EFFECTS OF FIRE INJURY ON WATER RELATIONS OF PONDEROSA PINE

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ABSTRACT

Heat was used to injure foliage and cambium of 36 juvenile, approximately 9-meter-tall, ponderosa pine (*Pinus ponderosa*) in western Montana. The objective was to determine the effects of crown scorch (0%, 40%, and 80% leaf area reduction), stem heating (0%, 70%, and 100% of basal circumference), and their interactions with water relations. Measurements were taken for 2 growing seasons following an autumn heat treatment. The first growing season was warmer and drier than normal. The second season was wetter than normal. Seasonal differences in precipitation had a relatively greater effect on water relations than did fire treatments except for 100% basal heating. Before August in the drought year, trees with 80% crown scorch had 50% greater stomatal conductance (g_s) than unscorched trees, whereas midday xylem pressure potential (ψ_m) was 0.16 megapascal higher in undefoliated trees. In the second growing season, a low moisture stress year, g_s and transpiration (E) increased with crown scorch, but predawn xylem pressure potential (ψ_b) and ψ_m were not significantly affected. In the second season half of the trees in the 100% basal heating class failed to break bud. They were under severe moisture stress (i.e., $\psi_b < -2.6$ megapascal, and g_s and E were negligible) in early June, and died by early July.

keywords: fire injury, ponderosa pine, Rocky Mountains, water relations.

INTRODUCTION

Prescribed burning is a valuable forest management tool. It is used to reduce competition from understory vegetation, reduce fuels and the potential for wildfire, prepare seedbeds, control disease, and improve wildlife habitat. Recurrent fire is a natural process in the development of many forests. Its absence contributes to a variety of forest health problems (Hungerford et al. 1991). Recognition of this fact has led to increased use of prescribed fire in the management of wilderness areas and parks (Lotan et al. 1985) and commercial forests (Kilgore and Curtis 1987, Hardy and Arno 1996). Effective application of prescribed fire and informed management of fire-injured stands need to be based on sound knowledge of the effects of fire on the survival and growth of trees. To understand and model survival and growth of burned trees, better information is needed on relationships between fire injury and stress physiology.

Burning can injure any of 3 basic parts of a tree: crown (foliage, twigs, and buds), stem (functional phloem and xylem), and roots. Significant injuries either singly or in combination negatively affect a tree's physiology, thereby reducing growth and the chances of survival. A search of the literature reveals that the effects of fire injury on physiology have received little attention (e.g., Hare 1961, Grissom 1985, Chambers et al. 1986, Ryan 1990, 1993, Ducrey et al. 1996). However, inferences on the possible effects of fire injury can be drawn from the general physiology literature.

Defoliation should lead to at least a temporary reduction of whole-tree moisture stress, which could have a positive effect on stomatal conductance (g_s) and transpiration (E). The remaining leaf area on partially defoliated trees may photosynthesize more efficiently because of increased availability of leaf water and carboxylating enzymes (Kramer and Kozlowski 1979). In the 9 months following a fire that killed approximately 50% of the foliage of slash pine (*Pinus elliottii*), Grissom (1985) found that during periods of high evaporative demand, midday xylem pressure potential (ψ_m) was up to 0.15 megapascal higher in burned trees. Predawn xylem pressure potentials (ψ_b) were not significantly different. Wright and Berryman (1978) found similar reductions in ψ_m in both artificially and insect-defoliated Douglas-fir (*Pseudotsuga menziesii*). Stress was not significantly reduced during the second and third growing seasons following defoliation. The recovery to pre-defoliation stress levels after 1 year was inferred to be a strong indication that the root-shoot ratio had returned to the previous level.

In addition to the direct effects on water relations defoliation can set in motion a variety of secondary feedback effects. Defoliation reduces the size of the supporting root system, leading to a resumption of the pre-defoliation root-shoot ratio (Kulman 1971, Tyree 1989, Kozlowski et al. 1991). Reductions in the total photosynthate production at higher defoliations should seriously affect basipetal transport of carbohydrates, leading to reduced stem growth and possibly root growth. Significant reductions in root growth should decrease available water and nutrients in subsequent growing seasons.
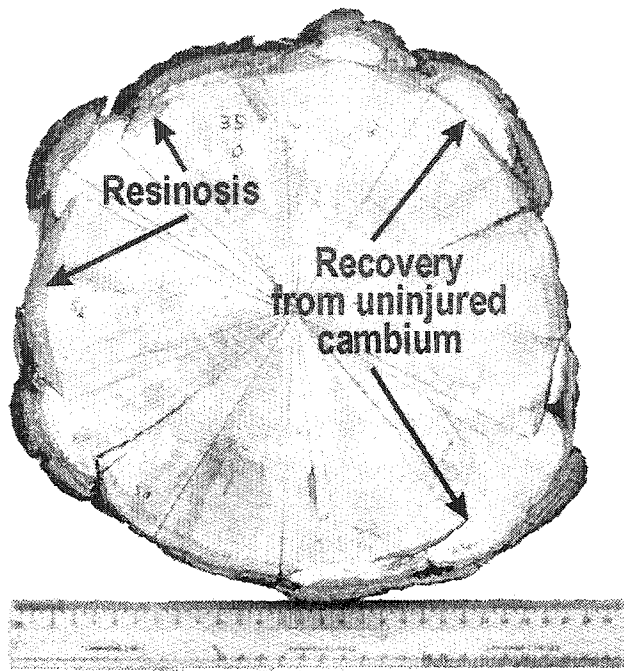
Fig. 1. Example of resinosis, and regrowth from uninjured stringers of cambium on ponderosa pine 2 years after basal heating treatment to 100% of the circumference.

