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Plant community composition, tree physiology, and bark-beetle mortality in relation to open and enclosed irrigation channels: a case study within a wildland-urban interface forest in western Montana

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ABSTRACT

Dry coniferous forests within the wildland–urban interface (WUI) in the northwestern US have experienced long-term drought and increasing bark-beetle infestations. An unexamined factor potentially affecting WUI forests are irrigation channels used to convey water to nearby farms. I studied the effects of two irrigation channels (a downslope, open channel and an upslope, recently enclosed channel) on plant community composition, tree water status and growth, and patterns of bark-beetle mortality in a WUI ponderosa pine/Douglas fir forest experiencing drought. Low-lying swale areas below the recently enclosed, upper channel had extensive down dead wood and showed shifts from mesic understory plant species to more xeric species. Tree density and basal area declined in swale areas below both channels. Ponderosa pine below the enclosed channel showed evidence of water stress (low water potentials) and negative growth responses to the channel enclosure. In contrast, hillslope trees below the open channel had higher growth rates and water potentials compared to trees above that channel. Beetle-kill was highest between the two channels, the area most likely affected by upper channel enclosure. The study provides evidence that plant community composition, tree physiology, and patterns of tree mortality in forests may be affected by irrigation channels interacting with small-scale topography.

RÉSUMÉ

Les forêts résineuses sèches à l'interface des milieux naturels et urbains (INU) dans le nord-ouest des USA subissent des sécheresses prolongées et une augmentation des épidémies de dendroctone. Les canaux d'irrigation utilisés pour alimenter les fermes en eau peuvent affecter les forêts de l'INU, mais ont été peu étudiés. Dans une forêt de pin ponderosa et de douglas de Menzies soumise à la sécheresse à l'INU, j'ai étudié les effets de deux canaux d'irrigation (un canal ouvert en bas de pente et un canal récemment fermé en haut de pente) sur la composition des communautés de plantes, sur la croissance et l'équilibre hydrique des arbres, ainsi que sur les patrons de mortalité par le dendroctone. Les cuvettes basses en aval du canal fermé avaient beaucoup de débris ligneux au sol et montraient une transition d'espèces végétales de sous-bois mésiques vers des espèces davantage associées aux milieux xériques. La densité des arbres et la surface terrière diminuaient dans les cuvettes en aval des deux types de canaux. Les pins en aval du canal fermé montraient des signes de stress hydrique (faibles potentiels hydriques) et une réponse de croissance négative à la fermeture du canal. À l'opposé, les arbres en aval du canal ouvert avaient des taux de croissance et des potentiels hydriques plus élevés que les arbres en amont. La mortalité par le dendroctone était plus élevée entre les deux canaux, dans la zone la plus affectée par la fermeture du canal en haut de pente. Cette étude montre que la composition des communautés végétales, la physiologie des arbres et les patrons de mortalité des arbres peuvent être affectés par les canaux d'irrigation, en fonction de la topographie fine.

Introduction

The wildland–urban interface (WUI) is an area where wild, protected public lands are found adjacent to private lands that may include homes, farms or pasture. The WUI comprises approximately 9% of the land area in the US, and includes over 40 million housing units (Radeloff et al. 2005; Theobald 2010). It may also include important natural and semi-managed ecosystems that buffer more remote, protected lands. Sustainable management of these areas is important for homeowners, forest managers, and the general public. However, research and management in the WUI is challenging because of continuous expansion of housing, rapid environmental changes, and the private/public division in land ownership (Theobald and Romme 2007).

In parts of the western US, the WUI is commonly dominated by dry, coniferous forests. In recent decades, these forests have experienced widespread drought and drought-related forest changes (Vose et al. 2015) such as bark-beetle infestations (Raffa et al. 2008; Kretchun et al. 2016) and increasing numbers of fires (Westerling et al. 2006; Schoennagel et al. 2009). Parts of western Montana, which include the study site considered here, have been identified as being under a 'triple threat' of development, beetles, and fire (Kline et al. 2013). The US Forest Service has proposed and implemented various management responses to reduce risks of bark-beetle infestation and fire across the west (USDA 2004; USFS 2011). However, there is still scientific uncertainty about the relative effectiveness of different management treatments (Fettig et al. 2007) and some proposed management actions are controversial (Six et al. 2014). Given the likelihood of climate change in the coming decades, more research is needed to understand WUI forest responses to drought, bark-beetle infestations, changing forest management, and the interactions between these change agents.

A potentially significant factor affecting WUI forests are irrigation channels used to convey water to nearby pastures and farms. On the eastern front of the Bitterroot Mountains in Montana, irrigation channels are extensive, with multiple diversions and branching channels running laterally off every major creek flowing into the Bitterroot Valley (DNRC 1965). Open channels very likely allow excess water to percolate into the soil, providing plants downslope from the channel with an artificial water source (Fernald and Guldan 2006; Sueltenfuss et al. 2013). In recent years, some landowners are opting to enclose these channels in buried pipes to avoid water losses. Many of these channels have been open and in continuous summer use for decades. Plant communities growing downslope from open channels may be acclimated to artificially moist soil conditions and enclosing a channel probably deprives plant communities of historical levels of soil moisture (Stromberg et al. 1996). The combination of both open and recently enclosed channels running across the same landscape may create a complex mosaic of differing and changing soil moisture conditions. This mosaic could have significant effects on plant community structure and composition, which in turn can affect forest resilience to drought, beetle infestation, and fire (Schoennagel et al. 2004; Gilliam 2007; Raffa et al. 2008).

Although irrigation channels are known to recharge groundwater (Stohlgren et al. 2007; Dages et al. 2009; Dollinger et al. 2015) and increase the presence of riparian plant species in the areas below the channel (Sueltenfuss et al. 2013), these effects have not been well documented or investigated in pine forests in the western US. In particular, irrigation channels may add complexity to forest responses to long-term drought. Because drought can increase pine beetle outbreaks (Shore and Safranyik 2003; Taylor et al. 2006), irrigation channels may affect patterns of bark-beetle mortality across a forested landscape, with more severe mortality in drier areas (Kaiser et al. 2013). Although the precise mechanistic connection between low water availability and plant defenses is complex and may be non-linear (Herms and Mattson 1992), drought and other biotic stresses are known to influence early stages of beetle infestation (Raffa et al. 2005, 2008) and water deficit can reduce tree defenses to bark-beetles (Mattson and Haack 1987; McDowell et al. 2008, 2011; Tague et al. 2013). Open and recently enclosed irrigation channels have been found to affect growth and morphology in conifers (Rigling et al. 2003; Feichtinger et al. 2014, 2015), and growth is generally correlated with defenses in ponderosa pine (Kane and Kolb 2010). However, relationships between irrigation channels, tree growth, tree water status, and bark-beetle infestation have not been studied in North American forests. Given the urgency of sustainable management of WUI forests in western Montana and similar areas across the northwestern US, research is needed to study how patterns of plant community composition and tree mortality in forests may be potentially affected by past and current irrigation channel usage

In the forested WUI of western Montana, irrigation channels are located mostly at the interface of private and public lands, a possible impediment to the design of broad-scale studies. However, place-based approaches in ecology (Billick and Price 2010) can explore variables (such as irrigation channels, in this case) that have yet to be fully tested at larger scales (Krebs 2010). For the current study, I took advantage of pre-existing forest survey data and the fortuitous co-occurrence of one open and one recently enclosed irrigation channel in a forest experiencing long-term drought and bark-beetle infestation. The objectives of the study were to document and characterize changes in plant community composition and tree physiology (growth and water status) and explore the association of those changes with the locations of the two irrigation channels. I also monitored and mapped bark-beetle mortality from 2012 to 2017 to explore patterns of tree mortality in relation to the locations of the two irrigation channels.

