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Nelson, Kellen N., Drivers of fuels, flammability, and fire behavior in young, post-fire lodgepole pine forests, Wyoming, USA, Ph.D., Program in Ecology, May 2017.

Fire and bark beetles have affected vast areas of forest over the past several decades raising concern about the risk of subsequent burning. Little is known about how fuel loads and fire behavior vary shortly after burning, nor how forest flammability might differ between stands recovering from fire and bark beetles. To address this, we investigated the variation and drivers of fuel characteristics (Chapter 2) and fire behavior (Chapter 3) in 24-year-old post-fire lodgepole pine (*Pinus contorta* var. latifolia) stands that regenerated after the 1988 Yellowstone Fires. To assess differences in flammability between disturbance types (Chapter 4), we intensively sampled meteorological conditions and fuel moisture content in adjacent burned and bark beetle-affected forest sites. Both sites were approximately 24 years since disturbance. Our results indicate that fuel characteristics varied tremendously across the post-1988 Yellowstone landscape and were sufficient to support fire in all stands. Total surface-fuel loads in post-disturbance forests were similar or greater than those reported in mature lodgepole pine stands; however, 88% of fuel was in the 1000-hr fuel class, and litter, 1-hr, and 10-hr surface fuel loads were lower than values reported for mature lodgepole pine forests. Pre-fire successional stage was the best predictor of 100-hr and 1000-hr fuel and strongly influenced the size and proportion of sound and rotten logs, where post-fire stand structure was the best predictor of litter, 1-hr, and 10-hr fuels. Available canopy fuel loads and canopy bulk density met or exceeded loads observed in mature lodgepole pine forests, exhibited a strong positive relationship with post-fire lodgepole pine density, and were the primary drivers of crown fire behavior. Meteorological conditions in post-fire sites exhibited symptoms of earlier snowmelt, greater evapotranspiration, and greater drought stress than

post-bark beetle sites, and live fuel moisture content mimicked these differences as post-fire sites broke dormancy earlier and experienced longer, more severe drought conditions than post-bark beetle sites. Dead fuel moisture content was similar in burned and bark beetle affected sites in July, but had a greater response to heavy August precipitation that resulted in higher dead fuel moisture content on the post-burn sites. In sum, our data suggest that 76% of the young post-fire lodgepole pine forests have 1000-hr fuel loads that exceed levels associated with high-severity surface fire, and 63% exceed canopy bulk densities associated with spreading crown fire. Fire simulation modeling predicted active crown fire in 90% of stands at wind speeds >20 km hr^{-1}, regardless of fuel moisture condition. We conclude that 24-year old lodgepole pine forests can readily support fire intervals shorter than those observed historically in Yellowstone National Park, and that dead fuel moisture content appears more dynamic while foliar fuel moisture content might be less dynamic on post-fire sites than post-bark beetle sites. Overall, the potential for crown fire is high across the post-1988 Yellowstone landscape, and post-fire sites appear to be more flammable than post-bark beetle sites during dry periods. Given a less developed canopy seed bank and a high potential for crown fire, young post-fire lodgepole pine forests are likely to have lower reproductive potential than comparable mature forests. Progressive reductions in tree recruitment after short-interval fires may lead to self-limiting dynamics where lack of fuels limit continued short-interval burning.

Drivers of fuels, flammability, and fire behavior in young, post-fire lodgepole pine forests

By

Kellen N. Nelson

A dissertation submitted to the University of Wyoming in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY

Laramie, Wyoming

May 2017

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ACNOWLEDGEMENTS

I dedicate my dissertation to Monique L. Nelson and our two boys, Eli S. Nelson and Bridger L. Nelson. Your ceaseless encouragement, sacrifice, and love has enabled me to live my dreams as a naturalist, alpinist, and conservationist. I cannot imagine better companions with whom to share my life. I am proud to be your husband and father, and look forward to helping you achieve your aspirations throughout our lifetimes. With love and thanks, - Kellen (aka Dad-oh).

Special thanks to:

Dan Tinker, *my advisor, for guiding me through the weeds of my overactive imagination and teaching me how to maintain work-life balance.*

Shannon Albeke, Ken Driese, Brent Ewers, Chad Hoffman, and Melanie Murphy, *my committee, for digging into my research and providing critical, constructive feedback.*

Paige Copenhaver, Paul Hood, Greg Pappas, and Gail Stakes*, the Tinker lab, for their constructive feedback and kind hearts.*

Christy and the Feinstein fellas, Jesse Grant, Nate and Katie Haynes, Nathaniel Hazelton, Jen House, Nathaniel Kitchel, Dave Pomeranz, Heather Rockwell, Bekah Smith, the Sherrills, and Vicky Zero, *our kind and supportive friends, for great times and help when times felt challenging.*

Mike Battaglia, Daniel Beverly, Dan Binkley, Molly Cavaleri, Jonas Feinstein, Heather Speckman, Patrice Janiga, Dan Kashian, Michael Lefsky, Bill Romme, Chuck Rhoades, Monique Rocca, Mike Ryan, Chip Scott, Monica Turner, and Jim Westfall, *my past and present collaborators and mentors, for helping shape my professional perspective*.

The Boges, Grants, Mahalins, Nelsons, LaPerrieres, and Ruepes *for their interest and support*.

Paige Copenhaver, Daniel Donato, Winslow Hansen, Ronald Harned, Paul Hood, Natalie Kaner, Erik Larsen, Eric McDevitt, Andy Muench, Eli Nelson, Monique Nelson, Stephen Nelson, Valerie Nelson, Alan Renneisen, Bill and Judy Romme, Dan Tinker and Gail Stakes, Monica Turner, and Tim Whitby *for lending a hand with logistics, field surveys, laboratory sample prep and data entry, and weather station building*.

Marty Alexander, Miguel Cruz, Chad Hoffman, Matt Jolly, Bob Keane, and Russ Parsons *for advice on fire behavior models*.

Diane Abendroth, Stacey Gunther, Mike Johnston, Andy Norman, Roy Renkin, and Becky Smith *for their knowledge and support in the Greater Yellowstone Ecosystem*.

The Joint Fire Science Program (Grants 11-1-1-7 and 15-2-01-63), Boyd Evison Graduate Fellowship, UW-NPS AMK Research Station grants program, and the American Alpine Club grants program *for providing funding; my degree would not have been possible without your support*.

University of Wyoming—National Park Service research station, Grant Teton National Park, and Yellowstone National Park *for housing and logistical assistance.*

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1.1 BACKGROUND

An unprecedented extent of forest land in the western US was affected by wildland fire and bark beetles between 2000 and 2010, and was the result of the greatest frequency of large fire seasons on record (e.g., >500,000 ha was affected by each disturbance per year in five of ten years (Figure 1)). Much of the impact was concentrated in temperate conifer forests including those in the Rocky Mountains (Littell et al. 2009, Meddens et al. 2012, Dennison et al. 2014) and resulted in substantial socioeconomic consequences, including loss of human life and infrastructure, escalating costs of fire prevention and suppression, and changes in ecosystem services (e.g., water, timber, carbon storage, and recreation resources). These events bring a new issue to the forefront: the potential for short-interval burning across historic extents of recently disturbed forests, a phenomenon likely to increase with elevated disturbance activity over the next century (Schoennagel et al. 2006). Forest managers and scientists will be challenged to anticipate successional dynamics that ultimately generate the fuels, fire behavior, and fuel moisture conditions for future fires.

Recent research suggests that bark beetle outbreaks have little effect on fire occurrence (Mietkiewicz and Kulakowski 2016) and severity (Harvey et al. 2014); however, depending on pre-outbreak forest structure and time-since-outbreak, variation in fuel loads (Jenkins et al. 2008, Simard et al. 2011, Hicke et al. 2012), energy budgets (Edburg et al. 2012), and wind speeds (Hoffman et al. 2012) can make post-bark beetle stands prone to extreme fire behavior including profuse firebrand production (Jenkins et al. 2008, Page et al. 2013). Fewer empirical studies have investigated short-interval reburning after high-severity fire, but existing studies report that either (i) post-fire stands have high fuel loads and are immediately capable of supporting fire (e.g., western hemlock/Douglas-fir (*Tsuga heterophylla/Pseudotsuga menziesii*), Washington, USA

(Agee and Huff 1987a) and subalpine fir (*Abies lasiocarpa*), Montana, USA (Fahnestock 1976)), or (ii) post-fire stands have extremely low fuel loads and require an extended period of fuel accumulation to support fire (e.g., Scots pine/Norway spruce/birch (*Pinus sylvestris/Picea abies/Betula* spp.), northern Sweden (Schimmel and Granström 1997a) and lodgepole pine, Wyoming, USA (Romme 1982a, Tinker and Knight 2000)). In the case of Rocky Mountain conifer forests, recent geospatial studies indicate that extensive tracts of young forests may soon support fire, as any reduction in fire potential lasts for only 12 to 18 years (Parks et al. 2016b).

The following three chapters aim to improve understanding of how forest dynamics affect wildfire in recently disturbed lodgepole pine stands. The first two chapters employ forest structure and fuel data from a landscape assessment of fuel conditions in 24-year old, post-fire lodgepole pine stands. Chapter 1 investigates the drivers of landscape variation in fuel abundance, and Chapter 2 investigates how variation in fire weather and fuel abundance affect simulated fire behavior. Chapter 3 uses intensive weather and fuel moisture measurements in adjacent burned and bark beetle-affected lodgepole pine stands and investigates how fuel moisture conditions (as a proxy for fuel flammability) differ between disturbance types of similar age.

1.2 REFERENCES

Agee, J. K., and M. H. Huff. 1987. Fuel succession in a western hemlock/Douglas-fir forest. Canadian Journal of Forest Research 17:697–704.

Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014. Large wildfire trends in the western United States, 1984–2011. Geophysical Research Letters 41:2014GL059576.

Edburg, S. L., J. A. Hicke, P. D. Brooks, E. G. Pendall, B. E. Ewers, U. Norton, D. Gochis, E. D. Gutmann, and A. J. Meddens. 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Frontiers in Ecology and the Environment 10:416–424.

Fahnestock, G. R. 1976. Fires, fuel, and flora as factors in wilderness management: the Pasayten case. Tall Timbers Fire Ecology Conference 15:33–70.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014. Recent mountain pine beetle outbreaks , wildfire severity , and postfire tree regeneration in the US Northern Rockies:6–11.

Hicke, J. a., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Hoffman, C. M., P. Morgan, W. E. Mell, R. A. Parsons, E. K. Strand, and S. Cook. 2012. Numerical simulation of crown fire hazard immediately after bark beetle-caused mortality in lodgepole pine forests. Forest Science 58:178–188.

Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecology And Management 254:16–34.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications 19:1003–1021.

Meddens, A. J., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22:1876–1891.

Mietkiewicz, N., and D. Kulakowski. 2016. Relative importance of climate and mountain pine beetle outbreaks on the occurrence of large wildfires in the western USA. Ecological Applications 26:2523–2535.

Page, W. G., M. E. Alexander, and M. J. Jenkins. 2013. Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. The Forestry Chronicle 89:783–794.

Parks, S. A., C. Miller, L. M. Holsinger, S. Baggett, and B. J. Bird. 2016. Wildland fire limits subsequent fire occurrence. International Journal of Wildland Fire 25:182–190.

Romme, W. H. W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199–221.

Schimmel, J., and A. Granström. 1997. Fuel succession and fire behavior in the Swedish boreal forest. Canadian Journal of Forest Research 27:1207–1216.

Schoennagel, T., M. G. Turner, D. M. Kashian, and A. Fall. 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. Landscape Ecology 21:1281–1296.

Simard, M., W. H. Romme, J. M. Griffin, and M. G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs 81:3–24.

Tinker, D. B., and D. H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3:472–483.

1.3 FIGURES

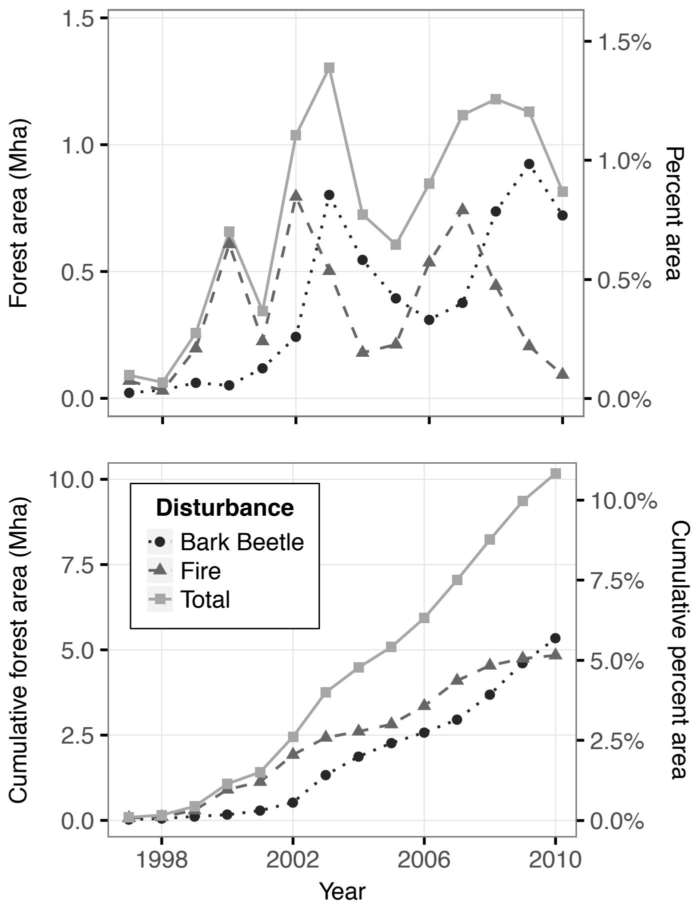

Figure 1: Variation in forest area affected by fire and bark beetles between 1997 and 2010 in the western Unites States. Data include recent aerial estimates of burned (Abatzoglou and Williams 2016) and bark beetle-affected (Meddens et al. 2012) forest land area in the western United States. Forest area was assumed to be 93.8 million ha (Smith et al. 2009b), slightly higher than that used for similar calculations by Littell et al. (2009).

CHAPTER 2: LANDSCAPE VARIATION IN TREE REGENERATION AND SNAG FALL DRIVE FUEL LOADS IN 24-YR OLD POST-FIRE LODGEPOLE PINE FORESTS

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Note: This chapter is published in Ecological Applications.

Citation: Nelson, KN, WH Romme, MG Turner, and DB Tinker. 2016. Landscape variation in tree regeneration and snag fall drive fuel loads in 25-yr old post-fire lodgepole pine forests. Ecological Applications, 26(8): 2424–2438.

2.1 ABSTRACT

Escalating wildfire in subalpine forests with stand-replacing fire regimes is increasing the extent of early-seral forests throughout the western US. Post-fire succession generates the fuel for future fires, but little is known about fuel loads and their variability in young post-fire stands. We sampled fuel profiles in 24-year-old post-fire lodgepole pine (*Pinus contorta* var. *latifolia*) stands (n=82) that regenerated from the 1988 Yellowstone Fires to answer three questions. (1) How do canopy and surface fuel loads vary within and among young lodgepole pine stands? (2) How do canopy and surface fuels vary with pre- and post-fire lodgepole pine stand structure and environmental conditions? (3) How have surface fuels changed between 8 and 24 years post-fire? Fuel complexes varied tremendously across the landscape despite having regenerated from the same fires. Available canopy fuel loads and canopy bulk density averaged 8.5 Mg ha^{-1} [range 0.0-46.6] and 0.24 kg m^{3} [range: 0.0-2.3], respectively, meeting or exceeding levels in mature lodgepole pine forests. Total surface-fuel loads averaged 123 Mg ha^{-1} [range: 43 - 207], and 88% was in the 1000-hr fuel class. Litter, 1-hr, and 10-hr surface fuel loads were lower than reported for mature lodgepole pine forests, and 1000-hr fuel loads were similar or greater. Among-plot variation was greater in canopy fuels than surface fuels, and within-plot variation was greater than among-plot variation for nearly all fuels. Post-fire lodgepole pine density was the strongest positive predictor of canopy and fine surface fuel loads. Pre-fire successional stage was the best predictor of 100-hr and 1000-hr fuel loads in the post-fire stands and strongly influenced the size and proportion of sound logs (greater when late successional stands had burned) and rotten logs (greater when early successional stands had burned). Our data suggest that 76% of the young post-fire lodgepole pine forests have 1000-hr fuel loads that exceed levels associated with high-severity surface fire potential, and 63% exceed levels associated with active crown fire potential. Fire rotations in Yellowstone National Park are predicted to shorten to a few decades and this prediction cannot be ruled out by a lack of fuels to carry repeated fires.

Keywords: succession, lodgepole pine, young forests, fire regimes, fuel dynamics, fuels, reburn, self-regulation

2.2 INTRODUCTION

Observed and projected increases in wildland fire extent and frequency have raised concern among scientists and forest managers regarding the consequences of escalating wildland fire activity (Flannigan et al. 2000, Scholze et al. 2006, Westerling et al. 2006, Krawchuk et al. 2009, Westerling et al. 2011a, Moritz et al. 2012, Stephens et al. 2013, Parks et al. 2016b). Extreme fire seasons have become more common over the last three decades and have had major social and ecological consequences including loss of human life and infrastructure, escalating costs of fire prevention and suppression, changes in ecosystem services (e.g., water, timber, carbon storage, and recreation resources), and increasing extents of young forests (Schoennagel et al. 2006b, Stephens et al. 2013). In subalpine forests across western North America, large fires historically burned during rare periods of extreme weather (Romme 1982b, Lotan et al. 1985, Bessie and Johnson 1995, Schoennagel et al. 2004). Projections of more frequent severe fire weather over longer fire seasons suggest that a new wildland fire issue may emerge—the potential for extensive reburning of young forests (Schoennagel et al. 2006b, Parks et al. 2016b, 2016a, Harvey et al. 2016). If realized, forest managers and scientists will be challenged to anticipate successional dynamics that ultimately generate the fuels for future fires. In this study, we evaluate patterns of fuel accumulation and abundance in young, post-fire lodgepole pine (*Pinus contorta* var. *latifolia*) stands originating from the 1988 Yellowstone Fires to understand variation in fuel loads in young, post-fire forests.

Observations of natural fires in Yellowstone during the 1970s and 1980s suggested that young ($\leq$ 40 yrs) post-fire lodgepole pine were unlikely to burn because combustion from the first fire had reduced fuel loadings (Renkin and Despain 1992). The spread of fires that burned early during the 1988 fire season fit that expectation, slowing when patches of young forest were encountered (M. G.

Turner and W. H. Romme, personal observations). However, fires that burned later in the 1988 fire season under extreme weather conditions burned readily through young lodgepole pine forests at seven (1981 Pelican Creek Fire) and 13 (1975 Arrow Fire) years post-fire. Recent fires in the Greater Yellowstone Ecosystem have reburned lodgepole pine stands at 12 (2000 Boundary fire), 24 (2012 Cygnet Fire) and 28 (2009 Bearpaw Fire) years post-fire. Parks et al. (2016b) rigorously tested the ability of young forests to act as fire breaks and found that the likelihood of re-burning was reduced for 14 to 18 years in four northern Rocky Mountain forest landscapes. Harvey et al. (2016) also conducted rigorous sampling and analysis in northern Rocky Mountain forest landscapes, and found that burn severity was reduced for 10 to 12 years in subalpine forests, but a second fire after that time was likely to be high severity. Both studies found that extreme burning conditions could negate any reduced likelihood of fire or burn severity in young forests.

Fuel dynamics following fire thus govern the likelihood that young stands will again burn (Parks et al. 2015, Harvey et al. 2016), but comprehensive measurements of post-fire fuel loads and variability in young stands are lacking. Previous fuel succession studies indicate that post-fire fuel loads capable of supporting fire vary by forest type. Western hemlock/Douglas-fir forests in Washington, USA (Tsuga heterophylla/Pseudotsuga menziesii; Agee and Huff 1987b) and subalpine fir forests in Montana, USA (*Abies lasiocarpa*; Fahnestock 1976) show high, post-fire fuel loads and potential for short-interval fire; however, lodgepole pine forests in Wyoming, USA (Romme 1982b, Tinker and Knight 2000) and Scots pine/Norway spruce/birch forests in northern Sweden (Pinus sylvestris/Picea abies/Betula spp.; Schimmel and Granström 1997b) appeared to require extended periods of biomass accumulation to support subsequent fire. The objective of this study was to quantify fuel loads and variability at the landscape scale following a large, severe wildfire. The 1988 Fires in Yellowstone National Park provide an ideal opportunity for such a study because the post-fire forest landscape has received minimal human intervention and the consequences of the fires have been studied extensively (e.g., Turner et al. 2003, Turner 2010, Romme et al. 2011).

After nearly 25 years of succession following high-severity fire, young lodgepole pine stands in Yellowstone National Park vary widely in structure and function (Turner et al. 2016), and have developed complex and varied fuel profiles. We sampled fuels across the forests regenerating from the 1988 fires to answer three questions: (1) How do canopy and surface fuel loads vary within and among young lodgepole pine stands across the burned landscape? (2) How do canopy and surface fuels vary with pre- and post-fire lodgepole pine stand structure and environmental conditions? (3) How have surface fuels changed between 8 and 24 years after the 1988 Yellowstone Fires?

2.3 STUDY AREA

The subalpine plateau of Yellowstone National Park is a mostly roadless landscape dominated by lodgepole pine but also contains Engelmann spruce (*Picea engelmanii*), subalpine fir, and whitebark pine (*Pinus albicalus*) in lower numbers. Most of the park ranges between 2100 and 2700 m in elevation. Soils include dry, infertile, rhyolitic substrates as well as more mesic and slightly less infertile andesitic and former lake-bottom substrates (Turner et al. 2004). The hydrologic regime is dominated by winter snowfall which generally persists from late-October to late-May at 2100 m elevation (Despain 1990a). Between 1981 and 2010 at Old Faithful, mean annual temperature was 1.2°C ranging from an average low of -17.6°C in January to an average high of 23.8°C in July (http://www.wrcc.dri.edu/). Mean annual precipitation ranges from 366 to 642 mm depending on geographic location and elevation (http://www.wrcc.dri.edu/).

Wildland fires within Yellowstone National Park generally ignite from lightning associated with convective summer storms and the 1988 Fires did so during the warmest, driest summer on record (Renkin and Despain 1992). These fires produced an extremely heterogeneous mosaic of burn severities across ~600,000 ha within the Greater Yellowstone Ecosystem (Christensen et al. 1989). Of the ~321,000 ha that burned inside the park, ~56% burned as stand-replacing fire, with 25% classified as severe-surface burn and 31% as high-severity crown fire (Turner et al. 1994). Post-fire lodgepole pine regeneration was rapid, abundant, and remarkably variable across the burned landscape, with post-fire tree densities ranging from zero to > 500,000 stems ha^{-1} (Turner et al. 1997, 1999, 2004; Turner 2010). Large stand-replacing fires historically occurred at a 100 to 300 year interval (Romme 1982b, Millspaugh and Whitlock 1995), but scientists and managers alike found the 1988 fires to be surprising and noteworthy in fire extent, severity, and rate of forest recovery (Romme et al. 2011). Extreme fire weather in the study area is projected to become more frequent and longer in duration over the next century leading to a reduction in fire rotation from > 100 to < 30 years (Westerling et al. 2011a).

2.4 METHODS

During the summer of 2012, we measured canopy, surface, and herbaceous fuels in 24-year-old post-fire forests across Yellowstone National Park. Ten plots were originally established in 1996 (Tinker and Knight 2000) and 72 plots were established in 1999/2000 (Turner et al. 2004). Plots encompassed a wide range of post-fire stem density, two 1988 stand-replacing fire-severity categories (i.e., crown and high-severity surface fire), and four substrate categories: rhyolite – till, rhyolite – glacial, rhyolite – low base saturation, and andesite includes lake bottom sediments. Surface fuels had previously been measured in 1996 in 10 plots (Tinker and Knight 2000) but no fuel measurements were collected in the Turner et al. (2004) plots in 1999/2000. All 82 plots were used to evaluate our first two questions, and the 10 plots sampled in 1996 were re-measured to address our third question. Sampling locations were separated by at least 1 km and spatial independence was confirmed using the Moran's I test (P=0.192). To our knowledge, this study includes one of only a few expansive fuels dataset collected within a single wildfire footprint.

Field measurements

2012 Canopy, surface, and understory vegetation fuels

We measured canopy, surface, and understory vegetation fuels at all 82 sites using a 0.25 ha (50 x 50 m) fixed-area plot. Plots were oriented northward with a southerly baseline that ran east-west (see Turner et al. 2004). Twelve 20 m planar intercept fuels transects were randomly oriented within each plot (Brown 1974, Brown et al. 1982). One-hr (<0.64 cm diameter) and 10-hr fuels (0.64–2.54 cm diameter) were tallied along the first 3 m of each transect, 100-hr fuels (2.54–7.62 cm diameter) were tallied along the first 10 m, and 1000-hr fuels (>7.62 cm diameter) were measured along the full 20 m. Litter depth (cm) was measured at 3 locations spaced at 2- m intervals at the beginning of each transect. Litter is defined as lightly decomposed recognizable organic matter and duff is defined as decomposed, unrecognizable organic matter. Duff was absent in all plots, which contrasts with boreal forests but is typical in young lodgepole pine forests.

We assessed canopy fuel profiles from estimates of stem density and size in each plot (Turner et al. 2016). Briefly, all trees were tallied by species inside three 2 m x 50 m belt transects that ran through the center and along the east and west boundaries of the plot. On a sample of lodgepole pine trees (n=25) in each plot, we measured basal diameter (0.1-cm), diameter at breast height (dbh=1.37 m, 0.1 cm), tree height (0.1 m), crown base height (0.1 m), and crown width (0.1 m). Understory vegetation cover was estimated visually by species within twenty-five 0.25 m^2 quadrats and converted to biomass using allometric equations developed in Yellowstone for these species (Turner et al. 2004, Simard et al. 2011b, Turner et al. 2016).

We also measured litter bulk density (kg m^{-3}) in 14 plots that spanned a representative range of post-fire seedling densities. Twelve subsamples of litter were collected using a 0.30 x 0.30 m quadrat and litter depth was recorded at the center of the quadrat. Litter was dried at 60°C for 24 hrs or until a constant mass was reached and weighed on an analytical balance to a hundredth of a gram. Care was taken to remove woody particles and mineral soil from each sample.

1996 surface fuels

In 1996, surface fuels were measured in 10 post-fire plots (Tinker and Knight 2000). At each plot, twenty-five 15.2 m transects were oriented at random azimuths on the east and west plot boundaries. Surface fuel loads were assessed along each transect using the planar intercept method (Brown 1974, Brown et al. 1982). One-hr (<0.64 cm diameter) and 10-hr fuels (0.64–2.54 cm diameter) were tallied along the first 1.83 m of each transect, 100-hr fuels (2.54–7.62 cm diameter) were tallied along the first 3.66 m, and 1000-hr fuels (>7.62 cm diameter) were measured along the full 15.2 m. Litter depth (cm) was measured along each transect at three locations (0.67 m apart). Duff was absent in all plots.

Data processing

Surface fuel loads were computed for each plot by summing intercept counts and transect lengths by size class, applying standard planar-intercept methods (Brown 1974, Brown et al. 1982, Harmon et al. 1986), then scaling to the hectare. 1000-hr fuel loads were summarized and grouped into two classes—sound and rotten—depending on their decay status (Maser et al. 1979). Sound logs include those with a sound bole regardless of branch, bark, and twig condition (i.e., decay classes 1 & 2). Rotten logs include those with a bole that breaks apart (i.e., decay classes 3, 4, & 5). Percent cover by species was converted to understory vegetation biomass using published relationships between percent cover and dry biomass (Turner et al. 2004, Simard et al. 2011b). Mean litter bulk density (kg m^3) was computed using a subsample of plots (n=14) and litter loads were computed for each plot by multiplying litter depth (m) by litter bulk density. Canopy fuel loads were calculated by applying custom lodgepole pine allometric equations (Copenhaver and Tinker 2014a) to the randomly subsampled trees, taking their plot-wise mean, then scaling to the hectare with tree density. Foliage, 1-hr branch wood, and available canopy fuel loads are reported. Available canopy fuel load is defined as the proportion of canopy fuels available for pyrolysis and is computed as 100% of foliage plus 50% of 1-hr branch wood (Reinhardt et al. 2006a). We define “crown” as pertaining to an individual tree and “canopy” as the sum of all individual trees within a stand (Cruz et al. 2003). Crown bulk density was computed using equation [1].

$$Available\ crown\ bulk\ density\ (kg\ m^{-3}) = \frac{foliage(kg) + 0.5(1\ hr\ branchwood(kg))}{\pi\left(\frac{crown\ width(m)}{2}\right)^2 * (tree\ height(m) - crown\ base\ height(m))} \quad [1]$$

Canopy bulk density was computed using the *biomass-percentile method* (Reinhardt et al. 2006a). Canopy length was determined by summing biomass through the canopy and reporting the distance between the 10th and 90th percentile of biomass. Vertical fuel profiles were created for each plot by splitting available canopy fuel load into 0.1 m vertical layers then dividing by the volume of each layer (plot area x layer depth) (Sando and Wick 1972, Reinhardt et al. 2006a). For plotting purposes, a 1 m running mean was used to smooth the fuel profile and reduce extreme values. Within-plot coefficient of variation (CV) was computed for each plot by computing fuel loads for each measurement unit (i.e., transects (n=12 plot^{-1}) and trees (n=25 plot^{-1})) and aggregating these estimates into plot-level means, standard deviations, and CVs. Among-plot (i.e., landscape-wide) CVs were also computed for each fuel category using among-plot means and standard deviations (n=82).

Statistical analyses

To examine fuel loads and their variability, we report means and standard errors of plot-level fuel loads (Table 1), and within-plot and among-plot coefficient of variation (Table 2) for three tree density classes and the total population. Differences among density classes were determined using one-way ANOVA and Tukey’s HSD at α=0.05. Landscape-wide CVs pertain to the whole study area and lack error estimates. We also calculated the proportion of the 82 plots that met or exceeded fuel loads associated with the potential for high-severity surface fire (1000-hr fuel loads greater than 60 Mg ha^{-1}; Sikkink and Keane 2012) and active or independent crown-fire spread (crown bulk density greater than 0.12 kg m-3; Reinhardt et al. 2006a).

To assess how fuel loads varied with pre- and post-fire stand structure and topo-climatic factors, we fit linear multiple regression models to predict fuel loads. Candidate predictor variables were selected based on the hypothesized ecological relationships and paired to each response variable (Table 3). Models were selected using the "best subsets" model selection routine to optimize the coefficient of determination (R^2) while maintaining α=0.05 (Lumley and Miller 2009). Model residuals, fits, and transformation criteria were checked using methods recommended by Venables and Ripley (2002) and the presence of multicollinearity was evaluated using variance inflation factors. After model construction, the importance of individual predictor variables was evaluated by computing the proportion of R^2 that each predictor variable contributes using the *lmg* metric in the relaimpo R package (Grömping 2006). *lmg* "quantifies the relative contributions of the regressors to the model's total explanatory value by averaging sequential sums of squares over orderings of regressors" (Grömping 2006, 2007). Significant differences in *lmg* between predictor variables were tested by generating bootstrapped confidence intervals (999 iterations).