If fire-induced defoliation significantly reduces whole-tree transpiration, soil water should not be limiting as often or as early in the summer. As a result, partially defoliated trees can be expected to have a higher xylem pressure potential (i.e., less water stress), E, and g_s. Transpiration, which is highly correlated with the rate of photosynthesis at any given time, and net carbon assimilation per unit of leaf area may increase. Because the total leaf area per tree is less, however, the total amount of water used and carbon assimilated should be less. Although leaf-level rates of photosynthesis and E may increase after fire due to an increase in xylem pressure potential, total tree carbon gain and growth will decrease, but this decrease will not be proportional to needle loss (Ryan 1990).

Fire frequently causes stem injuries, particularly near the ground line. Stem injuries can affect directly the overall water balance of the tree by disrupting water flow through xylem near the injury. When heat ruptures epithelial cells of the resin ducts, resinosis, a generalized wound response (Shigo and Marx 1977), occurs, leading to increased stem resistance (Figure 1). If the volume of sapwood injured is significant, stem capacitance also may be reduced (Rundel 1973). In addition to these direct effects, the tree's water budget may be indirectly affected by the disruption of flow of carbohydrates to the roots, leading to changes in root-shoot ratios. If carbon allocation to roots is substantially interrupted, fine root production should be less in the second growing season (Marshall and Waring 1985). Less fine root production may lead to earlier and stronger moisture stress exhibited by lower xylem pressure potentials, similar to the expected delayed response to defoliation. If this occurs, it should result in

lower E, g_s, and carbon assimilation. Thus, water availability could be substantially reduced the second year, particularly in undefoliated trees, where demand for water and foliar maintenance respiration have not been reduced. As a result, physiological changes should be expected to extend at least through the second growing season.

The literature indicates that the effects of fire injury on water relations are complex, with multiple feedbacks between water use and carbon allocation. The effects have been the subject of little direct investigation. The purpose of this study is to explore the effects of fire injury on stress physiology of ponderosa pine. It is part of a larger study (Ryan 1993) of the effects of fire injury on tree growth. The specific objective of this study is to determine the effects of controlled levels of fire injury on summer changes in water relations (predawn and midday xylem pressure potential, stomatal conductance, and transpiration).

METHODS

Study Area

The study area was located on the University of Montana's Lubrecht Experimental Forest 52 kilometers east of Missoula, Montana. The site was a relatively low-productivity Douglas-fir–nine bark (Pseudotsuga menziesii–Physocarpus malvaciace) habitat type (Pfister et al. 1977) on extremely stony Totelake loam (Nimlos 1986) located on a flat bench above the Blackfoot River at an elevation of 1,125 meters above sea level (T14N, R15W, Sec. 27, SE 1/4). Annual precipitation at the site is approximately 375 millimeters per year. In a normal year about 35% of annual precipitation is received from June through September.

Treatments and Experimental Design

A population of 36 ponderosa pine was selected from a stand of relatively vigorous, naturally regenerated trees. Trees averaged 9 meters in height (range 7–11 meters) and 185 millimeters in diameter (range 137–247 millimeters). A 3×3 factorial completely randomized experimental design with 9 treatments and 4 replicates was used. Defoliation was fixed at levels of 0%, 40%, and 80% of the leaf area and was accomplished by scorching foliage with heat from a propane burner. Experience indicated that conifer foliage is killed when a visual sheen caused by melting of the wax coating appears. This visual criterion was used to determine the amount of heat applied to each branch. Defoliation progressed upward from the base of the live crown and was quantified by ocular estimation as the proportion of the prefire leaf area scorched. Defoliation reduced the number of live whorls, somewhat in proportion to the percent defoliation. However, most trees did not have all of the buds killed on all of the defoliated branches. These buds put out new growth in 1988 and 1989, but the needles were short and internodes exhibited almost no elongation. It was concluded that because of the very low leaf area, these

branches did not have a significant impact on the tree's transpiration or water consumption during the 2 years of observation. Thus in the data analysis, no attempt was made to adjust the defoliation to account for the slight amount of regrowth. All analyses were conducted on the basis of the assigned treatment levels (0%, 40%, and 80%).

