Physiological responses of old growth ponderosa pine and western larch to restoration cutting and burning treatments

U.S.D.A. Forest Service
RMRS-99563-RJVA

Report June 2001

Anna Sala and Ragan Callaway

Division of Biological Sciences.
University of Montana
Missoula
MT-59812
Sala@selway.umt.edu (243 6009)
Callaway@selway.umt.edu (243 5077)

Abstract

In the interior northwest, preferential harvesting of old growth trees combined with fire exclusion since the early 1900's has resulted in a successional replacement of open ponderosa pine and larch stands to stands of interior Douglas-fir (*P. menziesii* var *glauca*) on several million hectares. Implications of this successional replacement include decreased resource availability for old growth trees due to strong competition with the understory. The inherent aesthetic and natural value of old growth trees has triggered a strong interest to protect the few remnant old growth stands in the Northern Rocky Mountains and restore them to pre-settlement conditions. However, data on the physiological response of old growth trees to different restoration practices are completely lacking. These data are crucial to ensure the successful restoration of old growth forests. The overall goal of this project was to assess the effectiveness of several management treatments to restore old growth ponderosa pine and western larch stands. The restoration treatments considered are: 1) Control: the old growth stand continues to be fire excluded, 2) Understory cutting followed by pile burning (pile burn), 3) Understory cutting followed by broadcast burning (broadcast burn), 4) Overstory thinning with understory cutting followed by pile burning (overstory thin and pile burn) and 5) Overstory thinning with understory cutting followed by broadcast burning (overstory thin and broadcast burn). In particular, we determined whether whole-tree water use, available soil moisture, water use efficiency, foliage nitrogen content, foliage production and radial wood increment of old growth ponderosa pine and western larch change in response to different restoration treatments. Results during the 2000 growing season corroborated to a larger extent our results from the first growing season after treatment implementation: all restoration treatments had a positive effect on soil moisture (particularly evident at 40 cm of soil depth), and on tree performance. Increased performance for western larch in treated plots was evident from; 1) significantly higher sap flow during the driest part of the summer relative to control plots, 2) increase in foliar nitrogen content in trees from all treated plots relative to the control plots and 3) slightly higher foliage production (although not statistically significant) in trees from all treated plots relative to the control plot. For ponderosa pine, increased performance was reflected in: 1) higher sap flow in the treated plots relative to the control plot, 2) highly significant increases in foliage production and bud size in trees from the treated plots and 3) significantly higher leaf nitrogen content in the broadcast burn plot

relative to the control and thin plots. While we observed a strong positive effect of the understory removal on the overstory old growth trees, we did not see large differences between specific restoration treatments. The only exceptions were a tendency in the overstory thin treatments to have higher soil moisture and increased leaf nitrogen in ponderosa pine in the broadcast burn treatment).

Introduction

Prior to 1900 most larch (*Larix occidentalis*) and ponderosa pine-dominated stands (*Pinus ponderosa*) experienced frequent surface fires (Arno 1988, Martin 1982). These frequent low-intensity fires helped maintain open, park-like ponderosa pine and larch stands, where old growth trees (> 200 years old) were common. In the interior northwest, preferential harvesting of old growth trees combined with fire exclusion since the early 1900's has resulted in a successional replacement of open ponderosa pine and larch stands to stands of interior Douglas-fir (*P. menziesii* var *glauca*) on several million hectares (Keane et al. 1989; 1996). In addition to the loss of the highly valued old growth trees, ecological implications of this successional replacement include increased stand-level transpiration, increased interception of water and snow, decreased snow pack accumulation and an increase in evaporation of intercepted water. As a result of these changes, water loss to the atmosphere increases and overall soil water availability decreases. Changes in biomass allocation may follow, resulting in a decrease of the above ground biomass production, and timber quality. Furthermore, increased density, canopy cover and LAI in fire excluded stands result in an increase of pathogen host availability, which combined with increased susceptibility to pathogen infection due to decreased resource availability (water and nitrogen), will result in a decrease of forest health.

In spite of the potential ecological implications of fire suppression policies relatively few studies have quantified changes in ecosystem properties such as water cycles and productivity resulting from fire suppression in the interior northwest. Because of the combination of fire suppression and harvesting, old growth stands in the interior northwest are very rare. The inherent aesthetic and natural value of old growth trees has triggered a strong interest to protect the few remnant old growth stands and restore them to pre-settlement conditions. However, data on tree physiological responses and ecological impacts (water and nutrient cycles and forest productivity) of different restoration practices are completely lacking. These data are crucial to ensure the effectiveness of potential restorations treatments and the maintenance of healthy old growth forests.

Objectives

The overall goal of this project is to assess the effectiveness of several management treatments to restore old growth ponderosa pine and western larch stands. The restoration treatments considered are:

1) Control: the old growth stand will continue to be fire excluded
2) Understory cutting followed by pile burning (pile burn)
3) Understory cutting followed by broadcast burning (broadcast burn)
4) Overstory thinning with understory cutting followed by pile burning (overstory thin and pile burn)
5) Overstory thinning with understory cutting followed by broadcast burning (overstory thin and broadcast burn).

These treatments are intended to simulate different fire regimes ranging from no fire (control) to low intensity understory fire without (treatment 3) or with some overstory mortality (treatment 5). They also allow to separate the effects of fire (treatments 2 and 4) from the effects of decreased understory and overstory competition for resources on forest function (treatments 2 and 4).

Specifically, the questions to be answered are:

1) Does understory removal release old growth ponderosa pine and western larch from competition for resources?

2) Does understory removal combined with overstory thinning of old growth trees release ponderosa pine and western larch to a greater extent than understory removal alone?

3) Does the response of old growth ponderosa pine and western larch change depending on the specific restoration treatment by which understory is removed (cutting + pile burning or cutting + broadcast burning)?

In particular, we will determine whether whole-tree water use, available soil moisture, water use efficiency, foliage nitrogen content, foliage production and radial wood increment of old growth ponderosa pine and western larch change in response to different restoration treatments. These treatments provide an extraordinary opportunity to *experimentally* assess changes in ecosystem properties due to fire suppression. Overall we hypothesized that increases in stand density and canopy cover associated with fire suppression results in an increase in whole-stand-level water use, with greater stress for old growth trees due to decreased soil water availability, increased competition for water and lower available nitrogen. Therefore, remnant fire-excluded old growth forests may be at risk due to the stresses associated with the lack of frequent fires.

Experimental Approach

The Fire Sciences Laboratory (U.S. Forest Service, Missoula Montana) located an old growth remnant stand of ponderosa pine and western larch at the Grant Creek valley of the Lolo National Forest (Missoula, Montana). The stand had not burned in about 80 years and had never had tree harvesting. Because of the lack of disturbance by fire the understory was dominated by Douglas-fir. Most of the overstory ponderosa pine and western larch are 320 to 380 years old. The stand is located on a steep slope oriented South-West and is divided by a Forest Service road that runs perpendicular to the slope. The overstory of the upper portion of the stand (above the road) is dominated by western larch, while the lower portion (below the road) is co-dominated by ponderosa pine and western larch.

During the summer of 1998 the stand was subdivided into 5 plots. From down slope to up slope, the assigned treatments described above were: control, pile burn, broadcast burn, overstory thin and pile burn and oversoty thin and broadcast burn. The two overstory plots are located above the road. All plots span the entire width of the old growth stand. Because of logistical restrictions, broadcast burning was assigned to the plots next to the road. The removal of the understory in treatment plots was performed in September 1998, while the burning (pile and broadcast burning) took place in March 1999.

Methods

Stand Function

Conifers respond to environmental change both by leaf-level physiological changes and by reallocating biomass among photosynthetic and respiratory tissues (Kaufmann 1979; Graham and Running 1984; Whitehead et al. 1984; Callaway et al. 1994a,b; See also Gower et al. 1995 and Pallardy et al. 1995). We are documenting changes in leaf- and tree-level water use in each species in response to treatment implementation as well as changes in foliage production, nitrogen content and water use efficiency.

Leaf production and Physiology

Branches of ponderosa pine (10-12 trees per treatment, one branch per treatment) were sampled in early September 2000 from all plots to determine foliage biomass for the three most recent foliage cohorts. Branches of western larch were also sampled and the dry weight of foliage removed from 30 cm long terminal branch sections was determined. Needles were detached and dried for 72 h at 65 C. The youngest fully mature leaf tissue for each ponderosa pine and western larch sampled were sent for analyses of total leaf nitrogen content and stable carbon isotope ratios. Stable carbon isotope data were used as long-term indicators of the ratio between leaf internal to ambient CO_2 concentrations (C_i/C_a) which is often correlated with water use efficiency (WUE, e.g. Marshall and Zhang 1994). Analyses were conducted at the Stable Isotope Laboratory of the University of Georgia, Athens and results were references to the Pee Dee Belemnite standard.

Whole-tree water use

Sap flow was measured using the heat pulse method, which uses pulses of heat as markers in the sap stream. Results from previous years (Sala and Callaway 2000) indicated that sap flow rates for ponderosa pine are generally so low that fall below the sensitivity level of the heat pulse method used here. Therefore the effect of the treatments on whole tree water use could not be detected. In contrast, western larch, a deciduous conifer with larger xylem vessel diameters, exhibits much higher sap flow rates. Consequently, during the 2000 summer we emphasized on water use in western larch as an indicator species of potential treatment effects on water availability and tree water use. Sap flow in western larch was monitored semi-continuously from June 1 to August 16, 2000, when the equipment was removed from the field due to the severe risk of wild fire. Measurements were resumed on September 18 until September 29, 2000. Sap flow was measured in at least 8 trees per treatment in the control, pile burn and broadcast burn treatments and in four trees in the overstory thin + pile burn and overstory thin + broadcast burn treatments. Concurrent with these measurements, sap flow was also measured in four Douglas-fir trees in the control plot. Sap flow for pines in the control, pile burn and broadcast burn treatments was measured from July 13 to July 18, 2000. During this period sap flow measurements for larch trees on these same treatments were interrupted due to lack of sufficient equipment to measure all trees at once. As for larches, eight pines were measured simultaneously per treatment.