Specifically, I asked: (1) Has there been a shift in plant community composition away from mesic/riparian species that may be related to the recently enclosed channel? (2) Do the open and recently enclosed channels affect the water status of ponderosa pine trees directly above and below channels? (3) Is there evidence of channel effects on growth rates of trees? (4) Is the enclosure of the upper channel a possible factor in

the pattern of observed beetle-kill in ponderosa pine trees?

Associated with these questions, I hypothesized: (1) a shift in community composition away from mesic understory plant species and trees, especially in swale areas most likely affected by the recently enclosed channel; (2) higher needle water potential in ponderosa pine trees below the open channel compared to trees above that channel, and lower needle water potential in trees below the recently enclosed channel compared to trees above that channel; (3) higher growth rates in trees below the open channel compared to trees above that channel, and a negative growth response to channel enclosure in trees growing below the recently enclosed channel compared to trees above that channel; and (4) higher bark-beetle mortality and evidence of negative growth responses to channel enclosure in beetle-kill areas likely affected by the enclosed channel.

Methods

Study area

The site is a mixed ponderosa pine (*Pinus ponderosa*)/ Douglas fir (*Pseudotsuga menziesii)* forest on gently sloping terrain within the WUI in the Bitterroot Valley near Hamilton, Montana, that includes private land and adjacent US Forest Service (FS) land slightly upslope, to the west. The private land has a history of forest-based scientific research (see e.g., Pataki et al. 2003) supported by memoranda of understanding with the USFS dating back to 1994. My role in continuous monitoring of the site dates from 1998, when a timber inventory was completed for the private property.

The study area and salient features of the site were mapped (Figure 1; see methods in Appendix 1), and for study purposes the site was divided into three zones: (1) an area downslope from an open irrigation channel (low zone), (2) an area upslope from the open channel, but downslope from a higher channel that was recently enclosed in 2007 (mid zone), and (3) an area upslope from both channels (high zone). In addition, low, depression areas (swales) likely receiving extra water from irrigation channels or natural downslope water movement were distinguished from adjacent hillslopes. The study took advantage of two unpublished baseline vegetation surveys – the 1998 inventory (low zone and lower section of the mid zone) and a combined overstory/understory survey in 2002 (swale and hillslope areas in all zones). The site also includes an area within the FS land (high zone) that was burned in a low-severity prescribed fire in 1997.

Monitoring of beetle-killed trees

A mountain pine beetle (Dendroctonus ponderosae) infestation was first detected in spring 2013. In mid-July 2013, the entire private property area was surveyed carefully to detect ponderosa pine trees killed by mountain pine beetle. All recently killed trees with pitch tubes in the bark were marked and counted. In each July of 2014–2016, the entire private property area was resurveyed, all previously recorded dead trees were revisited, and new beetle-killed trees were marked and recorded. No new beetle-kill was observed in 2017.

Beetle infestation in the public land (FS) followed approximately the same progression; however, beetle-kill trees had been cut on FS land by a local resident from 2012 to 2016, leaving groups of stumps. In other areas on FS land, uncut standing dead and fallen trees were found. The entire FS area was systematically surveyed for these dead stands and stump groups during July 2016 and 2017. Dead trees (standing and down) with pitch tubes were counted as beetle-killed. Fresh stumps were assumed to be beetle-killed, based on the testimony of the woodcutter. An extensive area (2.8 ha) of fallen trees below the upper, enclosed channel (see Figure 1) was not surveyed for beetle-killed trees except for standing dead trees along the perimeter of this area.

Down dead trees above and below upper channel

To characterize the fallen-tree area below the recently enclosed channel, down dead stems longer than 2.5 m were counted and tallied into four size classes along 25 m transects running perpendicular to the slope. Sub-counts of mesic tree species such as black cottonwood (*Populus trichocarpa*), quaking aspen (*Populus tremuloides*), and grand fir (*Abies grandis*) were also recorded. Transects were spaced to adequately sample the extent of the fallen-tree area (five transects below the burn area, five below the unburned area) and corresponding areas above the channel (five transects in the burn area, five outside the burn). Comparisons that included the burn area were analyzed separately from comparisons that included the unburned area. In addition, in 2014, standing mesic tree species, both alive and dead, were counted within 10 m immediately above and below the channel along the section of the channel above the fallen-tree area.

Plant community composition – understory changes

A baseline understory plant study was conducted in early October 2002. Within the three zones, areas were designated as either 'swale' or 'hillslope' based on
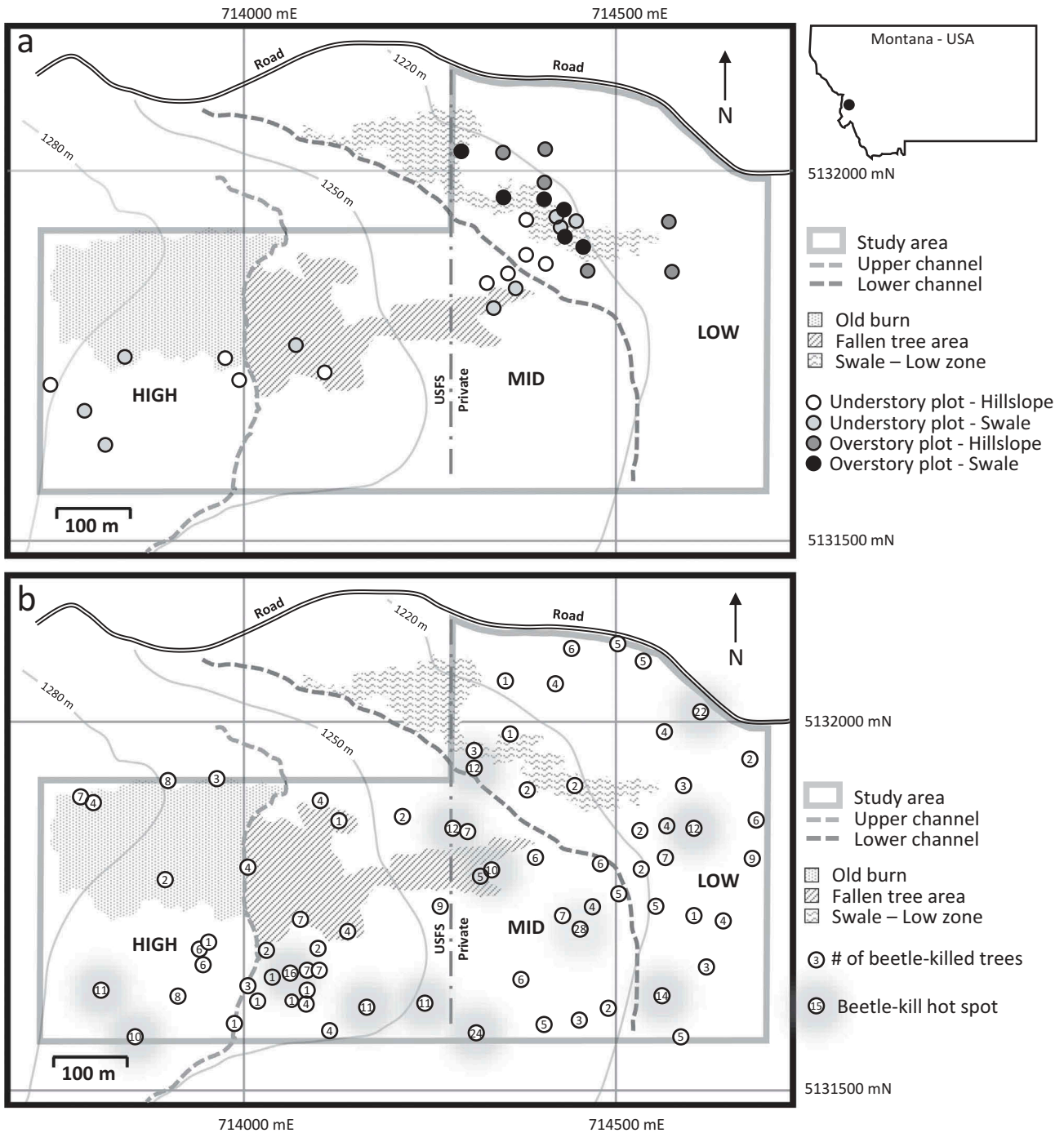
Figure 1. Study area, irrigation channels, landscape features, and (a) understory and overstory hillslope and swale plots, and (b) beetle-killed trees and beetle-kill hotspots (>10 dead trees), within 3 zones (High, Mid, Low). Beetle-kill numbers are cumulative from 2013 to 2017.