Basal stem heating was fixed at levels of 0%, 70%, and 100% of the circumference at the root crown. This was accomplished with heat from a burning wick at the base of the tree (Hare 1965). The duration of burning was adjusted in an attempt to cause cambium death with minimal disruption of the functional conducting xylem due to resinosis. The duration of heating was adjusted by monitoring temperatures beneath the wick during burning and predicting the depth of lethal heat penetration (Peterson and Ryan 1986). Cambium mortality was determined by spot checking the cambium with an increment borer and testing for the enzyme peroxidase (Ryan 1982). Two samples were taken from each tree (n = 48) at a height corresponding to the top of the wick, which was where the deepest charred bark occurred. One sample yielded a positive viability test. Stem dissection upon completion of the study revealed that heat treatments killed an average of 65% (range 55–73%) of the circumference of trees in the 70% heating class and an average of 95% (range 85–100%) in the 100% class. Errors in the heat treatment resulted from small intermittent stringers of undamaged cambium beneath thicker bark plates (Figure 1). All analyses were conducted on the basis of the assigned treatment levels (0%, 70%, and 100%).

Fire injury treatments were performed during October 1987. A combination of shrub clipping and light surface fire was applied to the area beneath each tree to simulate fire effects on competing understory vegetation, nutrients, and microenvironment. A light water spray was used to extinguish the fire once the surface litter was consumed. This action precluded fire spread to the fermentation and humus layers and minimized the potential for any direct heat impact on roots.

Water Relations

Tree water relations were measured once a month from July–September 1988 and from June–September 1989. All sampling was conducted during a 4-day period under relatively uniform weather conditions between 1200–1600 hours local sun time. Because leaf age affects g_s (Davies et al. 1981), and to minimize variation, all physiological measurements were conducted on 1-year-old needle tissues from the main stem and top 3 whorls of the trees. At each sampling period predawn and midday xylem pressure potentials were measured (megapascal) in 2 needle fascicles and averaged. Pressures were measured with a model 1000 PMS pressure chamber using standard procedures (Ritchie and Hinckley 1975). In addition, fascicle diameter was measured with a micronometer after removing the sheath. Stomatal conductance (micromoles per square meter per second), based on Cowan's (1977) definition, and transpiration (micromoles per square meter

per second) were measured using a Licor 1600M Steady State Porometer and procedures described in the manufacturer's manual and Beardsell et al. (1972). Measurements were made on 2 needle fascicles (6 needles), replicated (n = 2 in 1988, n = 5 in 1989), and averaged to characterize E and g_s for each sample period. Analysis of needle diameters revealed small, but statistically significant, differences between trees. Therefore, the leaf area used in porometer measurements was adjusted for each tree by using the tree's average needle diameter and calculating the surface area of a trisected cylinder.

A portable aluminum platform was used for canopy access in 1988. In 1989 a hydraulic lift bucket was used. To reduce the number of days required for sampling and thereby achieve relatively uniform environmental conditions in each sample period, a compromise was made between sampling logistics and complete randomization. Clusters of adjacent trees were assigned to 1 of 8 groups. At each sampling period, groups were chosen at random. In preliminary analysis of the data, group membership was not found to significantly affect any response variables and it was dropped from further analysis.

Although environmental conditions were generally very uniform during each sampling period, photosynthetically active radiation (Q, microeinsteins per square meter per second), ψ_b, and vapor pressure deficit (VPD, kilopascals) were used as covariates when analyzing treatment effects on g_s and E. Saturation vapor pressure was calculated from equations in Buck (1981) using the porometer temperature sensor. Vapor pressure deficit was computed from the saturation vapor pressure and the porometer relative humidity. Photosynthetically active radiation was measured with a Licor LI-190s-1 quantum sensor supplied with the porometer.