Sap flow probes (Thermalogic, Pullman, Washington) consisted of two 1.25-mm needles inserted in the sapwood: a lower heater needle and an upper thermocouple needle installed 6 mm above the heater. Each thermocouple needle had three individual thermocouples regularly spaced along the length of the needle (so that the heat pulse was sensed at increasing sapwood depths). Probe lengths varied from 30 mm (inserted in the smallest trees) to 35 mm (inserted in the larger trees). Data loggers (Models CR10 and 21X, Campbell Scientific, Logan, Utah) were used to control the relays operating the heaters and record the data. One probe was inserted per tree on the west-side of the trunk at a height of approximately 2 m. Once installed, probes were insulated with 6-cm thick foam and wrapped with padded reflective material to minimize the effect of external temperature fluctuations. The convective velocity of a heat pulse (V) was calculated as (Cohen et al. 1981; Schiller and Cohen 1995):

$$V = (r^2 - 4\,k\,t_m)^{1/2} / t_m \qquad \text{(equation 1)}$$

Where r is the distance between the heater and the thermocouple needles (6 mm), k the thermal diffusivity of wet wood, and t_m the time to the maximum temperature rise following the heat pulse. When no sap flow takes place, V = 0 and equation 1 yields:

$$k = r^2 / 4t_{m0} \qquad \text{(equation 2)}$$

where t_{m0} is the time to maximum temperature rise at zero flow. Combining equations 1 and 2 yields:

$$V = r\,(1 - t_m/t_{m0})^{1/2} / t_m \qquad \text{(equation 3)}$$

Sap flux density at each sapwood depth (J_i) is calculated as:

$$J_i = V \rho c / \rho_w c_w \qquad \text{(equation 4)}$$

Where ρc and $\rho_w c_w$ are the volumetric specific heat of wood and water, respectively.

Zero sap flow conditions were assumed to occur at dawn (4 A.M., local time). The volumetric specific heat (Campbell et al. 1991) of wet wood was determined gravimetrically from sapwood samples taken in 6 trees of each species. For the purposes of this report our emphasis will be on relative differences in sap flow between the different treatments during each measurement period, rather than on absolute values.

Weather variables (relative humidity, air temperature, global radiation and wind velocity) were measured concurrently with sap flow measurements at 60 second intervals and averaged every 30 min. in a nearby clearing. Potential evapotranspiration (PET) was calculated from these measurements using the Penman-Monteith equation as modified by van Bavel (1966), which gives an estimate equivalent to open water evaporation under a given set of environmental conditions.

Soil moisture

Seasonal changes in soil moisture were monitored in each treatment with a Frequency-Domain Reflectometer. In each plot 15 to 2 inch diameter PVC pipe were inserted in the soil as deep as substrate conditions permit. Eight additional pipes were located outside each treatment plot to quantify the influence of the slope gradient (or microsite) on soil moisture. Soil moisture was measured periodically at 15, 30 and 40 cm deep during the growing season.

Data analyses

Treatment differences of tree water use were assessed by using maximum sap flow velocity (from 1400 to 1800) in the outer sapwood (where sap flow is highest). Water transport is typically higher in the outer, most recent sapwood and decreases in the inner sapwood. Therefore, maximum sap flow velocity in the outer sapwood will be used here as an indicator of maximum tree water transport. For simplicity, for western larch and Douglas-fir where measurements were semi-continuous, only selected days during the summer were analyzed for treatment differences (approximately weekly). Treatment differences in maximum sap flow velocity were analyzed using one way ANOVA per selected date. Treatment differences in soil moisture at each soil depth were analyzed using one way ANOVA per date. Similar separate analyses were performed for measurements outside each plot, which measure the effect of the slope gradient or microsite (the measures in the treatment plots indicate the combined effect of treatment and microsite). Treatment differences in foliage production of ponderosa pine were analyzed separately for each age cohort with a one way ANOVA. Differences between specific treatments were tested using the Least Significant Difference test. Data were log transformed when necessary to meet ANOVA assumptions of normality.

Results

Soil moisture within and outside each treatment plots was highest at 40 cm and lowest at 15 cm (Figures 1-3). For all treatments and soil depths, soil moisture was highest during late spring (May) and decreased gradually to minimum values in mid-August, prior to the first summer rain events. After precipitation events during late August, soil moisture in all treatments and soil depths increased (Figures 1-3). Consistent with our previous results (Sala and Callaway 2000), differences in soil moisture among treatments were largest at 40 cm depth (Figures 1-3). Therefore, analyses of results will focus on differences at 40 cm. Soil moisture from May to August at all soil depths outside (but adjacent to) treatment plots tended to be lower next to the control plot than next to the rest of the treated plots. As in previous years, these results suggest that there was a microsite effect which is independent of the treatment effect (Figures 1-3). However, at 40 cm depth differences in soil moisture between the 'outside plots' (plots adjacent to each treatment plot) were smaller than those inside the treatment plots suggesting a net treatment effect. Larger treatment differences inside the treated plots compared to those from outside plots were particularly apparent from the end of June (June 28) to the beginning of August (August 3; Figure 1). During this period, soil moisture at 40 cm depth within the control plot was significantly lower ($P < 0.05$) than within the rest of the treatment plots (Figure 1). This was also true for the outside plots, although differences between the outside plots were smaller than within the treatment plots and often not statistically significant thus indicating that the microsite effect was smaller than the treatment effect (i.e. that there was a net treatment effect; Figure 1). Overall, soil moisture at 40 cm depth tended to be higher in the treated plots where, in addition to the removal of the understory, the overstory had also been thinned (overstory thin + pile burn plot and overstory thin + broadcast burn plot) than in the treated plots where only the understory had been removed (pile burn and broadcast burn; Figure 1). These differences were larger within the treated plots than outside the treated plots suggesting again a net treatment effect. Differences in soil moisture at 40 cm depth between the treated plots where only the understory was removed (pile burn and broadcast burn) and between the treated plots where the overstory had been thinned (overstory thin + pile burn and overstory thin + broadcast burn) were generally not significant (Figure 1).

As in 1998 and 1999, maximum sap flow velocity during the summer of 2000 was much higher for larches than for pines or Douglas-firs (Figures 4 and 5). For simplicity, only maximum sap flow velocity at weekly intervals are shown for western larch and Douglas-fir. For western larch, maximum sap flow velocity was highest during clear days in June and declined as the summer drought advanced (Figure 4). Sap flow velocity in western larch declined substantially during cloudy days in response to lower evaporative demand. While during June sap flow velocity for western larch was similar in all plots, as the summer proceeded and soil moisture became limiting, sap flow velocity declined strongly in trees in the control plot to values significantly lower than for trees in the remaining treated plots (Figure 4). By the end of the season, sap flow for western larch trees in the control plots was similar to that for Douglas-fir. Overall there were no differences in maximum sap flow velocity between treated plots (understory removal and understory removal + overstory thin). Sapflow velocity for ponderosa pine (measured during mid-July) was generally below the accuracy level of the method used. Therefore, the differences we report here need to be taken with caution and only as a qualitative measure of potential treatment effects. On average, maximum sap flow velocity of ponderosa pines in the control plot were lower than in the pile-burn and broadcast burn plot (Figure 5). Differences were marginally significant ($P < 0.06$) only when the pile and broadcast burn treatments were combined. No differences in maximum sap flow could be detected between the pile burn and the broadcast burn treatments.

Foliage production in the two most recent needle cohorts of ponderosa pine at the end of the 2000 growing season was much higher for trees in the pile burn and broadcast burn plots than in the control plot (Figure 6; $P < 0.05$). For the third most recent needle cohort, needle biomass was also higher in the treated plots than in the control plot, but differences were not statistically significant. If, as for second growth ponderosa pine, on needle cohort is produced per year in these old growth trees, the three most recent needle cohorts were produced, from the youngest to the oldest, during the 2000, 1999 and 1998 growing seasons, respectively. Therefore, the two most recent needle cohorts where foliage production was significantly lower for trees in the control plot, were produced after treatments were applied. Foliage production for any of the three needle cohorts did not differ between ponderosa pines in the pile burn and broadcast burn treatments. Total length (Figure 7) and maximum diameter (not shown) of buds on terminal ponderosa pine branches sampled at the end of the growing season were also significantly smaller ($P < 0.01$) in trees in the control plot relative to trees in the pile burn and broadcast burn plots. Again, there were no differences in bud size between these two last treatments. For western larch, total foliage biomass along 30 cm long terminal branch sections tended to be lower for trees in the control plots relative to all other treatments (Figure 8). Differences, however, were not statistically different.

Needle nitrogen content in ponderosa pine was significantly higher ($P < 0.05$) in the broadcast burn plot relative to the pile burn and control plot (Figure 9). For western larch needle nitrogen content was significantly higher in trees of all treated plots relative to the control (Figure 9; $P < 0.05$). Carbon isotope ratio did not differ significantly between the control and treated plots for any of the two species studied (Figure 10).

Discussion

Our results indicate significant positive effects of the restoration treatments on soil water availability and performance of old growth ponderosa pine and western larch two growing seasons after treatments were applied. Pretreatment measurements generally indicated higher tree performance in the plots assigned to the control treatment relative to plots assigned to the pile burn and broadcast burn treatments (Sala and Callaway 2000). Unfortunately, no pre-treatment measurements were performed in the overstory thin + pile burn and overstory thin + broadcast burn treatments and we do not know how these treatments compared to the control plot before treatments were applied. Measurements during the first growing season after treatments were applied (1999) also indicated positive treatment effects on soil water availability and tree performance (Sala and Callaway 2000): at the end of the 1999 growing season there were significant increases in soil moisture in the treated plots relative to the control plots. However, soil moisture did not differ between the understory pile burn and broadcast burn treatments (soil moisture for the overstory thinning treatments was not measured until the end of the 1999 growing season). Consistent with increases in soil moisture in treated plots, maximum sap flow velocity for western larch during the 1999 summer was significantly higher in most treated plots relative to trees in the control plot (Sala and Callaway 2000). Sap flow velocity for ponderosa pine during 1999 was generally below the accuracy limits of the heat pulse technique we used and treatment differences were not detected. However, data on foliage production in ponderosa pine collected at the end of the 1999 growing season suggested that removal of the understory (followed by pile burning or broadcast burning) ameliorated foliage production (Sala and Callaway 2000).