observed topography and soil moisture. Within each of these areas, three 10 × 10 m plots were selected randomly, making 18 plots altogether (3 zones x 2 topographic types x 3 replicates). Within each plot, percent cover was estimated visually to the nearest 5% for shrubs and herbaceous plant species and trees were identified and counted.

The understory survey was repeated in early October 2014. Plots in 2014 were located based on written plot descriptions and GPS coordinates from 2002. In both 2002 and 2014, most plants were identified to the species level (see Table 2). Cover for grasses was recorded as one, lumped, % estimate. To validate the designation of 'swale' vs. 'hillslope', soil volumetric

water content was measured in each plot using a Campbell's HydroSense II probe with 5–7 replicate measurements per plot. All soil moisture data was collected within a two-hour period on the same day in October 2016.

Multivariate analyses were carried out in PC-Ord, version 7 (McCune and Mefford 2016; Peck 2016). Species were deleted from the data set if they were (a) not in the knowledge base in 2002, (b) absent in 2002 and occurred in 2014 in only one plot with ≤ 5% abundance, or (c) absent in 2014 and possibly misidentified in 2002. Twenty-three species (11.4% of total observations across both years) were deleted based on these criteria, leaving 41 species in the dataset. Data was split by topographic category (swale, hillslope) and species absent in both years within a topographic category were deleted (2 for swale, 11 for hillslope). Species cover values (untransformed) were arranged in two response matrices (39 species x 9 swale plots, 30 species x 9 hillslope plots) and matrices were analyzed using Sorenson distance measure and non-metric multidimensional scaling (NMS) ordination. Two-dimensional NMS solutions were chosen for both response matrices based on stress tests and after verifying consistency of interpretation among several solutions. Ordination axes were rotated to highlight shifts in ordination space locations of plot pairs from 2002 and 2014. Two-way PERMANOVA was used to test for differences in species composition between year and zone. To further interpret PERMANOVA results, indicator species analyses (Dufrêne and Legendre 1997) with Monte Carlo tests were used on the combined dataset (all plots, 41 species) to determine species significantly ($p < .05$) associated with topographic category (swale vs. hillslope) and zones (low, mid, high). Species correlations with NMS axis 1 (after rotation), additional PC-ORD tools (joint plot overlays, overlays of individual species, 'hilltop' contour overlays) and examination of the original data matrix facilitated determination of species mainly responsible for differences between 2002 and 2014.

Plant community composition – overstory changes

Mean tree density per 100 m^2 plot was calculated for four subcategories (alder [*Alnus species*], quaking aspen, ponderosa pine, other) and compared between 2002 and 2016 for swale and hillslope plots separately. Percent cover was estimated for down dead trees and shrubs in the 100 m^2 plots in 2016, but not in 2002. Separate tree inventories were conducted using 400 m^2 plots on the private land in 1998 and again in 2015 (see Appendix 2 for methods). From the 1998 data, six plots (labeled 'overstory plots' in

Figure 1(a)) falling within both swale and hillslope areas were analyzed within the low zone because no 1998 plots fell within the mid-zone swale area. Mean basal area for total trees (living and dead) was calculated and compared between 1998 and 2015 for swale and hillslope plots separately.

Needle water potential of trees above and below the two irrigation channels

Ponderosa pine trees of similar sizes were selected for water potential measurements above (>10 m from channel) and below both the upper and lower irrigation channels (n = 3–4 trees per zone). The lower channel was studied on 17 July 2014 and the upper channel on 26 July 2016. Each sampling day consisted of six separate sampling times (5:30, 8:30. 11:30, 14:30, 17:30, and 22:45). Within a sampling time period, branches were selected for sampling on the southeast side of trees and were either all sun-exposed or all shaded, depending on time of day. However, this could not be perfectly controlled at the upper channel due to the paucity of healthy, reachable branches on some trees. Branches were cut using an extendable pole pruner at 3.2–4.4 meters from the ground, immediately placed in hydrated ziplock bags, and stored in a cooler until measuring. For a given sampling time, all branches were cut within a 15-minute period, and samples were read within 90 minutes of branch cutting. From each branch, one 1-year-old healthy fascicle was sliced cleanly at the base and water potential was measured using a PMS 600 pressure chamber. Below the lower channel, one sample (at 8.30 am) was unreadable and was not measured. Mean water potential (in MPa) was calculated and compared (above vs. below channel) for each time period.

Diameter growth of living ponderosa pine trees growing above and below irrigation channels and in beetle-infested stands

Cores were extracted from living ponderosa pine trees > 10 m above and similar distances below both channels (1 core per tree, n = 8 at the upper channel, n = 6 at the lower channel) in 2014 and 2017 (upper channel) and in 2015 (lower channel). Healthy (uninfested) living trees within beetle-infested stands (see Figure 1(b)) were also cored in 2014 (n = 13 for both mid and low zones). Field protocols, core processing, measuring, and cross-dating, and age estimation for all trees followed conventional methods (see Appendix 3). Field data for each tree included tree diameter and four bark-depth measurements at coring height (1.37 m). All cores were successfully cross-dated.

However two cores from beetle-infested stands (one in mid zone, one in low zone) were omitted from further analysis due to anomalous patterns of growth suppression and release. To calculate tree basal area growth, the inside-bark radius was determined by dividing the diameter at coring height by 2 and subtracting the average bark depth. Annual ring widths from each core were converted to proportions of the total inside-bark radius (Bakker 2005) and then converted to annual basal area increments (BAI) by assuming circular basal area with the pith at the center (Biondi and Qeadan 2008).

For individual trees, growth responses (Nowacki and Abrams 1997; Keeling and Sala 2012) to the 2007 upper channel enclosure were calculated as ratios of post-enclosure to pre-enclosure growth using two separate time periods of pre-enclosure growth (ShortPRE, LongPRE), as follows:

$$Growth\ Response_{ShortPRE} = \frac{BAI_{2007-2014}}{BAI_{1999-2006}} - 1,$$

$$Growth\ Response_{LongPRE} = \frac{BAI_{2007-2014}}{BAI_{LT-2006}} - 1,$$

where $BAI_{2007-2014}$ and $BAI_{1999-2006}$ are the mean annual BAIs in the two eight-year periods post- and pre-enclosure, and $BAI_{LT-2006}$ is the long-term mean annual BAI through the year 2006. Mean long-term growth ($BAI_{LT-2006}$) and mean growth response to channel enclosure (see formulas above) for each sample of trees were calculated and compared for each study (below vs. above for upper and lower channels; mid zone vs. low zone for beetle-kill stands). The start-years for $BAI_{LT-2006}$ were determined by the first year of complete sample sizes for each study. As a reference for interpreting tree growth patterns over time, annual Palmer Hydrologic Drought Indices (PHDI) for the western climatic region of Montana were obtained (NOAA 2017) and plotted.