Empirical response variables and transformations include: litter ($\log_{10}$), 1-hr ($\log_{10}$), 10-hr, 100-hr ($\log_{10}$), 1000-hr rotten ($\log_{10}$), 1000-hr sound ($\log_{10}$), total surface fuel, live herbacious biomass, live shrub biomass ($\log_{10}$), available canopy fuel load ($\log_{10}$), mean crown base height ($\log_{10}$), and canopy bulk density ($\log_{10}$). Empirical predictor variables and transformations include: live stem density ($\log_{10}$), live foliage, herbaceous, shrub biomass, live tree density, live basal area, canopy base height, and 1000-hr fuel load. Geospatial predictor variables were extracted from the following datasets using plot coordinates: pre-fire successional stage (Despain 1990a, NPS-YELL 1990), substrate (NPS-YELL 1997), mean annual precipitation and temperature (PRISM Climate Group

2012), and burn severity (dNBR; USDA Forest Service-RSAC 2012). The following geomorphometric predictor variables were computed using a digital elevation model (Gesch 2007) and extracted using plot coordinates: derived slope and aspect (Gesch 2007), compound topographic index (i.e., wetness) (Evans et al. 2014), and potential solar radiation (Pierce et al. 2005). Aspect was transformed to a continuous distribution using Beers et al. (1966). Categorical dummy variables—pre-fire successional stage and substrate—were defined in our models using deviance (effects) contrasts to compare individual levels with the mean of all levels. Pre-fire successional stage reflects lodgepole pine successional stages identified by Despain (1990a). LP0 represents post-fire stands where lodgepole pine has recolonized the site but has not yet produced a closed canopy. LP1 consists of a single cohort of dense, young lodgepole pine without tree seedlings in the understory. LP2 stands have closed canopies dominated by lodgepole pine with tree seedlings in the understory. LP3 and LP4 are multi-cohort stands with ragged canopy characteristics dominated by lodgepole pine. LP3 contains Engelmann spruce and subalpine fir in the sub-canopy whereas LP4 stands occur on dry sites that do not support Engelmann spruce and subalpine fir.

Total crown area was modeled using linear regression between summed tree crown area and stand density. Changes in fuel loads and their variability between 1996 and 2012 were compared using paired t-tests and the ratio of change was calculated using the ratio of means for each surface fuel type plus standard error (Scheaffer et al. 2011).

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3b15s.

2.5 RESULTS

Fuel characteristics and variability

Total surface fuel loads varied tremendously across the post-1988 Yellowstone fire landscape, ranging from 43.3 to 206.7 Mg ha^{-1} (Figure 1; Table 1). Thousand-hr fuels averaged 110.0±4.6 Mg ha^{-}

$^{-1}$ and composed 88% of the total fuel—by far the greatest proportion. Sound logs accounted for nearly 70% while rotten logs accounted for 30% of 1000-hr biomass but the distribution of biomass also varied with log size (Figure 2). 75.9% of stands had 1000-hr fuel loads greater than 65 Mg ha^{-1}—a threshold specified by Sikkink and Keane (2012) for high-severity surface fire. Litter accounted for the greatest share of fine surface fuels—more than 1-hr surface fuels, herbaceous fuels, shrub fuels, and 10-hr fuels combined. Mean litter bulk density was 50.2±6.1 kg m^{-3}, mean litter depth was 1.1±0.1 cm, and mean litter biomass was 5.61±0.46 Mg ha^{-1}. Fuel loads increased with density class for litter, 1-hr, and 100-hr fuel types but decreased for herbaceous biomass, rotten 1000-hr and total surface fuel loads (Table 1). Litter and rotten 1000-hr fuel within-plot variation decreased by density class but other fuel classes did not. Across all density classes, mean within-plot CVs were higher than landscape-wide CVs for the same fuel type (Table 2). In general, within- and among plots, surface fuel variability was less than canopy fuel variability.

Live lodgepole pine densities in 2012 averaged 19,500 stems ha^{-1} and ranged from 0 to 344,000 trees ha^{-1} (Turner et al. 2016). Available canopy fuels averaged 8.5 Mg ha^{-1} and varied from 0.0 to 48.6 Mg ha^{-1} over this wide range of stem density (Figure 1; Table 1). All canopy fuel characteristics (i.e., foliar biomass, 1-hr biomass, crown base height) increased with stem density. Within-plot CV for canopy fuels did not differ among density classes but was greater than the among-plot CV for canopy fuels (Table 2). Canopy bulk density ranged from 0.00 to 2.28, and 63.9% of stands in this study are greater than the 0.12 kg m^{-3} threshold for active and independent crown fire spread (Reinhardt et al. 2006a).

Effects of pre- and post-fire stand conditions and topo-climatic factors on fuels

Models predicting dead and downed surface fuel loads fell into two general groups: fine fuels (e.g., litter, 1-hr, and 10-hr fuels) were best predicted by post-fire stand structure and coarse fuels (e.g., 100-hr, 1000-hr) were best predicted by pre-fire forest structure variables (Table 3). Needle litter fuel load was positively associated with 1000-hr fuel load (both sound and rotten) and live stand density, but was negatively associated with mean annual precipitation (R^2=0.43). Live stem density showed the greatest importance in predicting litter fuel loads (Table 6). One-hr fuel load was positively related to crown base height, mean annual precipitation, topographic wetness index, and slope (R^2=0.49) with crown base height having greater importance than the other variables in our model (Table 6). Variation in lodgepole pine density and annual temperature were related to 10-hr fuels, but explained little variance (R^2=0.08). One hundred-hr fuels were best predicted by pre-fire successional stage and annual precipitation (R^2=0.22). Sound 1000-hr fuels were positively related to pre-fire successional stage (R^2=0.24), whereas rotten 1000-hr fuels were negatively related to pre-fire successional stage (R^2=0.30; Table 4; Figure 2). Total surface fuel loads were best predicted by pre-fire successional stage, mean annual temperature, mean annual precipitation, and aspect (R^2=0.31). Herbaceous fuel load was best predicted by soil class and live tree basal area (R^2=0.25; Table 5). Shrub fuels were miniscule but were positively related to live stand density, elevation, and slope (R^2=0.25; Table 5). Importance values for predictors were not different from one another in 10-hr, 100-hr, 1000-hr, total fuel load, herbaceous, and shrub models (Table 6).

Live stem density was a strong, positive predictor of available canopy fuel (R^2=0.78), canopy bulk density (R^2=0.87), and crown base height (R^2=0.66; Table 4), and had the greatest importance in predicting canopy fuel loads (Table 6). Vertical profiles of canopy bulk density display a shift in the distribution of canopy fuels with stem density (Figure 3). Low-density stands have lower canopy bulk density and a uniform vertical distribution whereas high-density stands had high canopy bulk density concentrated at lower heights. Crown area increased with stand density (R^2=0.80) and equaled ground area at ~12,000 trees ha^{-1} (Figure 4).

Change in surface fuel loads with time since fire

Surface down and dead fuel loads in post-1988 wildfire forests generally increased with time since fire; however, 1-hr fuels did not change between 1996 and 2012 (Table 6). Rotten 1000-hr fuels increased by a factor of four; other fuel classes increased by approximately half that rate (Table 6). Increasing fuel loads coincided with a sharp decrease in within-plot variability (Figure 5). 1000-hr fuel loads greater than the 65 Mg ha^{-1} threshold for severe surface fire (Sikkink and Keane 2012) were present in 10% of stands in 1996 and 90% of stands in 2012.

2.6 DISCUSSION

A quarter-century after the 1988 fires in Yellowstone National Park, substantial fuel loads cover much of the young forest landscape indicating that extensive and severe reburning may be possible, especially under severe fire weather conditions. Post-fire stand structure, especially live lodgepole pine stem density, was the single greatest predictor of canopy and fine fuel loads, but pre-fire successional stage was the most important predictor of large woody surface fuels. Stands in this study have passed the 10-to-18 year period where severe reburning potential is reduced (Parks et al. 2014, 2016b, Harvey et al. 2016); however, some stands with low post-fire regeneration have low fuel loads and may provide some resistance to subsequent fire.

Substantial spatial variability was evident across the post-fire landscape in all fuel types. Fine surface fuel loads in these 24-year old forests were generally less than those reported in mature lodgepole pine forests, but most stands contained sufficient litter and 1-hr fuels to support rapid surface fire spread. Coarse fuel loads were similar or higher than values observed in mature lodgepole pine forests after other disturbance types (e.g., bark beetles and blowdown; Veblen 2000, Woodall and Nagel 2007, Kulakowski and Veblen 2007), and stands with abundant coarse fuels are especially susceptible to prolonged smoldering with high biomass consumption and heat release (Byram 1959, Rothermel 1972, Scott and Reinhardt 2001, Sikkink and Keane 2012). Canopy fuel loads, and particularly canopy bulk density, attained or exceeded values reported in mature lodgepole pine forests, and ubiquitous low canopy base heights indicate that young stands may be susceptible to crown fire initiation and many stands can support active and independent crown fire spread. Fuel conditions in most stands suggest that fire may be difficult to control, particularly in places where fires must be suppressed (e.g., near infrastructure).

Surface fuel loads in developing lodgepole pine forests differed from those found in other young and mature forest types. Litter and 1-hr fuels were about *half* that found in 1, 3, and 19 year old western hemlock/Douglas-fir stands in Washington, USA (Agee and Huff 1987b) and 2, 27, and 30 year old subalpine fir stands in Montana, USA (Fahnestock 1976), similar to Swedish Scots pine/Norway spruce/birch boreal forests <20-year-old (Schimmel and Granström 1997b) and mixed-conifer stands in the Cascade range, USA measured one year after high-severity fire (Hudec and Peterson 2012), but *greater* than a 48-year-old Jack pine (*Pinus banksiana*) stand that originated from fire in Ontario, Canada (Stocks 1987). The complete absence of duff in our study also differs from these studies but reflects results from other studies that documented little duff accumulation in lodgepole pine stands across Yellowstone National Park (Romme 1982b, Litton et al. 2004, Kashian et al. 2013a). Previous studies in mature, Rocky Mountain lodgepole pine forests report similar litter, 2-4 times *higher* 1-hr fuel loads, similar 10-hr fuel loads, and 10-20 times *lower* 100-hr and 1000-hr fuel loads than were found in this study (Lawson 1973, Alexander 1979, Lotan et al. 1985, Battaglia et al. 2010). Studies in mature, Rocky Mountain ponderosa pine (*Pinus ponderosa*) forests documented similar litter loads, 2 times *higher* 1-hr fuel loads, 2-10 times *higher* 10-hr fuel loads, and similar or lower 100-hr and 1000-hr fuel loads than levels observed in post-1988 lodgepole pine forests (Mason et al. 2007, Klutsch et al. 2009, Battaglia et al. 2010). Studies in mixed conifer forests (i.e., *Pinus spp. /Abies spp./Calocedrus spp./Quercus spp.*) in the Sierra and Cascade Mtn ranges observed 1-10 times *greater* litter and 1-hr fuel loads, 1-5 time *higher* 10-hr fuel loads, and 100-hr and 1000-hr fuel loads similar to loads observed this study (Schmidt et al. 2008, Van de Water and North 2011, Pierce et al. 2012, Hudec and Peterson 2012, Banwell and Varner 2014, Lydersen et al. 2015).

Our hypothesis that the legacy of pre-fire forest structure would greatly influence 100-hr and 1000-hr fuel loads and the proportion of rotten and sound logs was supported by the distribution of log sizes stratified by successional stage (Figure 2) but only weakly supported by our regression models (Table 4). Pre-1988 successional stages, as defined in this study, were derived from a geospatial cover type map produced via aerial photo classification and field verification (Despain 1990a, NPS-YELL 1990). We expect that regression results involving pre-fire successional stage could be improved if more detailed pre-fire stand structure measurements had been available. Still, our findings highlight the influence of pre-fire successional stage on coarse fuel loads and indicate that all old coniferous forests, or forests that otherwise had large trees at the time of the fire, will likely have more coarse wood after fire, as has been demonstrated after short-interval fire in the Pacific Northwest (Donato et al. 2016). Subsequent fires that burn in stands that had large tress prior to the first fire will likely have greater biomass consumption, flame residence time, heat release, and smolder for longer than will forests of small trees or sparse trees prior to the initial fire.

Lodgepole pine forests are unique in being able to develop an enormous canopy seedbank that facilitates abundant seedling establishment after fire (Clements 1910, Lotan et al. 1985). Twenty-four years' post-fire, canopy fuel loads attained or exceeded values reported in other young and mature forest types. On average, canopy fuel loads in these stands were ~5 times *higher* than values observed in 19 year old western hemlock/Douglas-fir forests in Washington, USA (Agee and Huff 1987b) but similar to subalpine fir stands 27 and 30 years post-fire in Montana, USA (Fahnestock 1976). Approximately 45% of stands in this study have available canopy fuel loads *greater* than 10 Mg ha^{-1} and the highest available canopy fuel load (48 Mg ha^{-1}) in our study is *greater* than the maximum value found in mature lodgepole pine forests (Cruz et al. 2003, Reinhardt et al. 2006a, Simard et al. 2011b). Canopy bulk density was ~2-5 times *greater* than values found in mature lodgepole pine, ponderosa pine, and mixed conifer stands in Colorado, Idaho, and Montana, USA (Cruz et al. 2003, Fulé et al. 2004, Reinhardt et al. 2006a, Simard et al. 2011b, Roccaforte et al. 2015) but similar to untreated ponderosa pine and mixed conifer stands affected by fire suppression in Arizona, USA (Cruz et al. 2003, Hall and Burke 2006, Reinhardt et al. 2006a, Mason et al. 2007). Results from this study highlight the link between post-fire tree regeneration and the development of canopy and fine surface fuels suggesting that stands with the highest rates of light capture and biomass production also have the highest canopy and fine surface fuel loads. In forest types lacking such a seedbank, we would expect slower canopy fuel development and reduced crown fire potential after a quarter century of post-fire recovery.

Just how much of the landscape is now vulnerable to high-severity re-burning and/or active crown fire spread? If we assume that sampled stands represent the proportion of a given fuel characteristic across the burned landscape, then approximately 76% of the post-1988 fire landscape is susceptible to high-severity surface fire and 63% is capable of active or independent crown fire spread. In a simulation study investigating surface-fire severity using the First Order Fire Effects Model (FOFEM), Sikkink and Keane (2012) found that dry coarse fuel loads above the 60 Mg ha^{-1} threshold resulted in a mean fire line intensity greater than 120 Kw m^{-2}, a mean fire residence time greater than 2 hours, and soil temperatures greater than 60° C to a > 6 cm depth. Using the mean intensity reported by Sikkink and Keane (2012), canopy fuels would be capable of igniting at 0.8 m canopy base height and 100% live foliar moisture content using van Wagner's (1977) crown fire initiation equation—encompassing approximately 90% of the stands sampled in this study.

Changes in surface fuels between 1996 and 2012 showed that fuel deposition from growing young trees and falling fire-killed trees were the dominant factors shaping surface woody fuels during the first 24 years of forest development (Table 7). Though our sample size is limited, these plots bridged the 10-18 year post-fire period beyond which fire potential and severity are not reduced by previous fire (Parks et al. 2014, 2016b, Collins et al. 2015, Harvey et al. 2016). Fuel loads increased by 175-430% during this window of time (1-hr fuels excepted; Table 7) and within-plot variability declined, indicating a transition from patchy to more spatially continuous fuel beds (Figure 5). Severe surface fire potential increased dramatically during this period due to snag fall from 10% of stands in 1996 to 90% of stands in 2012. Overall, the rapid increase in surface fuel loads is consistent with Kashian et al.'s (2013a) finding that ~50% of maximum needle and woody litter is recovered in the first 25 years after fire. Delayed post-fire snag fall likely accounts for increases in 100-hr and 1000-hr fuel loads since large fuel classes are subject to slow biomass turnover rates and can take ~125 years to decompose completely (Kashian et al. 2013). The lack of change in 1-hr fuels was not surprising given the high biomass turnover rate for small diameter wood observed by Simard et al (2012).

2.7 CONCLUSION

For land management agencies to develop informed adaptation and mitigation strategies to attenuate adverse impacts of increased fire activity to human life, infrastructure, and ecological services, quantitative data on the variability and dynamics of fuel beds in young forests will become increasingly important. On lands implementing passive management strategies such as 'wildland fire use', management personnel should acknowledge that young forests may have heavy fuel loads—like those in many of the stands in this study—capable of sustaining stand-replacing fire. On lands under active management, post-fire salvage logging may be implemented to reduce long-term coarse fuel loads and lessen resistance to control.

In conclusion, the tremendous variation in fuel loads across the post-1988 fire landscape suggest that stand age alone is a poor surrogate for predicting fuel conditions in young lodgepole pine stands that regenerated naturally from stand-replacing fire. Surprisingly, these stands have already developed fuel conditions that are likely to sustain reburning. Most of the post-1988 fire lodgepole pine forests can likely sustain high-severity surface fire and active crown fire, although we anticipate that fire behavior and effects will vary spatially across the landscape. In the future, fire rotations in Yellowstone National Park are predicted to be shorter than were typical historically (Westerling et al. 2011a), and this prediction cannot be ruled out by a lack of fuels to carry repeated fires at intervals of a few decades.

2.8 ACKNOWLEDGEMENTS

Special thanks to Paige Copenhaver-Parry, Daniel Donato, Winslow Hansen, Ronald Harned, Natalie Kaner, Andy Muench, Monique Nelson, Gail Stakes, and Tim Whitby for field and laboratory support, Judy Romme for logistic support, and Ken Gerow for statistical assistance. We also thank Yellowstone National Park staff Roy Renkin and Stacey Gunther for their knowledge and support in the park. Housing and logistical assistance were provided by the University of Wyoming—National Park Service research station and Yellowstone National Park. We thank two anonymous reviewers for constructive comments that improved this manuscript. Funding was provided by the Joint Fire Science Program (Grant 11-1-1-7) and the Boyd Evison Graduate Fellowship.

2.9 LITERATURE CITED

Agee, J. K., and M. H. Huff. 1987. Fuel succession in a western hemlock/Douglas-fir forest. Canadian Journal of Forest Research 17:697–704.

Alexander, M. E. 1979. Fuels description in lodgepole pine stands of the Colorado Front Range. Thesis, Colorado State University.

Banwell, E. M., and J. M. Varner. 2014. Structure and composition of forest floor fuels in long-unburned Jeffrey pine-white fir forests of the Lake Tahoe Basin, USA. International Journal of Wildland Fire 23:363–372.

Battaglia, M. A., M. E. Rocca, C. C. Rhoades, and M. G. Ryan. 2010. Surface fuel loadings within mulching treatments in Colorado coniferous forests. Forest Ecology and Management 260:1557–1566.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect Transformation In Site Productivity Research. Journal Of Forestry 64:691–692.

Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in sub-alpine forests. Ecology 76:747–762.

Brown, J. K. 1974. Handbook for inventorying downed woody material. USDA Forest Service, GTR-INT-16.

Brown, J. K., R. D. Oberhau, and C. M. Johnston. 1982. Inventorying surface fuels and biomass in the Interior West. USDA Forest Service, INT-GTR-129.

Byram, G. M. 1959. Combustion of forest fuels. Forest Fire: Control and Use 1:61–89.

Christensen, N. L., J. K. Agee, P. F. Brussard, J. Hughes, D. H. Knight, G. W. Minshall, J. M. Peek, S. J. Pyne, F. J. Swanson, and J. W. Thomas. 1989. Interpreting the Yellowstone fires of 1988. BioScience:678–685.

Clements, F. E. 1910. The life history of lodgepole burn forests. USDA Forest Service.

Collins, L., T. D. Penman, O. F. Price, and R. A. Bradstock. 2015. Adding fuel to the fire? Revegetation influences wildfire size and intensity. Journal of Environmental Management 150:196–205.

Copenhaver, P. E., and D. B. Tinker. 2014. Stand density and age affect tree-level structural and functional characteristics of young, postfire lodgepole pine in Yellowstone National Park. Forest Ecology and Management 320:138–148.

Cruz, M. G., M. E. Alexander, and R. H. Wakimoto. 2003. Assessing canopy fuel stratum characteristics in crown fire prone fuel types of western North America. International Journal of Wildland Fire 12:39–50.

Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart. Inc, Boulder, CO.

Donato, D. C., J. B. Fontaine, and J. L. Campbell. 2016. Burning the legacy? Influence of wildfire reburn on dead wood dynamics in a temperate conifer forest. Ecosphere 7:no. 5.

Evans, J. S., S. A. Cushman, and D. M. Theobald. 2014. An ArcGIS toolbox for surface gradient and geomorphometric modeling, version 2.0-0. http://evansmurphy.wix.com/evansspatial.

Fahnestock, G. R. 1976. Fires, fuel, and flora as factors in wilderness management: the Pasayten case. Tall Timbers Fire Ecology Conference 15:33–70.

Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest fires. Science of the Total Environment 262:221–229.

Fulé, P. Z., J. E. Crouse, A. E. Cocke, M. M. Moore, and W. W. Covington. 2004. Changes in canopy fuels and potential fire behavior 1880–2040: Grand Canyon, Arizona. Ecological Modelling 175:231–248.

Gesch, D. B. 2007. The National Elevation Dataset. Pages 99–118 in Maune, D., ed., Digital Elevation Model Technologies and Applications: The DEM Users Manual, 2nd Edition. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. Journal of statistical software 17:1–27.

Grömping, U. 2007. Estimators of relative importance in linear regression based on variance decomposition. The American Statistician 61:139–147.

Hall, S. A., and I. C. Burke. 2006. Considerations for characterizing fuels as inputs for fire behavior models. Forest Ecology and Management 227:102–114.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in ecological research 15:133–302.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. Ecology 97:2272–2282.

Hudec, J. L., and D. L. Peterson. 2012. Fuel variability following wildfire in forests with mixed severity fire regimes, Cascade Range, USA. Forest Ecology and Management 277:11–24.

Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta -dominated forests. Ecological Monographs 83:49–66.

Klutsch, J. G., J. F. Negron, S. L. Costello, C. C. Rhoades, D. R. West, J. B. Popp, and R. Caissie. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (Dendroctonus ponderosae Hopkins) outbreak in Colorado. Forest Ecology and Management 258:641–649.

Krawchuk, M. A., M. A. Moritz, M. A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. Global pyrogeography: The current and future distribution of wildfire. PLoS ONE 4:e5102.

Kulakowski, D., and T. T. Veblen. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88:759–769.

Lawson, B. D. 1973. Fire behavior in lodgepole pine stands; related to the Canadian Fire Weather Index. Canadian Forest Service, Victoria, Canada.

Litton, C. M., M. G. Ryan, and D. H. Knight. 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. Ecological Applications 14:460–475.

Lotan, J. E., J. K. Brown, and L. Neuenschwander. 1985. Role of fire in lodgepole pine forests. Lodgepole Pine: The Species and Its Management Symposium Proceedings:133–152.

Lumley, T., and A. Miller. 2009. leaps: Regression subset selection. R package version 2.9. https://CRAN.R-project.org/package=leaps.

Lydersen, J. M., B. M. Collins, E. E. Knapp, G. B. Roller, and S. Stephens. 2015. Relating fuel loads to overstorey structure and composition in a fire-excluded Sierra Nevada mixed conifer forest. International Journal of Wildland Fire 24:484–494.

Maser, C., R. G. Anderson, K. Cromack Jr, J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service agricultural handbook no. 553 553:78–95.

Mason, G. J., T. T. Baker, D. S. Cram, J. C. Boren, A. G. Fernald, and D. M. VanLeeuwen. 2007. Mechanical fuel treatment effects on fuel loads and indices of crown fire potential in a south central New Mexico dry mixed conifer forest. Forest Ecology and Management 251:195–204.

Millspaugh, S. H., and C. Whitlock. 1995. A 750-year fire history based on lake sediment records in central Yellowstone National Park, USA. The Holocene 5:283–292.

Moritz, M. A., M. A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. Ecosphere 3:art49.

NPS-YELL. 1990. Pre-1988 cover types of Yellowstone National Park, Wyoming, Montana, Idaho (Vector Version). Spatial Analysis Center - Yellowstone National Park.

NPS-YELL. 1997. Soils of Yellowstone National Park, Wyoming, Montana, Idaho. Spatial Analysis Center - Yellowstone National Park.

Parks, S. A., C. Miller, J. T. Abatzoglou, L. M. Holsinger, M.-A. Parisien, and S. Z. Dobrowski. 2016a. How will climate change affect wildland fire severity in the western US? Environmental Research Letters 11:35002.

Parks, S. A., C. Miller, L. M. Holsinger, S. Baggett, and B. J. Bird. 2016b. Wildland fire limits subsequent fire occurrence. International Journal of Wildland Fire 25:182–190.

Parks, S. A., C. Miller, C. R. Nelson, and Z. A. Holden. 2014. Previous fires moderate burn severity of subsequent wildland fires in two large western US wilderness areas. Ecosystems 17:29–42.

Pierce, A. D., C. A. Farris, and A. H. Taylor. 2012. Use of random forests for modeling and mapping forest canopy fuels for fire behavior analysis in Lassen Volcanic National Park, California, USA. Forest Ecology and Management 279:77–89.

Pierce, K. B., T. R. Lookingbill, and D. L. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. Landscape Ecology 20:137–147.

PRISM Climate Group. 2012. Oregon State University. http://prism.oregonstate.edu, created on 2 Nov 2012.

Reinhardt, E. D., J. H. Scott, K. Gray, and R. E. Keane. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. Canadian Journal of Forest Research 36:2803–2814.

Renkin, R. A., and D. G. Despain. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. Canadian Journal of Forest Research 22:37–45.

Roccaforte, J. P., D. W. Huffman, P. Z. Fule, W. W. Covington, W. W. Chancellor, M. T. Stoddard, and J. E. Crouse. 2015. Forest structure and fuels dynamics following ponderosa pine restoration treatments, White Mountains, Arizona, USA. Forest Ecology and Management 337:174–185.

Romme, W. H., M. S. Boyce, R. Gresswell, E. H. Merrill, G. W. Minshall, C. Whitlock, and M. G. Turner. 2011. Twenty Years After the 1988 Yellowstone Fires: Lessons About Disturbance and Ecosystems. Ecosystems 14:1196–1215.

Romme, W. H. W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199–221.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, GTR-INT-115:1–50.

Sando, R. W., and C. H. Wick. 1972. A method of evaluating crown fuels in forest stands. Research Paper NC-84.

Scheaffer, R., W. Mendenhall III, R. Ott, and K. Gerow. 2011. Elementary survey sampling. Cengage Learning.

Schimmel, J., and A. Granström. 1997. Fuel succession and fire behavior in the Swedish boreal forest. Canadian Journal of Forest Research 27:1207–1216.

Schmidt, D. A., A. H. Taylor, and C. N. Skinner. 2008. The influence of fuels treatment and landscape arrangement on simulated fire behavior, Southern Cascade range, California. Forest Ecology and Management 255:3170–3184.

Schoennagel, T., M. G. Turner, D. M. Kashian, and A. Fall. 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. Landscape Ecology 21:1281–1296.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across rocky mountain forests. Bioscience 54:661–676.

Scholze, M., W. Knorr, N. W. Arnell, and I. C. Prentice. 2006. A climate-change risk analysis for world ecosystems. Proceedings of the National Academy of Sciences of the United States of America 103:13116–13120.

Scott, J. H., and E. D. Reinhardt. 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service, RMRS-RP-29:1–59.

Sikkink, P. G., and R. E. Keane. 2012. Predicting fire severity using surface fuels and moisture. USDA Forest Service, RMRS-RP-96.

Simard, M., W. H. Romme, J. M. Griffin, and M. G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs 81:3–24.

Simard, M., W. H. Romme, J. M. Griffin, and M. G. Turner. 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Reply. Ecology 93:946–950.

Stephens, S. L., J. K. Agee, P. Z. Fulé, M. P. North, W. H. Romme, T. W. Swetnam, and M. G. Turner. 2013. Managing Forests and Fire in Changing Climates. Science 342:41–42.

Stocks, B. J. 1987. Fire behavior in immature jack pine. Canadian Journal of Forest Research 17:80–86.

Tinker, D. B., and D. H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3:472–483.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Turner, M. G., W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5:731–742.

Turner, M. G., W. H. Romme, and R. H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. International Journal of Wildland Fire 9:21–36.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411–433.

Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7:751–775.

Turner, M. G., T. G. Whitby, D. B. Tinker, and W. H. Romme. 2016. Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? Ecology 97:1260–1273.

USDA Forest Service-RSAC. 2012. Monitoring Trends in Burn Severity (MTBS). http://www.mtbs.gov/index.html.

Van de Water, K., and M. P. North. 2011. Stand structure, fuel loads, and fire behavior in riparian and upland forests, Sierra Nevada Mountains, USA; a comparison of current and reconstructed conditions. Forest Ecology and Management 262:215–228.

Van Wagner, C. E. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7:23–34.

Veblen, T. T. 2000. Disturbance patterns in southern Rocky Mountain forests.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York, NY, USA.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences of the United States of America 108:13165–13170.

Woodall, C. W., and L. M. Nagel. 2007. Downed woody fuel loading dynamics of a large-scale blowdown in northern Minnesota, USA. Forest Ecology and Management 247:194–199.

2.10 TABLES

Table 1: Fuel characteristics in low, moderate, and high density stands. Means are reported with one standard error. Letters indicate row-wise differences (Tukey's HSD, α=0.05).