Measurements during the 2000 growing season corroborated to a larger extent our results from the first growing season after treatment implementation: all restoration treatments had a positive effect on soil moisture (particularly at 40 cm of soil depth), and on tree performance. Increased performance for western larch in treated plots was evident from; 1) significantly higher sap flow during the driest part of the summer relative to control plots, 2) increase in foliar nitrogen content in trees from all treated plots relative to the control plots and 3) slightly higher foliage production (although not statistically significant) in trees from all treated plots relative to the control plot. For ponderosa pine, increased performance was reflected in: 1) higher sap flow in the treated plots relative to the control plot, 2) highly significant increases in foliage production and bud size in trees from the treated plots and 3) significantly higher leaf nitrogen content in the broadcast burn plot relative to the control and thin plots.

Soil moisture measured during May and June (wettest part of the season) outside each treatment (i.e. following the slope gradient where treatment plots are laid out, but not affected by the specific treatment) was lowest adjacent to the control plot located at the lower end of the slope gradient (Figures 1-3). While higher soil moisture down the slope is counterintuitive, these results are consistent with those obtained during the 1998 and 1999 growing seasons. Differences in soil texture and microtopography may explain higher soil relative water content in the control plot. However, we found that differences in soil moisture due to the slope gradient were generally smaller than those found in the treated plots, indicating that there was a net treatment effect on soil moisture, particularly at 40 cm depth. The consistent tendency of higher soil moisture in the plots subjected to overstory thinning and understory removal by either pile burn or broadcast burn relative to plots subjected only to understory removal, suggests that the decrease in tree density in plots where the overstory was thinned resulted in increased soil water availability. However, microsite alone influenced soil moisture as measurements taken adjacent to the treated plots indicated also a tendency (although generally not significant) for higher soil moisture in the overstory thin + undertory removal plots. The slight increase in soil moisture in the plots where the overstory was thinned did not translate into higher water use in western larch in these plots relative to those in plots where only the understory was removed (Figure 4). Overall, treatment effects on soil moisture during the 2000 growing season were smaller than those measured during 1999. This may be due to a combination of factors including an unusually dry season and the fact that treatment-induced growth (Figures 6-8) and water use (Figures 4 and 5) may partially offset the effects of the understory removal on soil water resources.

The increases in soil relative water content in the treated plots relative to the control plot were most apparent during July and beginning of August. Consistent with these results, sap flow of western larch was similar for all plots in June, but declined strongly for trees in the control plot during July and August while it remained high in all treated plots. Lower water use in larches in the control plot suggests strong competition for water with the understory (Figure 4). Similarly, sap flow for old growth ponderosa pine in the control plot in July was somewhat lower than in the treated plots (Figure 5) suggesting again competition of water between the understory and the old growth trees. Our results during the dry 2000 season showed that although water use by individual Douglas-fir trees was low, the high density of Douglas fir trees in the understory of the control plot significantly reduced water availability for old growth ponderosa pine and western larch (Figures 4 and 5). Overall, however, sap flow of ponderosa pine and western larch was not affected by the specific restoration treatment. This is not surprising, however, because the understory, which is what competes for water with the old growth trees was removed in all treatments.

Increased water transport for old growth ponderosa pines in treated plots was accompanied by strong increases in foliage production and terminal bud size relative to trees in the control plot (Figures 6 and 7). These results and the fact that prior to the implementation of the restoration treatments foliage production tended to be higher in trees in the control plot (Sala and Callaway 2000) clearly demonstrate that the restoration treatments strongly ameliorated old growth ponderosa pine performance. However, as for water use, the type of restoration treatment did not affect foliage production of ponderosa pine. This is in contrast with the fact that nitrogen content of ponderosa pine foliage was significantly higher for trees in the broadcast burn plot relative to the control and thin plots (Figure 9). This suggests that the most limiting factor for ponderosa pine growth during the dry 2000 season was water rather than nitrogen. For western larch we did not find significant differences in foliage production between trees in the control plot relative to the treated plots (although values were lower for the control plot; Figure 8). However, our estimates of foliage production for western larch, a deciduous species, were very coarse. Further, the 2000 growing season was very dry and leaf senescence may have occurred prior to our harvest at the end of the summer thus obscuring potential treatment differences. Higher nitrogen content in western larch foliage in all treated plots relative to the control plot also indicate that the restoration treatments had a positive effect on western larch resource availability.

The observed increase in leaf nitrogen content in response to the restoration treatments is an additional positive response that was not observed at the end of the 1999 season (Sala and Callaway 2000). These results suggest that old growth trees respond slowly to increase nitrogen availability in response to understory removal (i.e. release from competition) or to fire. We have no immediate explanation for the fact that ponderosa pine leaf nitrogen responded to the specific restoration treatment (i.e. it increased only in the broadcast burn plot) but western larch responded to all treatments (Figure 9). While DeLuca (2001) reported higher soil ammonium in the treated plots (pile burn and broadcast burn) relative to the control during the 1999 growing season, at the end of the 1999 growing season only understory shrubs in the broadcast burn treatment exhibited increased leaf nitrogen (Sala and Callaway 2000). The differential response to the specific restoration treatment between ponderosa pine and western larch, may indicate that ponderosa pine nitrogen uptake is more responsive to fire than to removal of the understory, while the reverse is true for western larch. Future measurements of leaf nitrogen will indicate whether the responses observed in 2000 persist and whether they relate to the different physiology of the two species.

The lack of differences in leaf carbon isotope ratio between treatments (Figure 10) are not surprising. Stable carbon isotope ratios are long-term indicators of the ratio between leaf internal to ambient CO_2 concentrations (C_i/C_a) which is often correlated with water use efficiency (WUE, e.g. Marshall and Zhang 1994). It is possible that the observed increase in leaf nitrogen content (which is likely related to increased photosynthesis rates and to decreases of leaf internal CO_2 concentration) may have offset increases of water use (which is likely associated with increases of stomatal conductance and leaf internal CO_2 concentration). In other words, increased water use in treated plots would translate to decreased water use efficiency and to lower (more negative) carbon isotope ratios only if leaf photosynthesis remains unchanged. However, increases in nitrogen suggest that photosynthesis may differ between the treatments as reported in other similar studies (Feeney et al. 1998).

While we observed a strong positive effect of the understory removal on the overstory old growth trees, we did not see consistent differences between specific restoration treatments. The only exceptions were a tendency in the overstory thin treatments to have higher soil moisture and increased leaf nitrogen in ponderosa pine in the broadcast burn treatment). Additional measurements of soil moisture, tree water use, foliage function and production during successive growing seasons are needed to determine whether the effects we observed are maintained in the long term and whether responses in the long term are treatment- and species-specific.

The results reported here are very similar to those reported by Feeney et al. (1998) and Stone et al. (1999) for southwestern old growth ponderosa pine. These authors concluded that restoration thinning (of the understory) increased water uptake and nitrogen of presttlement trees and that these changes contributed to greater rates of photosynthesis and stem radial growth. These authors also reported small differences between thinning and thinning + burning treatments.

Acknowledgements

Funding was supported by funds provided by the Rocky Mountain Research Station and the Bitterroot Ecosystem Management Research Project of the Forest Service, U.S. Department of Agriculture. We are very thankful to Mick Harrington for all the logistical support and to Judy Perkins, Gregory Grallo, Jeremy Moran, Mauren O'Mara, and Molly White for their help in the field and with the sample processing.

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Figure Legends

Figure 1. Soil relative water content (% weight) at 15cm below the surface during 2000 (post-treatment) within the treatment plots (left) and outside each treatment plot (right). Treatments are: control (open triangles), understory removal by pile burn (P-Burn, open squares), understory removal by broadcast burn (B-Burn, open circles), overstory thin with understory removal followed by pile burning (O-PBurn, shaded squares) and overstory thin with understory removal followed by broadcast burning (O-BBurn, shaded circles). Bars are standard errors of the mean (N=15-20 per treatment and date). Within a given date, significant differences between the control plot and the rest of treated plots are indicated with a star.

Figure 2. Soil relative water content (% weight) at 30 cm below the surface during 2000 (post-treatment) within the treatment plots (left) and outside each treatment plot (right). Treatments are: control (open triangles), understory removal by pile burn (P-Burn, open squares), understory removal by broadcast burn (B-Burn, open circles), overstory thin with understory removal followed by pile burning (O-PBurn, shaded squares) and overstory thin with understory removal followed by broadcast burning (O-BBurn, shaded circles). Bars are standard errors of the mean (N=15-20 per treatment and date). Within a given date, significant differences between the control plot and the rest of treated plots are indicated with a star.

Figure 3. Soil relative water content (% weight) at 40 cm below the surface during 2000 (post-treatment) within the treatment plots (left) and outside each treatment plot (right). Treatments are: control (open triangles), understory removal by pile burn (P-Burn, open squares), understory removal by broadcast burn (B-Burn, open circles), overstory thin with understory removal followed by pile burning (O-PBurn, shaded squares) and overstory thin with understory removal followed by broadcast burning (O-BBurn, shaded circles). Bars are standard errors of the mean (N=15-20 per treatment and date). Within a given date, significant differences between the control plot and the rest of treated plots are indicated with a star.

Figure 4. Maximum sap flow velocity for Douglas-fir (black triangles) and western larch in the different treatments (control, open triangles; pile burn open squares; broadcast burn open circles,

overstory thin + understory pile burn, shaded squares; and overstory thin + broadcast burn, shaded circles) during the 2000 growing season (date in Julian day). Bars are standard errors of the mean (N=5-8 per treatment). Arrows indicate cloudy days followed by precipitation events. Stars indicate statistically significant differences between control and treated plots for western larch.