Data Analysis

Preliminary analyses included plotting of data, computing descriptive statistics, and analyzing correlation. Ratios of maximum to minimum variances were used to screen for homogeneity of variance. Hypothesis testing relied on repeated measures analysis of variance (Moser et al. 1990, Meredith and Stehman 1991). Tests were considered significant at the $P \leq$ 0.05 level. The GLM procedure (SAS Institute Inc. 1990) was used to analyze treatment effects. Seasonal effects on E and g_s were analyzed with a repeated-measures analysis of variance (ANOVA) for each sample month. Predawn xylem pressure potential, Q, and VPD were used as covariates. Treatment effects on seasonal ψ_b, ψ_m, and the diurnal recovery ($\psi_m - \psi_b$) were also evaluated with repeated-measures ANOVA. Early in 1989, 6 members of the 100% basal heating class died. Because changes in the population size resulted in an unbalanced experimental design, statistical analysis was conducted using all trees in 1988 but excluding the 100% heated trees in 1989. Normal probability, stem and leaf, and box plots were used to observe departures from normality.
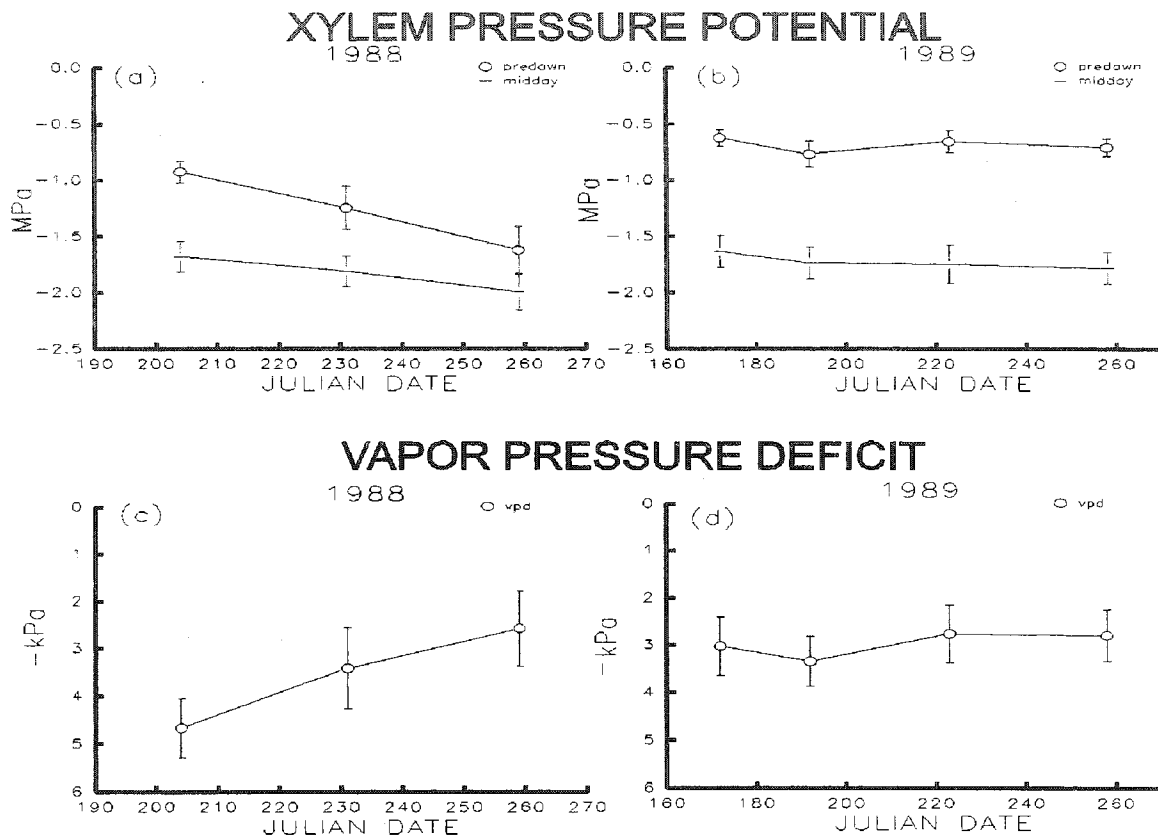
Fig. 2.   Seasonal variations in predawn and midday xylem pressure potential and vapor pressure deficit in 1988 and 1989. Data are combined for all treatments to show general seasonal patterns.

RESULTS

Environmental conditions during the summer of 1988 were unfavorable for growth and development (Figure 2). Extremely dry conditions during the last 5 months of 1987 and first 3 months of 1988 were followed by a somewhat wetter than normal spring. However, precipitation during July, August, and September was 29% of normal.

All measures of tree water status declined throughout the 1988 field season. Due to the lack of available soil water, E and g_s were low, particularly in August and September (Figures 3 and 4). In contrast to 1988, the trees experienced cooler temperatures, lower VPD (Figure 2), and substantially more growing season precipitation in 1989. From March–September precipitation was 82% above normal. All measures of tree water status showed significant seasonal variations, but heavy August rains limited the amount of moisture stress (Figures 3 and 4). July had the lowest 1989 ψ_b, but it was 0.15 megapascal higher than in 1988 (Figure 2). In the drought year 1988 the environmental conditions Q, VPD, and ψ_b did not explain a significant amount of variation in E or g_s (Table 1). In the wet year 1989 Q and VPD explained a significant amount of variation in E and g_s, but ψ_b did not (Table 1).

Relative to the environmental effects associated with the 2 years, crown scorch had minor effects on summer water relations. In 1988 the trend for g_s to increase with increasing defoliation was significant (P

= 0.032), but the trend was not statistically significant for E (P = 0.106) (Table 1). On average 80% defoliated trees had a 1.5 times higher g_s than undefoliated trees. The pattern for g_s was that 0% and 40% defoliated trees had the same g_s, which was less than that for 80% defoliated trees. The difference was most pronounced early in the summer (Figure 3c). In 1989 the percent crown scorch explained a significant amount of variation in E (P = 0.034) but not in g_s (P = 0.120). Again, the trend was for E and g_s to increase with the level of defoliation. Crown scorch did not affect ψ_b in either 1988 or 1989 (Table 1). Seasonal average ψ_m and diurnal recovery (ψ_m − ψ_b) were significantly affected by crown scorch (P = 0.001) (Table 1). The pattern was for 0% crown scorch to have the highest ψ_m, i.e., lowest moisture stress, and the smallest diurnal recovery. Results for 40% and 80% defoliation were not significantly different from each other. There was, however, monthly variation (Figure 3). In July 1988, undefoliated trees had ψ_m 0.16 megapascal higher than 80% defoliated trees and 0.10 megapascal higher than 40% defoliated trees. Late season differences were minor. In contrast, 1989 had more favorable moisture conditions, and ψ_m and diurnal recovery were not related to crown scorch.