	Density class			
	Low (<1000 stem ha^{-1})	Moderate (1000–50,000 stem ha^{-1})	High (>50,000 stem ha^{-1})	All
Sample size	n = 17	n = 56	n = 9	n = 82
Stand density (trees ha^{-1})	430 (67)	8,771 (1149)	124,474 (36482)	19508 (5645)
Crown				
Mean crown base height (m)	0.14 (0.02)^{a}	0.47 (0.03)^{b}	0.69 (0.07)^{c}	0.42 (0.03)
Crown bulk density (kg m^{3})	0.60 (0.07)^{a}	0.75 (0.04)^{a}	1.51 (0.17)^{b}	0.80 (0.04)
Canopy				
Foliage biomass (Mg ha^{-1})	0.84 (0.18)^{a}	8.27 (0.73)^{b}	15.12 (3.65)^{c}	7.49 (0.76)
1-hr branch biomass (Mg ha^{-1})	0.26 (0.06)^{a}	2.43 (0.21)^{b}	3.81 (1.09)^{b}	2.14 (0.22)
Available canopy fuel load† (Mg ha^{-1})	0.97 (0.20)^{a}	9.50 (0.84)^{b}	16.64 (4.25)^{c}	8.53 (0.87)
Total canopy biomass (Mg ha^{-1})	3.52 (0.74)^{a}	34.94 (3.11)^{b}	63.73 (15.62)^{c}	31.63 (3.25)
Canopy length (m)	3.48 (0.34)^{a}	3.77 (0.12)^{a}	1.77 (0.32)^{b}	3.49 (0.13)
Canopy bulk density§ (kg m^{3})	0.03 (0.00)^{a}	0.24 (0.02)^{b}	0.66 (0.12)^{c}	0.24 (0.03)
Live surface fuels				
Herbaceous (Mg ha^{-1})	1.71 (0.10)^{a}	0.98 (0.09)^{b}	0.81 (0.15)^{b}	1.11 (0.07)
Shrub (Mg ha^{-1})	0.10 (0.03)^{a}	0.15 (0.02)^{a}	0.13 (0.05)^{a}	0.13 (0.02)
Dead surface fuels				
Litter depth (cm)	0.59 (0.16)^{a}	1.19 (0.10)^{b}	1.73 (0.36)^{b}	1.10 (0.09)
Litter (Mg ha^{-1})	2.98 (0.78)^{a}	5.96 (0.51)^{b}	8.70 (1.80)^{b}	5.61 (0.46)
1-hr (Mg ha^{-1})	0.10 (0.01)^{a}	0.18 (0.02)^{b}	0.29 (0.04)^{c}	0.17 (0.01)
10-hr (Mg ha^{-1})	2.02 (0.19)^{a}	2.35 (0.11)^{a}	2.35 (0.33)^{a}	2.28 (0.09)
100-hr (Mg ha^{-1})	4.45 (0.32)^{a}	4.95 (0.23)^{a}	7.18 (1.13)^{b}	5.08 (0.22)
Sound 1000-hr (Mg ha^{-1})	78.48(7.54)^{a}	82.52 (5.64)^{a}	53.96 (7.83)^{a}	78.55 (4.31)
Rotten 1000-hr (Mg ha^{-1})	39.24(4.84)^{a}	31.13 (2.68)^{a,b}	17.64 (5.33)^{b}	31.42 (2.23)
Total surface fuel load (Mg ha^{-1})	127.27 (10.62)^{a}	127.09 (5.62)^{a}	90.12 (10.33)^{b}	123.12(4.70)

† Available canopy fuel load = foliage + 0.5*(1-hr branch wood)

§ Computed using the biomass-percentile method (Reinhardt et al. 2006)

Table 2: Within- and among-plot variability of fuel loads and fire behavior parameters in low, moderate, and high density stands. Within-plot variability estimates are mean coefficient of variation (CV, in percent) with one standard error. Letters indicate row-wise differences (Tukey's HSD, α=0.05). Among-plot coefficient of variation was computed using the population standard deviation and mean and do not include error rates.

	Within-plot variation (CV) by stem-density class				
	Low (<1000 stems ha^{-1})	Moderate (1000–50,000 stems ha^{-1})	High (>50,000 stems ha^{-1})	Within all plots	Among-plot variation
Sample size	n = 17	n = 56	n = 9	n = 82	n=82
Crown					
Mean crown base height	113.1 (26.7)^{a}	70.8 (3.9)^{b}	45.3 (4.8)^{b}	76.7 (3.4)	65.5
Available crown bulk density	116.8 (26.9)^{a}	103.2 (5.4)^{a}	93.9 (7.9)^{a}	105.0 (6.6)	112.4
Canopy					
Foliage biomass	123.4 (25.3)^{a}	113.8 (3.8)^{a}	97.4 (11.6)^{a}	114.0 (5.9)	96.3
1-hr branch biomass	128.8 (25.2)^{a}	120.6 (4.0)^{a}	105.2 (12.6)^{a}	120.6 (5.9)	96.1
Available canopy fuel load	124.1 (25.3)^{a}	114.7 (3.9)^{a}	98.5 (11.8)^{a}	114.9 (5.9)	96.2
Total canopy biomass	123.1 (25.3)^{a}	113.4 (3.8)^{a}	97.0 (11.5)^{a}	113.6 (5.9)	96.1
Dead surface fuels					
Litter	131.7 (17.5)^{a}	97.2 (5.7)^{b}	75.8 (4.8)^{b}	101.9 (5.6)	74.4
1-hr	89.5 (7.0)^{a}	85.7 (4.3)^{a}	65.7 (6.2)^{a}	84.3 (3.4)	70.4
10-hr	84.0 (7.4)^{a}	74.2 (3.1)^{a}	80.2 (10.6)^{a}	76.9 (2.9)	36.5
100-hr	59.1 (3.3)^{a}	60.3 (3.5)^{a}	68.3 (5.0)^{a}	60.9 (2.6)	39.8
Sound 1000-hr	51.0 (3.8)^{a}	47.8 (6.0)^{a}	52.8 (4.0)^{a}	49.0 (1.9)	49.9
Rotten 1000-hr	68.9 (4.1)^{a}	67.5 (4.0)^{a}	53.0 (8.8)^{a}	66.2 (3.1)	64.9
Total surface fuel load	39.5 (2.6)^{a}	35.5 (1.5)^{a}	34.5 (2.3)^{a}	36.2 (1.2)	34.9

Table 3. Candidate predictor variables, their sources, and the models that used them as candidates in model selection.

		Candidate variables used in model selection by response variable type			
Predictor variable	Acquisition method	Fine surface fuels	Coarse surface fuels	Live surface fuels	Canopy fuels
Live foliage, herb, shrub biomass	Empirical	X			
Live tree density	Empirical	X		X	X
Live basal area	Empirical			X	
Canopy base height	Empirical	X			
1000-hr fuel load	Empirical	X		X	
Pre-fire successional stage (Despain 1990, NPS-YELL 1990)	Downloaded		X	X	
Substrate (NPS-YELL 1997)	Downloaded			X	
Mean annual precipitation (PRISM Climate Group 2012)	Downloaded	X	X	X	X
Mean annual temperature (PRISM Climate Group 2012)	Downloaded	X	X	X	X
Compound topographic index (Evans et al. 2014)	Derived	X	X	X	X
Potential solar radiation (Pierce et al. 2005)	Derived	X	X	X	X
Elevation (Gesch 2007)	Downloaded	X	X	X	X
Slope (Gesch 2007)	Downloaded	X	X	X	X
Aspect (Gesch 2007)	Downloaded	X	X	X	X
dNBR fire severity (USDA Forest Service-RSAC 2012)	Derived		X	X	

Table 3: References

Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart. Inc, Boulder, CO.

Gesch, D. B. 2007. The National Elevation Dataset. Pages 99–118 in Maune, D., ed., Digital Elevation Model Technologies and Applications: The DEM Users Manual, 2nd Edition. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

NPS-YELL. 1990. Pre-1988 Cover Types of Yellowstone National Park, Wyoming, Montana, Idaho (Vector Version). Spatial Analysis Center - Yellowstone National Park.

NPS-YELL. 1997. Soils of Yellowstone National Park, Wyoming, Montana, Idaho. Spatial Analysis Center - Yellowstone National Park.

Pierce, K. B., T. R. Lookingbill, and D. L. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. Landscape Ecology 20:137–147.

PRISM Climate Group. 2012. Oregon State University. http://prism.oregonstate.edu, created on 2 Nov 2012.

USDA Forest Service-RSAC. 2012. Monitoring Trends in Burn Severity (MTBS). http://www.mtbs.gov/index.html.

Table 4: Predictive linear models illustrating the effects of post-fire stand structure, topo-climatic factors, and pre-fire successional stage on dead surface fuel loads in 24-year-old lodgepole pine stands.

Dead surface fuels	df	R^2	Parameter	ß	se	t-value	*p*-value
Log_{10} (Litter fuels)	78	0.43	Intercept	0.41	0.57	0.72	0.474
(Mg ha^{-1})			1000-hr fuel biomass	0.003	0.000	3.11	0.003
			Log_{10}(lodgepole pine density)	0.31	0.05	6.31	<0.001
			Mean annual precipitation	-0.002	0.001	-2.70	0.009
Log_{10} (1-hr fuels)	77	0.49	Intercept	-2.19	0.31	-7.11	<0.001
(Mg ha^{-1})			Mean crown base height	0.71	0.09	7.75	<0.001
			Mean annual precipitation	0.001	0.000	2.83	0.006
			Topographic wetness index	0.02	0.009	2.15	0.034
			Slope	0.02	0.007	2.08	0.041
10-hr fuels	79	0.08	Intercept	0.89	0.55	1.63	0.106
(Mg ha^{-1})			Log_{10}(lodgepole pine density)	0.36	0.14	2.55	0.013
			Mean annual temperature	-0.03	0.01	-1.96	0.053
Log_{10} (100-hr fuels)	78	0.22	Intercept	0.67	0.02	28.91	<0.001
(Mg ha^{-1})			Early pre-fire successional stage (LP1)	-0.15	0.06	-2.63	0.012
			Middle pre-fire successional stage (LP2)	0.17	0.04	4.66	<0.001
			Late pre-fire successional stage (LP3/4)	-0.01	0.03	-0.49	0.62
Log_{10} (Sound-1000-hr fuels)	77	0.24	Intercept	0.65	0.52	1.25	0.216
(Mg ha^{-1})			Early pre-fire successional stage (LP1)	-0.32	0.09	-3.72	<0.001
			Middle pre-fire successional stage (LP2)	0.07	0.06	1.10	0.275
			Late pre-fire successional stage (LP3/4)	0.17	0.05	3.66	<0.001
			Elevation	0.001	0.000	2.08	0.040
Log_{10} (Rotten-1000-hr fuels)	77	0.30	Intercept	2.62	0.44	5.91	<0.001
(Mg ha^{-1})			Early pre-fire successional stage (LP1)	0.22	0.12	1.82	0.073
			Middle pre-fire successional stage (LP2)	-0.38	0.08	-4.71	<0.001
			Late pre-fire successional stage (LP3/4)	0.004	0.07	0.07	0.95
			Mean annual precipitation	-0.002	0.000	-2.79	0.007
Total surface fuels	75	0.31	Intercept	379.68	59.70	6.36	<0.001
(Mg ha^{-1})			Early pre-fire successional stage (LP1)	-24.23	14.40	-1.68	0.10
			Middle pre-fire successional stage (LP2)	-6.89	10.81	-0.64	0.53
			Late pre-fire successional stage (LP3/4)	18.99	8.01	2.37	0.02
			Mean annual precipitation	-0.042	0.10	-4.03	<0.001

	Mean annual temperature	-2.42	0.72	-3.34	0.001
	Aspect	-15.94	6.28	-2.54	0.013

Table 5: Predictive linear models illustrating the effects of post-fire stand structure, topo-climatic factors, and pre-fire successional stage on live surface and canopy fuel loads in 24-year-old lodgepole pine stands.

Live surface fuels	df	R^2	Parameter	ß	se	t-value	*p*-value
Live herbaceous fuels ($Mg\ ha^{-1}$)	77	0.25	Intercept	2.09	0.34	6.25	<0.001
			Log_{10}(lodgepole pine density)	-0.24	0.09	-2.78	0.007
			Rhyolite–till	-0.14	0.19	-0.73	0.470
			Rhyolite–glacial	-0.12	0.16	-0.70	0.484
			Rhyolite–low base saturation	-0.23	0.11	-2.12	0.037
Log_{10}(Live shrub fuels) ($Mg\ ha^{-1}$)	78	0.25	Intercept	-8.75	1.63	-5.36	<0.001
			Log_{10}(lodgepole pine density)	0.35	0.10	3.60	<0.001
			Elevation	0.002	0.01	4.27	<0.001
			Fire severity (dNBR)	0.001	0.01	2.70	0.009
Live canopy fuels							
Log_{10}(Available canopy fuels) ($Mg\ ha^{-1}$)	81	0.78	Intercept	-1.27	0.12	-10.70	<0.001
			Log_{10}(lodgepole pine density)	0.54	0.03	16.95	<0.001
Log_{10}(Mean crown base HT) ($Mg\ ha^{-1}$)	79	0.66	Intercept	-1.16	0.08	-15.12	<0.001
			Log_{10}(lodgepole pine density)	0.24	0.02	12.01	<0.001
			Slope	-0.01	0.004	-2.24	0.028
Log_{10}(Canopy bulk density) ($kg\ m^{-3}$)	81	0.91	Intercept	-3.39	0.09	-39.62	<0.001
			Log_{10}(lodgepole pine density)	0.70	0.02	29.98	<0.001

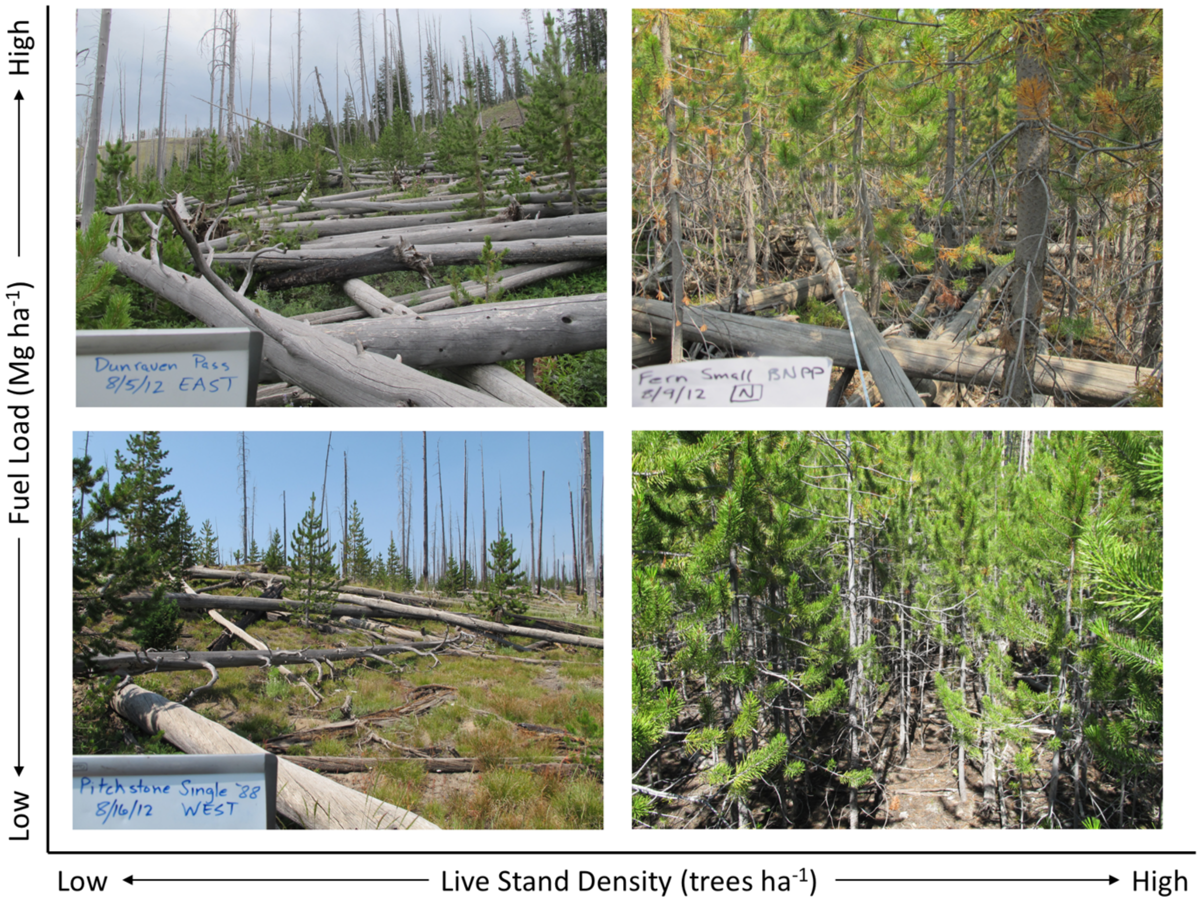
Table 6: The relative contribution of predictor variables to the models explanatory power with significant differences evaluated using bootstrapped confidence intervals. Each predictor's effect on the response is denoted using positive (+) and negative signs (-).

Fuel class response variables	**Stand structure and environmental predictor variables**												**Interpretation**
	Live stand density	Crown base height	1000-hr fuel load	Pre-fire successional stage	Substrate	Mean annual precipitation	Mean Annual Temperature	Compound topographic index	Elevation	Slope	1988 dNBR	Aspect	
Dead surface fuels													
Litter	0.66[a] (+)	-	0.13[b] (+)	-	-	0.21[a,b] (-)	-	-	-	-	-	-	• Litter biomass varied positively with post-fire stand attributes linked to litter deposition (i.e., stand density) and 1000-hr fuel loads, which promote drier soil conditions found on site with high numbers of logs (Remsburg and Turner 2006). Annual precipitation was negatively related to litter biomass possibly due to suppressed decomposition rates.
1-hr	-	0.78[a] (+)	-	-	-	0.09[b] (+)		0.02[b] (+)	-	0.01[b] (+)	-	-	• 1-hr fuels increased with post-fire stand attributes (i.e. canopy base height and stand density) related to lower branch pruning and with moisture availability.
10-hr	0.70[a] (+)	-	-	-	-	-	0.30[a] (-)						• 10-hr fuels were weakly predicted by post-fire stand attributes linked to litter deposition (i.e., stand density) and mean annual temperature.
100-hr	-	-	-	1.0 (+,-)	-	-	-	-	-	-	-	-	• 100-hr fuels varied negatively with early and late pre-fire successional stages and positively with middle pre-fire successional stages. These relationships are believed to stem from the sizes of pre-fire trees and logs.

1000-hr—sound	-	-	-	0.99[a] (+,-)	-	-	-	-	0.01[b] (+)	-	-	-	• Sound 1000-hr fuels varied negatively with early and middle pre-fire successional stages and positively with late pre-fire successional stages. The greatest sound 1000-hr fuel loads occurred on sites with large size classes of pre-fire trees and logs.
1000-hr—rotten	-	-	-	0.99[a] (-)	-	-	-	-	0.01[b] (-)	-	-	-	• Rotten 1000-hr fuels varied positively with early pre-fire successional stage and negatively with middle and late pre-fire successional stages. Rotten 1000-hr fuels are highest on sites with small size classes of pre-fire trees and logs.
Total surface	-	-	-	0.28[a] (+)	-	0.34[a] (-)	0.27[a] (-)	-	-	-	-	0.12[a] (-)	• Total surface fuel load varied positively with pre-fire successional stage and negatively with mean annual temperature, mean annual precipitation, and aspect.
Live surface fuels													
Live herbaceous	0.38[a] (-)	-	-	-	0.61[a] (-)	-	-	-	-	-	-	-	• Herbaceous biomass declined with post-fire stand basal area (i.e., restricted light and soil resources) and increased with substrate quality.
Live shrub	0.25[a] (+)	-	-	-	-	-	-	-	-	0.50[a] (+)	0.25[a] (+)	-	• Shrub biomass varied positively with post-fire stand density (i.e., restricted light and soil resources) and elevation.
Live Canopy fuels													
Available canopy fuel	1.0 (+)	-	-	-	-	-	-	-	-	-	-	-	• Available canopy fuel load varied positively with post-fire stand density.
Crown base height	0.96[a] (+)	-	-	-	-	-	-	-	-	0.04[b] (-)	-	-	• Canopy bulk density increased with post-fire stand density. High density stands were found to have the greatest foliar biomass and the lowest canopy length.
Canopy bulk density	1.0 (+)	-	-	-	-	-	-	-	-	-	-	-	• Canopy base height increased with post-fire stand density as a result of density-dependent lower branch pruning.

Table 7: Changes in surface fuel loads between 1996 and 2012 in 10 remeasured plots. Means are reported with one standard error and the range of observations in each time period. Statistics reflect paired t-tests.

Surface fuel type	1996 ($Mg\ ha^{-1}$)	2012 ($Mg\ ha^{-1}$)	t	p-value (two-tailed)	Ratio of change (2012/1996)
1-hr fuels	0.13±0.02 [0.07, 0.22]	0.14±0.02 [0.06, 0.26]	-0.34	0.744	1.07±0.22
10-hr fuels	0.98±0.15 [0.00, 1.92]	2.37±0.16 [1.52, 3.27]	-5.96	<0.001	2.41±0.43
100-hr fuels	2.92±0.39 [0.40, 4.42]	5.07±0.46 [1.97, 6.66]	-3.82	0.004	1.74±0.26
1000-hr fuels–Sound	26.85±4.14 [11.40, 50.16]	60.61±7.42 [25.54, 95.78]	-3.99	0.003	2.26±0.44
1000-hr fuels–Rotten	11.07±2.08 [1.72, 19.71]	47.66±6.79 [23.15,79.20]	-6.18	<0.001	4.31±0.70
Total Fuel Load	41.95±5.16 [24.01, 74.92]	115.84±9.61 [60.17, 160.54]	-7.49	<0.001	2.76±0.37



2.11 FIGURES

Figure 1: The great range of variability in 24-year-old lodgepole pine forest structure and fuel characteristics developing after the 1988 Yellowstone fires. Photos taken in 2012 by K. N. Nelson and M. G. Turner.

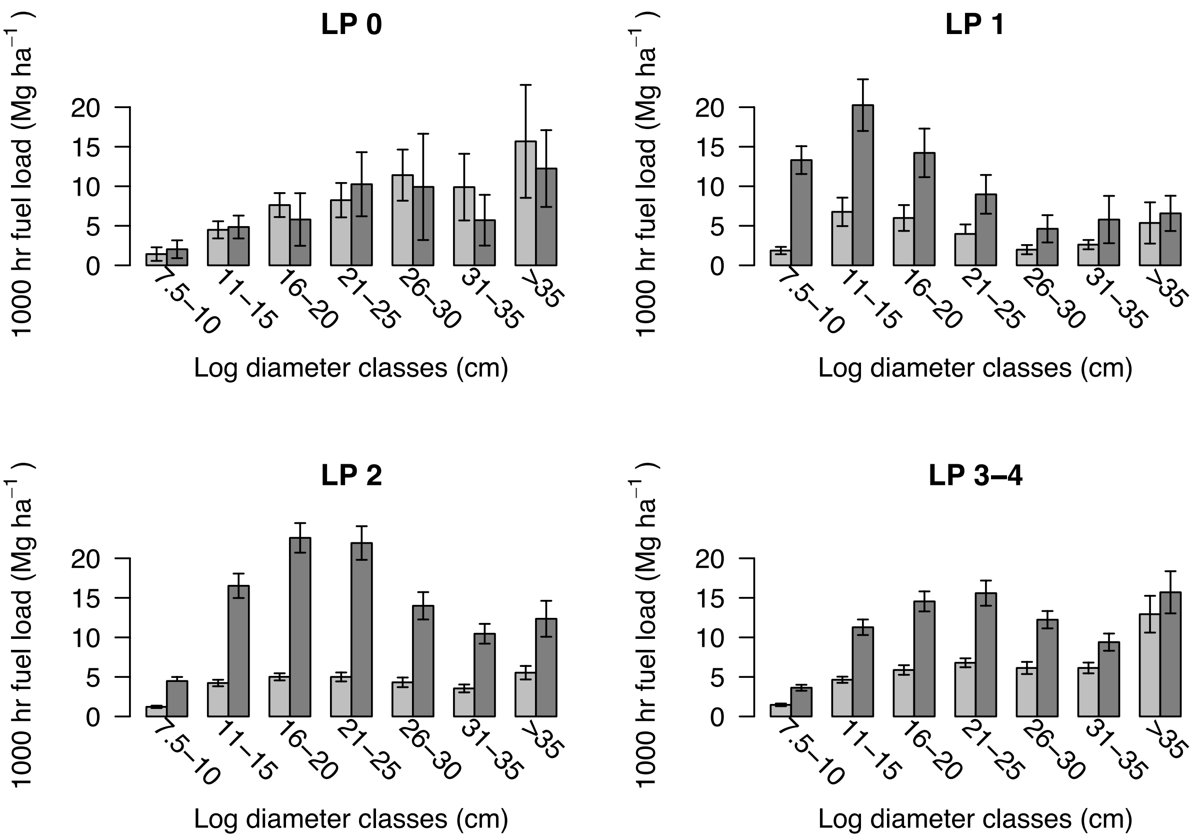


Figure 2: Coarse fuel loads by log size and decay status for each pre-fire successional stage. Rotten log fuel loads are depicted with light gray bars and sound log fuel loads are depicted with dark gray bars. Pre-fire vegetation successional stages (Despain 1990a) include: LP0—post-fire stands where lodgepole pine has recolonized the site but has not yet produced a closed canopy, LP1—dense, young lodgepole pine in a single cohort without tree seedlings in the understory, LP2—closed canopy lodgepole pine with tree seedlings in the understory, LP3—multi-cohort stands with ragged canopy characteristics dominated by lodgepole pine but containing Engelmann spruce and subalpine fir in the sub-canopy, LP4—seral lodgepole pine stands on dry sites wtihout Engelmann spruce and subalpine fir. LP3 and LP4 have similar above-ground biomass characteristics and were combined to enhance sample size.

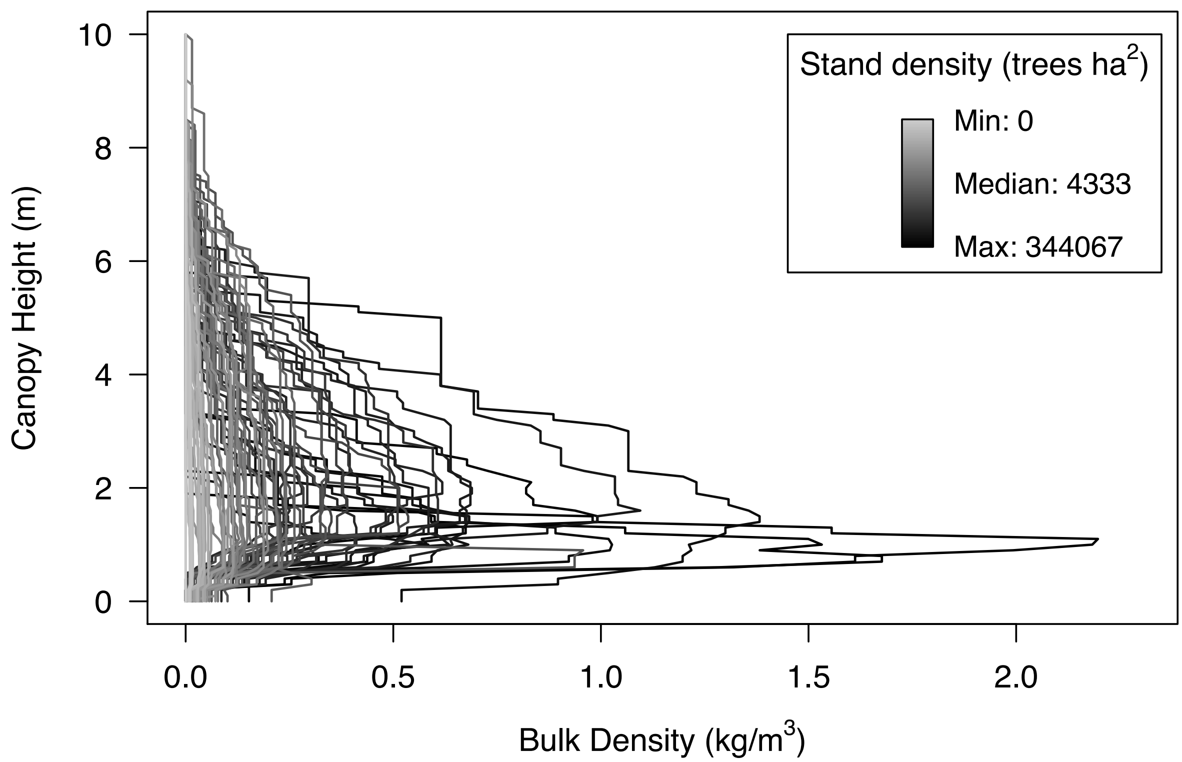


Figure 3: Vertical variation in canopy bulk density by stand density. Canopy bulk density was estimated for 0.1 meter vertical strata by summing available canopy fuel load within each strata then dividing by the volume of each layer (plot area x strata depth) for each plot and smoothed for plotting using a 1 meter running mean.

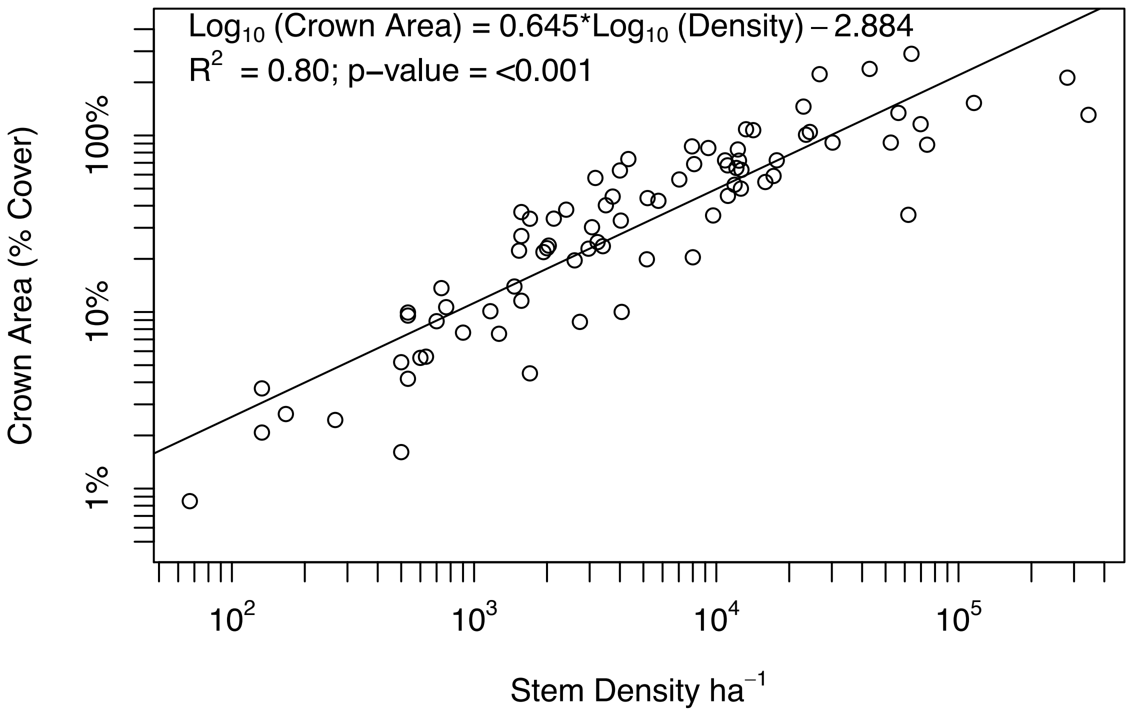


Figure 4: The relationship between stem density and percent crown area. Crown area is defined as the percent of ground area covered by tree crowns assuming circular crowns and even tree spacing.