Statistical tests

Univariate statistical tests were carried out in SPSS 24.0. Means of all variables – down dead stems, tree density, tree basal area, needle water potential, and tree growth variables (long-term BAI, post-2007 growth responses with both short and long pre-periods) – were tested for normality and homogeneity of variance using Kolmogorov-Smirnov and Levene's tests, respectively. Variables that did not meet normality assumptions (dead-tree basal area) were transformed using a square-root transformation. A Kolmogorov-Smirnov test was not possible for water potential data because of small sample sizes, but distributions were assumed to be normal based on other research on ponderosa pine near the

study area (Sala et al. 2005). Differences (above vs. below channels for down wood, needle water potential, and tree growth; between years for tree density and basal area in swale vs. hillslope plots were tested using t-tests, or, in the case of tree density, a paired t-test. Variables that did not pass Levene's test for homogeneity of variance (down wood, live-tree basal area) were tested with non-parametric Mann-Whitney-U tests. Tree growth variables in beetle-killed stands (mid vs. low zone) were tested with two-way ANOVA with zone and topographic type (swale vs. hillslope) as fixed factors. Multivariate tests (PerMANOVA, Indicator Species Analysis) were carried out in PC-ORD as described above.

Results

Beetle-killed trees

Beetle-killed trees were detected in all three zones (Table 1, Figure 1(b)). The mid zone had the highest occurrence of beetle-killed trees (18.4 trees/ha) compared to the low zone (10.1 trees/ha) and high zone (7.1 trees/ha). The low-zone beetle-kill occurrence was lower (7.8 trees/ha) when the area directly along the road was excluded. Within the mid zone, the private land section had more beetle-killed trees (25.1 trees/ha) than the FS zone (11.7 trees/ha).

Down dead trees above and below upper channel

The fallen-tree area below the recently enclosed upper channel had ~12 down dead stems per 25 m transect compared to ~1 stem per transect above the channel (Figure 2). Differences were significant for comparisons both including and not including the burn area (Mann-Whitney-U tests, p = .008). Six dead black cottonwood stems were found below the channel, whereas no mesic down dead species were identified above the channel. Directly below the channel, 25 standing dead mesic species were found (16 black cottonwood, 2 grand fir, 7 quaking aspen), whereas 4 living mesic species (3 black cottonwood, 1 grand fir) were found directly above the channel (within 10 m).

Table 1. Areas, elevation ranges, and number of beetle-killed trees per area for three zones and selected sub-areas within the study area. The mid-zone area and beetle-kill per area values do not include the 'fallen-tree' area (2.8 ha, see methods).

	Area (ha)	Elevation range (m)	Beetle-killed trees (per ha)
High zone	9.3	1252–1288	7.1
Mid zone	14.1	1219–1257	18.4
Private land	7.1		25.1
FS land	7.0		11.7
Low zone	15.2	1205–1231	10.1
Excluding road	14.3		7.8
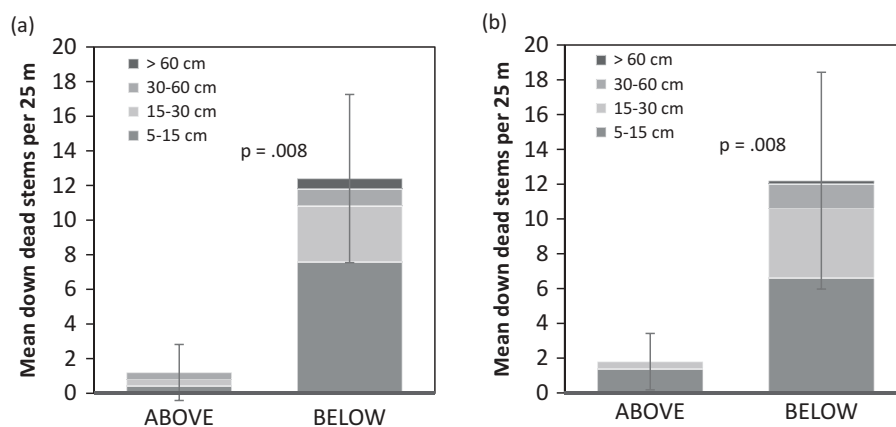
Figure 2. Mean down dead stems in four diameter size-classes along 25 m transects above and below the upper irrigation channel with the area above the channel in (a) the old burn area and (b) the unburned area. P-values for significant differences (Mann-Whitney-U tests, n = 5) in total down dead stems are shown. Error bars are 95% confidence intervals.
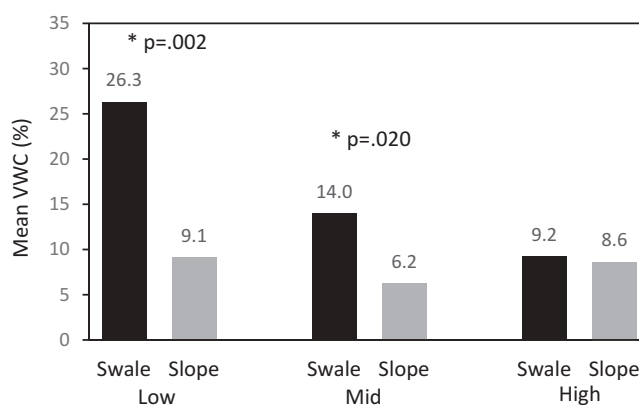

Figure 3. Mean percent volumetric water content (VWC) for swale and hillslope plots in three zones (Low, Mid, High). Mean values are shown above each bar, n = 3 plots per mean. Comparisons with * are statistically significant (t-tests, p < .05).

Changes in plant community composition – understory

Soil moisture measurements confirmed that 100 m^2 swale plots in the low and mid zones, but not the high zone, had significantly higher volumetric water content than hillslope plots (Figure 3, t-tests, p < .05). For understory plants in swale plots, the final two-dimensional NMS ordination (Figure 4) had a final stress = 11.43 (randomized test p = .004) and explained .533 and .327 of the variance on axes 1 and 2, respectively (cumulative variance explained = .871). Differences between years and zones were significant (PerMANOVA, p = .039 for year, p < .000 for zone). The ordination space was rotated to highlight shifts between 2002 and 2014, with increasing abundance of mesic spp in the positive direction and xeric species in the negative direction along axis 1. Shifts away from mesic species were evident for all mid plots, for 2 out of 3 low plots, but not for high plots (arrows in Figure 4).

Seven mesic species correlated positively with axis 1 (r^2 > 0.200), five of which were indicator species for swale areas in general (Table 2). Six xeric species correlated negatively with axis 1 (r^2 > 0.200). The community composition shifts between years appeared to be driven, in the mid zone, by decreases in horsetail (*Equisetum hyemale*) and willow (*Salix species*), and increases in Oregon grape (*Mahonia repens*), spotted knapweed (*Centauria maculosa*), and snowberry (*Symphoricarpos albus*); and in the low zone, by decreases in red raspberry (*Rubus idaeus*) and wintergreen (*Pyrola asarifolia*). Figure 4 includes shaded overlays showing the portion of the ordination space where these species have their peak abundances (Peck 2016).