Basal heating had minor effects on water relations. In 1988 the trend for ψ_b to increase, i.e., reduced moisture stress, with increasing basal injury was not significant (P = 0.055). However, ψ_m followed the same
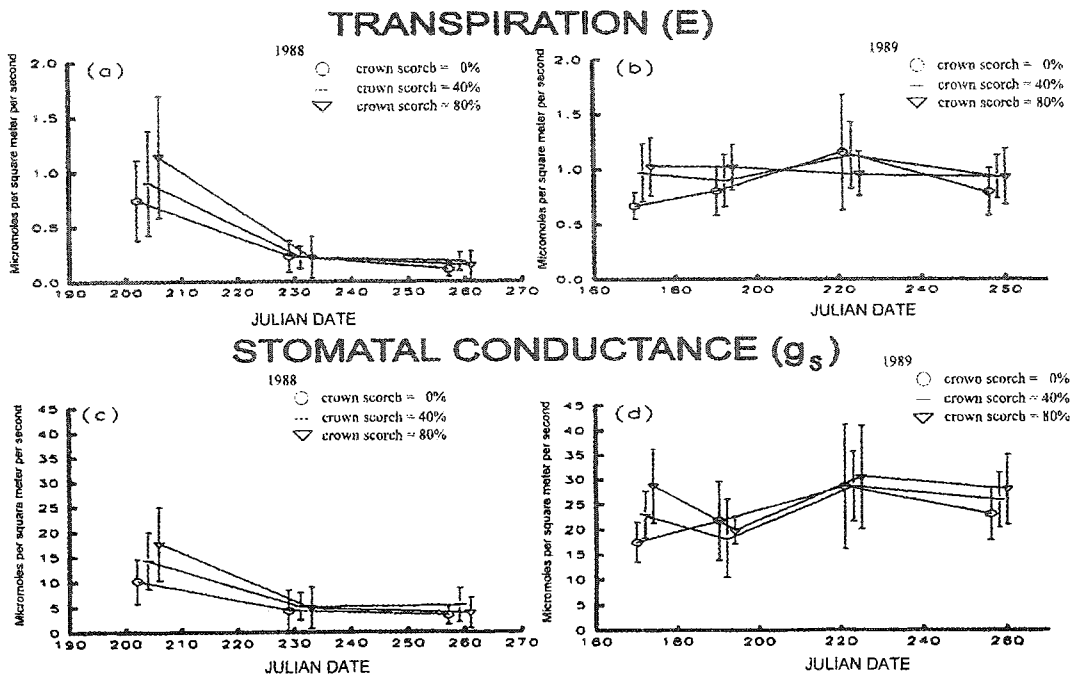
TRANSPIRATION (E)

STOMATAL CONDUCTANCE (g_s)

Fig. 3.   Seasonal variations in transpiration and stomatal conductance of ponderosa pine following crown scorch. Means ± 1 standard deviation are plotted at 2-day intervals in order to have visual separation of the treatments. All measurements were taken at random during each sample period.

TRANSPIRATION (E)

STOMATAL CONDUCTANCE (g_s)