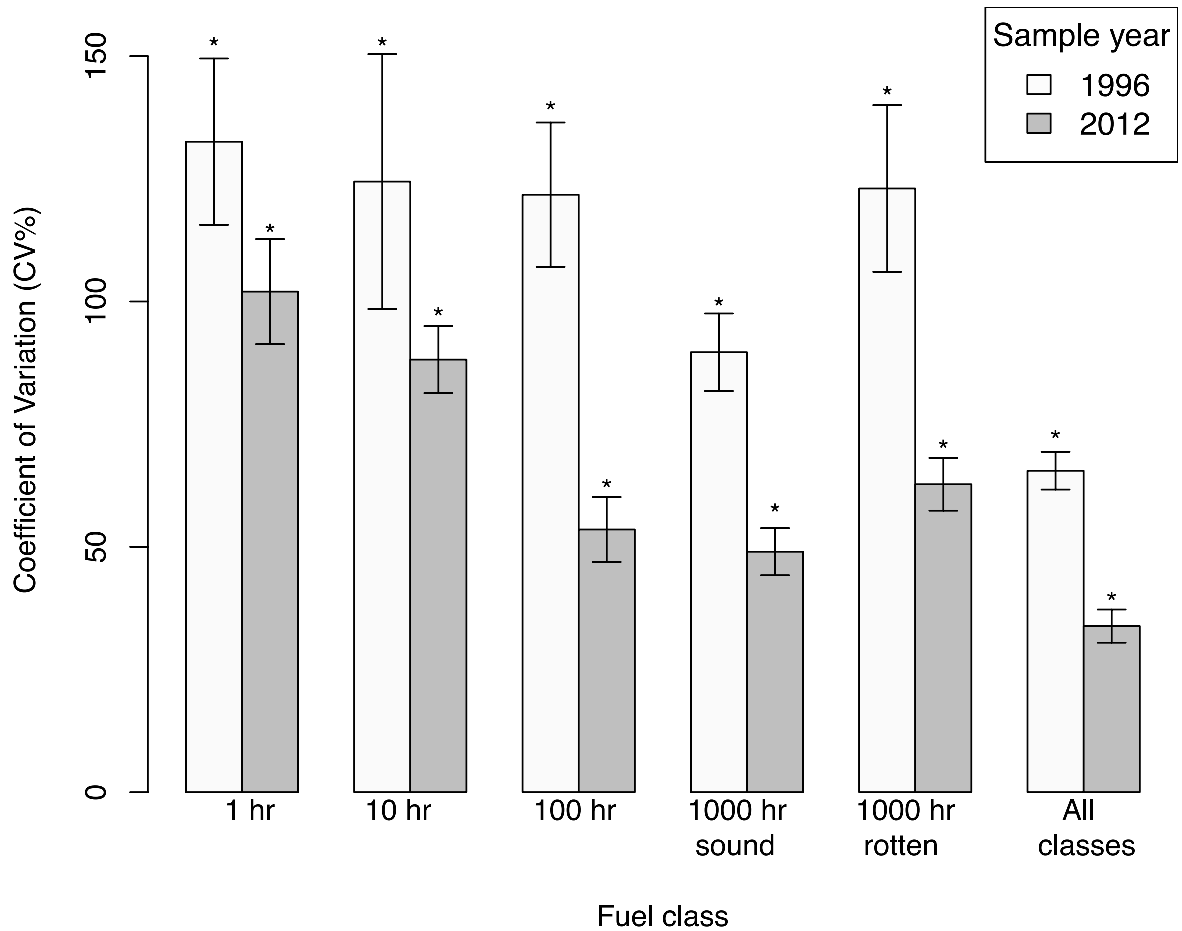


Figure 5: Within-plot coefficient of variation for surface fuel loads in 1996 and 2012. Asterisks indicate significant differences between years using a two-sided, paired t-test (α=0.05).

CHAPTER 3. WIND AND FUELS DRIVE FIRE BEHAVIOR IN YOUNG, POSTFIRE LODGEPOLE PINE FORESTS

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Note: This chapter was submitted for publication to the International Journal of Wildland Fire in December 2016.

3.1 ABSTRACT

Early successional forests are expanding throughout western North America as fire frequency and annual area burned increase, yet fire behavior in young postfire forests is poorly understood. We simulated potential fire behavior in 24-yr-old lodgepole pine (*Pinus contorta* var. *latifolia*) stands (*n*=82) in Yellowstone National Park (Wyoming, USA) to address two questions. [1] How does potential fireline intensity, crown fire initiation, and crown fire spread vary among post-1988 lodgepole pine stands? [2] What is the relative importance of fuels, fuel moisture conditions, and wind on potential fire behavior? Simulations used operational fire behavior models and empirical fuel characteristics, 50% to 99% fuel moisture conditions, and 1 to 60 km hr^{-1} winds. Fuel loads were sufficient to support fire in all stands. Wind was most important for predicting fireline intensity and crown fire initiation, but fuels were an important secondary driver under moderate burning conditions. Canopy bulk density was the most important predictor of crown fire spread. At higher wind speeds, active crown fire was predicted in 90% of stands under all fuel moisture conditions. We conclude that twenty-four-year-old lodgepole pine forests can readily support fire intervals shorter than those observed historically in Yellowstone National Park.

3.2 INTRODUCTION

Shifting patterns in global temperature and precipitation have been observed over the past three decades (Westerling et al. 2006), and are projected to accelerate over the next century, leading to increases in the frequency and extent of wildland fire (Flannigan et al. 2000, 2009, Scholze et al. 2006, Moritz et al. 2012, Abatzoglou and Williams 2016). In subalpine forest ecosystems prone to stand-replacing fire, increased burned area will lead to larger areas of young, regenerating forest stands. Until recently, effects of postfire succession on subsequent fire have been poorly described. A growing body of evidence indicates that time-since-fire plays an important role in the self-regulation of fire, especially as fires overlap at shortened intervals (Peterson 2002, Collins et al. 2009, 2015, Price and Bradstock 2010, Teske et al. 2012, Parks et al. 2015, 2016b, Coppoletta et al. 2016, Nelson et al. 2016, Stevens-Rumann and Morgan 2016). To understand how young subalpine forests might burn in short-interval fire, we investigated the relative contributions of fuels, weather, and wind on potential fire behavior in 24-yr old postfire lodgepole pine (*Pinus contorta* var. *latifolia*) forests that established after the 1988 fires in Yellowstone National Park (YNP).

Extensive stand-replacing fires (i.e., complete tree death) are common in subalpine lodgepole pine forests during periods of severe fire weather (Romme 1982a, Lotan et al. 1985, Bessie and Johnson 1995, Schoennagel et al. 2004). Greater frequency and severity of drought over the next century are projected to reduce fire return intervals and shift the forest mosaic toward a greater abundance of young forests (Schoennagel et al. 2006a, Westerling et al. 2011b). Stand replacing fires temporarily reduce forest biomass (Kashian et al. 2006) and initiate a period of reduced burn probability as fuels accumulate. Such a negative feedback does not preclude fire from burning in young forests during extreme wind and drought, but does imply that fuel limitation may reduce fire extent and severity during the first decades following fire. In the northern Rocky Mountains, the likelihood of a second fire may be reduced for 14 to 18 years (Parks et al. 2016b) while burn severity may be reduced for 10 to 12 years (Harvey et al. 2016).

Historically, fires in YNP's young lodgepole pine stands rarely transitioned from surface-to-crown fire in the absence of high winds, and predominantly occurred when fire spread from adjacent mature stands under severe fire weather (Despain 1990b; D Abendroth, A Norman, M Johnston, R Renkin, B Smith, personal communication, 2015). Recent fires, including the 2012 Cygnet, 2010 Antelope, and 2002 Phlox fires were consistent with these observations. However, severe burning conditions during the 2016 fire season led to the greatest burned extent in YNP since 1988 and re-burned over 18,000 ha of post-1988 forests (http://inciweb.nwcg.gov/incident/4944/). We previously quantified fuel loads in 24-yr old lodgepole pine stands that regenerated after the 1988 fires and found fuels suitable for high-severity surface fires in 76% and crown-fire spread possible in 63% of our sample of the post-1988 Yellowstone landscape (Nelson et al. 2016). These estimates of fire potential were based on simplified thresholds applied to fuels (Sikkink and Keane 2012, Reinhardt et al. 2006). Thresholds did not incorporate the myriad processes affecting surface and crown fire behavior, including effects of wind, fuel moisture, and detailed fuel characteristics that are represented in more sophisticated fire models. More rigorous fire behavior analyses are needed to fully understand and predict the controls exerted by weather and fuel conditions on surface and crown fire behavior in young postfire forests.

The objective of this study was to assess the variation and drivers of potential fire behavior in young, post-1988 lodgepole pine stands burned under a range of weather conditions using a comprehensive set of operational fire behavior and effects models. We simulated potential fire behavior in 82 lodgepole pine stands that regenerated following the 1988 fires in Yellowstone National Park (Wyoming, USA) to address two questions: [1] How does potential fireline intensity, crown fire initiation, and crown fire spread vary among post-1988 lodgepole pine stands? [2] What is the relative importance of fuel loads, fuel moisture conditions, and wind on potential fire behavior? Yellowstone National Park is the premiere landscape for such a study because human intervention on fire regimes and forest dynamics has been minimal, substantial reductions in the fire interval have been projected in recent empirical studies (Schoennagel et al. 2006a, Westerling et al. 2011b), and the scale of the 1988 fires represents the anticipated magnitude of mega-disturbances under projected climate conditions (Running 2006).

3.3 MATERIALS AND METHODS

Study area

Yellowstone National Park is a mostly roadless landscape primarily managed as wilderness encompassing approximately 900,000 ha along the continental divide in northwestern Wyoming, USA. The park ranges from 2100 to 2700 m in elevation with ~ 80% of the landscape covered in forests. At the Old Faithful weather station, mean annual precipitation is 645 mm and mean annual temperature is 1.2°C with winter lows averaging -17.6°C in January and summer highs averaging 23.8°C in July (NCDC normals between 1981 and 2010; http://www.wrcc.dri.edu). Lodgepole pine is the dominant tree species, occurring primarily on infertile, rhyolitic substrates and slightly less infertile andesitic substrates (Turner et al. 2004). Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) can dominate on moister sites, and whitebark pine (*Pinus albicalus*) can be found in pure stands at high elevations.

In 1988, extensive fires burned across 45% of the subalpine plateau (Turner et al. 1994). Twenty-four years later, regenerating lodgepole pine trees varied in density from 0 to 344,000 stems per hectare and produced a wide range of available canopy fuel loads [range 0.0-46.6 Mg ha^{-1}] and canopy bulk densities [range: 0.0-2.3 kg m^{3}], with canopy fuels in the densest stands exceeding those found in mature lodgepole pine forests (Nelson et al. 2016). Litter and 1-hr fuels varied positively with post-1988 stem density and averaged 5.61 Mg ha^{-1} and 0.17 Mg ha^{-1}, respectively. Mean total surface fuel loads were 123 Mg ha^{-1}, with 1000-hr fuels accounting for 88% of surface fuel loads. Surface fuels, in many stands, were in direct contact with canopy fuels. In total, fuel profiles quantified for 82 stands of 24-yr old postfire lodgepole pine (Nelson et al. 2016) provided the basis for this simulation.

Fire model formulation

Our objective was to simulate potential fire behavior across the post-1988 Yellowstone landscape using empirical fuel characteristics, fuel moisture, and wind conditions (Table 1). Fuel characteristics for each study site (n=82) were input into a custom-built fire simulation system that links operational fire behavior models to predict head fire (aka fireline) intensity and crown fire initiation and spread (Figure 1, Table 1). This approach assumed that: [1] fuels are homogeneously distributed within each study site, [2] forest fires are capable of equilibrium conditions (i.e., we do not account for temporal variation in fire behavior), [3] fuel moisture and wind conditions observed at the Old Faithful RAWS station are representative of the range of conditions observed across the broader landscape, [4] empirical relationships in sub-model components result in a *reasonable* estimate for that model component in our system (i.e., standard *fire behavior fuel models* (FBFM) may be used to estimate surface rate of spread (sROS) when fuel conditions in a study site are deemed reasonably similar to a standard FBFM), and [5] the sites sampled in this study reflect a random sample of the post-1988 forest conditions across Yellowstone National Park. Slope in our study sites ranged from 0 to 10 degrees and was set to zero in our modeling framework for ease of comparison.

Surface fireline intensity (I_b)— Surface fireline intensity (I_b) was estimated using a derivation of Byram's (1959) fire intensity equation (Eqn. 1; Andrews and Rothermel 1982, Scott and Reinhardt

$$I_b = sROS * HPA \tag{1}$$

2001) where sROS is forward rate of fire spread (m min^{-1}) and HPA is heat release per unit area (kW m^{-2}) in the flaming front. sROS was estimated using a reduced set of standard FBFMs that best represent the empirical fuels data at each site and adjusted mid-flame windspeed (Andrews 2012). To assign standard FBFMs to each site, we [1] applied a cluster analysis to our site-wise litter, 1-hr, 10-hr, 100-hr, herbaceous, and shrub fuel estimates using a k-medoid clustering algorithm (Supplementary Figures 1 and 2), [2] estimated surface rate of spread (sROS) for each resulting fuels group using a custom FBFM, [3] selected the most similar FBFM from a subset of Scott and Burgan's (2005) FBFMs representing arid climate types (Rebain et al. 2010) by comparing custom model output with standard FBFM output using root mean square error and mean bias between custom and standard fuel models via the Rothermel R-package (Vacchiano and Ascoli 2015), and [4] assigned the most similar standard FBFM to each site according to its cluster group (sFigure 1; sFigure 2). Twenty-three sites were assigned to the *Low Load, Dry Climate Grass-Shrub (GS1)* model representing sparse grass with small amounts of dead fuel particles with a RSME of 1.177, mean bias of -0.653, and mean cluster silhouette width of 0.17. Thirty-seven sites were assigned to the *Moderate Dwarf conifer with understory (TU4)* representing short conifer trees with grass or moss understory with a RSME of 1.023, mean bias of 0.447, and mean cluster silhouette width of 0.24. Twenty-three sites were assigned to the *Very High Load Broadleaf Litter (TL9)* representing heavy broadleaf litter, or heavy needle drape, with a RSME of 0.220, mean bias of 0.149, and mean cluster silhouette width of 0.24.

HPA was estimated using the first 60 seconds of combustion in the First Order Fire Effects Model (FOFEM). The Burnup model (Albini and Reinhardt 1995, 1997) used in FOFEM estimates fuel consumption and burn intensity using comprehensive empirical fuel profiles and fuel moisture conditions (Table 1).

Crown fire thresholds—Crown fire thresholds were estimated using Boolean logic. I' was evaluated by computing a critical surface intensity threshold (Eqn. 2; I') for crown fire initiation (Van

$$I'_{initiation} = \left(\frac{CBH(460 + 25.9FMC)}{100}\right)^{3/2} \quad (2)$$

Wagner 1977) where CBH is crown base height (m) and FMC is live foliar moisture content (%), then evaluating whether I_b exceeds this threshold. cROS was estimated using an empirical relationship developed in North American conifer forests (Eqn 3) where U_{10} is 10 m open wind speed (km hr^{-1}), CBD is crown bulk density (kg m^2), and $FMC_{1\text{-}hr}$ is 1-hr fuel moisture content (Cruz et al. 2005, Alexander and Cruz 2006). U_{10} was estimated in the cROS model by multiplying 6.1 m open wind speeds by 115% (Turner and Lawson 1978). Crown-to-crown fire spread was estimated using the criterion for active crowning (Eqn. 4, CAC; Cruz et al. 2005, Alexander and Cruz 2006), a metric that evaluates whether predicted crown fire rate of spread (Eqn. 4; cROS) exceeds a minimum cROS threshold that is based on canopy bulk density (CBD) (Van Wagner 1977, Alexander and Cruz 2006).

$$cROS_A = 11.02(U_{10})^{0.9} * CBD^{0.19} * e^{(0.17*FMC_{1-hr})}, CAC \geq 1.0 \tag{3}$$

$$CAC = \frac{cROS_A}{{}^{3}/_{CBD}} \tag{4}$$

To evaluate potential fire type, we combined I' and CAC using set theory in accordance with established fire type logic (Van Wagner 1977, Scott and Reinhardt 2001). Surface fire was assigned in cases where I_b was not capable of surface-to-crown initiation and cROS was not capable of crown-to-crown spread [I_b < I', cROS < CAC]. Passive crown fire was assigned in cases where I_b was sufficient for surface-to-crown initiation, but cROS was not capable of crown-to-crown spread [I_b ≥ I', cROS < CAC]. Conditional crown fire was assigned in cases where I_b was not capable of surface-to-crown initiation, but canopy fuel characteristics were sufficient for crown-to-crown spread [I_b < I', cROS ≥ CAC]. Active crown fire was assigned in cases where I_b was sufficient for surface-to-crown initiation and cROS was sufficient for crown-to-crown spread [I_b ≥ I', cROS ≥ CAC].

Model parameterization

Fuels—We used empirical surface and canopy fuel characteristics from 82 stands (see Nelson et al. 2016). Parameters derived from empirical field data and used to specify initial conditions in each stand included surface fuel loads, fuel bed depth, canopy fuel characteristics, and wind adjustment factor (WAF; Table 1). Thousand-hour fuel loads were summarized and grouped into two decay classes, sound and rotten, and four log diameter classes corresponding to those required in the FOFEM – Burnup model (Albini and Reinhardt 1995, 1997): 7.5–15 cm, 16–22 cm, 23–50 cm, and >50 cm diameter classes. Canopy bulk density was computed using the mass over volume approach used by Van Wagner (1977) and recommended by Cruz and Alexander (2010). Fuels data can be found at http://dx.doi.org/10.5061/dryad.3b15s.

Fuel moisture content (FMC)—Simulations were parameterized using FMC estimates spanning 50th—99th percentile conditions. Daily meteorological and fire occurrence data were downloaded via KCFAST (https://fam.nwcg.gov/fam-web/kcfast/mnmenu.htm) from the Old Faithful weather station (#480107) in YNP for all fire seasons (June through October) from 1981 and 2010. Data were input into the Fire Family Plus software system (Bradshaw and McCormick 2000), and percentile FMC conditions were generated for 1-hr, 10-hr, 100-hr, 1000-hr, herbaceous, and shrub fuel classes using National Fire Danger Rating System protocols. Live lodgepole pine foliar FMC was estimated by calculating a probability distribution of empirical FMC values extracted from the Flagg Ranch station in the National fuel moisture database (http://www.wfas.net/index.php/national-fuel-moisture-database-moisture-drought-103).

FMC declined in all fuel classes as the percentile (i.e., severity) of weather conditions increased in our simulation model framework (Figure 2). Over the 50^{th} to 99^{th} percentile range in FMC conditions, herbaceous FMC declined from 79% to 3%, woody shrub FMC from 122% to 70%, 1-hr FMC from 7% to 2%, 10-hr FMC from 9% to 2%, 100-hr FMC from 13% to 6%, 1000-hr FMC from 17% to 10%, and live lodgepole pine FMC from 118% to 84%.

Wind—Open wind speeds (6.1 m) were bound on the upper end at 60 km hr^{-1} representing 99.9th percentile wind speed at the Old Faithful RAWS station on days that reported fires in Yellowstone National Park. Wind adjustment factor (WAF) was computed using empirical stand structure variables (Table 1; Andrews 2012) and used to convert open wind speed to mid-flame wind speeds (i.e., approximately eye level winds) for input into the Rothermel surface fire spread model (Rothermel 1972, 1983).

Simulation experiment

Potential fire behavior was simulated for each study site (n = 82) across a range of 50th to 99th percentile weather conditions (n = 50 levels) and 1 to 60 km hr^{-1} open wind speeds (n = 60 wind speeds) resulting in 246,000 unique simulations. Weather and wind conditions were held constant within a given scenario; however, site specific fuels varied within each scenario representing empirical surface and canopy fuel characteristics at the 1 ha scale. Potential fire behavior response variables (Table 1) were simulated for each combination of weather (Figure 3), wind, and site-specific fuel profile.

Analysis

To quantify among-stand variability in potential fire behavior in 24-yr old lodgepole pine stands, we computed the median and inner quartile range for HPA and I', and generated boxplots (depicting median, inner-quartile range, and upper and lower observation at 1.5 times the inter-quartile range) for sROS and I_b at 50^{th} and 99^{th} percentile moisture conditions and at 1, 25, and 50 km hr^{-1} open wind speeds. Binary canopy fire behavior response variables were reported as percent of stands exhibiting surface-to-crown initiation and/or crown-to-crown fire spread at 50th and 99th percentile moisture conditions and 1, 25, and 50 km hr^{-1} open wind speeds. The distributions of fireline intensity and percent of stands exhibiting successful surface-to-crown initiation and/or crown-to-crown fire spread were plotted using a kernel density function.

To quantify the relative importance of wind and fuel characteristics on potential fire behavior, we fit generalized linear models to fire behavior response variables using wind and empirical fuel attributes as predictor variables. Independent predictor variables were (with transformations): open wind speed (6.1 m), fuel moisture percentile, litter, 1-hr, 10-hr, 100-hr, sound 1000-hr, rotten 1000-hr, all 1000-hr fuel loads, crown base height, and canopy bulk density. Continuous response variables were fit using the *identity* link function and binary response variables were fit using a *Gaussian* link function. Model selection routines (Lumley and Miller 2009, Calcagno et al. 2010) were used to optimize AIC while maintaining α=0.05. Model residuals, fits, and transformation criteria were checked using methods recommended by Venables and Ripley (2002); the presence of multicollinearity was evaluated using variance inflation factors.

To evaluate the relative contribution of each predictor variable in the final models, we computed r^2 and pseudo-r^2 for each predictor variable using the *lmg* metric in the *relaimpo* R package (Grömping 2006). Variation in relative contributions of predictor variables was evaluated across the range of input wind speeds by iteratively fitting models at each wind speed and extracting the *lmg* metric for each wind speed. *lmg* estimates the relative contribution of each predictor to the model's total explanatory power by reordering predictor variables and taking the mean sums of squares (Grömping 2006, 2007). Significant differences in *lmg* between predictor variables were tested by generating 95% bootstrapped confidence intervals (999 iterations).

Analyses were completed using the R software program and the following r-packages: *base* (R Core Team 2016), *cluster* (Maechler et al. 2012), *dplyr* (Wickham and Francois 2015), *ggplot2* (Wickham 2009), *glmulti* (Calcagno and de Mazancourt 2010), *leaps* (Lumley and Miller 2009), *relaimpo* (Grömping 2006, 2007), *spatialEco* (Evans 2016), and *Rothermel* (Vacchiano and Ascoli 2015).

3.4 RESULTS

Variation in potential fire behavior—Potential fire behavior varied among the 24-yr old lodgepole pine stands depending upon surface and canopy fuel characteristics, fuel moisture conditions, and open wind speed. Dense canopy conditions reduced open wind speed by 52 to 90% (WAF ranged from 0.10 to 0.48; Figure 3). At 50th and 99th percentile weather conditions, median and inner-quartile range for surface fire rate of spread (sROS) was 0.33 [0.32, 0.37] and 0.55 [0.52, 0.57] m min^{-1} at 1 km hr^{-1} and 3.52 [2.08, 6.58] and 7.91 [5.5, 11.33] m min^{-1} at 50 km hr^{-1} open wind speed (Figure 4). Median HPA was 104.9 and 111.8 kW m^2 under 50th and 99th percentile moisture (Table 2), and ranged from a minimum of 27.8 kW m^2 to a maximum of 318.1 kW m^2 depending on the load and composition of the fuel bed. Critical surface-to-crown initiation intensity (I') varied from 0 kW m^2 in stands where canopy fuels contact surface fuels to 259 kW m^2 in stands with the greatest crown base heights (Table 2). At 50^{th} and 99^{th} percentile moisture conditions median and inner-quartile range for surface fireline intensity (I_b) was 46.8 [28.9, 70.9] and 112.7 [75.3, 168.4] kW m^2 at 1 km hr^{-1} and 607.5 [440.3, 903.4] and 1588.7 [991.4, 27.7.4] kW m^2 at 50 km hr^{-1} open wind speed (Figure 4). The distribution of fireline intensity exhibited a strong positive skew that diminished slightly under 99th percentile moisture conditions (Figure 5). Distributions of the percent of stands capable of surface-to-crown initiation and crown-to-crown spread were negatively skewed and increased under 99th percentile moisture conditions (Figure 5). At 50th and 99th percentile moisture conditions, surface fire intensity was sufficient to overcome the surface-to-crown initiation threshold in 49 and 94% of stands at 1 km hr^{-1} and 99% of stands under all moisture conditions at 50 km hr^{-1} open wind speed (Figure 6). The threshold for crown spread was met in a minimum of 17% of stands at 1 km hr^{-1} and a maximum of 90% of stands at 50 km hr^{-1} (Figure 6). Even under extreme wind and weather conditions, 10% of stands were not capable of achieving spreading crown fire due to sparse tree cover and insufficient canopy bulk density.

Relative importance of fuels, weather and wind speed—Simulated sROS and I_b were strongly and positively influenced by wind speed; fuels had less influence (Table 3). Wind attenuation via the WAF was strongly driven by post-1988 tree density (Table 3; Figure 4), and WAF was a significant driver of sROS and I_b (Table 3), increasing in importance as wind speed increased (Supplementary Figure 3). Heat per unit area was driven entirely by fuels, specifically litter fuel load, which positively influenced I_b as the second best predictor (Table 3). When models of I_b were fit over the input range of open wind speeds, litter fuel loads and WAF increased in their relative importance and explanatory power, whereas fuel moisture conditions explained the same amount of variance and decreased slightly in relative contribution of explanatory power (Figure 6) .

Successful surface-to-crown fire initiation was driven nearly equally by a negative relationship with crown base height and a positive relationship with wind speed, but weakly by moisture conditions. Explained variance varied inversely with wind speed until ~20 km hr^{-1} where 100% of stands produced I_b sufficient for crown fire initiation (Figures 6). At wind speeds less than 5 km hr^{-1}, crown base height and percent moisture explained nearly 50% of the variability in crown fire initiation across our stands (Figure 6). Successful crown fire spread was driven by crown bulk density, and to a minor degree, wind speed. Crown bulk density's explanatory power spiked at wind speeds 5 and 20 km hr^{-1}, but were steady at higher wind speeds (Figure 6).

Simulation results predicted obligate surface fire in a very small percentage of stands when wind speeds were less than 5 km hr^{-1} under 50th and less than 2 km hr^{-1} under 99th percentile moisture conditions (Figure 7). The prevalence of passive crown fire varied inversely with wind speed, declining from 50% of stands when wind speed was less than 5 km hr^{-1} and a minimum of 10% of stands at 35 km hr^{-1} under 50^{th} and 18 km hr^{-1} under 99^{th} percentile moisture conditions (Figure 7). Conditional crown fire was possible in the greatest percent of stands (i.e., 40%) at 5 km hr^{-1} and 50^{th} percentile moisture; however, this value declined sharply until wind speeds reach 20 km hr^{-1} (Figure 7). Conditional crown fire was predicted to occur in a very small percentage of stands when moisture conditions were greater than 90%. Under 50^{th} and 99^{th} percentile moisture conditions, active crown fire was predicted in 50% of stands at 10 and 2 km hr^{-1}, and was present in the maximum percent of stands (i.e., 90%) at 35 and 18 km hr-1 wind speeds, respectively (Figure 7).

3.5 DISCUSSION

Our results indicate high potential for reburning in 24-year-old lodgepole pine stands that originated after the 1988 Yellowstone Fires. Potential for severe fire activity was evident across the entire range of 50th to 99th percentile moisture conditions, especially with high wind speeds. These results confirm that post-1988 stands exceed the suggested 10-18 year window of time in which fuel limitation might reduce fire occurrence (Parks et al. 2016b) and fire severity (Harvey et al. 2016) and add to evidence that any reduction in fire activity due to postfire fuel limitation is fleeting. Regenerating trees in early successional subalpine forests form closed-canopy stands with abundant canopy fuels, and litter fuel loads accumulate with density dependent lower branch pruning. Furthermore, 100-hr and 1000-hr fuels are abundant because postfire snags have fallen to the forest floor.

Our expectation of variation in fire type across the post-1988 Yellowstone landscape was supported when open wind speeds were less than ~20 km hr^{-1} and fuel moisture conditions were below the 90th percentile (Figure 7). However, nearly 90% of stands exhibited active crown fire as wind speeds and moisture conditions became severe (Figure 7). Crown-to-crown fire spread was possible in stands with dense canopy fuels, even when surface-to-crown initiation criteria was not met. At low to moderate wind speeds, fire managers should be prepared for crown fire spread from adjacent stands into dense, young lodgepole pine stands. If wind speeds decrease, crown fire spread in the densest stands may drop to the forest floor and not transition back to the crown. At wind speeds greater than 20 km hr^{-1}, crown fire spread is anticipated in all but the sparsest sites due to greater lateral heat transfer among tree crowns (Rothermel 1972, Cruz 2003, Alexander 2006). Thus, our data suggest that these young forests should not be expected to serve as fire breaks.

Wind speed was most important in predicting potential fire behavior, although fuels and moisture were also significant. Large fires in boreal and subalpine forests are associated with severe weather conditions (i.e., high wind and low fuel moisture conditions; Lotan et al. 1985, Turner and Romme 1994, Bessie and Johnson 1995, Schoennagel et al. 2004), and our study supports the notion that open wind speed is the primary, positive driver of fire potential in young subalpine forests (when fuels are present). Fuel moisture explained a surprisingly small amount of variance in our regression models, aligning with other variables typically considered secondary drivers of fire behavior (i.e., variables that drive how instead of whether a fire burns). A positive shift in our fire behavior simulation results with the severity of moisture conditions supports observations of lower fire severity early in the 1988 fire season (Turner et al. 1994), and between 1972 and 1987 when cooler, wetter conditions (analogous to moisture conditions < 90% in this study) may have suppressed fire in young lodgepole pine forests (i.e., less 40 years of age) when compared to their relative abundance on the landscape (Renkin and Despain 1992). Our findings emphasize the relative importance of fuel characteristics over moisture conditions; differences between our interpretation and that of previous fire occurrence versus weather studies may arise because our model output represents equilibrium fire conditions and does not attempt to model ignition success including pre-heating and pre-ignition phases of combustion. Weather and variation in fuel moisture may play a greater role during early combustion phases when heat fluxes are low in comparison to the quantity of water that must be evaporated from fuels to initiate flaming combustion and greater spread rates (Simard 1968).

Heterogeneity in fuel characteristics is likely to produce varied fire behavior if wind and weather conditions are not extreme. Surface fuel characteristics in post-1988 lodgepole pine forests have transitioned from sparse, patchy fuel beds observed at 8 years postfire (Tinker and Knight 2000) to continuous surface fuel beds composed of high litter loads with low bulk density (Nelson et al. 2016). Canopies are closing in most stands, making available canopy fuel loads dense and continuous (Nelson et al. 2016, Turner et al. 2016). Post-1988 tree density was the strongest predictor of these fuel variables (Nelson et al. 2016), suggesting that postfire regeneration may positively affect HPA, I_b, and crown-to-crown fire spread, and negatively affect surface-to-crown fire initiation through the pruning of lower branches. Further, forest stands occupied by late-seral forests prior to 1988 had the greatest 1000-hr fuel loads (Nelson et al. 2016), which are prone to extreme fire behavior (Rothermel 1991), extended periods of burning, and are a receptive medium for firebrands (Page et al. 2013).

