natural Resources Competitive Grants program. Field and laboratory assistance were provided by E. Asarian, K. Eldridge, and N. Hancock. Advice on statistical analysis was provided by R. Van Kirk. Comments on the design and on previous versions of the manuscript were provided by L. Arguello, E. Engber, E. Jules, and J. Kane. Managers at Redwood National Park (L. Arguello, S. Samuels, and L. Julian) graciously allowed access to study sites and provided information on site history and management. Comments and suggestions by reviewers improved the quality and clarity of the manuscript.

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