Figure 5. Maximum sap flow velocity for ponderosa pine during July 2000 (two growing seasons post-treatment) in the control plot (C) and the two restoration treatment plots: understory removal by pile burn (PB) and by broadcast burn (BB). Bars are standard errors of the mean (N=3-8). When the pile burn and broadcast burn treatments were combined, differences were marginally significant (P = 0.06).

Figure 6. Foliage biomass of consecutive leaf cohorts of ponderosa pine in the control (black bars), understory removal by pile burn (P-Burn, gray bars) and by broadcast burn (B-Burn, white bars) plots at the end of the 2000 growing season (two seasons post-treatment). Bars are standard errors of the mean (N=8-10). Within a given leaf cohort, different letters indicate statistically significant differences (LSD, P < 0.05).

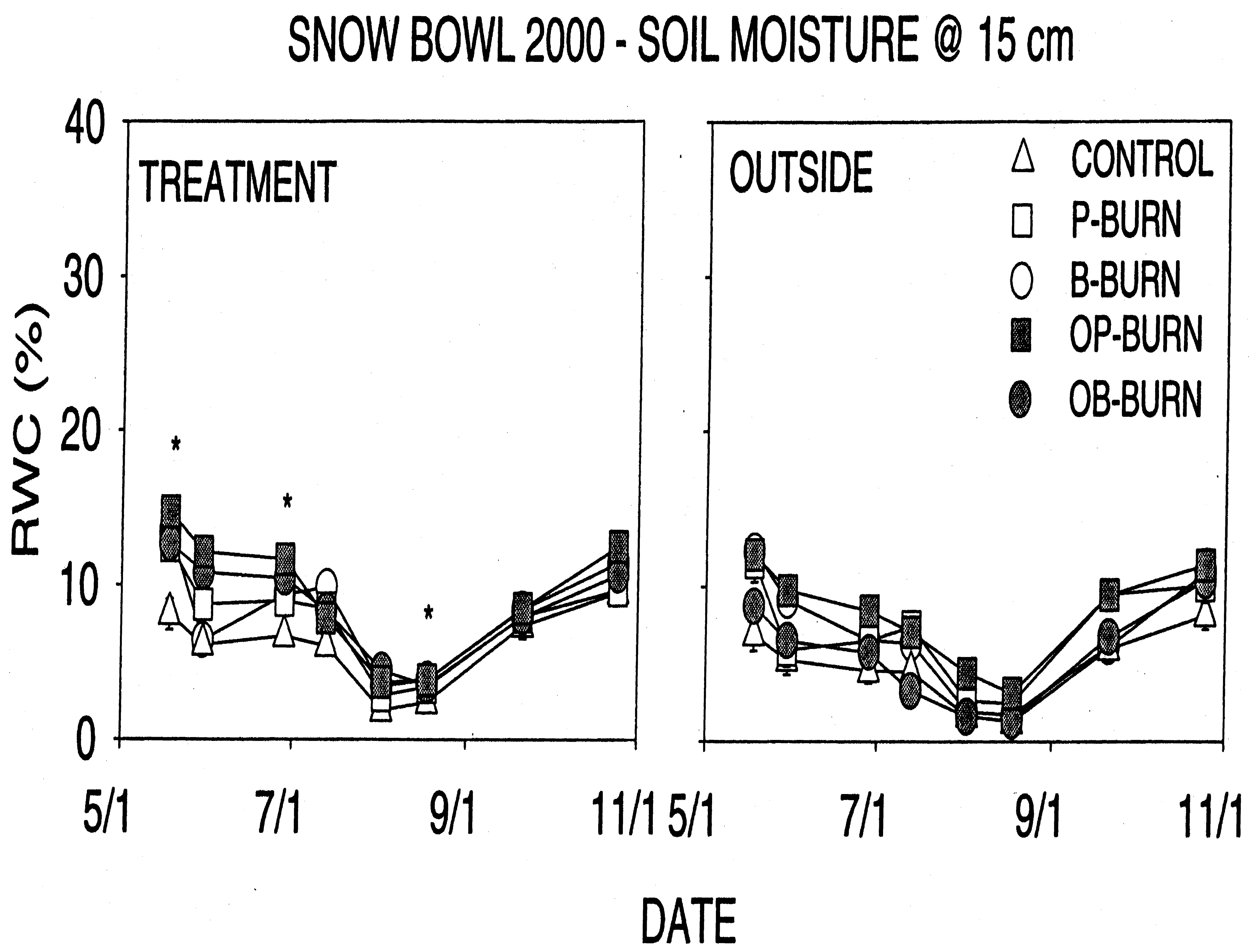
Figure 7. Terminal bud length of ponderosa pine branches in the control, understory removal by pile burn (PB) and by broadcast burn (BB) plots at the end of the 2000 growing season (two seasons post-treatment). Bars are standard errors of the mean (N=8-10). Different letters indicate statistically significant differences (LSD, P < 0.05).

Figure 8. Foliage biomass along 30 cm terminal branch sections of western larch in the control, understory removal by pile burn (PB), by broadcast burn (BB), overstory thin + pile burn (OPB) and overstory thin and broadcast burn (OBB) plots at the end of the 2000 growing season (two seasons post-treatment). Bars are standard errors of the mean (N=8-10).

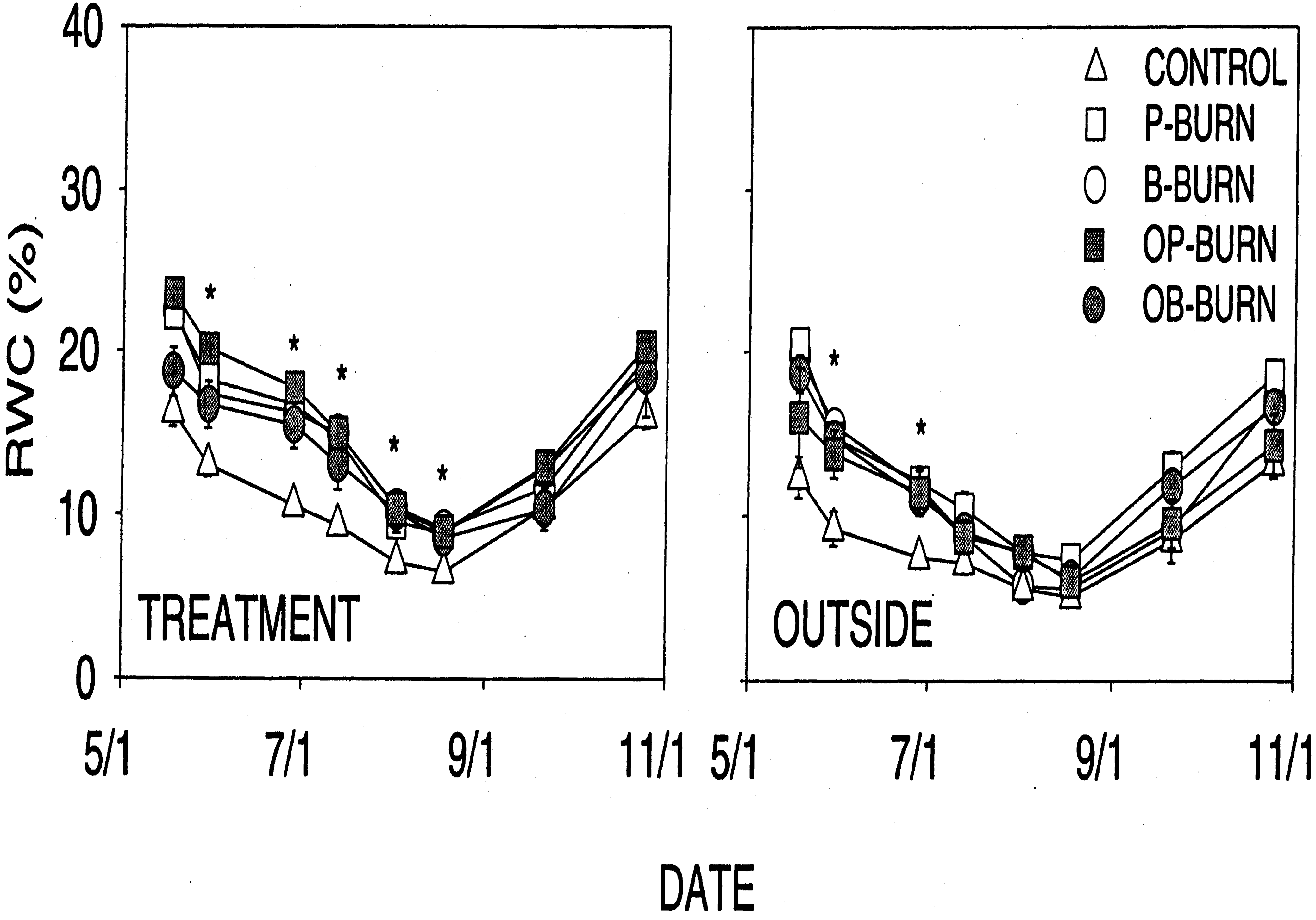
Figure 9. Leaf nitrogen content of Ponderosa pine (white bars) and western larch (shaded bars) at the end of the 2000 growing season (two seasons after treatment) for the control (C), pile burn (PB), broadcast burn (BB), overstory thin+ pile burn (O-PB) and overstory thin + broadcast burn

(O-BB) plots. Bars are standard errors of the mean (N=8-10). Within a species, different letters indicate statistically significant differences (LSD, $P < 0.05$).

Figure 10. Stable carbon isotope ratios of Ponderosa pine (white bars) and western larch (shaded bars) at the end of the 2000 growing season (two seasons after treatment) for the control (C), pile burn (PB), broadcast burn (BB), overstory thin+ pile burn (O-PB) and overstory thin + broadcast burn (O-BB) plots. Bars are standard errors of the mean (N=8-10).