Our model formulation follows nearly 60 years of wildland fire modeling in forest ecosystems (Byram 1959, Anderson 1969, Rothermel 1972, Albini and Alder 1976, Van Wagner 1977, Albini and Reinhardt 1995, 1997, Cruz et al. 2004, 2005), and adheres to the long-standing tradition of linking surface fire intensity to the ignition and spread of crown fire (Van Wagner 1977). Fireline intensity (I_b), as modeled in this study, reflects the product of HPA and sROS. A recent review found that underestimates of fireline intensity are pervasive in operational fire modeling software and may exaggerate wind speeds required for crown fire initiation due to systematically low approximations of HPA (Cruz and Alexander 2010). To overcome this issue, we estimated HPA using median fire intensity calculated during the first minute of combustion in FOFEM. This increased I_b estimates by 2+ times when compared to the commonly used residence time method, and successfully resulted in shifting estimates of crown fire initiation to lower wind speeds where crown fires have been observed in coniferous fuel beds (Cruz and Alexander 2010). sROS was estimated from standard FBFMs selected using a cluster analysis. Empirical head fire data are required for bias estimates but were not available in our specialized fuel type (but see Miller et al. 2009). Further research is required to rigorously compare HPA estimates using 60 second median fire intensity from FOFEM against other methods (e.g., Nelson Jr 2003), and improve the integration of these fire modeling systems for use in novel fuel beds.

Fireline intensity and sROS estimates were similar to those found in other studies conducted in coniferous fuel beds. sROS values from this study were approximately 10% of values observed in 48-year-old Jack pine (*Pinus banksiana*) stands with higher fuel loads in Ontario, Canada (Stocks 1987), ~30% those found in 1, 3, and 19 year old western hemlock/Douglas-fir stands with greater fuel loads in Washington, USA (Tsuga heterophylla/Pseudotsuga menziesii; Agee and Huff 1987a), but similar to Swedish Scots pine/Norway spruce/birch boreal forests <25 years old with similar fuel loads (Pinus sylvestris/Picea abies/Betula spp.; Schimmel and Granström 1997a) and 1 year postfire mixed-conifer forest with heavy uncombusted ground fuel loads in the Cascade Range, USA (Hudec and Peterson 2012). Observations of crown fire spread in young forests were not available for comparison; however, open wind speeds associated with crown fire activity in this study (Figure 7) fell within the range of open wind speeds observed during crown fires in mature conifer forests across western North American (Cruz and Alexander 2010).

We conclude that 24-year old lodgepole pine forests are capable of supporting all types of fire depending on wind and weather conditions. Any reduction in fire activity due to fuel limitation, as suggested in regional geospatial studies, appears to have passed. Simulation results from this study indicate that fuel characteristics may play a greater role than previously acknowledged in driving variation in fire behavior, and fuels 24-years postfire are unlikely to impede shorter fire intervals than those observed historically in Yellowstone National Park.

3.6 ACKNOWLEDGEMENTS

We are grateful to Paige Copenhaver, Daniel Donato, Winslow Hansen, Ronald Harned, Paul Hood, Natalie Kaner, Andy Muench, Monique Nelson, Gail Stakes, and Tim Whitby for field and laboratory support, Judy Romme for logistic support, and Marty Alexander, Miguel Cruz, and Bob Keane for advice on fire behavior models. We also thank Yellowstone National Park staff Roy Renkin, Stacey Gunther, Diane Abendroth, and Becky Smith, and USDA Forest Service staff Mike Johnston and Andy Norman for their knowledge and support in the Greater Yellowstone Ecosystem. Housing and logistical assistance were provided by the University of Wyoming—National Park Service research station and Yellowstone National Park. Funding was provided by the Joint Fire Science Program (Grant 11-1-1-7) and the Boyd Evison Graduate Fellowship.

3.7 LITERATURE CITED

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences:11700–11775.

Agee, J. K., and M. H. Huff. 1987. Fuel succession in a western hemlock/Douglas-fir forest. Canadian Journal of Forest Research 17:697–704.

Albini, F., and N. N. Alder. 1976. Estimating wildfire behavior and effects. USDA Forest Service, GTR-INT-30:1–90.

Albini, F., and E. D. Reinhardt. 1995. Modeling ignition and burning rate of large woody natural fuels. International Journal of Wildland Fire 5:81–81.

Albini, F., and E. D. Reinhardt. 1997. Improved calibration of a large fuel burnout model. International Journal of Wildland Fire 7:21–21.

Alexander, M. E., and M. G. Cruz. 2006. Evaluating a model for predicting active crown fire rate of spread using wildfire observations. Canadian Journal of Forest Research 36:3015–3028.

Anderson, H. E. 1969. Heat transfer and fire spread. USDA Forest Service, GTR-INT-69:1–20.

Andrews, P. L. ; 2012. Modeling wind adjustment factor and midflame wind speed for Rothermel's surface fire spread model. USDA Forest Service; RMRS-GTR-266. Fort Collins, CO:1–39.

Andrews, P. L., and R. C. Rothermel. 1982. Charts for interpreting wildland fire behavior characteristics. USDA Forest Service, GTR-INT-131:1–21.

Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in sub-alpine forests. Ecology 76:747–762.

Byram, G. M. 1959. Combustion of forest fuels. Forest Fire: Control and Use 1:61–89.

Calcagno, V., and C. de Mazancourt. 2010. glmulti: an R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34:1–29.

Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. Van Wagtendonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. Ecosystems 12:114–128.

Collins, L., T. D. Penman, O. F. Price, and R. A. Bradstock. 2015. Adding fuel to the fire? Revegetation influences wildfire size and intensity. Journal of Environmental Management 150:196–205.

Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26:686–699.

Cruz, M. G., and M. E. Alexander. 2010. Assessing crown fire potential in coniferous forests of western North America: A critique of current approaches and recent simulation studies. International Journal of Wildland Fire 19:377–398.

Cruz, M. G., M. E. Alexander, and R. H. Wakimoto. 2004. Modeling the likelihood of crown fire occurrence in conifer forest stands. Forest Science 50:640–658.

Cruz, M. G., M. E. Alexander, and R. H. Wakimoto. 2005. Development and testing of models for predicting crown fire rate of spread in conifer forest stands. Canadian Journal of Forest Research 35:1626–1639.

Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart. Inc, Boulder, CO.

Flannigan, M. D., M. A. Krawchuk, W. J. de Groot, B. M. Wotton, and L. M. Gowman. 2009. Implications of changing climate for global wildland fire. International Journal of Wildland Fire 18:483–507.

Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest fires. Science of the Total Environment 262:221–229.

Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. Journal of statistical software 17:1–27.

Grömping, U. 2007. Estimators of relative importance in linear regression based on variance decomposition. The American Statistician 61:139–147.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. Ecology 97:2272–2282.

Hudec, J. L., and D. L. Peterson. 2012. Fuel variability following wildfire in forests with mixed severity fire regimes, Cascade Range, USA. Forest Ecology and Management 277:11–24.

Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon storage on landscapes with stand-replacing fires. BioScience 56:598–606.

Lotan, J. E., J. K. Brown, and L. Neuenschwander. 1985. Role of fire in lodgepole pine forests. Lodgepole Pine: The Species and Its Management Symposium Proceedings:133–152.

Lumley, T., and A. Miller. 2009. leaps: Regression subset selection. R package version 2.9. https://CRAN.R-project.org/package=leaps.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2012. Cluster: cluster analysis basics and extensions. R package version 1:56.

Miller, E. A., R. A. Renkin, S. C. McEldery, and T. J. Klukas. 2009. Fire behavior, weather, and fuels: A case study of crown fire in an early post-fire lodgepole pine forest [extended abstract]. Page 26 in R.E. Masters, K.E.M. Galley, and D.G. Despain (eds.). The '88 Fires: Yellowstone and Beyond, Conference Proceedings. Tall Timbers Miscellaneous Publication No. 16, Tall Timbers Research Station, Tallahassee, Florida, USA.

Moritz, M. A., M. A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. Ecosphere 3:art49.

Nelson, K. N., W. H. Romme, M. G. Turner, and D. B. Tinker. 2016. Landscape variation in tree regeneration and snag fall drive fuel loads in 25-yr old post-fire lodgepole pine forests. Ecological Applications 26:2424–2438.

Page, W. G., M. E. Alexander, and M. J. Jenkins. 2013. Wildfire's resistance to control in mountain pine beetle-attacked lodgepole pine forests. The Forestry Chronicle 89:783–794.

Parks, S. A., L. M. Holsinger, C. Miller, and C. R. Nelson. 2015. Wildland fire as a self-regulating mechanism: the role of previous burns and weather in limiting fire progression. Ecological Applications 25:1478–1492.

Parks, S. A., C. Miller, L. M. Holsinger, S. Baggett, and B. J. Bird. 2016. Wildland fire limits subsequent fire occurrence. International Journal of Wildland Fire 25:182–190.

Peterson, G. D. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems 5:0329–0338.

Price, O. F., and R. A. Bradstock. 2010. The effect of fuel age on the spread of fire in sclerophyll forest in the Sydney region of Australia. International Journal of Wildland Fire 19:35–45.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rebain, S. A., E. D. Reinhardt, N. L. Crookston, S. J. Beukema, W. A. Kurz, J. A. Greenough, D. C. E. Robinson, and D. C. Lutes. 2010. The fire and fuels extension to the forest vegetation simulator: updated model documentation. USDA-Forest Service:1–408.

Reinhardt, E. D., J. H. Scott, K. Gray, and R. E. Keane. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. Canadian Journal of Forest Research 36:2803–2814.

Romme, W. H. W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199–221.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, GTR-INT-115:1–50.

Rothermel, R. C. 1991. Predicting behavior and size of crown fires in the northern Rocky Mountains. USDA Forest Service, Intermountain Research Station, Research Paper:INT-RP-438.

Running, S. W. 2006. Is Global Warming causing more, large wildfires. Science 313:927–928.

Schimmel, J., and A. Granström. 1997. Fuel succession and fire behavior in the Swedish boreal forest. Canadian Journal of Forest Research 27:1207–1216.

Schoennagel, T., M. G. Turner, D. M. Kashian, and A. Fall. 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. Landscape Ecology 21:1281–1296.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across rocky mountain forests. Bioscience 54:661–676.

Scholze, M., W. Knorr, N. W. Arnell, and I. C. Prentice. 2006. A climate-change risk analysis for world ecosystems. Proceedings of the National Academy of Sciences of the United States of America 103:13116–13120.

Scott, J. H., and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. USDA Forest Service, RMRS-GTR-153:1–72.

Scott, J. H., and E. D. Reinhardt. 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service, RMRS-RP-29:1–59.

Simard, A. J. 1968. The moisture content of forest fuels: A review of the basic concepts. Department of Forestry and Rural Development, Canada Information Report FF-X-14:1–47.

Stevens-Rumann, C., and P. Morgan. 2016. Repeated wildfires alter forest recovery of mixed-conifer ecosystems. Ecological Applications.

Teske, C. C., C. A. Seielstad, and L. P. Queen. 2012. Characterizing fire-on-fire interactions in three large wilderness areas. Fire Ecology 8:82–106.

Turner, J. A., and B. D. Lawson. 1978. Weather in the Canadian forest fire danger rating system. A user guide to national standards and practices.

Turner, M. G., W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5:731–742.

Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape ecology 9:59–77.

Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7:751–775.

Vacchiano, G., and D. Ascoli. 2015. An implementation of the Rothermel fire spread model in the R programming language. Fire Technology 51.

Van Wagner, C. E. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7:23–34.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York, NY, USA.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences of the United States of America 108:13165–13170.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer Science & Business Media.

Wickham, H., and R. Francois. 2015. dplyr: A grammar of data manipulation. R package version 0.4 1:20.

3.8 TABLES

Table 1: Response variables and model parameters included in fire behavior models used to simulate potential fire behavior in 24-year old lodgepole pine (*Pinus contorta* var. latifolia) forests in Yellowstone National Park, WY, USA.

Response variable	Abbr.	Input parameters (units)	References
Wind adjustment factor (dimensionless)	WAF	Canopy height (m) Canopy cover (fraction) Crown ratio (fraction)	(Andrews 2012)
Surface rate of spread† ($m\ min^{-1}$)	sROS	Fuel loads ($Mg\ ha^{-1}$): duff, litter, 1-hr, 10-hr, 100-hr, herb, shrub Wind: 6.1 m open wind speed ($km\ hr^{-1}$), WAF Fuel moisture (%): duff, 1-hr, 10-hr, 100-hr, herbaceous, live woody (shrub)	(Rothermel 1972, Scott and Burgan 2005)
Heat per unit area‡ ($kW\ m^2$)	HPA	Fuel loads ($Mg\ ha^{-1}$): duff, litter, 1-hr, 10-hr, 100-hr, 1000-hr, herb, shrub Fuel moisture (%): duff, 100-hr, 1000-hr	(Albini and Reinhardt 1995, 1997, Reinhardt et al. 1997)
Fireline intensity (Eqn. 1; $kW\ m^2$)	I_b	Heat per unit area ($kW\ m^2$) Surface rate of spread ($m\ min^{-1}$)	(Byram 1959, Andrews and Rothermel 1982, Scott and Reinhardt 2001)
Critical crown initiation intensity (Eqn. 2; $kW\ m^2$)	I'	Crown base height (m) Fuel moisture (%): live foliar fuel moisture	(Van Wagner 1977, Cruz et al. 2004)
Crown fire rate of spread (Eqn. 3; $m\ min^{-1}$)	cROS	Crown bulk density ($kg\ m^{-3}$) Fuel moisture (%): 1-hr surface fuel moisture Wind: 10 m open wind speed ($km\ hr^{-1}$)	(Cruz et al. 2005, Alexander and Cruz 2006)
Criterion for active crown fire (Eqn. 4; $m\ min^{-1}$)	CAC	Crown fire rate of spread ($m\ min^{-1}$) Crown bulk density ($kg\ m^{-3}$)	(Cruz et al. 2005, Alexander and Cruz 2006)

[†] As implemented in the Rothermel R package (Vacchiano and Ascoli 2015).
[‡] Estimated using the median fire intensity during the first minute of combustion in the First Order Fire Effects Model (FOFEM; Albini and Reinhardt 1995, 1997, Reinhardt et al. 1997, Sikkink and Keane 2012).

Table 2: Median and inner-quartile range for heat per unit area (HPA) and critical surface-to-crown initiation intensity. HPA is the median intensity from the first 60 seconds of combustion in the First Order Fire Effects Model (FOFEM).

Percentile FMC	Heat per unit area (kW m^2 min^{-1})	Critical crown initiation intensity (kW m^2)
50%	104.9 [65.9, 157.6]	49.9 [17.6, 91.6]
99%	111.8 [80.0, 164.7]	34.2 [12.1, 62.9]

Table 3: Predictive linear models illustrating the effects of fuel characteristics, FMC conditions, and 6.1 m (open) wind speed on surface and crown fire behavior in 24-year-old lodgepole pine stands. Partial-R^2 was calculated using the *relaimpo* R package (Grömping 2006, 2007) with statistical differences calculated using 95% bootstrapped confidence intervals.

Surface fire	df	R^2	Parameter	Partial-R^2	ß	se	t-value	*p*-value
Log_{10}(Wind adjustment factor)	76	0.67	Intercept		-1.781	0.523	-3.4	<0.001
			Log_{10}(Post-1988 tree density)	0.51[a]	1.656	0.463	3.6	<0.001
(dimensionless)			Log_{10}(Post-1988 tree density)^2	0.06[b]	-0.592	0.132	-4.5	0.001
			Log_{10}(Post-1988 tree density)^3	0.10[b]	0.060	0.012	4.9	<0.001
Log_{10}(sROS)	245996	0.89	Intercept		-1.130	0.002	-667.9	<0.001
(m min^{-1})			Wind adjustment factor	0.18[a]	1.740	0.003	642.8	<0.001
			6.1 m open wind speed	0.67[b]	0.021	<0.001	1250.6	<0.001
			Percentile FMC	0.05[c]	0.006	<0.001	328.5	<0.001
Heat per unit area	4098	0.97	Intercept		62.267	0.543	114.6	<0.001
(kW m^2)			Litter fuel load	0.97	29.494	0.077	383.9	<0.001
Crown fire								
Log10(Fireline intensity)	245995	0.88	Intercept		0.802	0.002	375.6	<0.001
			Wind adjustment factor	0.07[a]	1.677	0.003	481.2	<0.001
(kW m2 min-1)			Litter fuel load	0.19[b]	0.060	<0.001	695.0	<0.001
			Percentile FMC	0.04[c]	0.007	<0.001	301.7	<0.001
			6.1 m open wind speed	0.57[d]	0.021	<0.001	1075.6	<0.001
Crown fire initiation success	245996	0.17	Intercept		0.804	0.002	385.0	<0.001
(dimensionless)			Crown base height	0.07[a]	-0.188	0.001	-142.3	<0.001
			6.1 m open wind speed	0.08[b]	0.003	<0.001	151.6	<0.001
			Percentile FMC	0.02[c]	0.002	<0.001	73.8	<0.001
Crown fire	245996	0.59	Intercept		0.938	0.001	818.8	<0.001
Spread success			Log_{10}(Crown bulk density)	0.34[a]	-0.108	0.003	-42.6	<0.001

(dimensionless)	Log_{10}(Crown bulk density)^2	0.20[b]	-1.063	0.003	-348.8	<0.001
	6.1 m open wind speed	0.05[c]	0.005	<0.001	176.4	<0.001

3.9 FIGURES

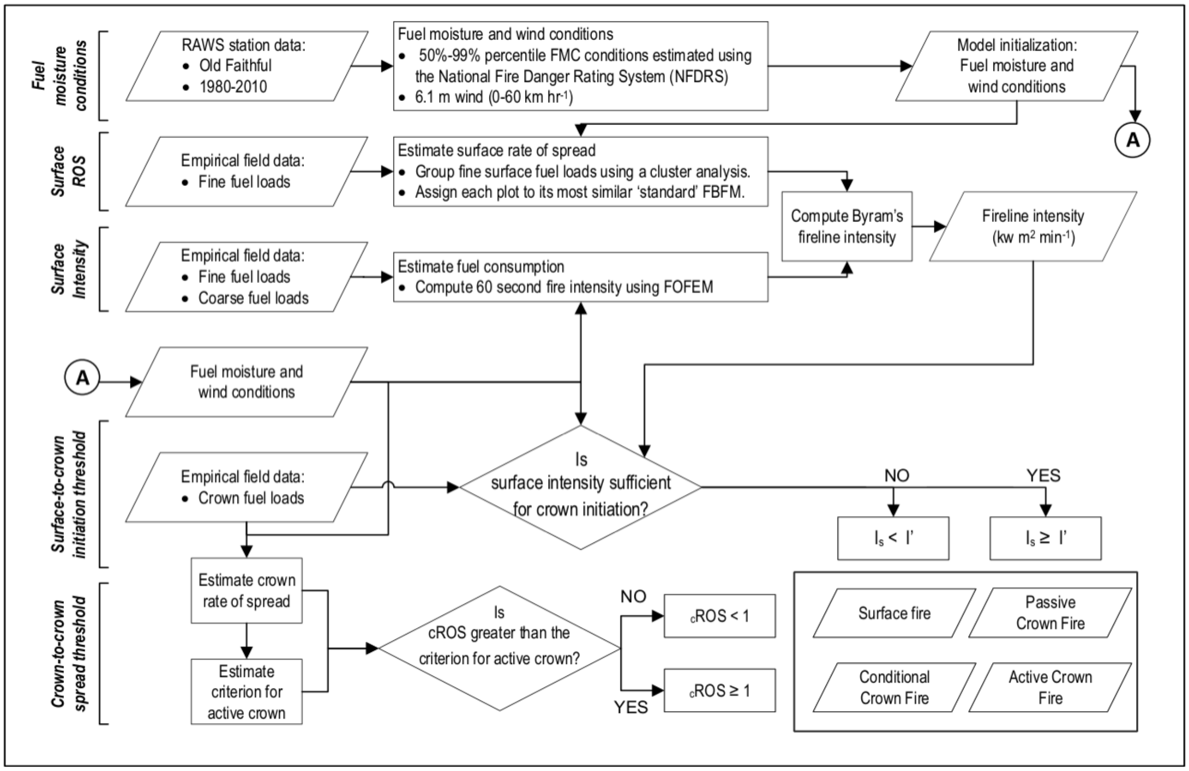


Figure 1: Data and modeling work-flow used to predict surface and crown fire in 24-year old lodgepole pine forests.

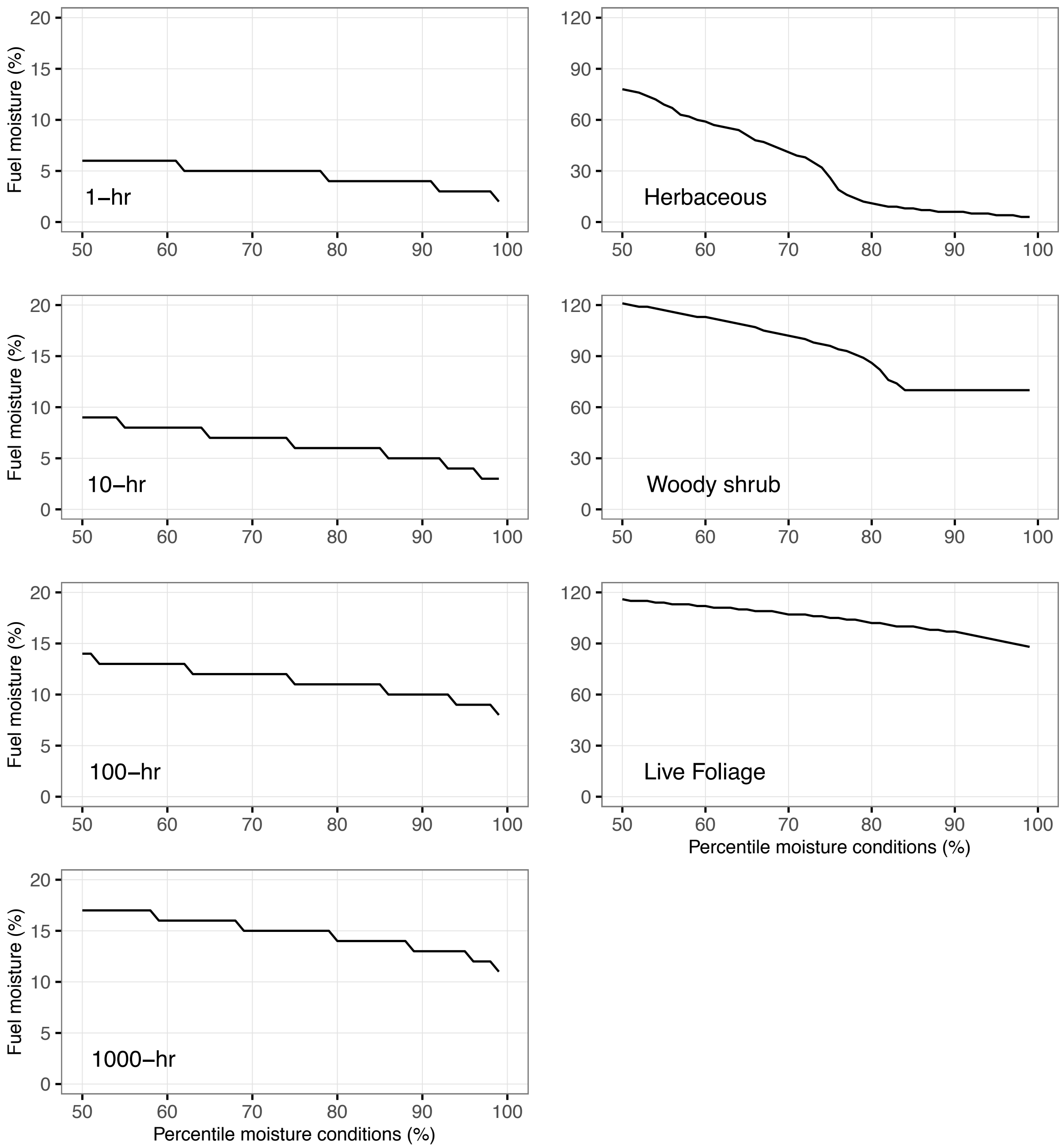


Figure 2: Fuel moisture and weather conditions over the fire season (i.e., June—October) in Yellowstone National Park. Fuel moisture content equals water mass divided by dry biomass and may exceed 100%. Surface fuel moistures were estimated using the National Fire Danger Rating System with weather measurements recorded at the Old Faithful RAWS station, Yellowstone National Park, Wyoming, USA for the period 1980 and 2010. All weather days were used to

represent overall fire season conditions. Live lodgepole pine fuel moisture was estimated using data from the National Fuel Moisture Database recorded at the Flagg Ranch station between 1996 and 2012. Temperature and relative humidity represents conditions found at the Old Faithful RAWS Station between 1980 and 2010.

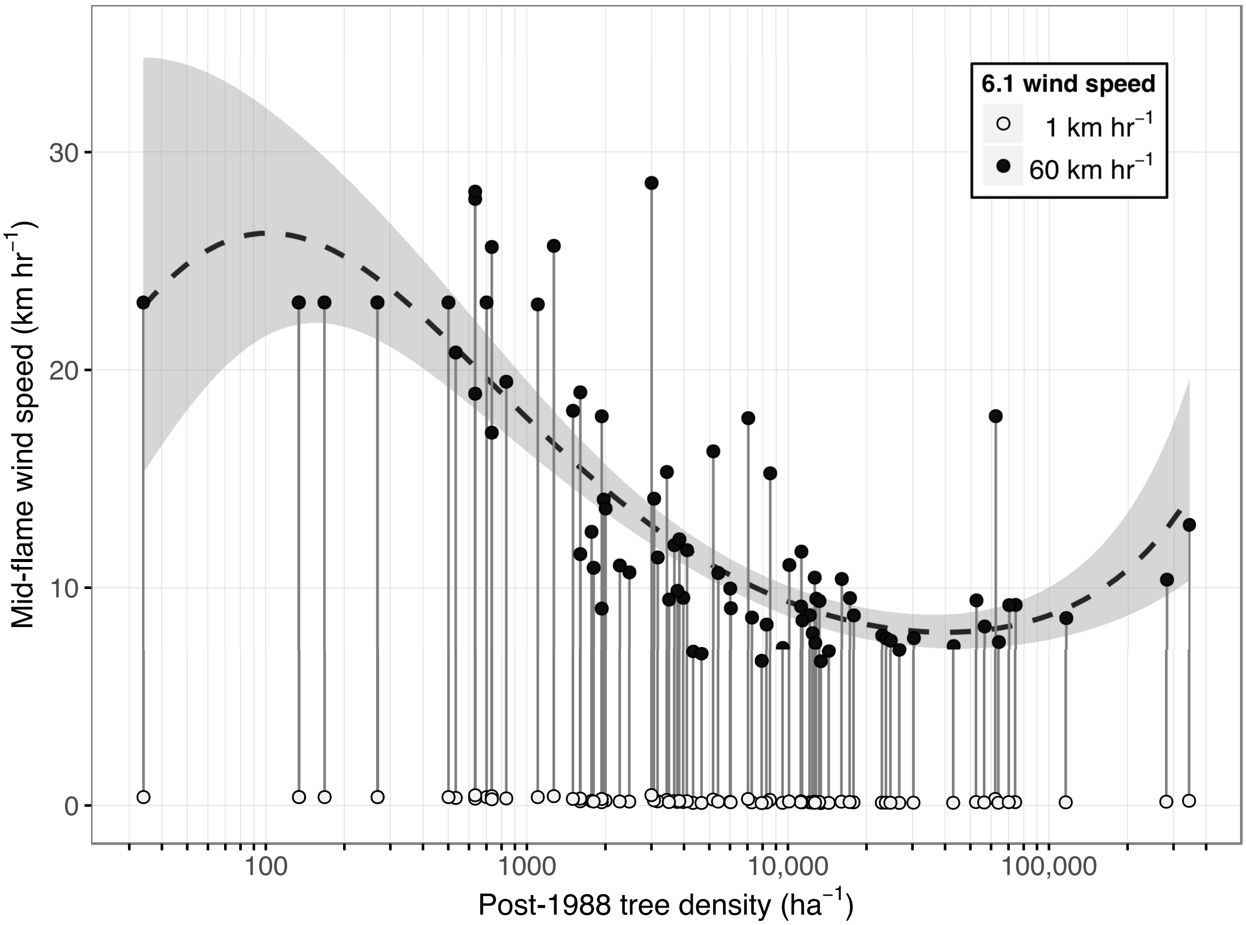


Figure 3: Variation in tree density leads to diminished ranges of mid-flame wind speed ($r^2 = 0.67$; p-value < 0.001). Each vertical line represents the input range of 6.1 m open wind speeds (i.e., 1 to 60 km hr^{-1}) and depicts the attenuating effect of forest structure on mid-flame wind speed (i.e., sub-canopy wind speed affecting surface fire). Mid-flame wind speed is an input to surface rate of spread (sROS) FBFMs.

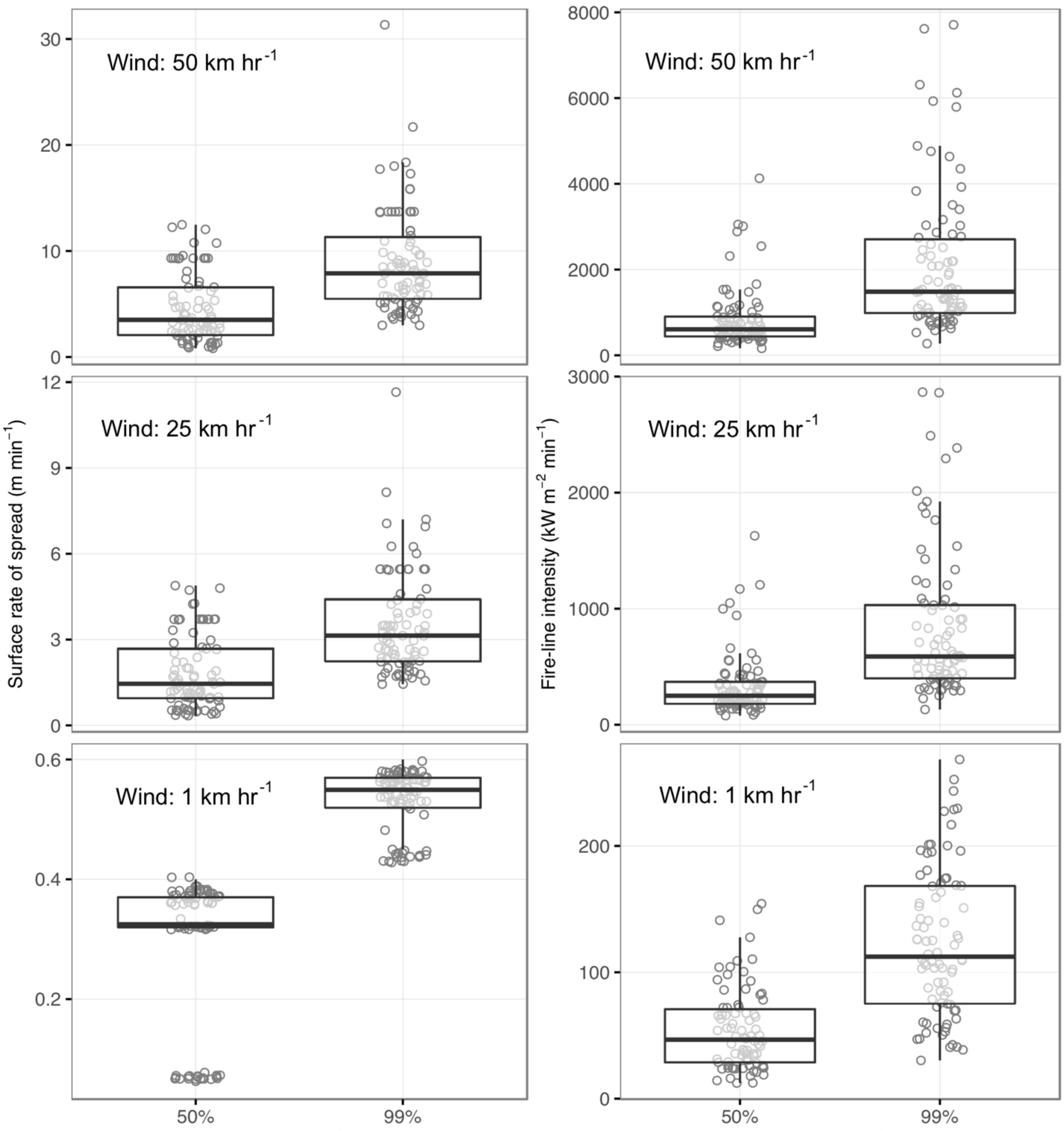


Figure 4: Boxplots and site-level estimates for surface rate of spread and fireline intensity at 50th and 99th percentile weather and 1, 25, and 50 km hr^{-1} open wind speed.