Fig. 4.   Seasonal variations in transpiration and stomatal conductance of ponderosa pine following basal heating. Means ± 1 standard deviation are plotted at 2-day intervals in order to have visual separation of the treatments. All measurements were taken at random during each sample period.
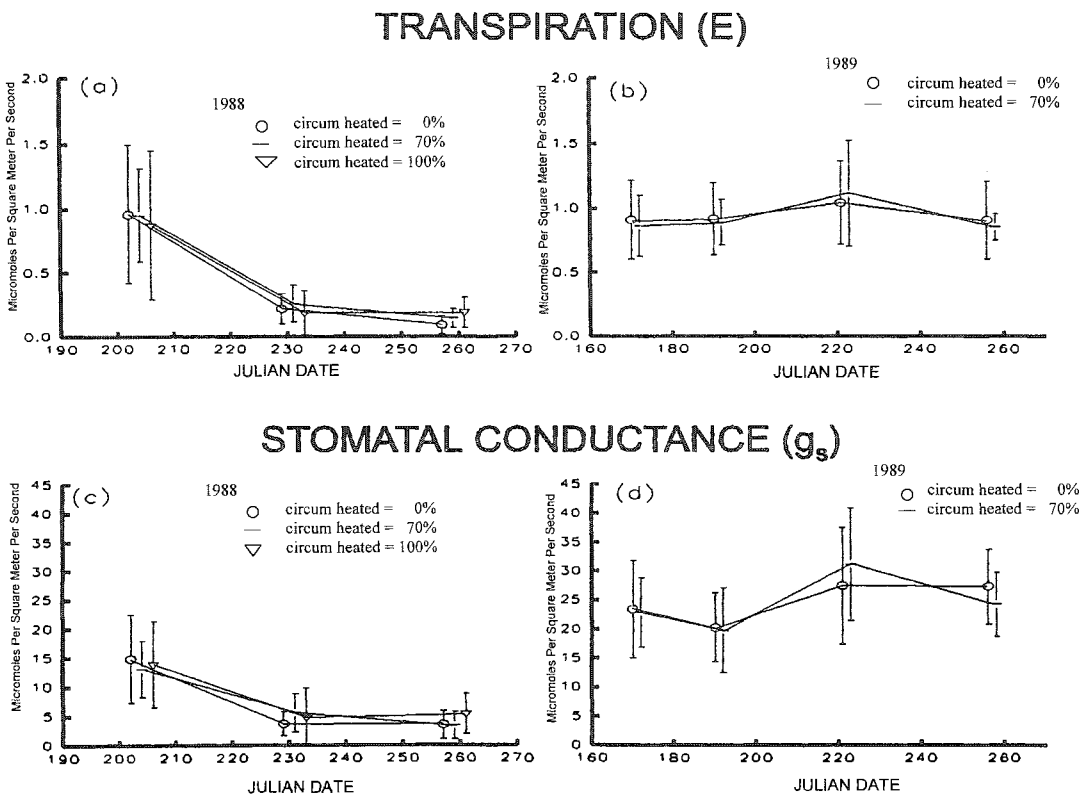
Table 1. Probability values from analysis of variance of the effects of crown scorch (CS) and basal girdling (GRDL) on seasonal water relations of 36 ponderosa pine in 1988 and 1989.

	Moisture response									
	Transpiration		Stomatal conductance		Predawn xylem pressure potential		Midday xylem pressure potential		Recovery (Midday–Predawn)	
					Significance level					
	Year		Year		Year		Year		Year	
Source[a]	1988	1989	1988	1989	1988	1989	1988	1989	1988	1989
Q (μE/sq. m./sec)	0.962	0.005	0.812	0.004						
VPD (kPa)	0.902	0.000	0.068	0.012						
Ψ_b (MPa)	0.393	0.323	0.992	0.095						
CS (%)	0.106	0.034	0.032	0.120	0.807	0.173	0.000	0.268	0.001	0.285
GRDL (%)	0.798	0.129	0.914	0.076	0.055	0.647	0.006	0.589	0.465	0.462
CS*GRDL	0.238	0.310	0.432	0.177	0.022	0.157	0.003	0.157	0.048	0.038
Period	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.003	0.000	0.016
CS*Period	0.0976	0.154	0.042	0.114	0.981	0.293	0.107	0.143	0.128	0.325
GRDL*Period	0.800	0.415	0.434	0.380	0.351	0.875	0.757	0.261	0.780	0.364
CS*GRDL*Period	0.103	0.541	0.313	0.592	0.943	0.109	0.967	0.857	0.996	0.505

[a] Q—photosynthetically active radiation (microeinsteins per square meter per second), VPD—vapor pressure deficit (kilopascals), Ψ_b—predawn xylem pressure potential, CS—% crown scorch (0%, 40%, 80%), GRDL—% basal circumference heated (0%, 70%, 100%), Period—measurement period. All trees were measured within a 5-day period 3 times (Jul–Sep) in 1988, 4 times (Jun–Sep) in 1989, and between solar noon and 4 hours past solar noon.

pattern (0% < 70% = 100%) and was significant (P = 0.014) (Table 1). The 100% basal heating treatment resulted in cambium death ranging from 85–100% of the circumference. Six trees in this class died. Three were completely girdled. The remaining 3 trees were girdled on 93%, 96%, and 98% of their circumference. Girdling on the 6 trees that lived was 85%, 85%, 86%, 96%, 97%, and 100%. Dead trees either failed to break bud in 1989 or died by early July. In June 1989, these trees were under severe moisture stress (ψ_b < −2.6 megapascal), and E and g_s were negligible. Basal girdling had a relatively minor effect on the remaining trees (Figure 4). Those trees that eventually died had higher E and g_s in July 1988, but lower E and g_s in later months (Table 2). Despite the worsening drought, E and g_s of the 100% heated class increased between August and September while these responses continued to decline in all other trees (Figure 4a, c). Inspec-

Table 2. Monthly means and standard deviations of tree water relations for the 6 live vs. 6 dead trees in the 100% basal heating class in 1988.