For the hillslope understory plots (ordination not shown), differences were significant between zones (PerMANOVA, p < .000), but not between years. For the entire study site, significant indicator species included, for the high zone, yarrow (*Achillia*
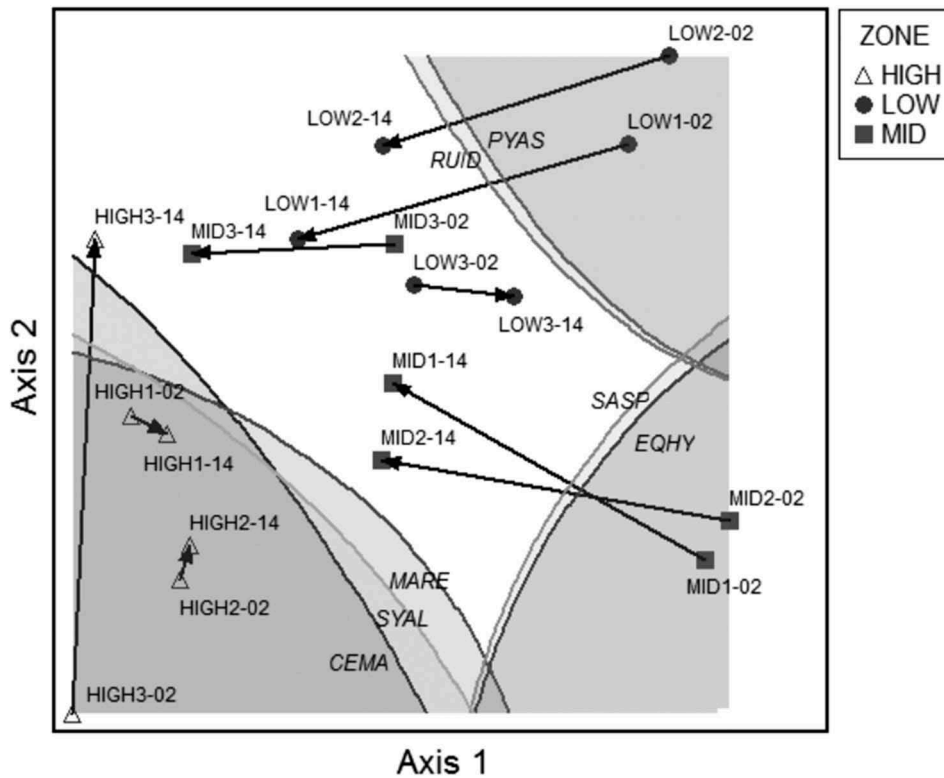
Figure 4. Non-metric multidimensional scaling (NMS) ordination of understory swale plots across three zones, 2002 and 2014. Plots are labeled by zone (LOW, MID, HIGH), replicate (1–3), and year (02 = 2002, 14 = 2014). Differences between zones and years were tested with PerMANOVA, p < .000 for zone, p = .039 for year. Arrows show species composition shifts between 2002 and 2014 for each plot. Shaded overlays show portion of the ordination space where selected species driving differences between years have their peak abundances. Four-letter species codes and species correlations with axis 1 are in Table 2.

mellifolium), grasses, and snowberry; and for the low zone, strawberry (*Fragaria species*), bedstraw (*Galium boreale*), and raspberry (Table 2). No understory species were significant indicators of the mid zone.

Changes in plant community composition – overstory

Total density of living trees declined significantly in 100m² swale plots (all zones pooled, Figure 5(a), p = .008) between 2002 and 2016. Tree species with the largest density decreases in living stems were alder, quaking aspen, and black cottonwood. There was no significant difference between 2002 and 2016 in density of living trees in the hillslope plots (Figure 5(b)). Although % cover of down dead woody plant species was not recorded in 2002, in 2016 low-zone understory swale plots had 5–20% down dead stems (willow, quaking aspen, black cottonwood) and mid-zone understory swale plots had 40–70% down dead stems (willow, quaking aspen).

In low-zone 400 m² swale plots, basal area of living trees significantly declined from 1998 to 2015 (Figure 5

(c), Mann-Whitney-U test, p = 0.026) and dead trees significantly increased (t-test, p = .014). All 400 m² swale plots in 2015 had standing dead, compared to only one plot with a single dead tree in 1998. Largest components of standing dead in 2015 were black cottonwood, ponderosa pine, and quaking aspen. Standing dead grand fir, sub-alpine fir (*Abies lasiocarpa*), and Douglas fir were also present in 2015 but not in 1998. In low-zone 400 m² hillslope plots, there were no significant differences between 1998 and 2015 in basal area of living or dead trees (Mann-Whitney-U tests, Figure 5(d)).

Needle water potential in ponderosa pine trees above and below channels

At the lower (open) channel, mean water potential in ponderosa pine needles was higher below the channel during morning hours and night-time periods (Figure 6(a)). Differences were statistically significant at 5.30pm (p = .034), 11.30am (p = .002), and 10.45pm (p = .001). At the upper (enclosed) channel, mean water potential was lower below the channel during

Table 2. Indicator species values (IV) for 2002 and 2014 combined. Significant associations with topographic category and zone (p < .05, Monte Carlo Test) and correlations with axis 1 of NMS ordination for swale plots ($r^2 > 0.200$) are in bold. For significant axis 1 correlations, mesic species are marked with * and xeric with †. Species highlighted as overlays on the NMS graph (Figure 4) are shaded.