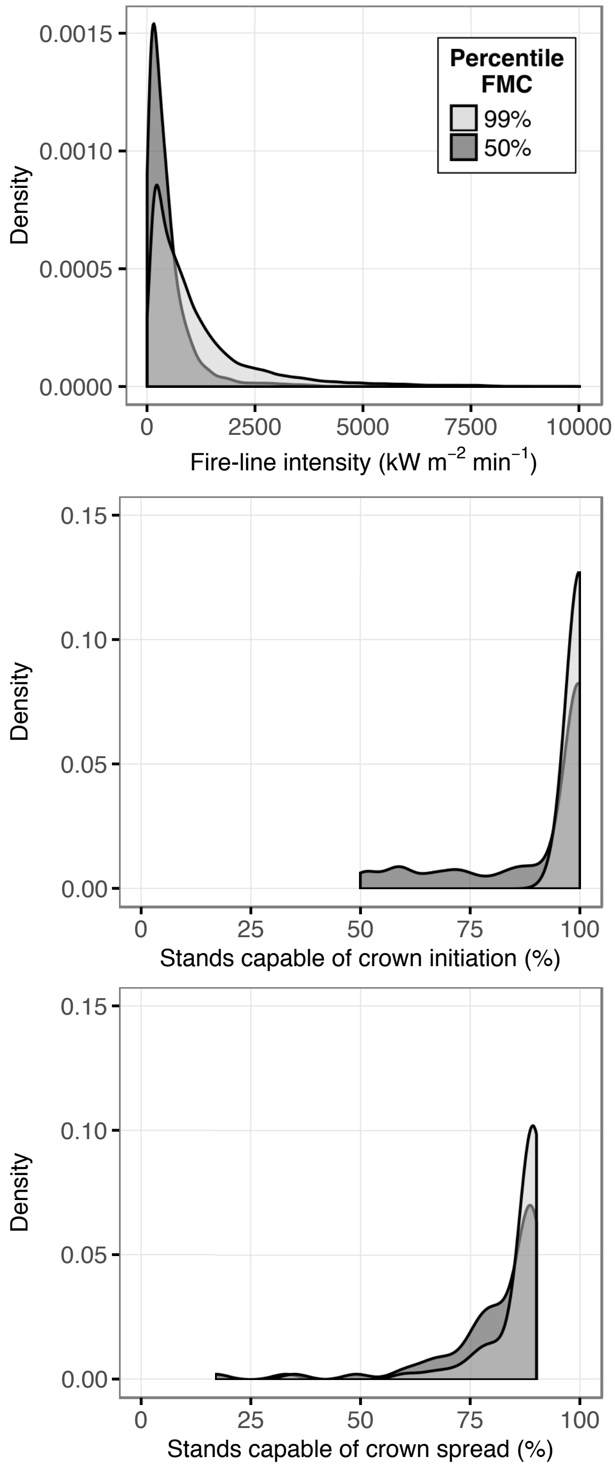


Figure 5: Density distributions for simulated surface fire intensity, surface-to-crown fire initiation, and crown-to-crown fire spread at 50th and 99th percentile weather conditions.

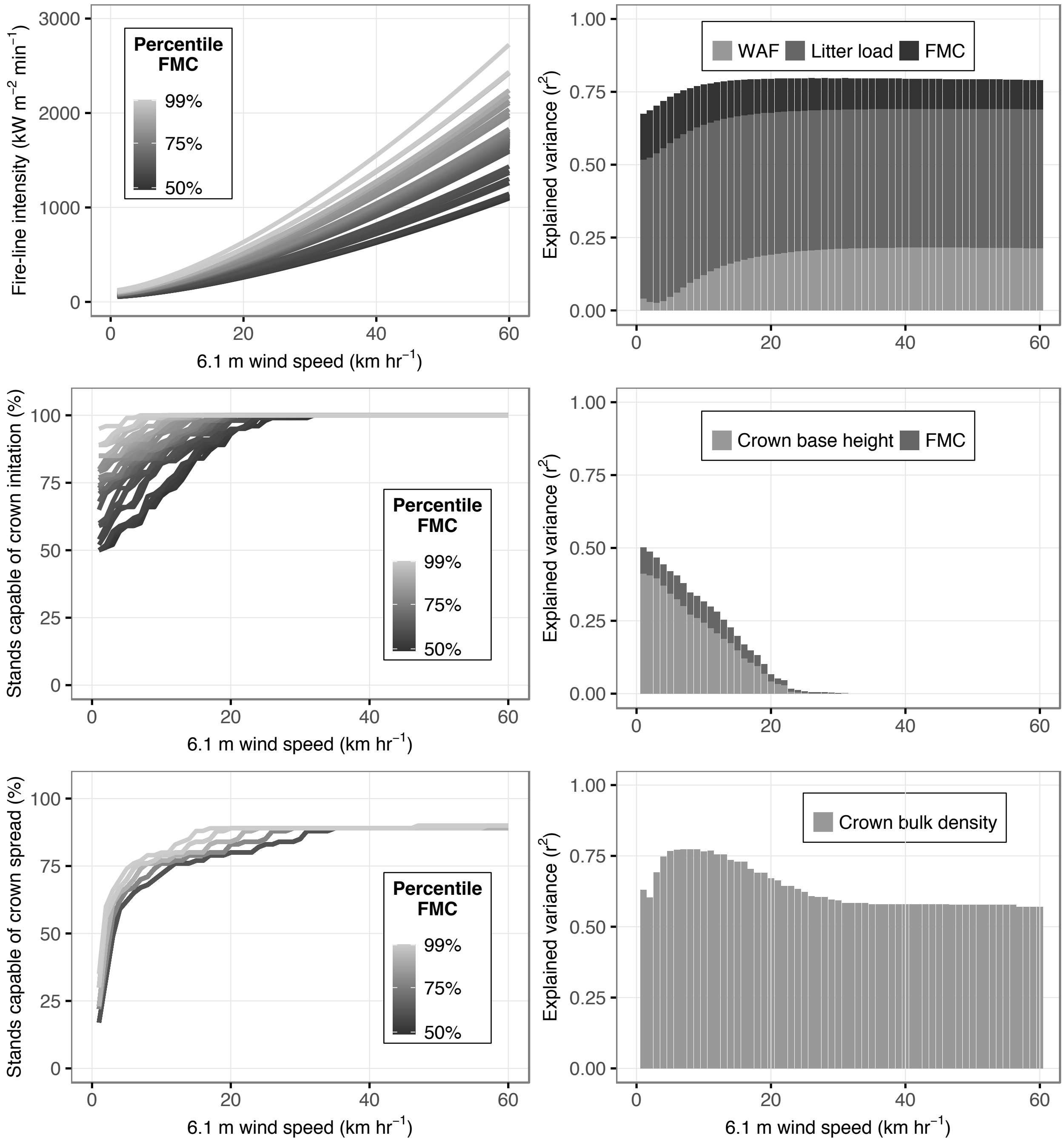


Figure 6: Median surface fire intensity, surface-to-crown fire initiation, and crown-to-crown fire spread, and regression model explanatory power for each significant predictor variable across the full range of weather conditions and open wind speeds.

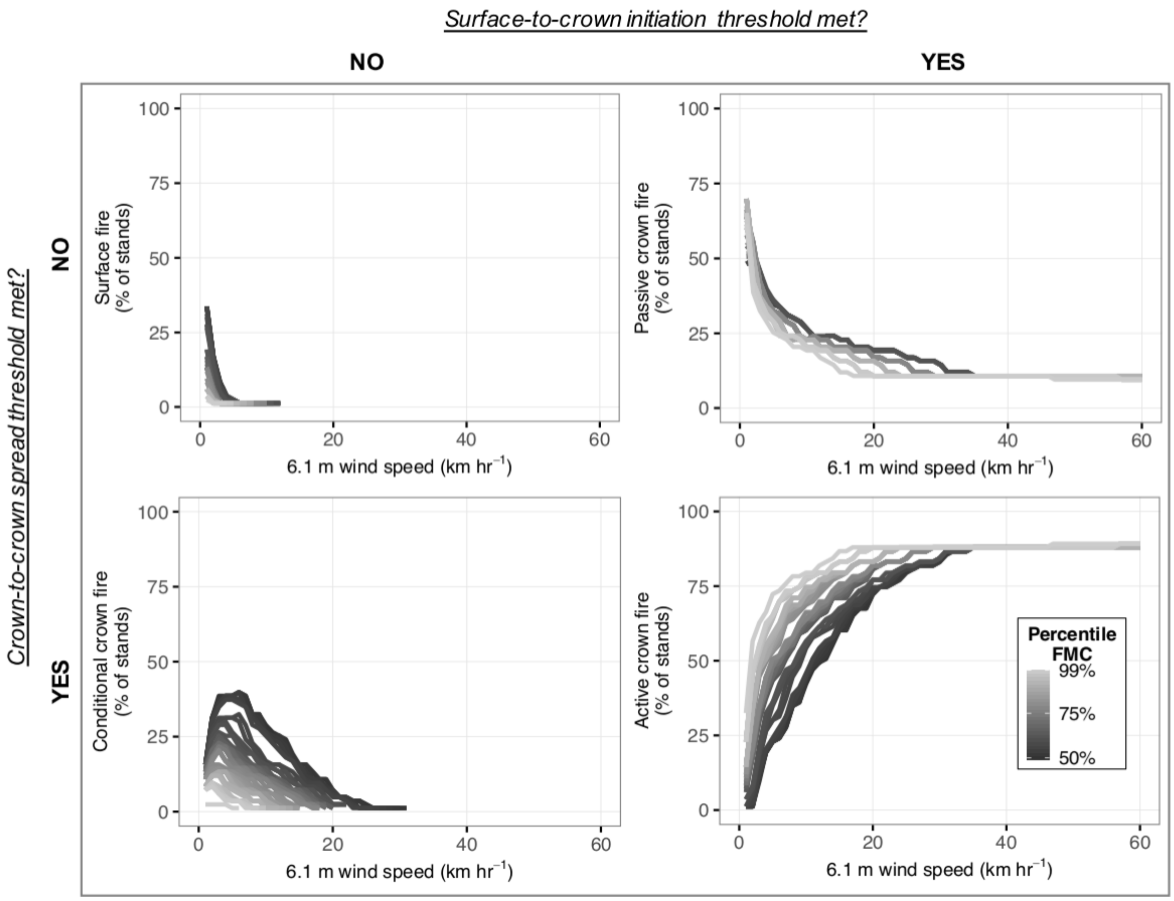
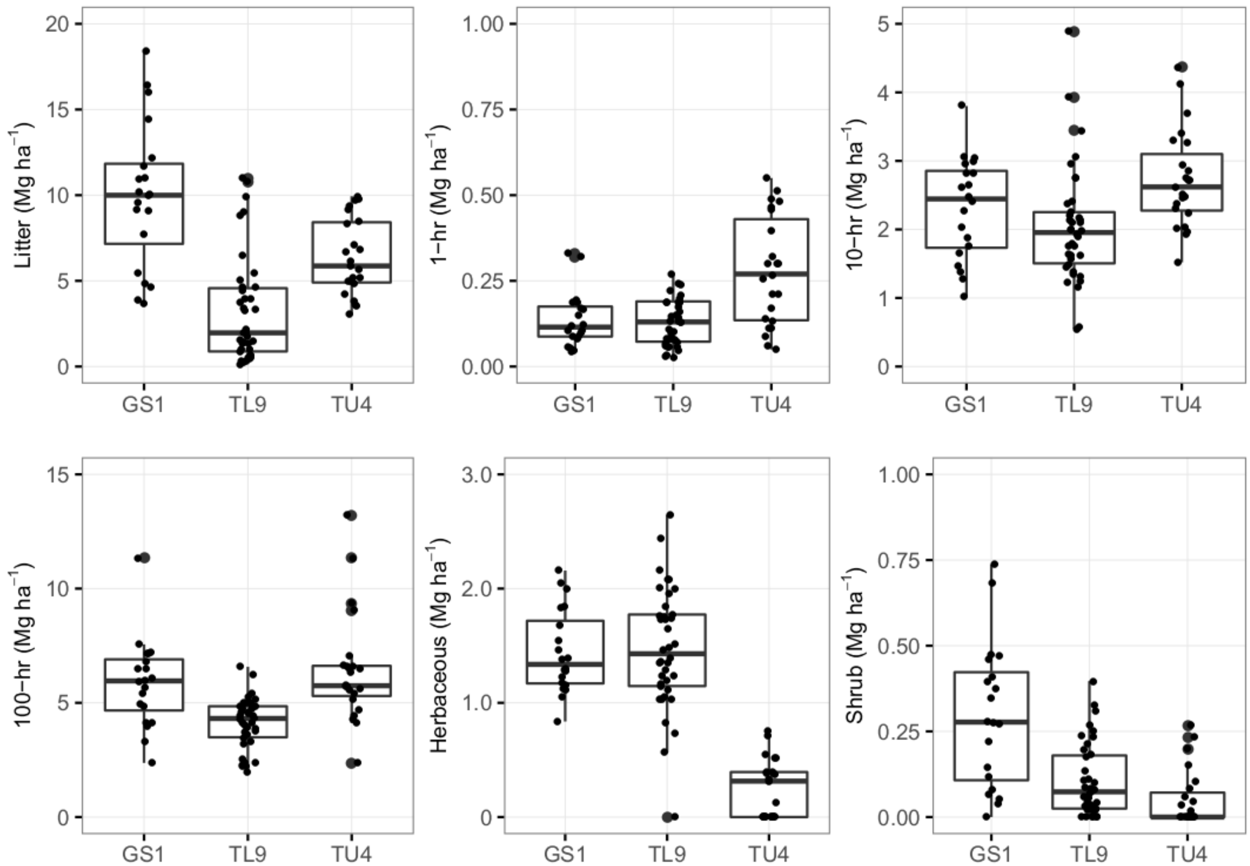
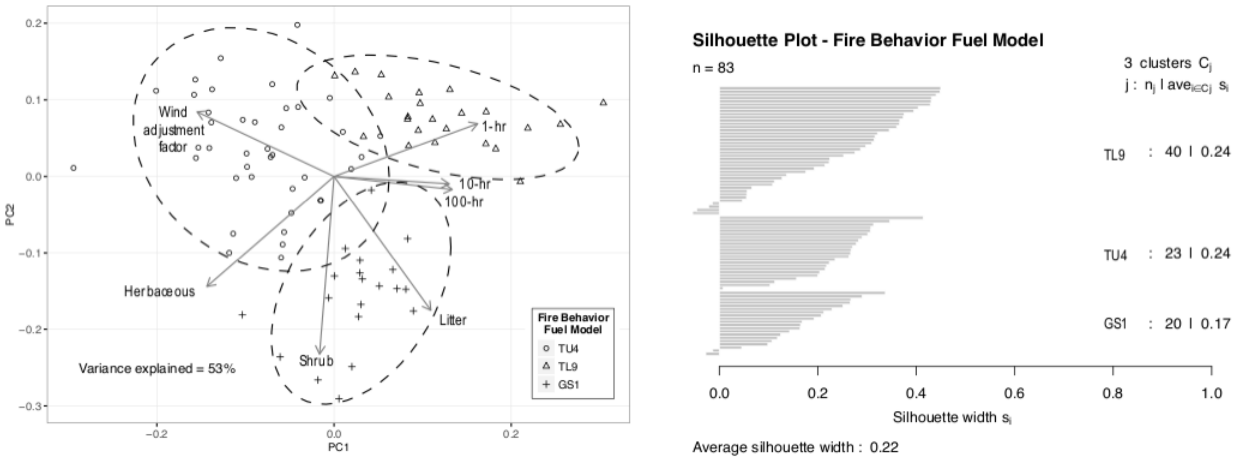


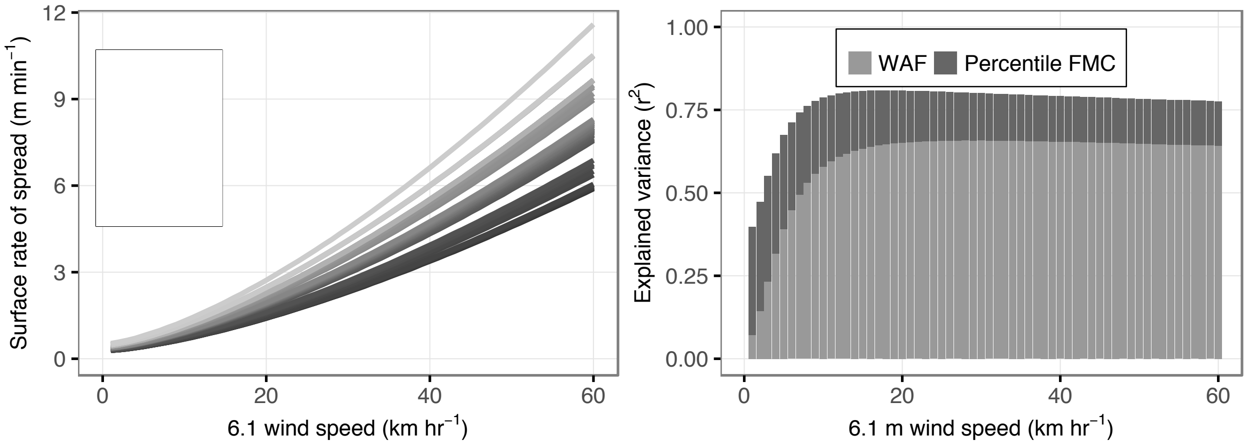
Figure 7: Percent of stands predicted to achieve each fire type by weather condition and 6.1 m open wind speed. Fire types were determined by contrasting results from the surface-to-crown and crown-to-crown thresholds for each stand using Boolean logic and include: surface fire, passive crown fire, conditional crown fire, and active crown fire (Van Wagner 1977, Scott and Reinhardt 2001).



Supplementary Figure 1: Cluster analysis results used to assign empirical fuel beds to their most similar standard fire behavior fuel model. Silhouette width indicates classification accuracy—values greater than 1 signify correct classification where values less than 1 indicate possible mis-classification.



Supplementary Figure 2: Empirical fuel loads for study sites assigned to their most similar standard Fire Behavior Fuel Models using a cluster analysis.



Supplementary Figure 3: Median simulated rate of spread (sROS) and regression model explanatory power for each significant predictor variable across the full range of open wind speeds. The relative importance of the wind adjustment factor (WAF) increased with wind speed, where weather conditions decreased in importance.

CHAPTER 4. FUEL MOISTURE DYNAMICS VARY WITH DISTURBANCE HISTORY

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****This manuscript is 'in preparation'.*

Keywords: fuel moisture content, lodgepole pine, press disturbance, pulse disturbance, flammability

4.1 ABSTRACT

Fire and bark beetles have affected tremendous areas of forest land over the past several decades, but little is known about how flammability differs between sites recovering from fire and bark beetles. To better understand this issue, we investigated how meteorological conditions and fuel moisture content (FMC) vary in adjacent lodgepole pine stands a quarter century since fire and bark beetle outbreak. Post-fire sites had higher sapling densities, but lower basal area, projected leaf area index, and quadratic mean diameter than bark beetle affected sites. Meteorological conditions on post-fire sites indicate earlier snowmelt, greater evapotranspiration, and greater drought stress than post-bark beetle sites. Live FMC mimicked meteorological differences between disturbance types as post-fire sites broke dormancy earlier and experienced longer, more severe drought conditions than post-bark beetle sites. Dead FMC was similar in burned and bark beetle affected sites in July, but had a greater response to heavy August precipitation that resulted in higher dead FMC on the post-fire sites. Overall, dead FMC was more dynamic while foliar FMC was less dynamic on post-fire sites than post-bark beetle sites.

4.2 INTRODUCTION

Wildland fire and bark beetle outbreaks are the most important disturbance agents affecting forest dynamics in temperate coniferous forests (Dale et al. 2001). Driven in part by drought and high temperatures, both disturbances have profound effects on terrestrial biogeochemical cycles, energy budgets, and ecosystem services (Kurz et al. 2008, Raffa et al. 2008, Edburg et al. 2012). Warm, dry climate conditions over the last several decades have increased high-severity burning (Westerling et al. 2006, Krawchuk et al. 2009) and bark beetle-related tree mortality across extensive tracts of forestland in North America (Dale et al. 2001, Kurz et al. 2008, Raffa et al. 2008). Projections of accelerated climatic warming over the next century have spurred concern among forest managers, policy makers, and scientists about the risk of fire in recently disturbed forests (Jenkins et al. 2008, Simard et al. 2011a, Hicke et al. 2012, Donato et al. 2013, Harvey et al. 2014, 2016, Parks et al. 2016b). Fuel moisture content (FMC) is an important and extremely variable fuel metric that limits fuel combustibility and is closely tied to fire risk. We investigated how FMC varies in adjacent lodgepole pine stands a quarter century since fire and bark beetle outbreak.

FMC is the ratio of water content to dry biomass (eqn. 1), and seasonal dynamics in live and dead FMC are driven in both fuel types by variation in water content (the numerator), and in the case of live fuels, variation in dry mass (the denominator).

$$FMC(\%) = \left(\frac{\text{water mass (g)}}{\text{dry biomass (g)}}\right)*100 \qquad (1)$$

The water content in live plant materials varies depending on the water demands of the plant and whether soil water resources are available to replenish plant water use (Nelson Jr., 2001). When soil water is limited and plant water needs are high, live plant materials may be forced to function under a water deficit and may not fully hydrate. Seasonal variations in the density of plant biomass is also important in explaining fluctuations in live FMC (Jolly et al., 2012, 2014; McAllister et al., 2012; Nelson Jr., 2001). Structural and non-structural carbohydrates and crude fat vary through the season with leaf elongation, photosynthate production and transport, and respiration processes (Kozlowski and Clausen 1965, Gary 1971, Riaño et al. 2005, Jolly et al. 2014). Processes affecting the FMC of dead fuels differ greatly from live fuels in that mass does not vary appreciably through the fire season, and structural and metabolic attributes allowing for the active regulation of water in live plants become degraded or absent when plant tissues die and decompose. Lacking active regulation of water, dead fuels are capable of both longitudinal and transverse sorption and desorption of water depending on the temperature and relative humidity surrounding the fuel particle (Matthews, 2013; Nelson Jr., 2001; Simard, 1968; Viney, 1991). Through these mechanisms, dead FMC follows seasonal trends in fire weather, whereas live FMC follow trends in plant phenology and water stress (Finney et al., 2013; Nelson Jr., 2001).

Bark beetle activity and high severity fire are common agents of tree mortality in western North America. Both increase with drought and high temperatures but represent contrasting ends of a press-pulse disturbance continuum defined by the duration of time required to realize disturbance effects (Lake 2000, Smith et al. 2009a). Bark beetles (a press disturbance) require protracted periods of warm, dry climate conditions that compromise host tree vigor and facilitate bark beetle brood size and winter survival (Amman and Cole 1980, Safranyik and Carroll 2006, Raffa et al. 2008). Rates of overstory tree mortality due to bark beetles vary with multi-year beetle population dynamics and often decline when the number of suitable host trees become limited or climate conditions become unfavorable for beetle reproduction and survival (Safranyik and Carroll 2006, Raffa et al. 2008, Nelson et al. 2014). In contrast, rapid drying of forest fuels can occur over days to weeks under warm, dry weather conditions (Simard 1968), and wildfires (a pulse disturbance) can cause complete, indiscriminant tree death during a single fire event or season. Ecological effects from bark beetles and high-severity fire include altered forest stand structure (Amman and Baker 1972), energy budgets (Edburg et al. 2012), fuel profiles (Jenkins et al. 2008, Hicke et al. 2012, Nelson et al. 2016), and a post-disturbance period of high variation in net primary production (Litton et al. 2003, Turner et al. 2004, 2016, Kashian et al. 2006, 2013b). Differences in effects primarily lie in the rate and severity of each disturbance: bark beetles result in gradual, where high-severity fires result in rapid changes to forest stand characteristics. Such alterations in vegetation structure ultimately affect the flammability of post-disturbance forests by changing FMC dynamics.

Fuel moisture content is an important driver of live and dead fuel flammability, and is routinely used by fire management personnel to monitor fire risk and parameterize fire modeling software to estimate fire behavior and effects (Rothermel 1972, 1983, Van Wagner 1977, Reinhardt et al. 1997, Scott and Reinhardt 2001, Cruz et al. 2004, 2005, Alexander and Cruz 2006). Despite an expansive literature on FMC (Simard 1968, Viney 1991, Nelson Jr. 2001, Matthews 2013), targeted studies are needed to improve understanding of the variation and drivers of FMC in recently disturbed forests. We looked at two adjacent forest stands with differing disturbance histories to explore the following questions: [1] How do meteorological conditions that affect live and dead FMC differ between stands affected by bark beetles versus high-severity fire? [2] How do physiological measurements of live fuel moisture differ between trees versus saplings in stands affected by bark beetles and high-severity fire? [3] How does FMC of dead and herbaceous fuel differ between stands affected by bark beetles versus high-severity fire?

4.3 MATERIALS AND METHODS

Study area

Yellowstone National Park (YNP) encompasses 900,000 ha along the continental divide in northwestern Wyoming, USA. Primarily managed as wilderness, ~80% of the park is covered in forests with lodgepole pine being the dominant species in most forest stands. Engelmann spruce (*Picea engelmanii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) can co-occur on fertile sites, and whitebark pine (*Pinus albicalus* Engelm.) can be found at high elevations. The park ranges from 2100 to 2700 m in elevation, and receives two-thirds of its precipitation as wintertime snowfall (Despain, 1990). At the Old Faithful weather station, less than 15 kilometers from our study site, mean annual precipitation was 645 mm, mean annual temperature was 1.2°C, mean annual minima were -17.6°C in January, and mean annual maxima were 23.8°C in July for the period 1981 and 2010 (http://www.wrcc.dri.edu).

Within YNP, extensive bark beetle outbreaks occurred in the mid-1970 and early-1980s with the outbreak peaking in 1982 with ~390,000 hectares affected. When extensive fires burned nearly ~321,000 ha in 1988, nearly no bark beetle activity was present (Despain 1990b). Fifty-six percent of the burned area was classified as high-severity surface or crown fire that resulted in complete canopy death (Turner et al., 1994). Between 1989 and 1993, fire girdled trees near the perimeter spurred an increase in bark beetle populations and nearby stands experienced moderate-levels of tree mortality (Amman and Ryan 1991, Rasmussem et al. 1996, Ryan and Amman 1996).

Our study was conducted during the 2014 fire season in south-central YNP. Study sites ranged from 2450 to 2530 m in elevation, and bark beetle sites were located between 250 and 1200 m from the perimeter of the 1988 Fires. Median weather conditions between June 1 and

September 31, 2014 at the Old Faithful weather station exhibited cooler temperatures and lower wind speeds, and higher relative humidity, precipitation, and 10-hr FMC than observed during the same months between 1981 and 2010 (Table 1). Abundant fallen snags and growth release of surviving trees (Figure 1) within our study plots suggest that tree mortality coincided with either the extensive early-1980s bark beetle outbreak (Despain 1990) and/or the less extensive post-1988 Fire outbreak between 1989 and 1993 (Figure 1; Amman and Ryan 1991, Rasmussem et al. 1996, Ryan and Amman 1996). Post-disturbance stand structure differed greatly between fire and bark beetle affected study sites (Table 2). Post-1988 fire sites exhibited single-cohort stand structure and were occupied exclusively by lodgepole pine that established after 1988. Overall, post-fire sites had higher sapling densities (stem ha^{-1}), but lower basal area (m^2 ha^{-1}), projected leaf area index (m^2 m^{-2}), and quadratic mean diameter (cm) than bark beetle affected sites. Saplings in post-fire sites were larger and had greater leaf area than those found on post-bark beetle sites. Unburned, bark beetle-affected sites exhibited multi-cohort stand structure with a sparse overstory composed of large diameter lodgepole pine, a mid-story composed of smaller diameter subalpine fir and Engelmann spruce, and a dense, patchy understory composed of lodgepole pine, subalpine fir, whitebark pine, and Engelmann spruce saplings. Overstory and mid-story trees accounted for the greatest share of basal area and projected leaf area in post-bark beetle sites, despite being present at much lower densities than saplings. Both sites exhibited similar stand structure characteristics as those found in recent, nearby studies of 24-year old post-fire (Turner et al. 2016) and 27 to 36 year post-bark beetle forests (Simard et al. 2011a).

Field measurements and data processing

In July and August 2014, we measured stand structure, live and dead FMC, and meteorological data in two adjoining lodgepole pine stands in Yellowstone National Park, Wyoming, USA. Using a 5:21 cyclic sampling design, we located five study sites along three 1000 m transects at the 48, 94, 240, 720, and 816 m positions on each transect. Two transects were located within unburned lodgepole pine forest stands affected by bark beetles and one was located nearby inside the 1988 burn perimeter. All sites were located a minimum of 150 m from the 1988 burn perimeter, and edge effects were assumed to be negligible. Each plot consisted of four subplots: subplot 1 was located at plot center, subplot 2 was located 15 m north of plot center, subplot 2 was located 10 m east-south-east of plot center, and subplot 4 was located 5 m west-south-west of plot center. Forest structure and live and dead FMC were measured at each subplot. Meteorological data were collected at a weather station positioned 5 m north of plot center.