	Dead		Alive	
Response[a]	Mean	Std. Dev.	Mean	Std. Dev.
July 1988, Julian Date = 204				
E (micromoles per sq. m. per sec.)	0.97	0.63	0.78	0.55
g_a (micromoles per sq. m. per sec.)	15.04	7.47	13.00	7.92
Ψ_p (megapascals)	0.89	0.06	0.90	0.06
Ψ_m (megapascals)	1.60	0.11	1.64	0.19
Diurnal Recovery ($\Psi_p - \Psi_m$)	0.71	0.09	0.74	0.18
Q (microeinsteins per sq. m. per sec.)	1523	420	1172	676
VPD (kilopascals)	4.56	0.86	4.44	0.54
August 1988, Julian Date = 231				
E (micromoles per sq. m. per sec.)	0.10	0.08	0.28	0.18
g_a (micromoles per sq. m. per sec.)	2.38	2.91	7.35	5.72
Ψ_p (megapascals)	1.25	0.23	1.17	0.17
Ψ_m (megapascals)	1.72	0.16	1.79	0.12
Diurnal Recovery ($\Psi_p - \Psi_m$)	0.48	0.22	0.63	0.17
Q (microeinsteins per sq. m. per sec.)	1119	57	1023	31
VPD (kilopascals)	3.12	0.58	2.93	0.41
September 1988, Julian Date = 259				
E (micromoles per sq. m. per sec.)	0.15	0.04	0.23	0.15
g_a (micromoles per sq. m. per sec.)	3.99	0.98	7.02	4.47
Ψ_p (megapascals)	1.71	0.24	1.48	0.23
Ψ_m (megapascals)	1.91	0.16	2.00	0.18
Diurnal Recovery ($\Psi_p - \Psi_m$)	0.22	0.10	0.52	0.22
Q (microeinsteins per sq. m. per sec.)	1066	243	839	388
VPD (kilopascals)	2.85	0.86	2.61	0.86

[a] E—Transpiration, g_a—stomatal conductance, Ψ_p—predawn xylem pressure potential, Ψ_m—midday xylem pressure potential, Q—photosynthetically active radiation, VPD—vapor pressure deficit.

tion of the means for the 6 trees that died versus the 6 that lived indicates that the increase in E and g_s came from those trees that lived (Table 2). In the late summer of 1989 the 6 trees in the 100% basal heating class that were still alive had somewhat higher ψ_m than the 0 and 70% heated classes (e.g., 0.2 megapascal higher in September). Other water status variables were not affected despite the complete girdling of one of the trees and >96% girdling of two of them.

Interactions between percent crown scorch and basal girdling were significant for ψ_m in 1988 (P = 0.022), and for diurnal recovery in 1988 and 1989 (P = 0.048 and P = 0.038, respectively) (Table 1). In 1988 the only treatment that differed significantly from the rest was 0% crown scorch × 100% girdling. It had the highest ψ_m and the lowest diurnal recovery. In 1989 the 80% crown scorch × 0% girdling class had the smallest diurnal recovery.

DISCUSSION

The complex physiological interactions resulting from foliage and stem injury are difficult to interpret except in the extremes, i.e., high defoliation versus no defoliation and high girdling versus no girdling. The working hypothesis behind the moisture status measurements was that major fire injuries would have serious consequences for tree water relations. It was assumed that major shifts in plant moisture status would be reflected in measurements taken at the most limiting times, midsummer and midday. Individual tree variations in water relations within each treatment replication were large enough that statistical significance was not achieved for most treatment effects on water relations, nor were the trends unambiguous.

The expected pattern of increased g_s and E with higher levels of defoliation was present only in some months (Figure 3). In July 1988 E and g_s increased with increasing defoliation. Later in 1988 water was not available regardless of the amount of transpiring leaf area. In 1989 the expected pattern occurred in June and September, and also in July for E only. The expected pattern may not be reflected in midday measurements, particularly at higher evaporative demand. If reductions in moisture stress are consistently associated with reduced leaf area, then other factors not addressed in this study must also exert significant control. Seasonal shifts in control of canopy function either by hormones, osmotic adjustment, or other factors may be contributing to midsummer deviations.

Several studies have reported increases in soil water following fire (Wells et al. 1979). However, treatment effects on ψ_b were not significant. Seasonal patterns in ψ_b were dominated by the drought in 1988. In 1989 ψ_b showed remarkably little seasonal variation (Figure 2). Defoliation did not result in more available soil water during the summer months. The area beneath the canopy of the trees was treated with a light surface burning to simulate fire effects on competing vegetation. The fire was purposely controlled to minimize soil heating and the confounding effects of root

injury. Under these conditions understory vegetation quickly refoliated the area. Furthermore, the rooted volume of an open-grown tree is unlikely to be contained beneath the canopy. Thus individual trees were likely competing for water with nearby uninjured trees and understory vegetation. If defoliation treatments reduced individual tree water use early in the growing season, then competing vegetation may have transpired any potential savings in soil water, thereby reducing water available for transpiration late in the growing season. Grissom (1985) also found that ψ_b was unaffected by crown scorch 9 months following an underburn through "Southern rough," which quickly revegetates. The results of this study and those of Grissom (1985) conflict with the stand-level results simulated by Ryan (1990), which showed substantial increases in late-season ψ_b. Thus, it appears that ψ_b would be useful as an indicator of fire injury only when the entire stand is similarly affected.