		By topographical type (swale vs. hillslope)			By zone (low, mid, high)			Correlation NMS axis 1 (see Figure 4)	
Code	Name	Group	IV	P-value	Group	IV	P-value	r	r²
ACMI†	Achillea millefolium	swale	22.2	1.0000	high	42.2	0.0390	−0.662	0.438
AMAL	Amelanchier alnifolia	**hillslope**	**65.0**	**0.0042**	high	40.0	0.1924	−0.407	0.166
ANMA	Anaphalis margaritaceae	swale	11.1	0.4795	low	16.7	0.3181	0.183	0.034
ANPU	Antennaria pulcherrima	hillslope	28.6	0.0832	high	29.8	0.0610	−0.311	0.097
ANRA	Antennaria racemose	hillslope	22.2	0.0976	low	18.8	0.2955	NA	NA
APAN	Apocynum androsaemifolium	**hillslope**	**48.1**	**0.0294**	high	19.4	0.9262	−0.291	0.085
ARCO	Arnica cordifolia	hillslope	6.7	1.0000	mid	13.3	0.3287	0.397	0.157
ARUV	Arctostaphylos uva-ursi	hillslope	35.6	0.0822	low	30.0	0.1490	−0.001	0.000
CARSP	Carex spp	swale	38.9	0.0078	low	29.3	0.0982	0.217	0.047
CEMA†	Centauria maculosa	swale	26.7	0.7273	high	32.7	0.1510	**−0.575**	**0.331**
CHUM	Chimaphila umbellata	hillslope	22.2	0.1512	low	23.3	0.1724	0.037	0.001
CISP	Cirsium spp	**swale**	**27.8**	**0.0456**	low	15.0	0.5849	0.318	0.101
COSE*	Cornus sericea	**swale**	**48.1**	**0.0024**	low	30.0	0.1264	**0.663**	**0.440**
EQHY*	Equisetum hyemale	swale	16.7	0.2286	mid	25.0	0.0882	**0.541**	**0.292**
FRASP	Fragaria spp	hillslope	30.6	0.7570	**low**	**41.7**	**0.0294**	−0.072	0.005
GABO*	Galium boreale	**swale**	**58.7**	**0.0018**	**low**	**42.2**	**0.0346**	**0.694**	**0.482**
GEMA	Geum macrophyllum	swale	16.7	0.2188	low	11.1	0.7582	0.404	0.163
GRSP	Grass spp	hillslope	57.1	0.1528	**high**	**44.5**	**0.0234**	−0.293	0.086
HISP	Hieracium spp	hillslope	27.2	0.2591	low	13.3	1.0000	−0.087	0.007
HODI	Holodiscus discolor	hillslope	5.6	1.0000	high	25.0	0.0862	−0.227	0.052
JUCO	Juniperus communis	hillslope	11.1	0.4807	low	16.7	0.3119	NA	NA
LEVU	Leucanthemum vulgare	swale	11.1	0.4815	mid	16.7	0.3201	0.041	0.002
MARE†	Mahonia repens	hillslope	33.3	0.4327	high	20.0	0.9072	**−0.542**	**0.293**
MEAR	Mentha arvensis	swale	11.1	0.4747	mid	16.7	0.3217	0.314	0.099
PEAL†	Penstemon albertinus	hillslope	28.1	0.3013	high	32.8	0.1572	**−0.462**	**0.214**
PHMA†	Physocarpus malvaceus	swale	17.7	0.5655	high	30.3	0.0530	**−0.527**	**0.278**
PRVI	Prunus virginiana	swale	14.8	0.6467	low	12.5	0.8614	−0.001	0.000
PRVU	Prunella vulgaris	**swale**	**27.8**	**0.0416**	low	26.7	0.0994	0.331	0.110
PTAN	Pterospora andromedea	swale	7.4	1.0000	low	11.1	0.7612	−0.102	0.010
PTAQ	Pteridium aquillnums	swale	2.8	1.0000	low	4.2	1.0000	0.037	0.001
PYAS*	Pyrola asarifolia	**swale**	**37.3**	**0.0278**	low	26.7	0.1622	**0.597**	**0.357**
RISP	Ribes spp	**swale**	**33.3**	**0.0186**	low	22.2	0.2464	0.444	0.197
ROAC*	Rosa acicularis	**swale**	**65.0**	**0.0014**	low	34.6	0.2547	**0.458**	**0.210**
RUID*	Rubus idaeus	**swale**	**42.3**	**0.0116**	**low**	**50.0**	**0.0050**	**0.529**	**0.280**
SASP*	Salix spp	**swale**	**43.1**	**0.0142**	mid	36.6	0.1046	**0.603**	**0.364**
SMST	Smilacina stellate	**swale**	**44.4**	**0.0032**	mid	18.5	0.4401	0.326	0.106
SOAU	Sorbus aucuparia	swale	23.8	0.1476	low	19.0	0.2274	0.412	0.169
SOCA	Solidago canadensis	swale	11.1	0.4795	low	16.7	0.3181	0.275	0.076
SPBE	Spiraea betulifolia	hillslope	42.0	0.6649	mid	33.8	0.5671	−0.395	0.156
SYAL†	Symphoricarpos albus	swale	50.0	0.2909	**high**	**54.7**	**0.0118**	**−0.659**	**0.434**
TRSP	Trifolium spp	swale	23.1	0.1798	low	12.5	0.8570	−0.008	0.000

morning hours and night-time periods (Figure 6(b)); however, differences were statistically significant only at 8.30am (p = .035).

Diameter growth and growth responses in ponderosa pine trees

At the upper channel, differences in long-term mean annual BAI between trees above and below the channel were non-significant (Figure 7(a)). However, post-2007 growth responses were significantly lower below the channel. Results were similar using both long (t-test, p = .022) and short (t-test, p = .003) pre-2007 time periods. At the lower channel, long-term mean annual BAI was significantly higher below the channel (Figure 7(b), t-test, p = .006) and growth responses to upper channel enclosure were non-

significant. In beetle-kill stands, growth response based on the short (eight-year) pre-2007 time period was significantly lower for mid-zone trees than for low-zone trees (ANOVA, p = .025), but other comparisons were non-significant (Figure 7(c)). There was no significant difference between growth responses of swale vs. hillslope trees across the two zones and no significant interaction between zone and topographic type.

Discussion

To my knowledge, this is the first study to investigate effects of irrigation channels in a western US WUI forest. The results of the case study suggest that plant community composition, tree water status and growth, and patterns of tree mortality, including mortality from

(a) Swale plots – all zones

(b) Hillslope plots – all zones
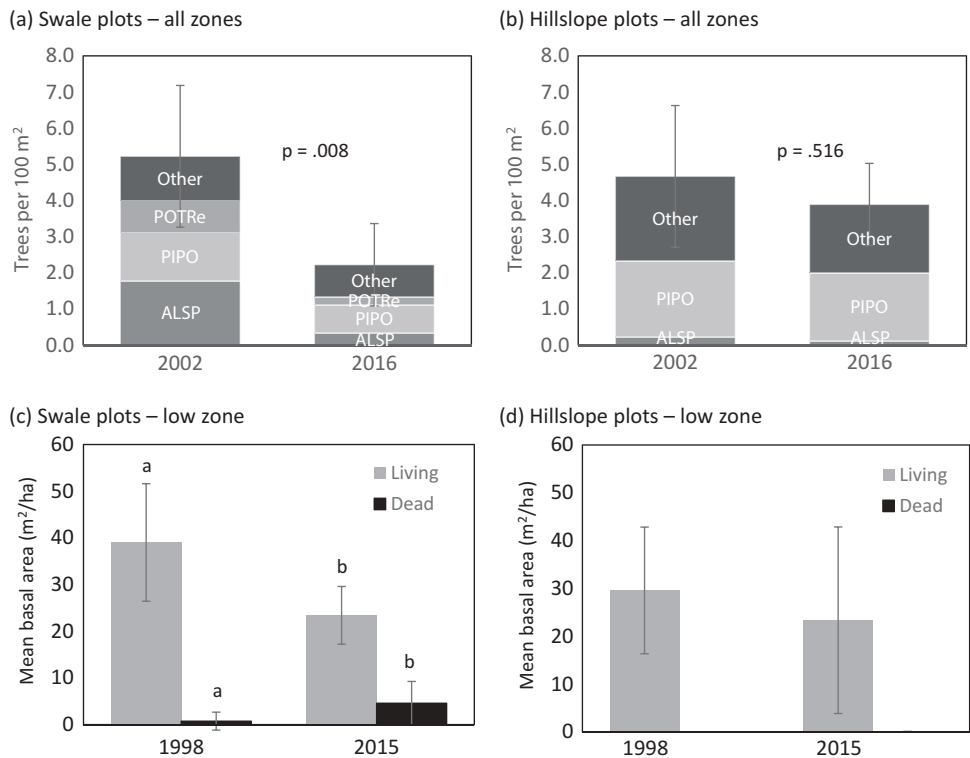
Figure 5. Mean density of trees in 2002 and 2016 in (a) swale areas and (b) hillslope areas across all zones (low, mid, high). POTRe = quaking aspen, PIPO = ponderosa pine, ALSP = Alder spp. Differences between years were tested with paired t-tests, n = 9 plots for each topographic type. Mean basal area of living and standing dead trees in 1998 and 2015 in (c) swale areas and (d) hillslope area within the low zone. Significant differences within each category (living/dead) are marked with different letters (Mann-Whitney-U tests, p < .05), n = 6 plots for each topographic type. Error bars are 95% confidence intervals in all panels.