Forest Structure

Within each subplot, trees greater than 10 cm diameter at breast height (dbh) were measured using a circular fixed area plot (5 m radius) and dbh (@ 1.37 m), live/dead status, and species were recorded. Saplings- trees less than 10 cm dbh but greater than 1.37 m height- were measured within a 3.5 m radius plot and dbh, basal diameter, live/dead status, and species were recorded. All trees measured in post-1988 burned plots established following the fires and were assigned “sapling” status for consistency and ease of comparison. Tree density and basal area were estimated for each tree size class using standard fixed area plot estimation procedures and scaled to the hectare (Avery and Burkhart 2002). Height was measured and tree cores were extracted on 3 trees/saplings nearest to subplot center (i.e., 12 per plot). Tree heights were estimated for the remainder of trees in each plot using a regression relationship between dbh and tree height. Increment cores were prepared using standard dendrochronological methods (Stokes and Smiley 1968) and annual increment was measured for the period 1964 to 2014 using a Velmex “TA” Measurement system. Mean annual increment was estimated for each subplot to evaluate growth release in response to nearby tree mortality. Projected leaf area index (one-sided) was estimated by predicting leaf area for all trees within each subplot using allometric equations (Kashian et al. 2013 for trees, Copenhaver and Tinker 2014 for saplings), summing leaf area over each subplot, and dividing by the ground-area represented by each subplot.

Meteorological data

We installed 15 hand-built, micro-controller-based weather stations (Fisher 2012), 5 in burned stands and 10 in mountain pine beetle-affected stands, and recorded meteorological conditions at 15 minute intervals between July 5 and August 23, 2014. Stations employed an Arduino Pro microcontroller with 5V/16MHz logic (https://www.arduino.cc/en/Main/ArduinoBoardPro), Adafruit Datalogger shield (https://learn.adafruit.com/adafruit-data-logger-shield), and were powered using an AA battery pack. Measurements and sensors included: air temperature/humidity (Sensiron SHT-15/75 sensor), soil water potential (Shock et al. 1998, Watermark 200ss; Fisher 2007, Fisher and Kebede 2010), and soil and litter temperature (Vishay NTC Thermistor-NTCLE100E3). Air temperature and humidity sensors were enclosed inside a Gill-type radiation shield (Tarara and Hoheisel 2007) and was positioned at 2.5 m height. Data were extracted and batteries were replaced on a bi-weekly basis to ensure that stations were working properly. Meteorological conditions were summarized daily, and plotted for each disturbance type through the growing season with 1 standard error.

FMC measurements

Surface and canopy FMC was assessed three times during the summer: mid-July (July 9, 16, 17), late-July (July 24, 25, 28), and late-August (August 18, 19, 20). At each sample date, 200-400 grams of each fuel type was collected between 11:00 and 17:00 hours at each sub-plot and placed in a large Ziploc bag. Samples were placed in a cool, dark location for the remainder of the field day, and refrigerated overnight. Field wet masses were measured within 48 hours on a scale to a hundredth of a gram, placed in a paper bag, and dried in a convection oven at 70° C for 48 to 72 hours until a constant mass was reached. Samples were stored until the end of the field season, and processed at the University of Wyoming during the following year. After storage, samples were dried a second time before dry masses were measured. Fuel moisture content was estimated by subtracting the wet mass from the dry mass and dividing by dry mass (eqn. 1; Jolly and Hadlow, 2012).

Dead surface FMC was assessed for duff, litter, 1-hr, 10-hr, and herbaceous fuel classes. At each subplot, duff, litter, and herbaceous fuels were collected from inside a 0.1 m^2 sample frame. 1-hr (<0.64 cm diameter) and 10-hr (0.64 to 2.54 cm diameter) woody fuels were collected from the surface of the litter layer in the immediate area surrounding each subplot. In some cases, woody fuels were not present and were not collected. Live canopy fuels were collected by clipping south-facing branches from mid-crown with a pole pruner (up to 14 m) on 3 trees/saplings nearest to subplot center (i.e., 12 per plot). On a subsample of 9 plots (6 on the post-MPB site and 3 on the post-fire site), a branchlet consisting of the last 4 years of growth was removed, bark was stripped from the oldest year exposing the bare stem, and leaf water potential was determined using a Pressure Chamber (PMS Instrument Company, Model 600). Samples used to assess leaf water potential were discarded in the field and a separate sample from the same tree branch was returned to the lab for FMC measurements. Sample trees were marked at the beginning of the field season and samples were taken from the same trees at each sample date. In the lab, annual growth for the current and the preceding 2 years were identified via needle whorls, bud scars, and bud scales, and needles and stem wood were separated from each branch sample. FMC was determined for each branch component.

In late-August, pressure-volume measurements were taken on 21 branch samples representing post-fire saplings, post-MPB saplings, and post-MPB trees. Samples were prepared by [1] collecting south-facing, mid-crown branches from each study site at mid-day, [2] clipping branches to the last 4 years of growth, [3] hydrating clipped branches in the dark using distilled water for 24 hours, [4] stripping the bark from the oldest year to expose the bare wood, and [5] recutting the stem using a razor blade. Over the next 36 hours, branch samples were air dried, and wet mass and leaf water potentials were repeatedly collected. Measurement intervals were progressively increased as changes in branch mass and water potential became less pronounced. After sampling ended, samples were dried in a convection oven at 70° C until a constant mass was achieved and dry mass was measured. Pressure volume curves were fit using polynomial regression with relative water content as the response variable and leaf water potential as the predictor variable.

Relative water content (RWC) was estimated for each tree using pressure-volume regression models and water potential measurements from each sample date. Total water holding capacity, as percent dry biomass, was assessed at each measurement date by dividing FMC estimates by relative water content.

Data analysis

We assessed differences in meteorological conditions, and live and dead FMC using Monte Carlo methods (Gotelli and Ellison 2013, Dale and Fortin 2014) to test the following null hypothesis: *Meteorological conditions and FMC do not differ between stands affected by bark beetles and fire.* Monte Carlo methods were selected because data were not normally distributed and violated assumptions used in parametric data analysis. To test the null hypothesis, we defined the test statistic as the absolute difference in the medians of observations collected in bark beetle and high-severity fire affected stands (DIF_{obs}; eqn. 2). Next, we randomly reassigned bark beetle and fire classes to the observations and

$$DIF = \left|\tilde{x}_{fire} - \tilde{x}_{MPB}\right| \tag{2}$$

recomputed the absolute difference in medians (DIF_{sim}). After repeating this process 10,000 times, we tallied the number of simulated differences that are less than or equal to our observed difference ($DIF_{sim} \leq DIF_{obs}$), and computed a one-sided tail probability by dividing by the number of simulations (n = 10,000). An analogous process was used to test for differences in leaf water potential, relative water content, water holding capacity, and FMC between post-fire sapling, post-MPB saplings, and post-MPB trees. Differences in the degree of change between sample periods within individual disturbance types and fuel classes were assessed by defining the test statistic as the absolute difference in the median FMC change observed between two measurement periods in bark beetle and high-severity fire affected stands ($DIF_{\Delta t}$; eqn. 3). Differences in the degree of change within fuel classes but between disturbance types were

$$DIF_{\Delta t} = \left|\left(\tilde{x}_{disturbance_{t_2}} - \tilde{x}_{disturbance_{t_1}}\right)\right| \tag{3}$$

assessed by defining the sample statistic as the difference in one disturbance type between measurement periods minus the difference in the second disturbance type between measurement periods ($DIF_{disturbance_{\Delta t}}$; eqn. 4). Random reassignment of bark beetle and fire classes was restricted to observations within respective measurement dates.

$$DIF_{disturbance_{\Delta t}} = \left|\left|\tilde{x}_{fire_{t_2}} - \tilde{x}_{fire_{t_1}}\right| - \left|\tilde{x}_{MPB_{t_2}} - \tilde{x}_{MPB_{t_1}}\right|\right| \tag{4}$$

4.4 RESULTS

Differences in meteorological conditions

Meteorological conditions generally differed between disturbance types; however, all variables showed convergent trends over the measurement period (Figure 2). While median air temperature did not differ between disturbance types, post-fire sites exhibited a greater difference between daily minimum and maximum temperatures, although this difference decreased in late-August. Median and maximum relative humidity was higher on post-fire sites, however minimum relative humidity showed no difference between disturbance types. Median and maximum litter temperature was higher on post-fire sites until late July, and the difference between daily minimum and maximum litter temperatures remained greater on post-fire sites throughout the measurement period. Soils were consistently warmer and drier in post-fire stands throughout the entire measurement period; however, differences between disturbances decreased steadily during the month of August. Precipitation increased through the measurement period with approximately 30 mm falling during the month of July and 70 mm falling during the month of August.

Differences in tree and sapling physiological measurements and fuel moisture content

Pressure-volume regression models indicate that saplings maintain a higher relative water content than trees across the range of leaf water potentials observed in the lab (Table 4; Figure 3). Differences between post-fire and post-bark beetle saplings were not present at leaf water potentials above -2 mPa; however, post-bark beetle saplings exhibited lower relative water content when leaf water potentials were below -2 mPa (Figure 3).

In mid-July, post-bark beetle sapling leaf water potential was 0.28 mPa greater than either post-fire saplings or post-bark beetle trees, and relative water content was 3.2% and 7.9% greater, respectively (Figure 4). Post-fire saplings displayed similar leaf water potentials but RWC was

4.7% greater than post-bark beetle trees. An ~8% greater water holding capacity than either post-bark beetle saplings or trees permitted post-fire saplings to attain similar FMC with post-bark beetle saplings despite greater leaf water stress, and greater FMC than post-bark beetle trees despite similar leaf water stress.

From mid-July to late-July, post-bark beetle saplings experienced a 2.3% greater change in RWC, 22% greater change in water holding capacity, and 18.7% greater change in FMC than post-fire saplings, and a 0.18 mPa greater change in leaf water potential and 2.6% greater change in RWC than post-bark beetle trees. During the same period, post-bark beetle trees experienced a 20.5% greater change in water holding capacity than post-fire saplings. By late-July, RWC was 4.4% greater in post-fire saplings and 5.3% greater in post-bark beetle saplings than post-bark beetle trees, but water holding capacity was 14.2% greater in post-bark beetle saplings and 13.0% greater in post-bark beetle trees than post-fire saplings. This increase in water holding capacity resulted in post-bark beetle sapling FMC 14.3% greater and post-bark beetle tree FMC similar to post-fire sapling FMC.

From late-July to late-August, post-fire saplings experienced a 0.13 mPa greater change in leaf water potential than post-bark beetle saplings or trees, and a 1.5% greater change in RWC than post-bark beetle saplings. By late-August, post-fire and post-bark beetle sapling leaf water potential was 0.20 mPa greater and RWC was 7.3% and 6.7% greater than post-bark beetle trees, respectively. Water holding capacity remained greater in post-bark beetle saplings and post-bark beetle trees than post-fire saplings. Post-bark beetle sapling FMC was 10.3% greater than post-fire sapling FMC, and 8.8% greater than post-bark beetle tree FMC.

Differences in surface fuel moisture content

Differences in duff, litter, 1-hr, and 10-hr FMC were not evident between post-fire and post-bark beetle sites in mid-July or late-July; however, live herbaceous FMC was greater on post-fire sites by 25.2% in mid-July and 56.3% in late-July (Table 6). By late-August, after nearly 70 mm of precipitation fell in the area, surface FMC on post-fire sites exhibited greater FMC than post-bark beetle sites by 40.3% for litter, 44.5% for 1-hr fuels, 19.8% for 10-hr fuels, and 40.8% for live herbaceous fuels.

From mid-July to late-July, post-fire sites experienced the greatest change in 1-hr, 10-hr, and herbaceous FMC and post-bark beetle sites experienced the greatest change in duff and litter FMC (Table 6). Over the same period, 1-hr and 10-hr FMC declined by 6.0% and 7.3%, respectively, within post-fire stands, but no changes were significant within bark beetle stands. From late-July to late-August, post-fire sites experienced a greatest change in litter, 1-hr, 10-hr, and herbaceous FMC and post-bark beetle sites experienced a greater change in duff FMC. Within post-fire stands over this period, FMC increased by 15.7% for duff 54.3% for litter, 45.5% for 1-hr fuels, and 23.7% for 10-hr fuels. Herbaceous fuels did not change between late-July and late-August on post-fire sites. On post-bark beetle sites from late-July to late-August, FMC increased by 24.2% for duff and 12.7% for litter, but decreased by 21.5% for herbaceous fuels. 1-hr and 10-hr fuels did not change in post-bark beetle sites over this period.

4.5 DISCUSSION

Our results indicate that disturbance history (i.e., fire and bark beetle outbreaks) in lodgepole pine forests can lead to substantial differences in fuel moisture dynamics. In July, dead FMC was similar among disturbance types, but heavy precipitation in August led to greater dead FMC on post-burn sites, a likely consequence of disturbance generated variation in canopy interception and evapotranspiration. Live FMC mimicked meteorological differences between disturbance types as post-fire sites broke dormancy earlier and experienced longer, more severe drought conditions than post-bark beetle sites. Overall, dead FMC was more dynamic while foliar FMC was less dynamic on post-fire sites than post-bark beetle sites.

Live FMC in conifers varies through the growing season because of two processes: changes in the density of needle biomass and the water status of the plant (eqn. 1). Prior to needle elongation, live FMC should temporarily dip while photosynthetically active older needles concentrate organic molecules in foliar tissues (Kozlowski and Clausen 1965, Gary 1971, Nelson Jr. 2001, Jolly et al. 2014). After bud break, organic molecules redistribute throughout elongating leaf tissues leading to an initial decline followed by stability in old needle biomass density. The approximate timing of needle elongation could be discerned on post-bark beetle sites between mid- and late-July via rising trends in the FMC of old needles (Supplementary Table 1) and total foliar FMC (Figure 4). Leaf water potential and relative water content on both sites exhibited far less variation through the season (Figure 4). Isohydric tree species such as lodgepole pine closely regulate mid-day minimum leaf water potential by actively limiting gas transfer as vapor pressure deficits increase (Ewers et al. 2005, Lambers et al. 2008). Had a drying trend continued through August 2014, we would have expected continued stability in mid-day minimum leaf water potentials and little change in live FMC. Had our study species been anisohydric (i.e., lower stomatal closing under higher vapor pressure deficit; Lambers et al. 2008), we would have expected a strong inverse relationship between leaf water potential and vapor pressure deficit resulting in lower mid-day live FMC.

Fluctuations in dead FMC are driven by their tendency toward equilibrium moisture content (EMC), a dynamic value that varies negatively with fuel temperature and positively with relative humidity (Simard 1968). We hypothesized that higher relative humidity in post-fire stands would result in greater dead FMC, but we substantially underestimated the effect of higher litter temperatures on the desorption of dead fuels on post-fire sites. To our surprise, dead fuel moisture content was similar among disturbance types in July. If a drying trend had continued through August, we anticipate that relative humidity, followed by dead FMC, might have experienced a sharp decline on post-fire sites as depleted soil water resources limited evapotranspiration. Instead, heavy rain disproportionately increased dead FMC on post-fire sites in August, likely due to lower rainfall interception and lower boundary layer mixing.

Since 1979, fire season lengths in North American temperate coniferous forests have increased by over five days and the aerial extent exposed to longer fire seasons (>1 σ above historic mean) has increased by 14.3% (Jolly et al. 2015). Our data suggest that after 25 years, burned sites experienced season lengthening and greater wetting from precipitation events when compared with post-bark beetle sites. This supports the notion that changes in vegetation structure tied to accelerating changes in climate over the next century may strengthen or weaken changes in disturbance potential, frequency, and extent (Littell et al. 2009). On adjoining forest sites, divergent disturbance histories appear to have shifted energy budgets and phenological trends that drive live and dead FMC dynamics. Young, post-fire lodgepole pine forests appear to experience longer fire seasons, greater rates of wetting and drying of dead fuels, and an earlier dip in live fuel moisture. Post-bark beetle sites appeared to break dormancy later and benefit less from late season precipitation.

Since the late 1990s, fire and bark beetle outbreaks have affected a tremendous area in the Rocky Mountains (Littell et al. 2009, Smith et al. 2009b, Meddens et al. 2012, Abatzoglou and Williams 2016), leading to a greater likelihood of burning on recently disturbed sites (based simply on land area). Our study indicates that disturbance history (i.e., fire vs. bark beetle) can influence the phase, period, and amplitude of live and dead FMC through the fire season, thus influencing the flammability of forest stands. Further investigation is needed to understand how vegetation dynamics in recently disturbed forests might affect a site's potential for subsequent disturbance.

4.6 ACKNOWLEDGEMENTS

We are grateful Erik Larsen, Eric McDevitt, Alan Renneisen, David Pomeranz, Paul Hood, Phillip Timpson, Monique Nelson, Stephen Nelson, Valerie Nelson, and Eli Nelson for field and laboratory support. We also thank US-DOI National Park Service staff Roy Renkin and Stacy Gunther for their knowledge and support in the park. Funding was provided by the Joint Fire Science Program-GRIN, Boyd Evison Graduate Fellowship, UW-NPS AMK Research Station small grant program and the American Alpine Club.

4.7 LITERATURE CITED

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences:11700–11775.

Alexander, M. E., and M. G. Cruz. 2006. Evaluating a model for predicting active crown fire rate of spread using wildfire observations. Canadian Journal of Forest Research 36:3015–3028.

Amman, G. D., and B. H. Baker. 1972. Mountain Pine Beetle Influence On Lodgepole Pine Stand Structure. Journal Of Forestry 70:204-.

Amman, G. D., and W. E. Cole. 1980. Mountain Pine Beetle Dynamics in Lodgepole Pine Forests Part 1: Course of an Infestation. USDA Forest Service GTR INT-89:1–59.

Amman, G. D., and K. C. Ryan. 1991. Insect infestation of fire-injured trees in the Greater Yellowstone Area. US Dept. of Agriculture, Forest Service, Intermountain Research Station.

Avery, T. E., and H. E. Burkhart. 2002. Forest measurements. McGraw-Hill.

Copenhaver, P. E., and D. B. Tinker. 2014. Stand density and age affect tree-level structural and functional characteristics of young, postfire lodgepole pine in Yellowstone National Park. Forest Ecology and Management 320:138–148.

Cruz, M. G., M. E. Alexander, and R. H. Wakimoto. 2004. Modeling the likelihood of crown fire occurrence in conifer forest stands. Forest Science 50:640–658.

Cruz, M. G., M. E. Alexander, and R. H. Wakimoto. 2005. Development and testing of models for predicting crown fire rate of spread in conifer forest stands. Canadian Journal of Forest Research 35:1626–1639.

Dale, M. R. T., and M.-J. Fortin. 2014. Spatial Analysis: A Guide For Ecologists. Cambridge University Press.

Dale, V. H., L. a Joyce, S. Mcnulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, B. M. Wotton, R. P, and M. P. 2001. Climate change and forest disturbances. Bioscience 51:723–734.

Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart. Inc, Boulder, CO.

Donato, D. C., B. J. Harvey, W. H. Romme, M. Simard, and M. G. Turner. 2013. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecological Applications 23:3–20.

Edburg, S. L., J. A. Hicke, P. D. Brooks, E. G. Pendall, B. E. Ewers, U. Norton, D. Gochis, E. D. Gutmann, and A. J. Meddens. 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Frontiers in Ecology and the Environment 10:416–424.

Ewers, B. E., S. T. Gower, B. Bond-Lamberty, and C. K. Wang. 2005. Effects of stand age and tree species composition on transpiration and canopy conductance of boreal forests. Plant Cell Environ. 28:660–678.

Fisher, D. K. 2007. Automated collection of soil moisture data with a low-cost microcontroller circuit. Applied engineering in Agriculture 23:493–500.

Fisher, D. K. 2012. Open-Source Hardware Is a Low-Cost Alternative for Scientific Instrumentation and Research. Modern Instrumentation 1:8–20.

Fisher, D. K., and H. Kebede. 2010. A low-cost microcontroller-based system to monitor crop temperature and water status. Computers and Electronics in Agriculture 74:168–173.

Gary, H. L. 1971. Seasonal and diurnal changes in moisture contents and water deficits of Engelmann spruce needles. Botanical Gazette:327–332.

Gotelli, N. J., and A. M. Ellison. 2013. A Primer of Ecological Statistics. Macmillan Education.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014. Recent mountain pine beetle outbreaks , wildfire severity , and postfire tree regeneration in the US Northern Rockies:6–11.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. Ecology 97:2272–2282.

Hicke, J. a., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecology And Management 254:16–34.

Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6:7537.

Jolly, W. M., A. M. Hadlow, and K. Huguet. 2014. De-coupling seasonal changes in water content and dry matter to predict live conifer foliar moisture content. International Journal of Wildland Fire 23:480–489.

Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon storage on landscapes with stand-replacing fires. BioScience 56:598–606.

Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta - dominated forests. Ecological Monographs 83:49–66.

Kozlowski, T. T., and J. J. Clausen. 1965. Changes in moisture contents and dry weights of buds and leaves of forest trees. Botanical Gazette:20–26.

Krawchuk, M. A., M. A. Moritz, M. A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. Global pyrogeography: The current and future distribution of wildfire. PLoS ONE 4:e5102.

Kurz, W. a, C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990.

Lake, P. S. 2000. Disturbance, Patchiness ad Diversity in Streams. Journal of American Benthological Society 19:573–592.

Lambers, H., F. S. Chapin, and T. L. Pons. 2008. Plant Physiological Ecology. Springer New York, New York, NY.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications 19:1003–1021.

Litton, C. M., M. G. Ryan, D. B. Tinker, and D. H. Knight. 2003. Belowground and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density. Canadian Journal of Forest Research 33:351–363.

Matthews, S. 2013. Dead fuel moisture research: 1991 – 2012. International Journal of Wildland Fire 23:78–92.

Meddens, A. J., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22:1876–1891.

Nelson Jr., R. M. 2001. Chapter 4 - Water Relations of Forest Fuels. Pages 79–149 in E. A. Johnson and K. Miyanishi, editors. Forest Fires. Academic Press, San Diego.

Nelson, K. N., M. E. Rocca, M. Diskin, C. F. Aoki, and W. H. Romme. 2014. Predictors of bark beetle activity and scale-dependent spatial heterogeneity change during the course of an outbreak in a subalpine forest. Landscape Ecology 29:97–109.

Nelson, K. N., W. H. Romme, M. G. Turner, and D. B. Tinker. 2016. Landscape variation in tree regeneration and snag fall drive fuel loads in 25-yr old post-fire lodgepole pine forests. Ecological Applications 26:2424–2438.

Parks, S. A., C. Miller, L. M. Holsinger, S. Baggett, and B. J. Bird. 2016. Wildland fire limits subsequent fire occurrence. International Journal of Wildland Fire 25:182–190.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. BioScience 58:501–517.

Rasmussem, L. A., G. D. Amman, J. C. Vandygriff, R. D. Oakes, A. S. Munson, and K. E. Gibson. 1996. Bark beetle and wood borer infestation in the Greater Yellowstone Area during four postfire years.

Reinhardt, E. D., R. E. Keane, and J. K. ; Brown. 1997. First Order Fire Effects Model: FOFEM 4.0, user's guide. USDA Forest Service, GTR-INT-344:1–65.

Riaño, D., P. Vaughan, E. Chuvieco, P. J. Zarco-Tejada, and S. L. Ustin. 2005. Estimation of fuel moisture content by inversion of radiative transfer models to simulate equivalent water thickness and dry matter content: Analysis at leaf and canopy level. IEEE Transactions on Geoscience and Remote Sensing 43:819–826.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, GTR-INT-115:1–50.

Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service, GRT-INT-143:166–166.

Ryan, K. C., and G. D. Amman. 1996. Bark beetle activity and delayed tree mortality in the Greater Yellowstone Area following the 1988 fires.

Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of mountain pine beetle in lodgepole pine forests. Pages 3–66 in L. Safranyik and B. Wilson, editors. The Mountain Pine Beetle: A Synthesis of its Biology, Management and Impacts on

Lodgepole Pine. Canadian Forest Service: Pacific Forestry Center, Natural Resources Canada, Victoria, Canada.

Scott, J. H., and E. D. Reinhardt. 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service, RMRS-RP-29:1–59.

Shock, C. C., J. M. Barnum, and M. Seddigh. 1998. Calibration of Watermark Soil Moisture Sensors for Irrigation Management. Proceedings of the International Irrigation Show:139–146.

Simard, A. J. 1968. The moisture content of forest fuels: A review of the basic concepts. Department of Forestry and Rural Development, Canada Information Report FF-X-14:1–47.

Simard, M., W. H. Romme, J. M. Griffin, and M. G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs 81:3–24.

Smith, M., A. Knapp, and S. Collins. 2009a. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. Ecology 90:3279–3289.

Smith, W. B., P. D. Miles, C. H. Perry, S. A. Pugh, and others. 2009b. Forest resources of the United States, 2007: a technical document supporting the forest service 2010 RPA Assessment. General Technical Report-USDA Forest Service.

Tarara, J. M., and G. A. Hoheisel. 2007. Low-cost shielding to minimize radiation errors of temperature sensors in the field. HortScience 42:1372–1379.

Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7:751–775.

Turner, M. G., T. G. Whitby, D. B. Tinker, and W. H. Romme. 2016. Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? Ecology 97:1260–1273.

Van Wagner, C. E. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7:23–34.

Viney, N. R. 1991. A review of fine fuel moisture modelling. International Journal of Wildland Fire 1:215–234.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943.

4.8 TABLES

Table 1: Median and inner-quartile ranges for meteorological conditions during the fire season at the Old faithful weather station for the study year and the historic period between 1981 and 2010.

	Old faithful weather station†	
Year	2014	1981-2010
T (°C)	18.9 [13.9, 22.2]	20.0 [15.0, 23.3]
RH (%)	35 [28, 55]	37 [27, 50]
Precip ‡ (mm)	245	153 [106, 220]
Wind (km hr^{-1})	3.2 [1.6, 4.8]	8.1 [5.8, 12.9]
10-hr FMC (%)	12 [10, 18]	9 [7, 14]

† Summary statistics computed using 1 pm daily measurements during the fire season (June 1—September 31).
‡ Total precipitation during the fire season (June 1—September 31).

Table 2: Mean and 95% confidence intervals for forest structure attributes by site

	Stands affected by bark beetles		Stands burned in 1988
	Sapling	Tree	Sapling
Sample size (n)			
Density (stems ha^{-1})	2196 (1376, 3016)	493 (386, 601)	5925 (4058, 7791)
Pinus contorta	1332 (624, 2040)	397.9 (299, 497)	5925 (4058, 7791)
Abies lasiocarpa	481 (205, 756)	86 (39, 133)	0 (0, 0)
Picea Engelmanii	72 (17, 126)	35 (7, 63)	0 (0, 0)
Pinus albicalus	260 (105, 415)	0 (0, 0)	0 (0, 0)
Basal area (m^2 ha^{-1})	2.2 (1.4, 2.9)	30.1 (22.5, 37.7)	12.0 (9.3, 14.7)
Pinus contorta	0.8 (0.3, 1.3)	27.2 (19.7, 34.6)	12.0 (9.3, 14.7)
Abies lasiocarpa	0.7 (0.2, 1.2)	2.5 (1, 3.9)	0 (0, 0)
Picea Engelmanii	0.1 (0, 0.2)	0.7 (0.1, 1.3)	0 (0, 0)
Pinus albicalus	0.2 (0, 0.3)	0 (0, 0)	0 (0, 0)
Projected leaf area index (m^2 m^2)	0.2 (0.1, 0.2)	1.2 (0.9, 1.4)	1.0 (0.8, 1.2)
Pinus contorta	0.1 (0, 0.1)	0.9 (0.7, 1.2)	1.0 (0.8, 1.2)
Abies lasiocarpa	0.1 (0, 0.1)	0.2 (0.1, 0.3)	0 (0, 0)
Picea Engelmanii	0 (0, 0)	0.1 (0, 0.1)	0 (0, 0)
Pinus albicalus	0 (0, 0)	0 (0, 0)	0 (0, 0)
Quadratic mean diameter (cm)	3.7 (3, 4.3)	26.9 (25, 28.9)	5.4 (4.9, 5.9)
Pinus contorta	2.6 (2.1, 3.1)	29 (27.0, 30.9)	5.4 (4.9, 5.9)
Abies lasiocarpa	3.8 (3.3, 4.2)	18.5 (15.4, 21.7)	0 (0, 0)
Picea Engelmanii	3.8 (3.2, 4.4)	15.8 (13.2, 18.3)	0 (0, 0)
Pinus albicalus	2.4 (1.9, 2.9)	0 (0, 0)	0 (0, 0)

Table 3: Median and inner-quartile ranges, and differences in meteorological conditions between post-fire and post-bark beetle affected stands. Measurements taken between July 5 and August 23, 2014. Probability of observed differences were computed using Monte Carlo methods.

Disturbance	Fire	Bark beetle	Fire – Bark beetles
n	5	9	10,000
Temperature (°C)	10.7 [5.8, 17.2]	10.6 [6.6, 16.3]	0.1^{ns}
Rel. humidity (%)	87.9 [53.5, 100]	80.7 [52.6, 95.8]	7.2^{***}
Litter T (°C)	10.9 [8.5, 14.3]	10.6 [8.8, 13.1]	0.3^{***}
Soil T @ 30 cm (°C)	10.4 [9.9, 11.2]	9.0 [8.3, 9.9]	1.3^{***}
Soil moisture (mPa)	-0.07 [-0.12, -0.05]	-0.02 [-0.03, -0.02]	0.05^{***}

Probability of observed difference: $^{ns}p > 0.05$, $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

Table 4: Regression results predicting relative water content from leaf water potential.

Dependent variable: Relative water content	df	r^2	*a*	*b*	*c*	MSE	F-statistic	*p*-value
Post-fire saplings	81	0.90	0.238	0.038	1.071	0.0007	359	<0.001
Post-MPB saplings	81	0.92	0.194	0.017	1.041	0.0006	483	<0.001
Post-MPB trees	67	0.86	0.279	0.046	1.064	0.0016	205	<0.001

† All equations take the form $y = a(x) + b(x)^2 + c$ where y is relative water content and x is leaf water potential (mPa). Relative water content is the proportion of total water content.

Table 5: Differences in canopy fuel moisture content between post-fire saplings, post-bark beetle saplings, and post-bark beetle trees. Probability of observed differences were computed using Monte Carlo methods.

	Post-fire saplings – post-bark beetle saplings	Post-fire saplings – post-bark beetle trees	Post-bark beetle saplings – post-bark beetle trees
mid-July			
Leaf water potential	-0.28^{***}	0.00^{ns}	0.28^{***}
Relative water content	-3.2^{**}	4.7^{***}	7.9^{***}
Water holding capacity†	8.1^{*}	7.8^{*}	0.2^{ns}
Total branch‡	5.5^{ns}	16.1^{***}	10.6^{***}
late-July			
Leaf water potential	-0.13^{ns}	-0.03^{ns}	0.1^{ns}
Relative water content	-0.9^{ns}	4.4^{***}	5.3^{**}
Water holding capacity†	-14.2^{**}	-13.0^{*}	1.2^{ns}
Total branch‡	-14.3^{**}	-2.6^{ns}	11.7^{ns}
late-August			
Leaf water potential	0.00^{ns}	0.20^{**}	0.20^{*}
Relative water content	0.6^{ns}	7.3^{***}	6.7^{***}
Water holding capacity†	-15.6^{***}	-17.5^{***}	-1.8^{ns}
Total branch‡	-10.3^{***}	-1.6^{ns}	8.8^{**}
Δ *mid-July to late-July*			
Leaf water potential	-0.15^{ns}	0.03^{ns}	0.18^{**}
Relative water content	-2.3^{*}	0.3^{ns}	2.6^{*}
Water holding capacity†	-22.0^{***}	-20.5^{**}	1.5^{ns}
Total branch‡	-18.7^{***}	-17.5^{**}	1.2^{ns}
Δ *late-July to late-August*			
Leaf water potential	0.13^{*}	0.13^{*}	0.0^{ns}
Relative water content	1.5^{*}	1.5^{ns}	0.0^{ns}
Water holding capacity†	1.4^{ns}	4.4^{ns}	3.0^{ns}
Total branch‡	-4.0^{ns}	-1.0^{ns}	2.9^{ns}

† Percent water holding capacity as percent of dry biomass.
‡ Needle and branch wood for the current and the two prior years of growth.
Probability of observed difference: $^{ns}p > 0.05$, $^{*}p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$.