Treatment effects on ψ_m were also minor. In 1988 undefoliated trees had higher ψ_m, i.e., less stress, than defoliated trees. This outcome was counter to what was expected. The shift in carbohydrate source/sink ratio in defoliated trees may have resulted in accelerated E and g_s in residual foliage causing them to expend available water sooner. Trees in the 100% basal heating class had higher ψ_m than ungirdled trees. Increased stem growth above the girdle in the lower bole would have been associated with increased unloading of carbohydrates from the phloem. Phloem unloading results in a net water flow to the xylem (Kozlowski 1992). This net water flow could increase stem capacitance, thereby making more water available for other physiological functions. However, Grissom (1985) found similar increases in ψ_m. If stem injuries occurred in his study, they were not recorded. Thus, at this point an explanation for the treatment effects on ψ_m would be entirely conjecture.

It is thought that root growth in the northern Rocky Mountains is limited primarily to the early growing season when soil temperature and moisture are adequate. Moreover, root growth relies heavily on carbohydrates stored during the previous growing season (Lyr and Hoffman 1967, Kramer and Kozlowski 1979). Thus, girdling was not expected to affect moisture status until the second year. Moisture stress was expected to be highest in undefoliated trees with basal girdling because of the relatively high demand for water and the reduced flow of carbohydrates to the roots. Comparing treatment means for undefoliated trees at 0% and 70% basal heating shows that this result did not occur consistently. Predawn xylem pressure potential decreased slightly while ψ_m, g_s, and E all increased slightly. Basal girdling either did not reduce phloem transport enough to affect fine root production, or 1989 fine root production relied heavily on previously stored carbohydrates. Given the harsh environmental conditions in 1987 and 1988, it seems intuitively implausible that these trees would have had adequate root reserves.

Decreased radial growth below girdled portions of the stem (Ryan 1993) probably reflects decreased car-

bohydrate transport to the subtending root system. Likewise, accelerations in growth on the ungirdled side of the tree probably reflect increased allocation to roots on that side. However, it is difficult to imagine that an even redistribution of the root system occurred in 1 growing season. Ryan (1993) reported an average 24% increase in basal area increment of 70% girdled trees in this study. This suggests a shift in carbon allocation to stem growth. Moreover, it is contrary to a considerable body of evidence on carbon allocation (Waring 1983, Kozlowski 1992) to argue that the allocation came at the expense of reduced leader growth, which also was not significantly affected by basal heating (Ryan 1993). From this evidence it seems likely that root reserves compensated for some of the effects of basal girdling. Supporting evidence in 1989 for high reliance on stored carbohydrates for root function can also be found in the fact that 6 trees in the 100% basal heating class were still alive at the end of the second growing season and suffered no apparent decline in water relations despite the fact that three of them were girdled >96% of their circumference. As a result, it is likely that the complete effects of basal girdling were not exhibited in 2 growing seasons. The failure of the 100% basal heating treatment to effectively kill all of the cambium undoubtedly led to increased variation in these data.

It was hypothesized that defoliated trees would have less leaf area and therefore use less water early in the growing season, thereby making more water available in midsummer. Evidence for reduced moisture stress in defoliated trees is not statistically strong for these midsummer data. The early season trends for higher E and g_s are consistent with greater water availability in 1988 and 1989 (Figure 3). In August and September of 1988 E and g_s were minimal for all treatments. In August and September 1989 there is not a clear pattern. Moreover, ψ_m was higher in undefoliated trees. Clearly, midday, midsummer tree water relations were not strongly affected by these fire injury treatments, and the patterns were not consistent. Growth data for these trees (Ryan 1993) suggests that fire injury is associated with complex changes in the timing and magnitude of carbon allocation that likely confound tree water status measurements. Future studies to understand the effects of fire injury on tree water relations should focus on early season and diurnal measurements.

CONCLUSIONS

The primary source of differences in water relations of these trees resulted from variations in year-to-year (i.e., drought versus normal precipitation) and month-to-month (i.e., seasonal soil moisture status and VPD) dryness. It was expected that increasing crown scorch would lead to reduced moisture stress. This trend was present in much, but not all, of the E and g_s data, and the opposite trend occurred in the ψ_m data. Treatment effects also were masked by high tree-to-tree variation. The high variation within treatments

suggests future studies should either be based on a more homogeneous population or have more replicates. It was expected that treatment differences would be greatest during periods of maximum stress, i.e., midsummer and midday. Results suggest that the greatest differences probably occur earlier in the growing season, or possibly earlier in the day. Studies of the effects of fire injury on tree water status should focus more attention on measurements at these times.

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