SNOW BOWL 2000 - SOIL MOISTURE @ 15 cm
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
RWC (%)
0
10
20
30
40
5/1
7/1
9/1
11/1
DATE

SNOW BOWL 2000 - SOIL MOISTURE @ 30 cm



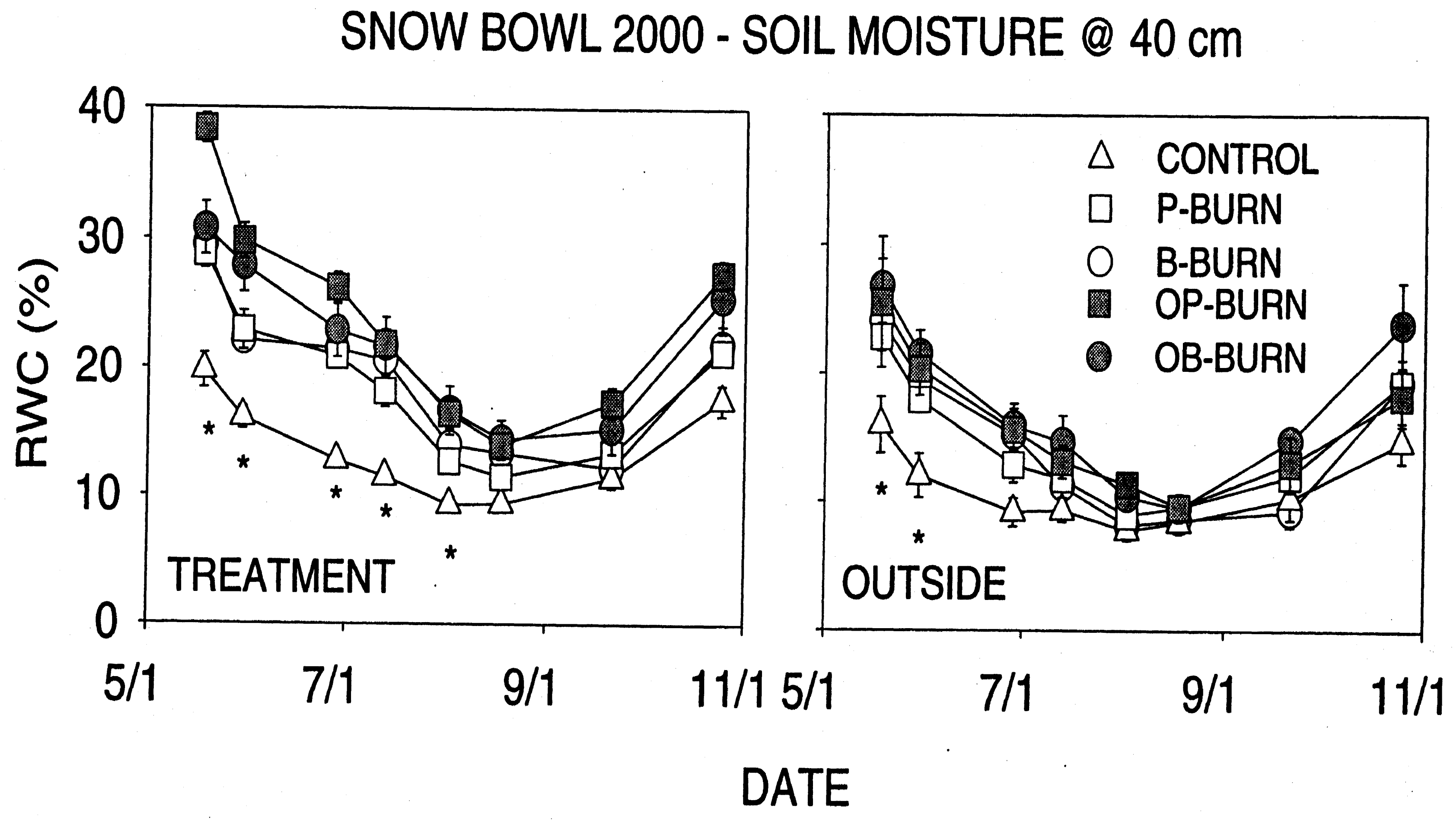

SNOW BOWL 2000 - SOIL MOISTURE @ 40 cm
RWC (%)
40
30
20
10
0
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
5/1
7/1
9/1
11/1
DATE