mountain pine beetle infestation, may be affected by the locations of open and recently enclosed irrigation channels, interacting with small-scale topography (swales vs. hillslopes). The vegetation changes documented here illustrate the potential for irrigation channels to produce a mosaic of effects that may be overlooked by forest managers and land owners in WUI forests. Although the overall pattern of beetle-kill at the site is likely driven by multiple factors (Raffa et al. 2008), higher beetle-kill and more negative growth responses in the mid zone at this site raise the possibility that channel enclosure may decrease tree growth and affect patterns of bark-beetle mortality. The study should inspire further research into whether
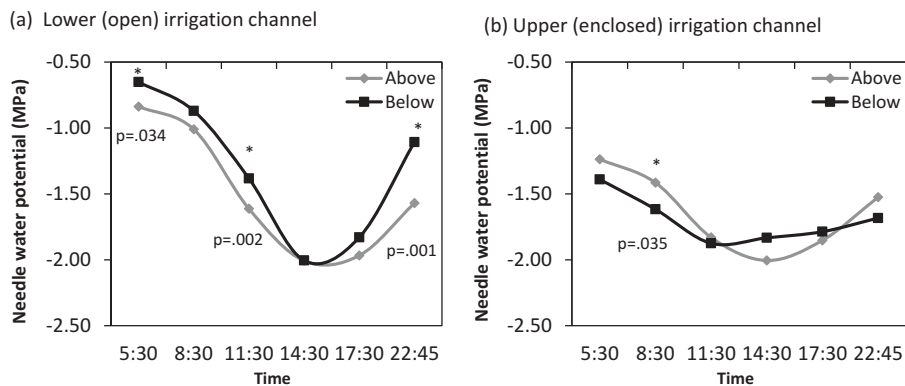
Figure 6. Diurnal mean needle water potential (in MPa) for ponderosa pine trees above and below (a) the lower (open), and (b) the upper (enclosed) irrigation channels. Significant differences between above and below channels are marked with an * and labeled p-value (t-tests, n = 3–4 for all tests).
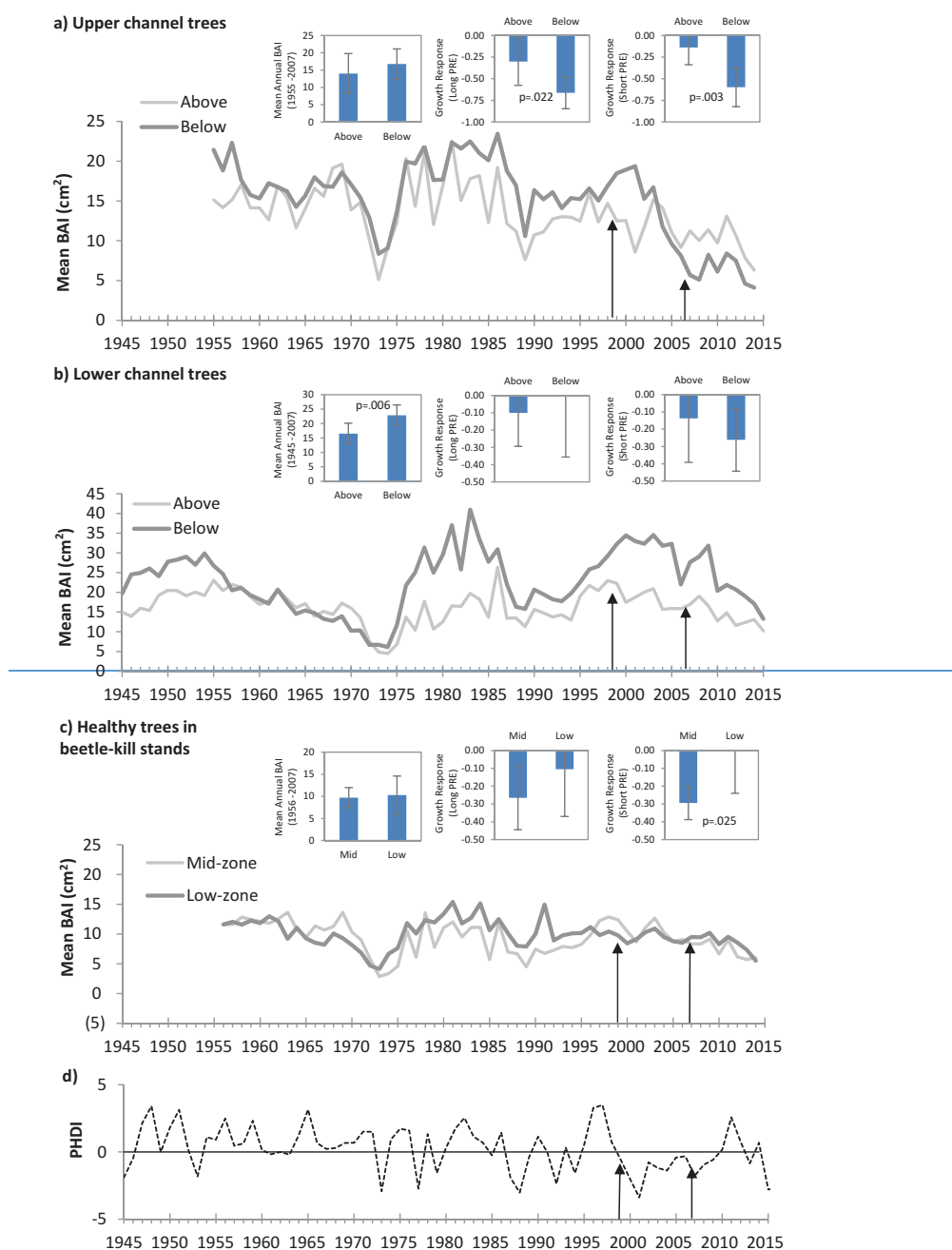
Figure 7. Mean annual basal area increment (BAI) for ponderosa pine trees above and below (a) the upper (enclosed) channel; (b) the lower (open) channel; and for (c) healthy trees in beetle-kill stands in the mid and low zones; and (d) annual Palmer hydrologic drought indices (PHDI). Long-term mean BAI in each panel starts in the year when full sample sizes are reached for both comparison groups (n = 8, n = 6, n = 13 for panels a, b, c respectively). Inset graphs show mean long-term annual BAI and two mean growth responses (POST/PRE −1) comparisons using long ('LongPRE') and short ('ShortPRE') periods (see Methods). P-values are included for all significant differences (t-tests, p < .05). Arrows show the year of upper channel enclosure (2007) and the boundary for short-PRE calculations (1999).

irrigation channels could be playing a role in vegetation changes and forest resilience to drought and insect infestation across broader WUI forested areas in the region.

A series of dramatic changes has occurred at the study site since 1998 and 2002. In swale areas of the mid zone, shifts toward a less mesic understory community, the extensive fallen-tree area, the loss of tree density, and observations of dead riparian tree species in the vicinity of the upper channel all suggest drying of soil moisture as a plausible cause. Similar patterns were found in swale areas of the low zone. The location of these effects in swale areas below channels, but not in hillslope areas or in the high

zone above both channels, is indicative of channel effects. In addition, several species in decline at the site, such as cottonwood, alder, aspen, and willow, are specifically associated with areas of high soil moisture in this forest type (Habeck 1987; Burns and Honkala 1990). Similar responses, including mortality events and shifts in forest species composition, have been observed due to human-caused water table changes (Stromberg et al. 1996; Scott et al. 1999; Caskey et al. 2015), but effects associated with recently enclosed irrigation channels have not been documented.

The low zone has been potentially affected by both channels. Although a high water table persists in some parts of the low zone, it is possible that enclosure of the upper channel, plus ongoing drought, may be causing drying of some previously wet areas in the low zone. Negative effects of waterlogged soils (Crow 2005) or natural self-thinning processes (Westoby 1984) may also be partially responsible for mortality of trees in the low zone, especially where tree densities may have been high before the study due to early-succession stand-age coupled with extra soil moisture. The results suggest that combined effects of open and enclosed channels may be patchy, likely a combination of fine-scale topography and drainage, proximity to channels, and stand age.