Table 6: Median and inner-quartile ranges for surface fuel moisture content at each sample date, and differences in surface fuel moisture content between post-fire and post-bark beetle affected stands. Changes in fuel moisture content between sample dates, and the differences in the rate of change between disturbance types. Probability of observed differences were computed using Monte Carlo methods. Note: 65 mm of precipitation fell between the late-July and late-August sample dates

	Fire	Bark beetle	Fire – Bark beetle
mid-July			
Duff	32 [26, 48]	55 [33, 75]	-23.2^{ns}
Litter	15 [11, 40]	14 [5, 39]	1.5^{ns}
1-hr	15 [7, 29]	11 [7, 16]	4.2^{ns}
10-hr	16 [10, 25]	12 [4, 23]	3.9^{ns}
Herb	141 [131, 150]	116 [104, 134]	25.2^{*}
late-July			
Duff	30 [12, 42]	45 [26, 61]	-15.0^{ns}
Litter	14 [11, 21]	16 [10, 25]	-1.4^{ns}
1-hr	9 [7, 11]	8 [6, 12]	0.5^{ns}
10-hr	8 [7, 11]	11 [7, 17]	-2.6^{ns}
Herb	167 [147, 242]	111 [98, 125]	56.3^{**}
late-August			
Duff	45 [37, 58]	69 [50, 94]	-23.6^{ns}
Litter	69 [32, 92]	29 [19, 49]	40.3^{**}
1-hr	54 [24, 81]	10 [7, 16]	44.5^{***}
10-hr	32 [21, 55]	12 [10, 35]	19.8^{*}
Herb	131 [109, 179]	90 [78, 110]	40.8^{***}
Δ *mid-July to late-July*			
Duff	-2.4^{ns}	-10.6^{ns}	-8.2^{***}
Litter	-1.0^{ns}	1.9^{ns}	-0.9^{***}
1-hr	-6.0^{*}	-2.3^{ns}	3.8^{***}
10-hr	-7.3^{**}	-0.8^{ns}	6.5^{***}
Herb	26.4^{ns}	-4.7^{ns}	21.7^{***}
Δ *late-July to late-August*			
Duff	15.7^{*}	24.2^{***}	-8.5^{***}
Litter	54.3^{***}	12.7^{***}	41.7^{***}
1-hr	45.5^{***}	1.5^{ns}	44.0^{***}
10-hr	23.7^{***}	1.3^{ns}	22.4^{***}
Herb	-36.9^{ns}	-21.5^{***}	15.4^{***}

Probability of observed difference: $^{ns}p > 0.05$, $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

Supplementary Table 1: Changes in fuel moisture content by disturbance type, canopy position, and measurement period.

	Post-fire sapling		Post-bark beetle		Post-MPB trees	
	late-July – mid-July	late-Aug – late-July	late-July – mid-July	late-Aug – late-July	late-July – mid-July	late-Aug – late-July
Leaf water potential	-0.03^{ns}	0.18^{***}	-0.18^{**}	0.05^{ns}	0.0^{ns}	-0.05^{ns}
Relative water content	-0.3^{ns}	2.2^{***}	-2.6^{**}	0.7^{ns}	0.0^{ns}	-0.7^{ns}
Water holding capacity†	-0.2^{ns}	-5.5^{ns}	22.1^{***}	-4.1^{ns}	20.7^{***}	-1.0^{ns}
Total branch‡	-0.6^{ns}	-0.1^{ns}	19.2^{***}	-4.1^{ns}	18.1^{***}	-1.1^{ns}

† Tissue water holding capacity as percent dry biomass.
‡ Combined needle and branch wood for the current and the two prior years of growth.
Probability of observed difference: $^{ns}p > 0.05$, $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

4.9 FIGURES

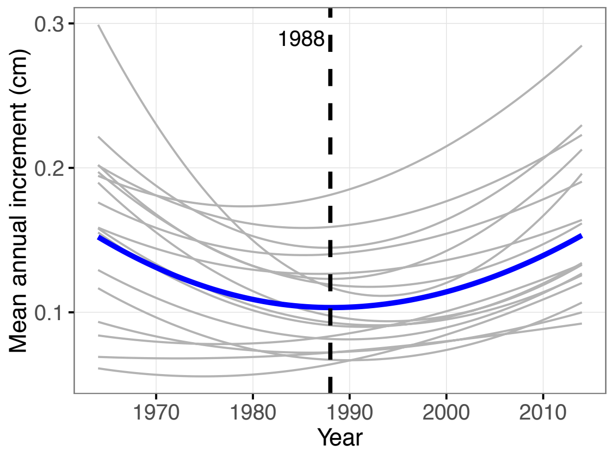


Figure 1: Mean annual diameter increment in surviving post-bark beetle trees increased during the late-1980s and early-1990s suggesting the timing of the bark beetle outbreak. Mean annual increment is displayed across all plots (blue line) and for each plot (gray lines).

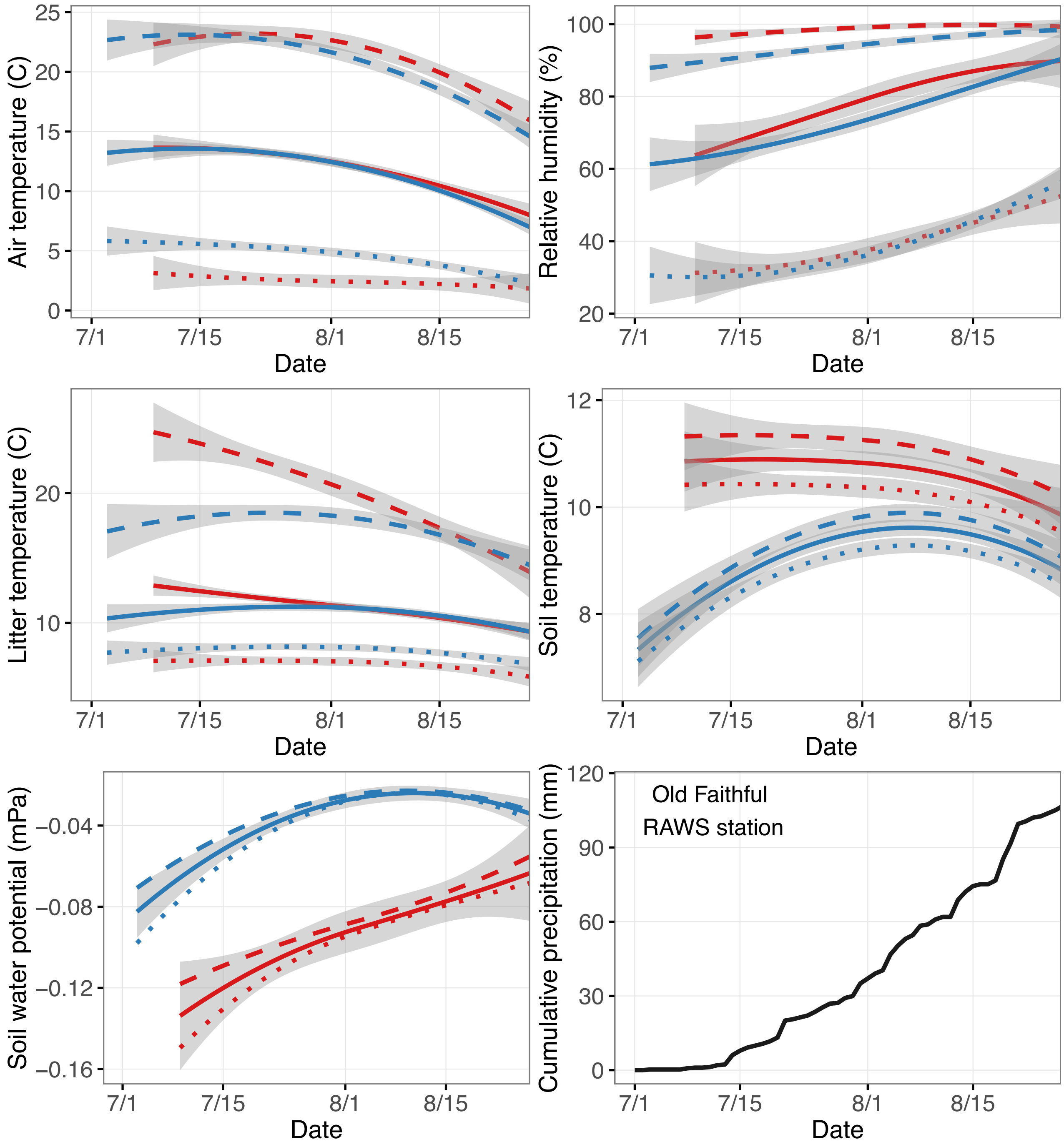


Figure 2: Daily variation in weather variables measured at 10 sites affected by the mountain pine beetle sites and 5 sites burned in 1988. Data were smoothed using a 3-day window. Red

lines indicate post-1988 fire; blue lines indicate Post-1988 MPB. Dotted lines are minima; solid lines are median, and dashed lines are maxima.

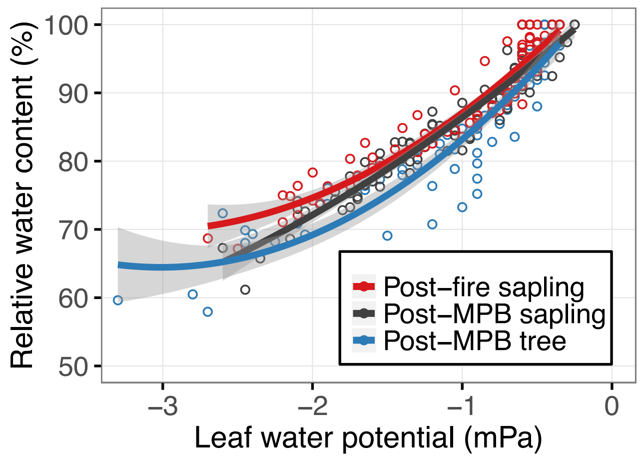


Figure 3: Pressure-volume relationships predicting relative water content from leaf water potential.

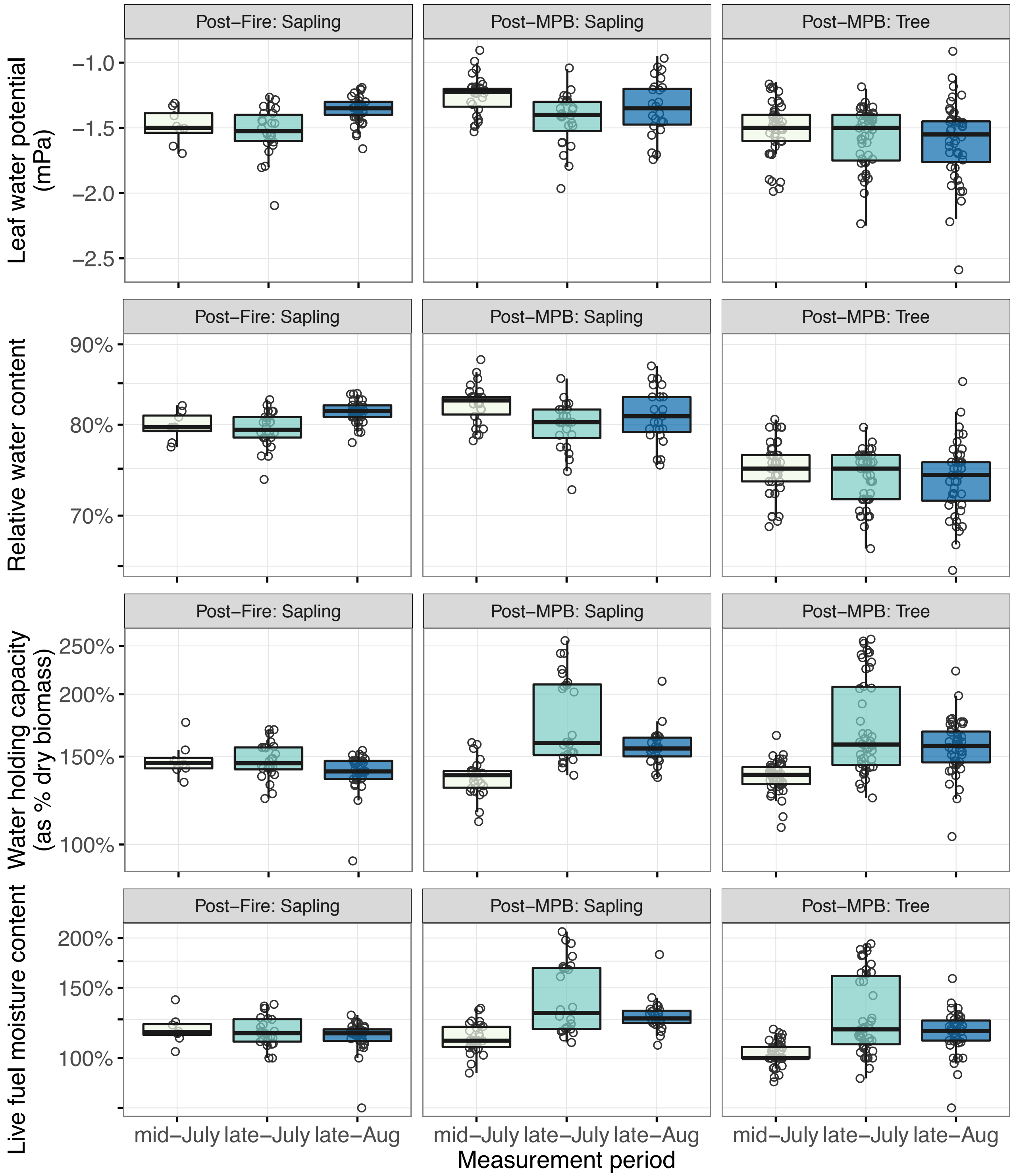
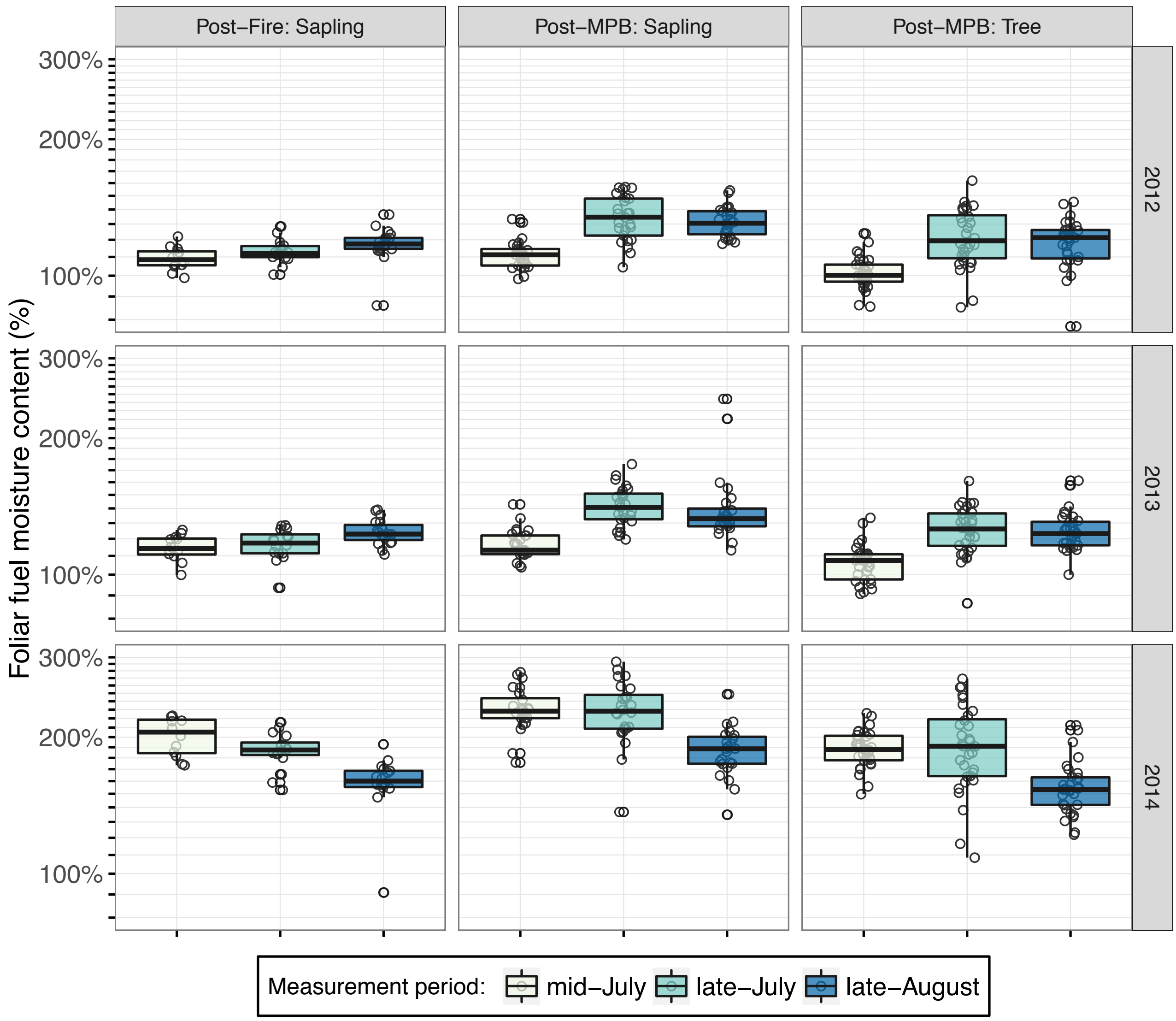
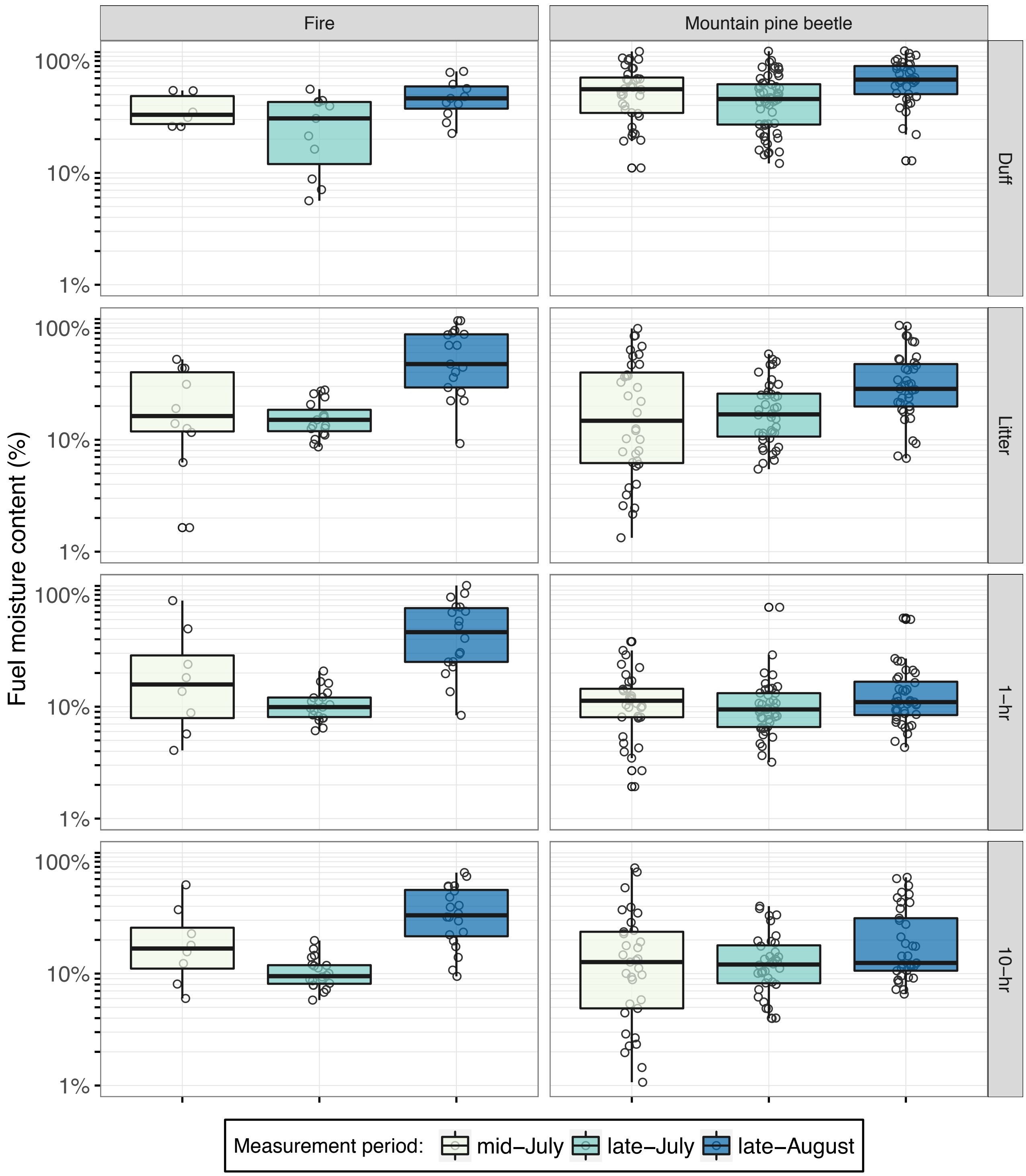


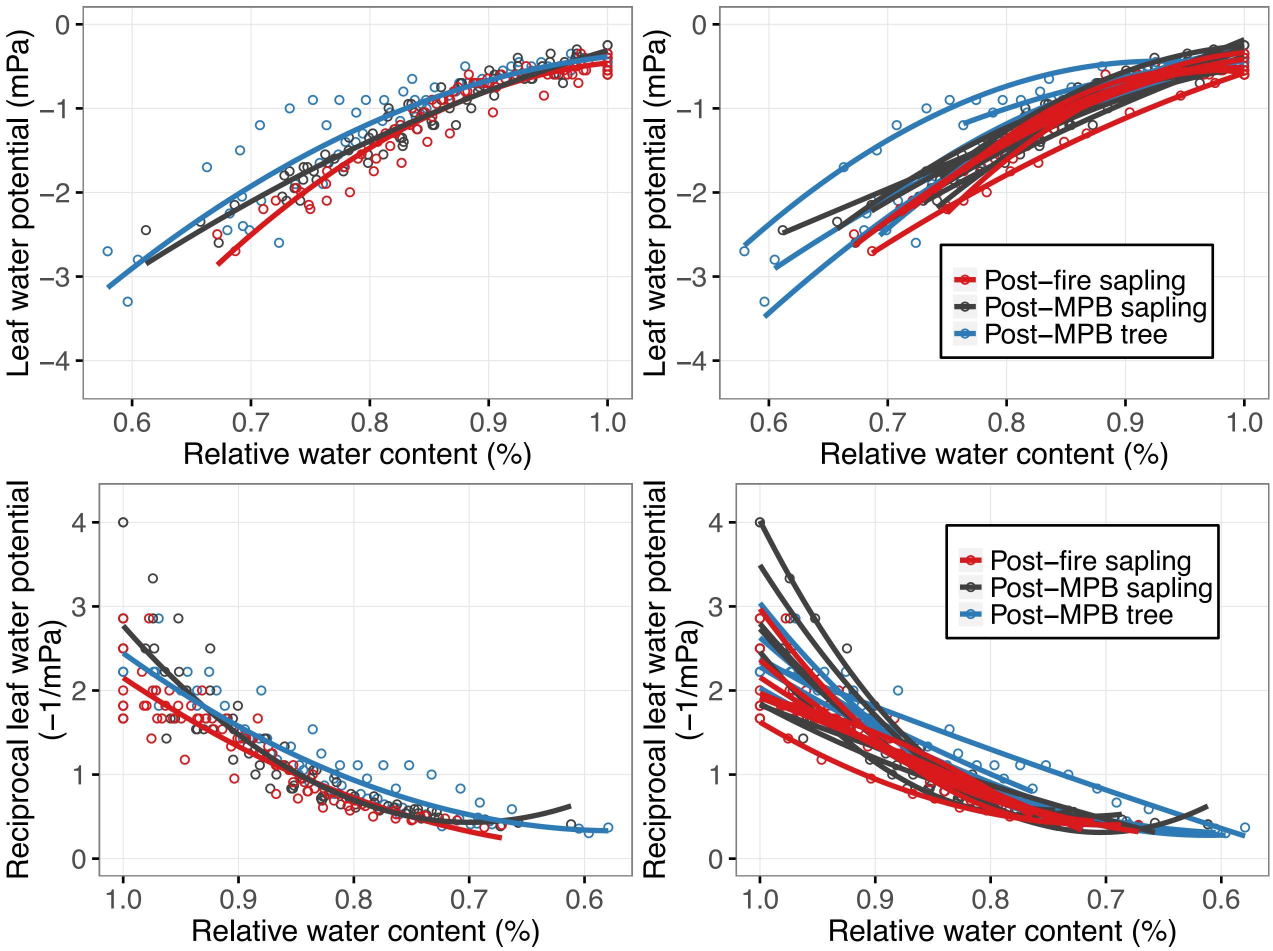
Figure 4: Variation in the constituents of foliar moisture content by measurement date.



Supplementary Figure 1: Live foliar fuel moisture content by disturbance type, measurement date, tree type, and needle age.



Supplementary Figure 2: Dead fuel moisture content by fuel class, disturbance type, and measurement date.



Supplementary Figure 3: Höfler diagrams Show a third row of figures that have a xlim set at 1.0.

CHAPTER 5:

5.1 CONCLUSIONS

Projections of warming temperatures over the next century suggest lengthening fire seasons (Jolly et al. 2015), greater vapor pressure deficits, and greater frequency and extent of wildfires and bark beetle outbreaks (Flannigan et al. 2000, Dale et al. 2001). Amplified disturbance regimes are expected to result in greater extents of young and/or recently altered forestland (Schoennagel et al. 2006b, Westerling et al. 2011b), and a greater likelihood of short-interval reburning. Little is currently known about wildfire potential in recently burned forest stands, nor how this potential differs between burned and bark beetle-affected stands.

The 1988 Yellowstone fires and subsequent short-lived bark beetle outbreaks are considered an early example of the magnitude of disturbance under anticipated climate change conditions (Running 2006), and recent evidence suggests that fire rotation (time to burn an area equivalent to the study extent) may decline in YNP from 120 years historically to less than 30 years by the middle of the 21st century (Westerling et al. 2011). To better understand fire potential in young, post-fire and/or recently disturbed forests, we investigated the variation and drivers of fuel abundance and simulated fire behavior across the post-1988 Yellowstone Fire landscape, and examined differences in fuel moisture conditions (as a proxy for fuel flammability) in burned and bark beetle affected forests. Key findings from this set of studies include:

Variation and drivers of fuel abundance in 24-year old, post-fire lodgepole pine forests

- Post-fire stem density was the strongest positive predictor of canopy and fine surface fuel loads, where pre-fire successional stage was the best predictor of 100-hr and

1000-hr fuel loads and strongly influenced the size and proportion of sound and rotten logs.

- 76% of sites exceeded 1000-hour fuel loads associated with high-severity surface fire.
- 63% of sites exceeded canopy bulk densities associated with spreading crown fire.
- Shorter fire rotations than were historically typical in Yellowstone National Park cannot be ruled out by a lack of fuels.

Variation and drivers of simulated fire behavior in 24-year old, post-fire lodgepole pine forests

- All types of fire are supported in 24-year old lodgepole pine forests; however, fire simulation results suggest that 90% of sites are likely to support crown fire when fuel moisture conditions are above 90th percentile and wind speeds are greater than 20 km hr^{-1}.
- Fire simulation results indicate that wind was the most important predictor of fire behavior, while fuel characteristics played a greater role than expected in driving variation in fire behavior.
- Shorter fire rotations than were historically typical in Yellowstone National Park cannot be ruled out by modeled relationships between fuels and fire behavior across the range of fuel moisture and wind conditions observed at Old Faithful in the center of the park.

Differences in fuel moisture conditions on post-fire and post-bark beetle sites

- Post-fire sites broke dormancy earlier, and showed signs of greater evapotranspiration and greater drought stress when compared with post-bark beetle sites.

- Variation in live FMC was primarily driven by phenological changes in leaf biomass density, and to a lesser degree by leaf water status. Mid-day leaf water potential and relative water content showed little variation, as would be expected in an isohydric species like lodgepole pine. Isohydric species closely regulate their mid-day leaf water potential by actively limiting gas transfer when vapor pressure deficits increase.
- Dead FMC was similar in burned and bark beetle affected sites in July; however, post-fire exhibited a greater response to heavy precipitation in August due to lower canopy interception.
- Dead fuel moisture content was more dynamic while foliar fuel moisture content was less dynamic on post-fire sites than post-bark beetle sites.

Overall, the potential for crown fire is high across the post-1988 Yellowstone landscape, and post-fire sites appear to be more flammable than post-bark beetle sites during dry periods. Although high post-fire stocking levels have resulted from stands with small proportions of serotinous cones (Turner et al. 1997), early-seral lodgepole pine forests generally have less developed canopy seed banks and lower reproductive potential than comparable mature forests (Buma et al. 2013, Turner et al. 2016). In the event of ignition, our results suggest that crown fire is likely under all but the mildest fuel moisture and wind conditions, and we anticipate sparse tree regeneration after crown fire on most sites. Given the strong positive effect that post-fire tree regeneration has on young forest fuels and fire behavior, we anticipate that progressive reductions in tree recruitment after short-interval fires will lead to progressive self-limitation of short-interval burning due to lack of fuels. Any such burning is likely produce a heterogeneous landscape where sites with healthy seedbanks and high potential for fire are interspersed with sites that have little to no regeneration and low potential for fire.

5.2 REFERENCES

Buma, B., C. D. Brown, D. C. Donato, J. B. Fontaine, and J. F. Johnstone. 2013. The Impacts of Changing Disturbance Regimes on Serotinous Plant Populations and Communities. BioScience 63:866–876.

Dale, V. H., L. a Joyce, S. Mcnulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, B. M. Wotton, R. P, and M. P. 2001. Climate change and forest disturbances. Bioscience 51:723–734.

Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest fires. Science of the Total Environment 262:221–229.

Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6:7537.

Running, S. W. 2006. Is Global Warming causing more, large wildfires. Science 313:927–928.

Schoennagel, T., M. G. Turner, D. M. Kashian, and A. Fall. 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. Landscape Ecology 21:1281–1296.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411–433.

Turner, M. G., T. G. Whitby, D. B. Tinker, and W. H. Romme. 2016. Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? Ecology 97:1260–1273.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences of the United States of America 108:13165–13170.