FIGURE 3

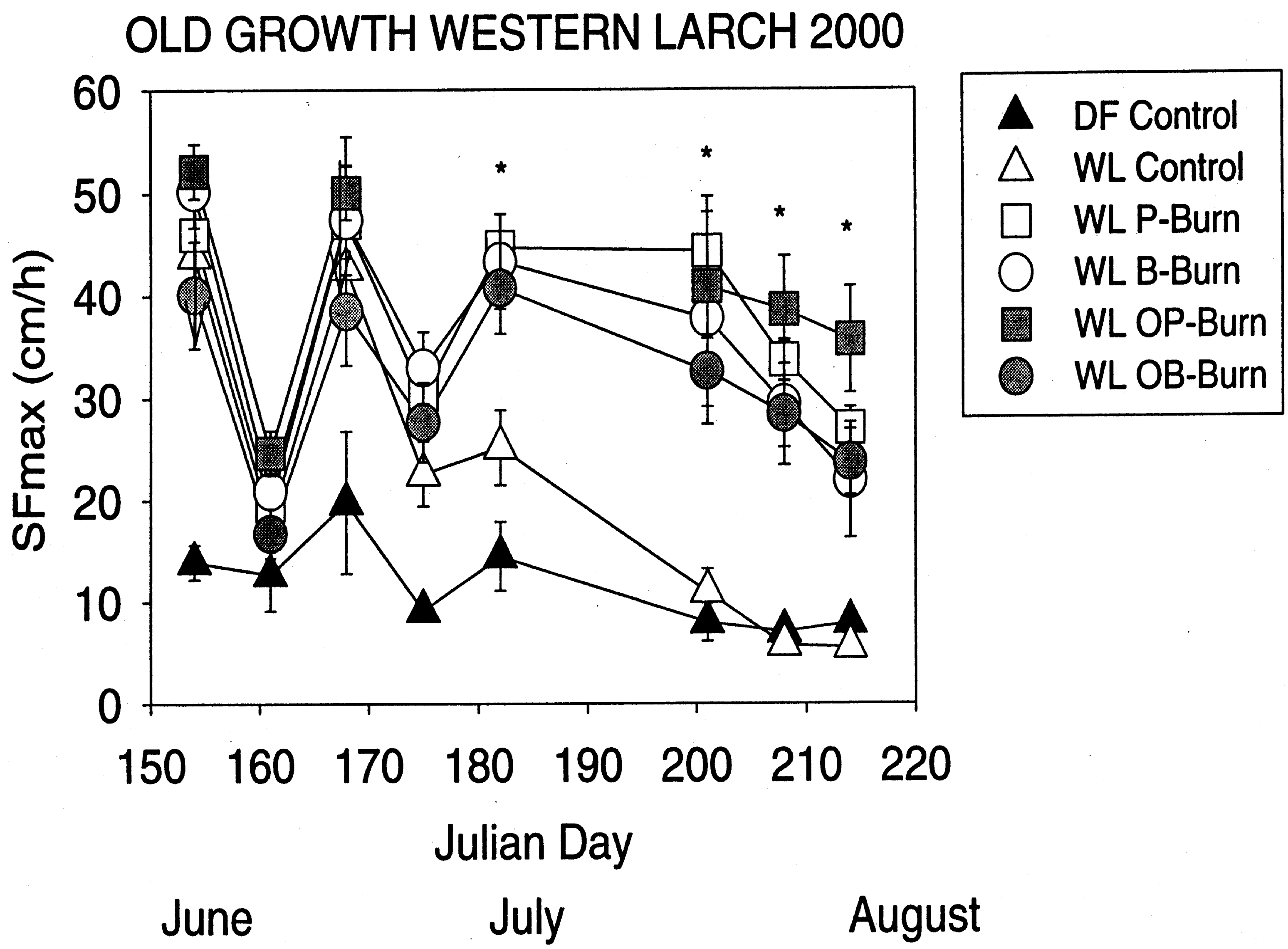
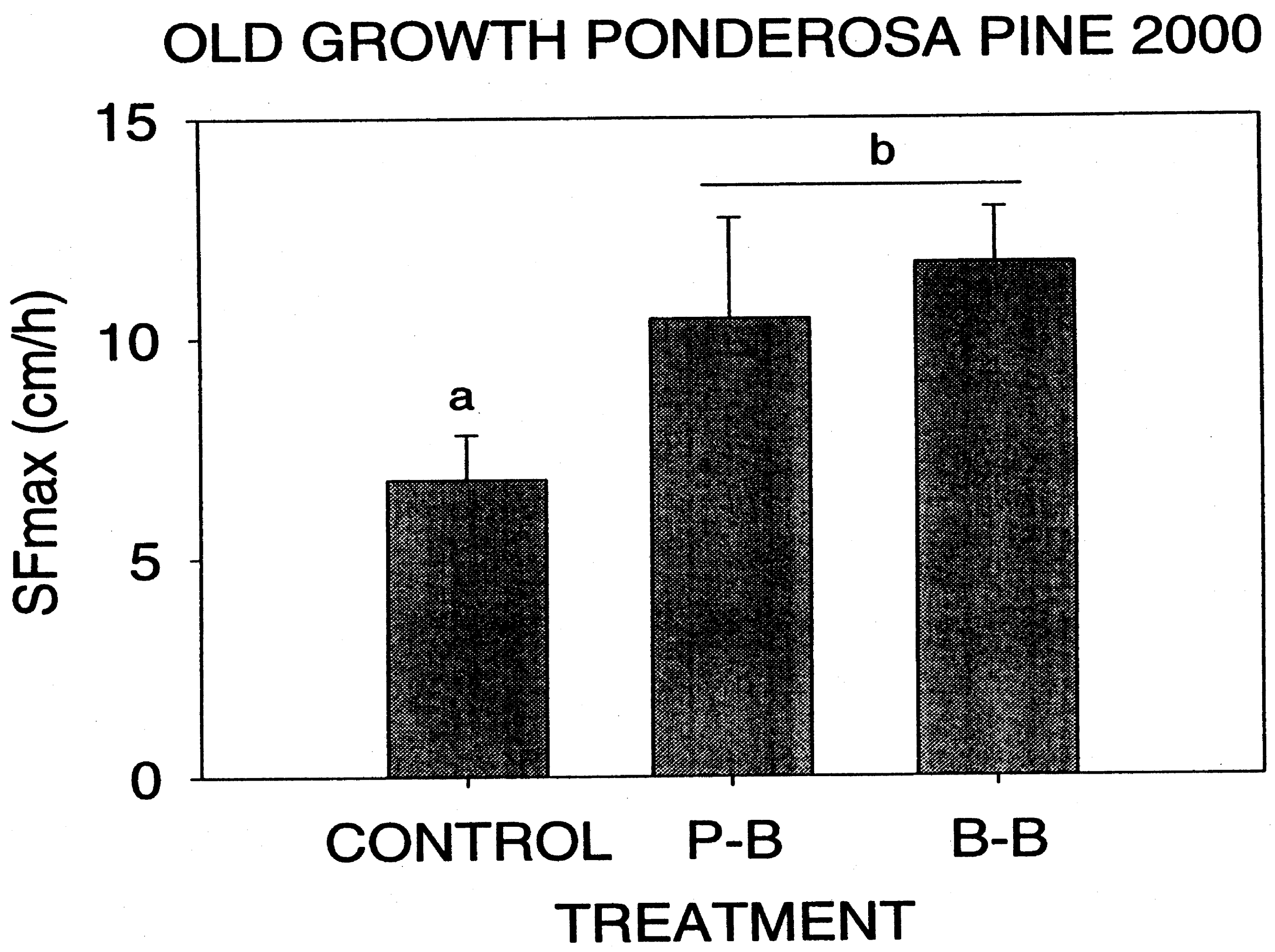
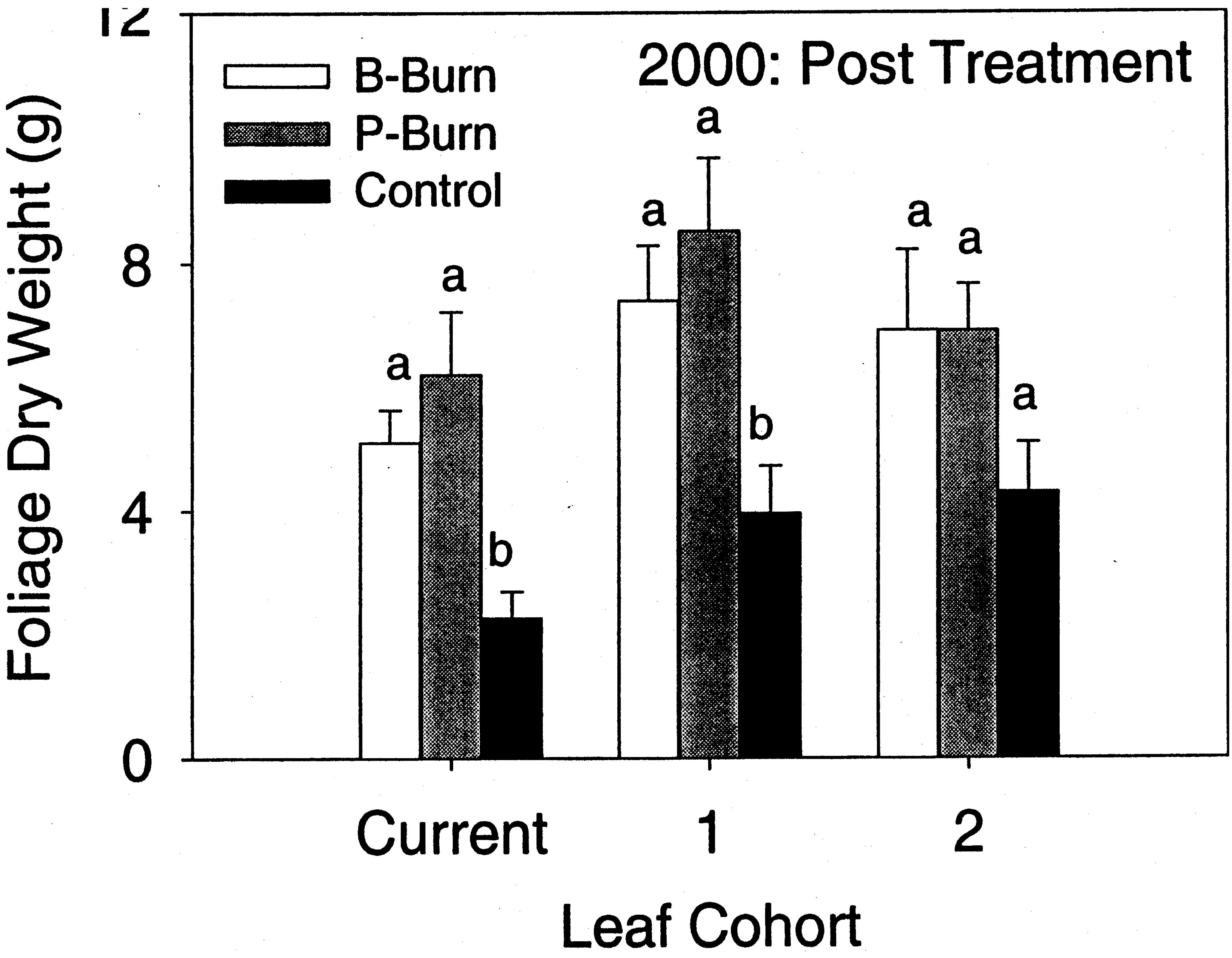
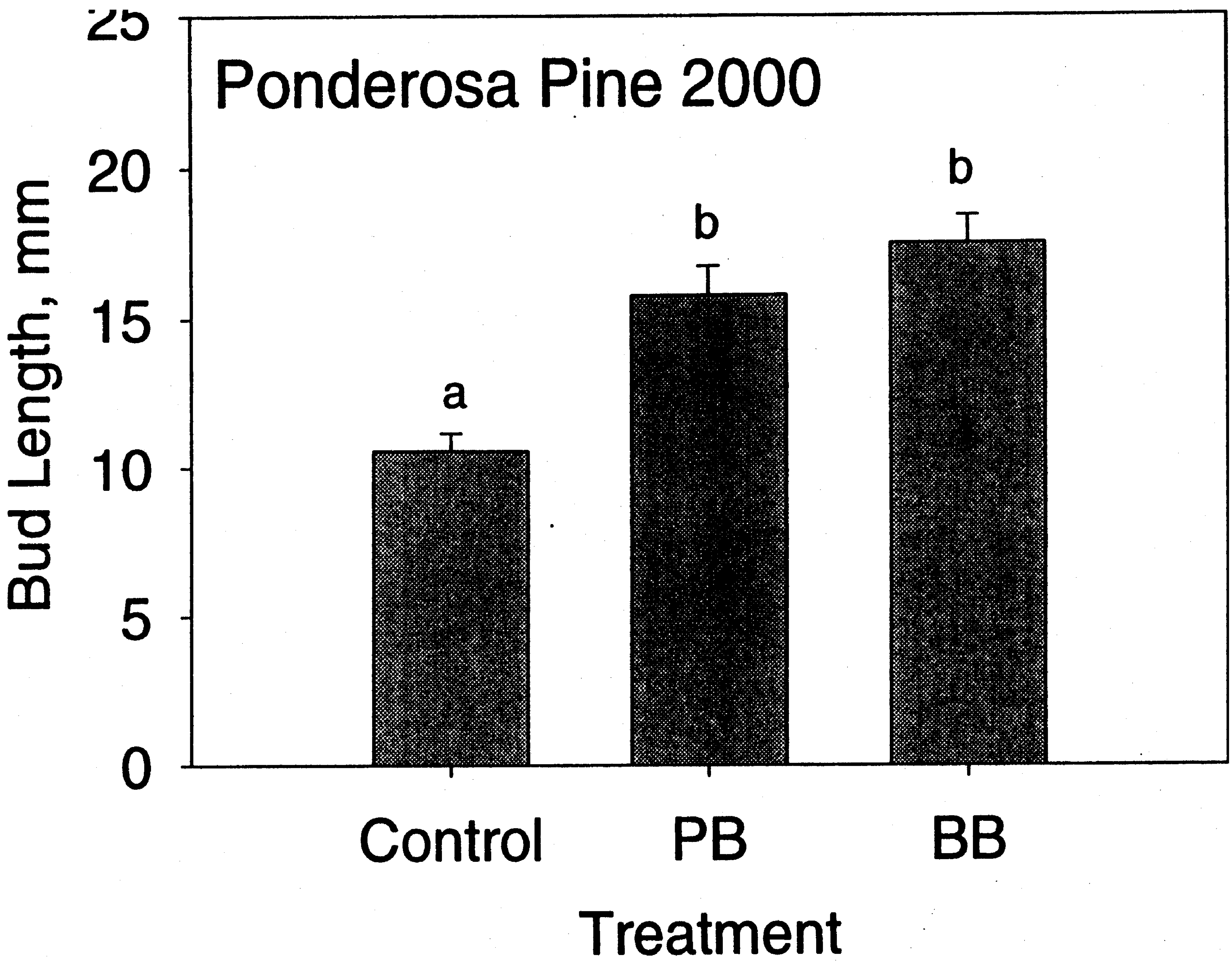

OLD GROWTH WESTERN LARCH 2000
SFmax (cm/h)
0
10
20
30
40
50
60
150
160
170
180
190
200
210
220
Julian Day
June
July
August
*
*
*
*
DF Control
WL Control
WL P-Burn
WL B-Burn
WL OP-Burn
WL OB-Burn