Water potential measurements above and below both channels show that channels could also be affecting water availability for ponderosa pine trees in proximity to the channels. At the open (lower) channel, water potentials were significantly higher in trees directly below the channel during times (morning and evening) when measurements are most likely reflecting soil moisture differences. At midday, water potentials converged to a similar minimum value in both treatments, indicating a general tolerance threshold for ponderosa pine (Maherali and DeLucia 2000). This pattern was not observed at the enclosed, upper channel. In fact, results at the upper channel suggest negative effects on water potentials in trees below the channel. The upper channel results may have been influenced by sampling challenges (see Methods). However, it is also possible that negative effects on water potential were underestimated because the trees below the upper channel potentially most affected by channel enclosure were already dead at the time of sampling. Channel effects on the water status of ponderosa pine have not been investigated in other studies. However, the water potential patterns observed here are consistent with studies of water deficit on ponderosa pine (Maherali and DeLucia 2000), and effects of stream diversions on other species (Stromberg and Patten 1990; Smith et al. 1991).

Tree growth rates above and below the channels also indicate likely channel effects. At the lower, open channel, trees below the channel had significantly higher long-term growth rates (Figure 7(b)) likely due to extra water from channel seepage. At the upper channel, growth response results indicate that enclosure has had significant negative effects on growth below the channel. Similar responses are seen in other studies (Stromberg and Patten 1990; Feichtinger et al. 2014) although none that investigated irrigation channels in WUI forests of the US.

Consistent with the possibility of channel effects on the water status and growth of trees, healthy trees in beetle-killed stands in the mid zone showed a significant and more negative post-enclosure growth response compared to the similar trees in the low zone, using the short (1999–2006) pre-enclosure period (Figure 7(c)). It is likely that growth differences between the mid and low zones would have been even greater with greater representation of swale areas in the samples. Also, because beetle-killed trees were not cored, there may have been stronger but undetected negative post-2007 growth responses in trees that died compared to trees that survived the beetle infestation within the same stands. The significant difference in growth response between mid and low zones could be an effect of general drought (Figure 7(d)) offset by extra water from the open channel ameliorating drought effects in the low zone.

The vegetation changes and tree physiological responses associated with irrigation channels in this study are an important context for the observed pattern of beetle-kill across the site (Figure 1(b)). Based on a total enumeration of beetle-killed trees in all three zones, beetle-kill was highest in the mid zone (Table 1), which is the area most likely affected by the enclosure of the upper channel. In fact, beetle-kill may have been even higher than reported here, because it is likely that many of the dead trees in the fallen-tree area of the mid zone were also killed by beetles. In addition, beetle-kill in the mid zone was substantially higher in the private section of the mid zone compared to the FS area where stumps were counted, suggesting that beetle-kill was not overestimated due to stump counts. The higher beetle-kill in the mid zone is consistent with the larger negative growth responses to channel enclosure and extensive areas of down dead trees in the mid zone.

It should be noted that beetle infestations are multi-causal, landscape-level processes (Raffa et al. 2008). At this site, beetle-kill was extensive in all zones, including areas directly below the open lower channel. Beetle-kill

also occurred in the high zone, and along the road in the low zone; areas not likely affected by channels at all. Therefore, it is difficult to fully assess the causality of channel enclosure with regard to the higher beetle mortality in the mid zone. However, the possibility that irrigation channels may affect bark-beetle mortality via drying effects is consistent with other research (Kaiser et al. 2013) and plausible given the results found here. Further research is needed to test this connection.

This study took advantage of long-term datasets and a place-based approach to explore the possible effects of irrigation channels on a WUI forest. The results are suggestive of important channel effects at this site. Although the findings require corroboration by further testing at broader spatial scales, the patterns observed here warrant the attention of WUI forest managers and land owners. The sustainability of dry coniferous forests in the WUI of the northwestern US is at substantial risk due to increasing fire, drought, and beetle infestation (Kline et al. 2013). Mapping locations of irrigation channels may aid in interpreting existing patterns of plant community composition and patterns of vegetation changes and tree mortality. Forest managers should also consider the locations of irrigation channels when making predictions about forest resilience to drought and bark-beetles.

Disclosure statement

No potential conflict of interest was reported by the author.

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Appendix 1

The study area was mapped using Gaia GPS software running on an Apple iPad, with a BadElf-Pro GPS receiver. In the high zone, the burn area was mapped by observing the boundary of trees with bark char. In the mid zone, the perimeter of a 'fallen tree' zone was mapped by GPS by encircling an area where fallen trees were encountered at least once every 10 paces. The 'fallen-tree area' encompassed a swale area below the upper irrigation channel. In the low zone, an additional wet, swale area was mapped by encircling an area where periodic standing water and riparian vegetation is encountered. A base map was made by saving screen shots from the Gaia app, and tracing perimeters, tracks, and waypoints in MS PowerPoint. Specific areas relevant to the data analyses were calculated by importing the maps into ImageJ software and measuring the areas of polygons, calibrated to the map scale.

Appendix 2

In 1998, sampling points were determined in advance on a map, and located in the field by pacing distances from property lines and known landmarks. A point-sampling method (Avery and Burkhart 2001) using a 20-factor forester's cruise angle was used to count 'in' trees > 12.7 cm DBH. Living and standing dead trees were identified to species and recorded in four diameter categories. Saplings (DBH < 12.7 cm, > 1.37 m ht) were also counted in fixed circular plots around the points (area = 81.4 m^2). In 2015, approximate point locations were determined by using the same map and pacing methods from 1998. Fixed circular plots (area = 400 m^2) were used in 2015, and all living and standing dead trees > 2 cm DBH falling within the plot were recorded, with DBHs. Seedlings (trees < 2 cm DBH, and less than head height) and saplings (trees < 2 cm DBH, and > 1.37 m tall) were also recorded.

For 1998 data, tree counts in each size-class were converted to basal area (m^2/ha) using form factors corresponding to the 20-factor cruise-angle (Avery and Burkhart 2001). Trees with diameters < 12.7 cm, but taller than 1.37 m were converted to basal area by assuming an average diameter of 7.6 cm. For 2015 data, individual measured diameters of all trees > 2 cm diameter in the plot were converted to basal area. Trees with diameters < 2 cm, but taller than 1.37 m were converted to basal area assuming an average diameter of 1 cm.

Appendix 3

Trees for coring above and below the channels were controlled for size, condition, microsite, and distances from the channel. At the upper channel, cored trees below the channel were in the swale/fallen-tree area, and at the lower channel, trees both above and below the channel were located away from the swale area. In the beetle-kill stands, approximately 1–2 healthy trees were chosen from infested stands that had mature trees across the mid and low zone in 2014. Cores were taken in both swale and hillslope areas, but these were roughly balanced for each zone (three and four from swale areas in the mid and low zones respectively). All trees were cored at breast height (1.37 m from the ground), perpendicular to the direction of the slope.

Cores were mounted on wooden core mounts and sanded until rings could easily be distinguished and cores were visually cross-dated against a previously cross-dated tree-ring chronology of ponderosa pine trees from the region (Keeling and Sala 2012). Relatively narrow and wide rings, rings with notable latewood, suspected false or missing rings, and years of growth suppression or release were recorded and used as an aid in cross-dating all cores (Yamaguchi 1991). Rings from all cores were then measured to an accuracy of .001 mm using a Velmex measuring station. The program COFECHA was used to verify the dating accuracy and as an aid in determining missing and false rings which were then checked and corrected on the cores (Holmes 1983).

Once cores were cross-dated, the year of the innermost ring established a minimum estimate of tree age. To estimate errors due to cores missing the pith, the distance from the innermost complete ring to the pith was calculated from the height and length of the last incomplete ring and this distance was divided by the average of the three inner rings (Duncan 1989). T-tests were used to confirm that age differences were not significantly different between test groups within each study