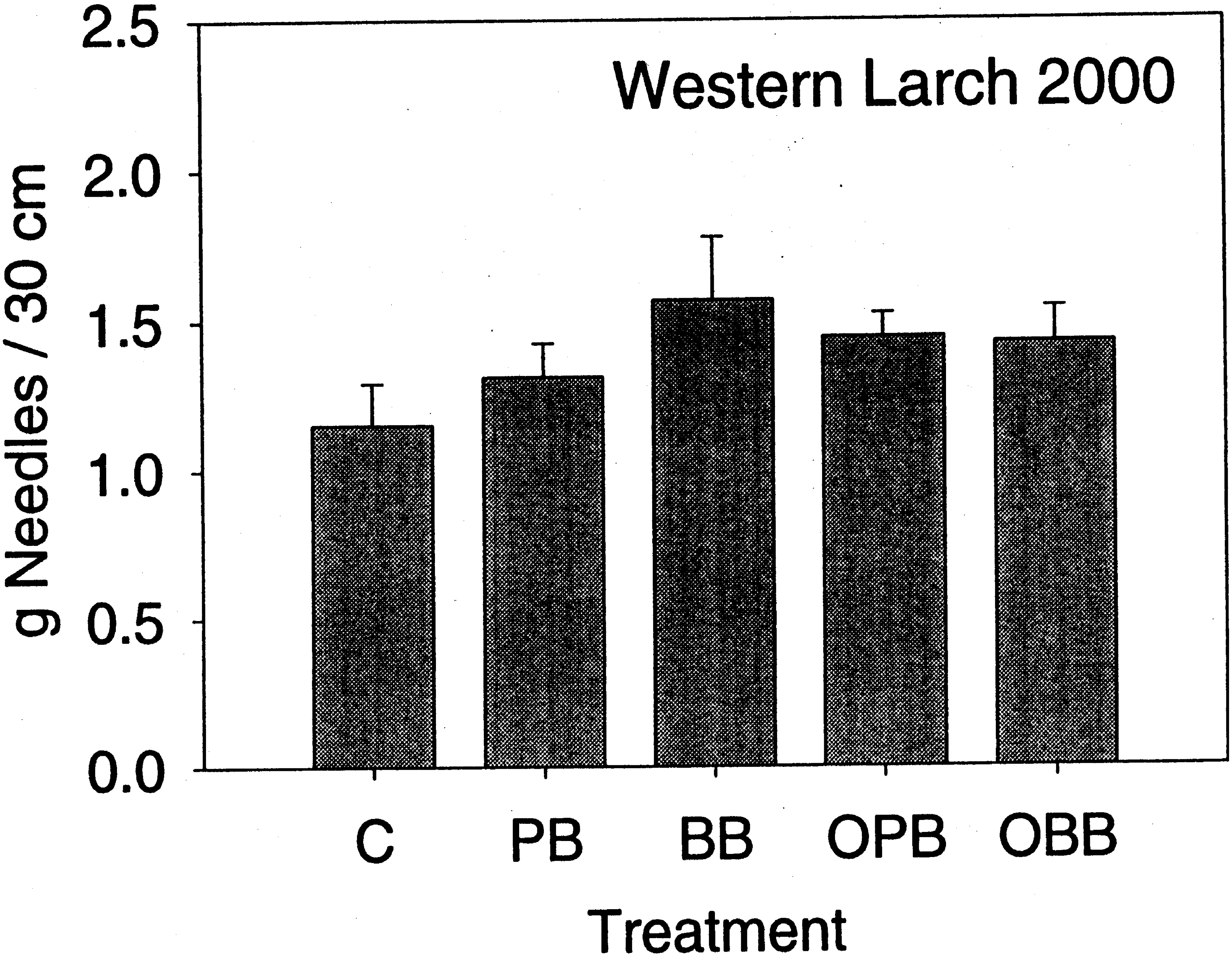
FIGURE 4

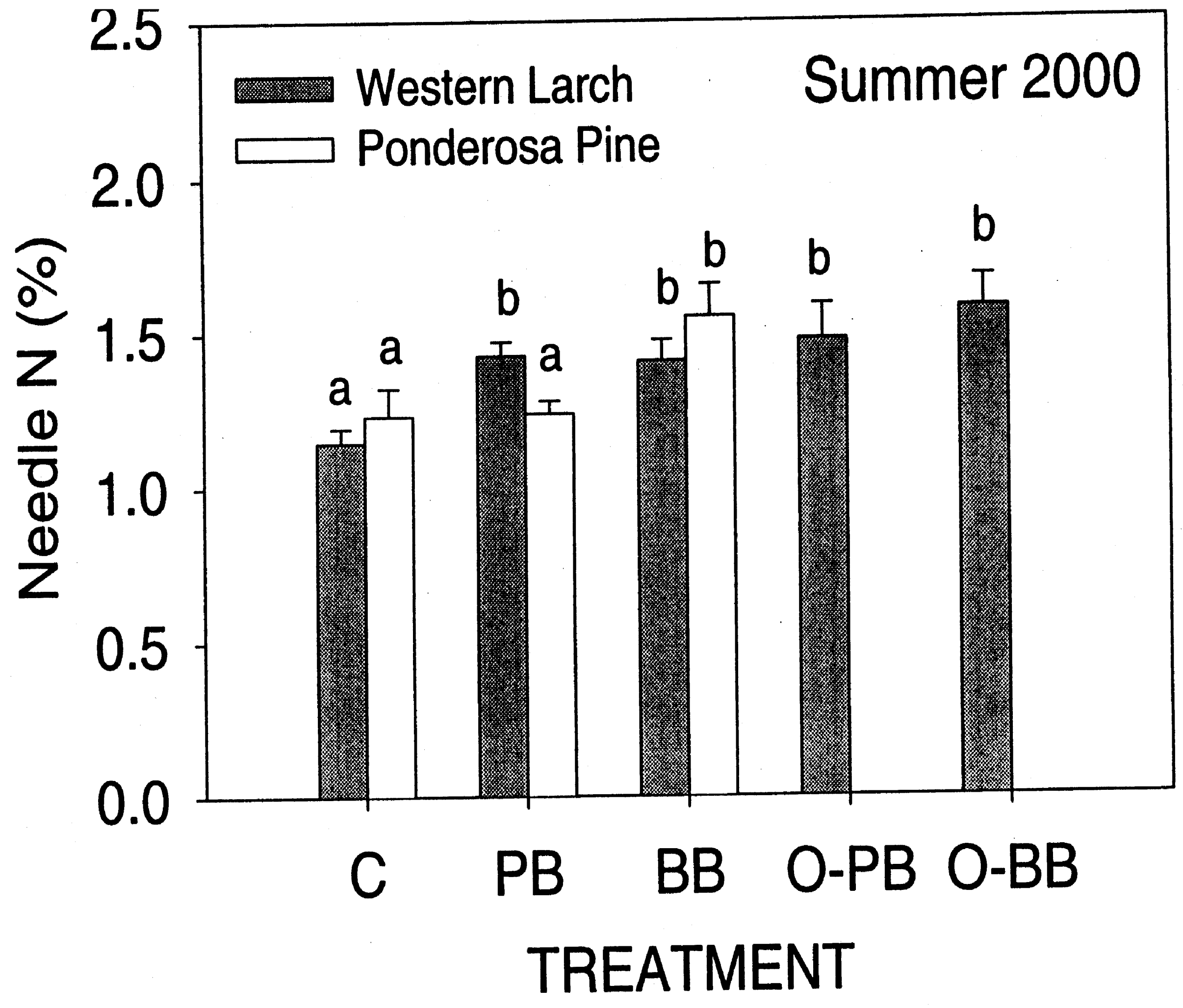

OLD GROWTH PONDEROSA PINE 2000
SFmax (cm/h)
15
10
5
0
a
b
CONTROL
P-B
B-B
TREATMENT



2000: Post Treatment
B-Burn
P-Burn
Control
Foliage Dry Weight (g)
12
8
4
0
a
a
b
a
a
b
a
a
a
Current
1
2
Leaf Cohort


Ponderosa Pine 2000
Bud Length, mm
25
20
15
10
5
0
a
b
b
Control
PB
BB
Treatment


Western Larch 2000
g Needles / 30 cm
2.5
2.0
1.5
1.0
0.5
0.0
C
PB
BB
OPB
OBB
Treatment



Western Larch
Ponderosa Pine
Summer 2000
Needle N (%)
2.5
2.0
1.5
1.0
0.5
0.0
a
a
b
a
b
b
b
b
C
PB
BB
O-PB
O-BB
TREATMENT

FIGURE 9

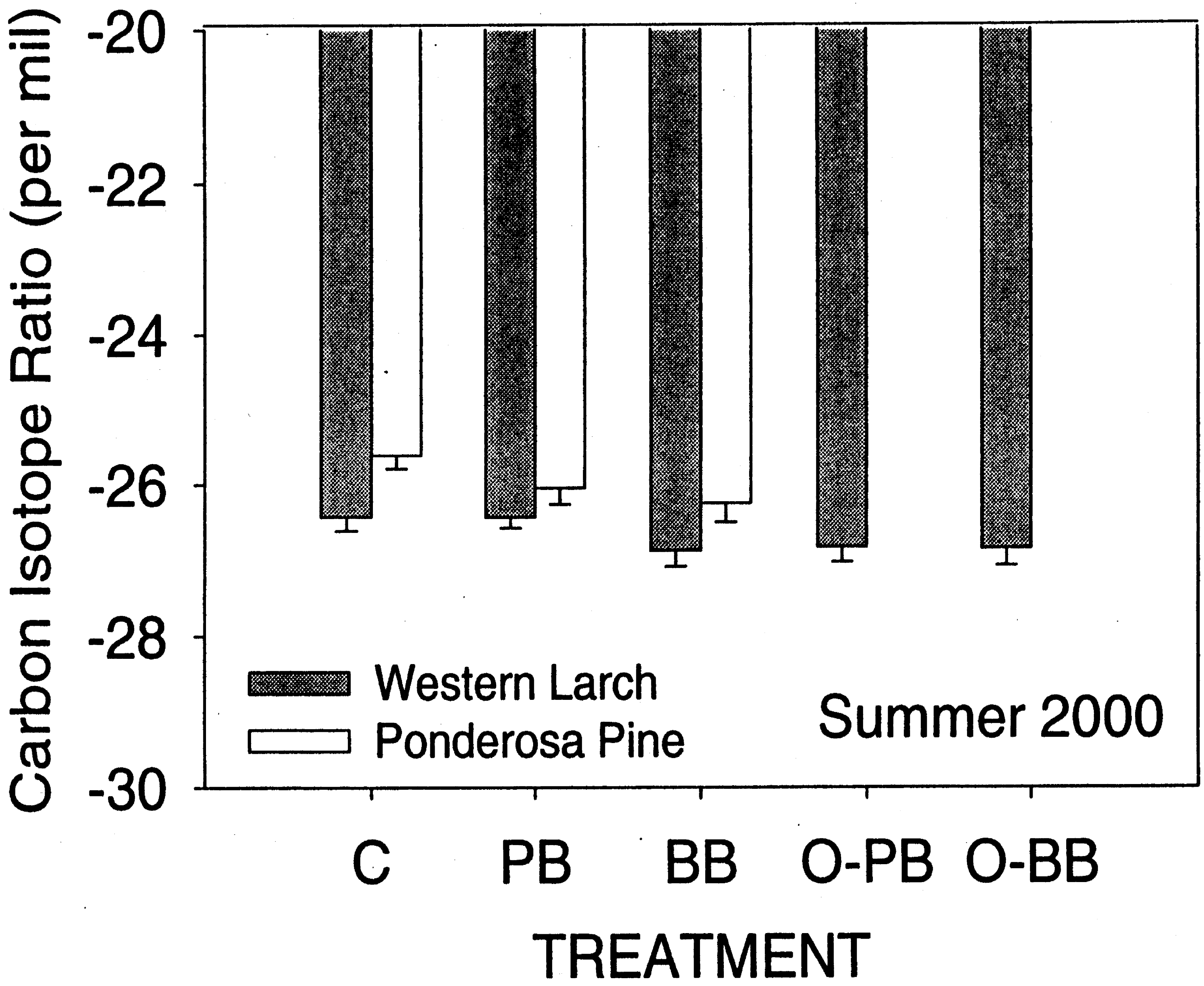

Carbon Isotope Ratio (per mil)
-20
-22
-24
-26
-28
-30
Western Larch
Ponderosa Pine
Summer 2000
C
PB
BB
O-PB
O-BB
TREATMENT

FIGURE 10

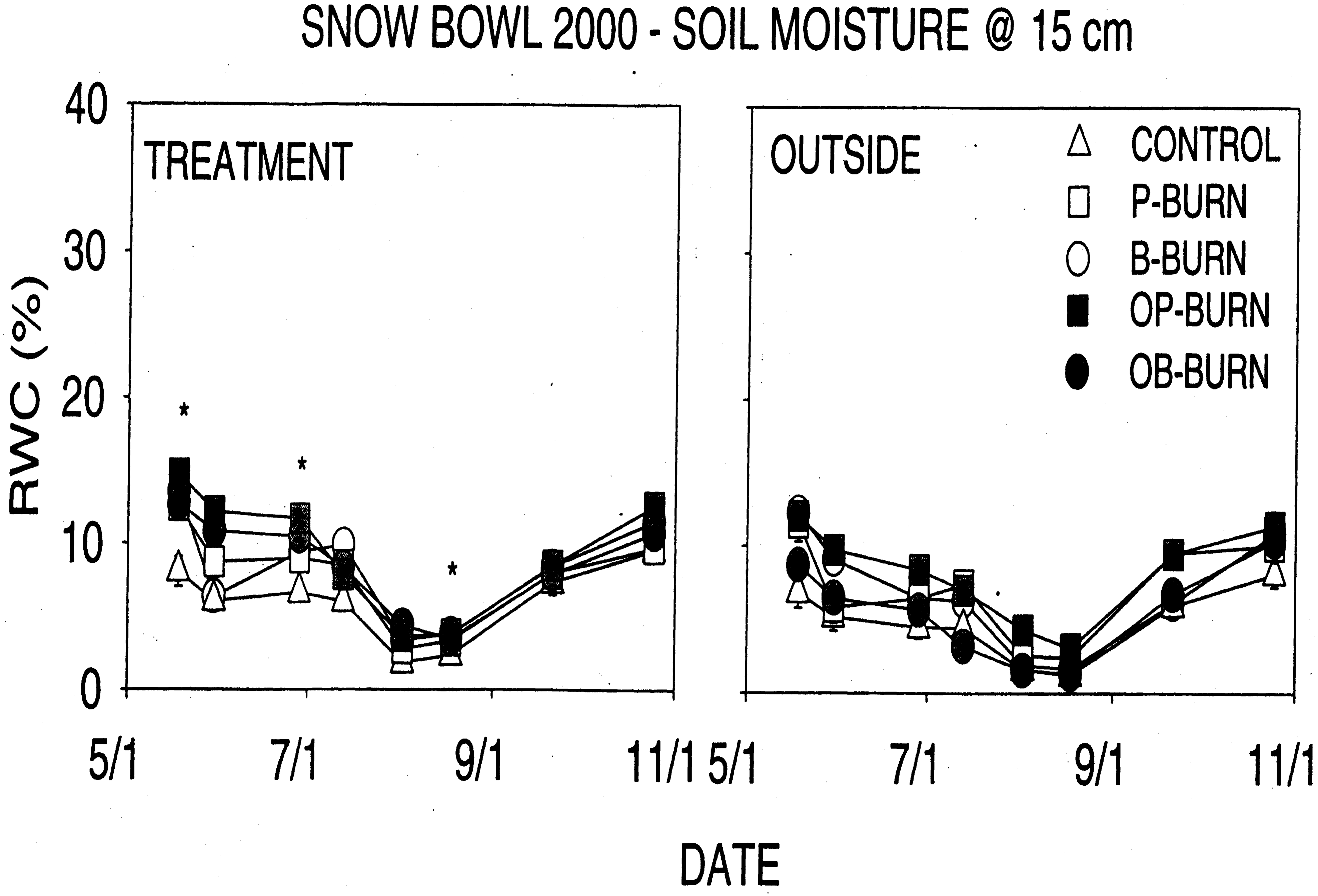

SNOW BOWL 2000 - SOIL MOISTURE @ 15 cm
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
RWC (%)
40
30
20
10
0
*
5/1
7/1
9/1
11/1
DATE

FIGURE 1

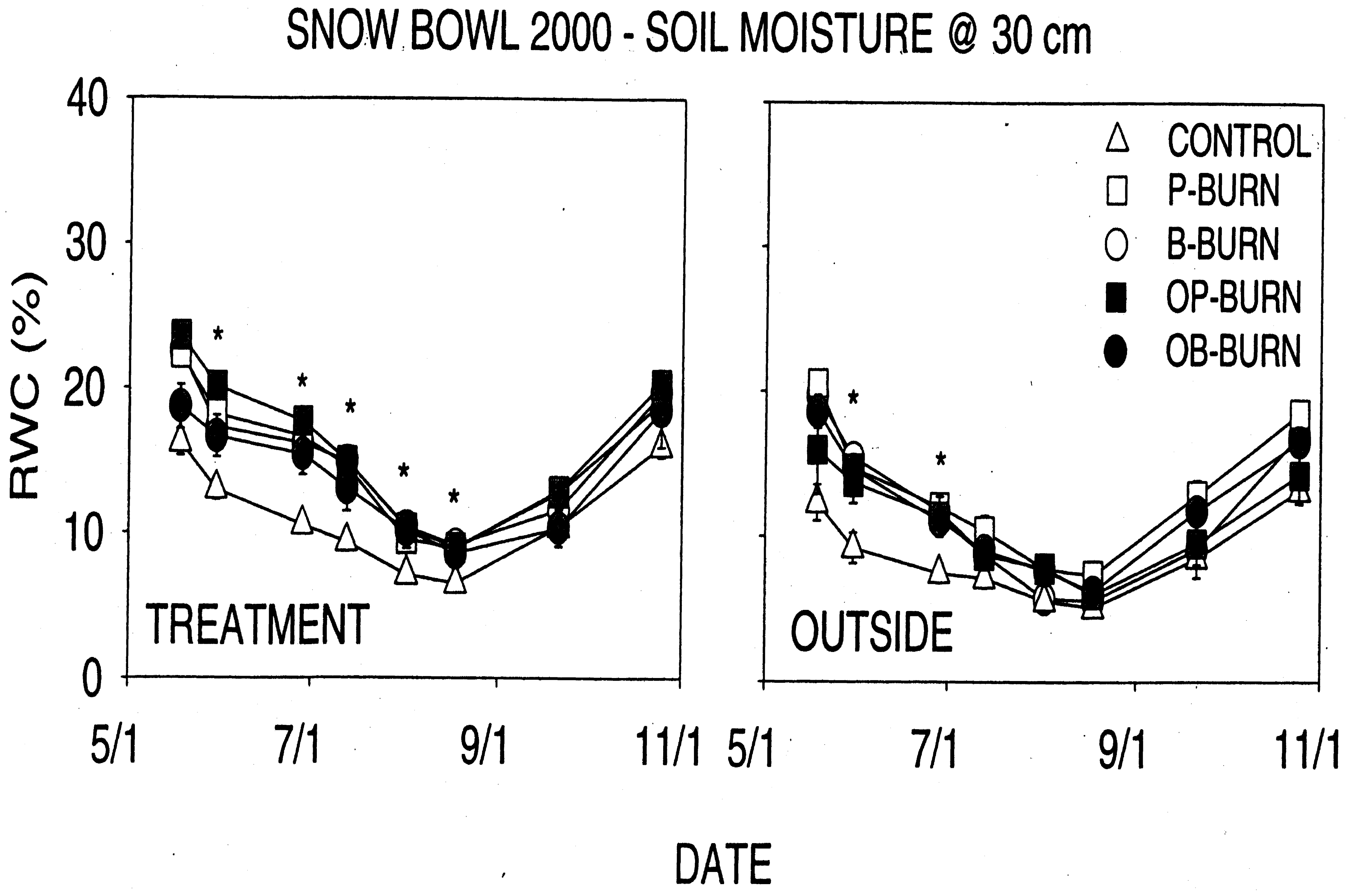

SNOW BOWL 2000 - SOIL MOISTURE @ 30 cm
RWC (%)
40
30
20
10
0
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
5/1
7/1
9/1
11/1
DATE

FIGURE 2

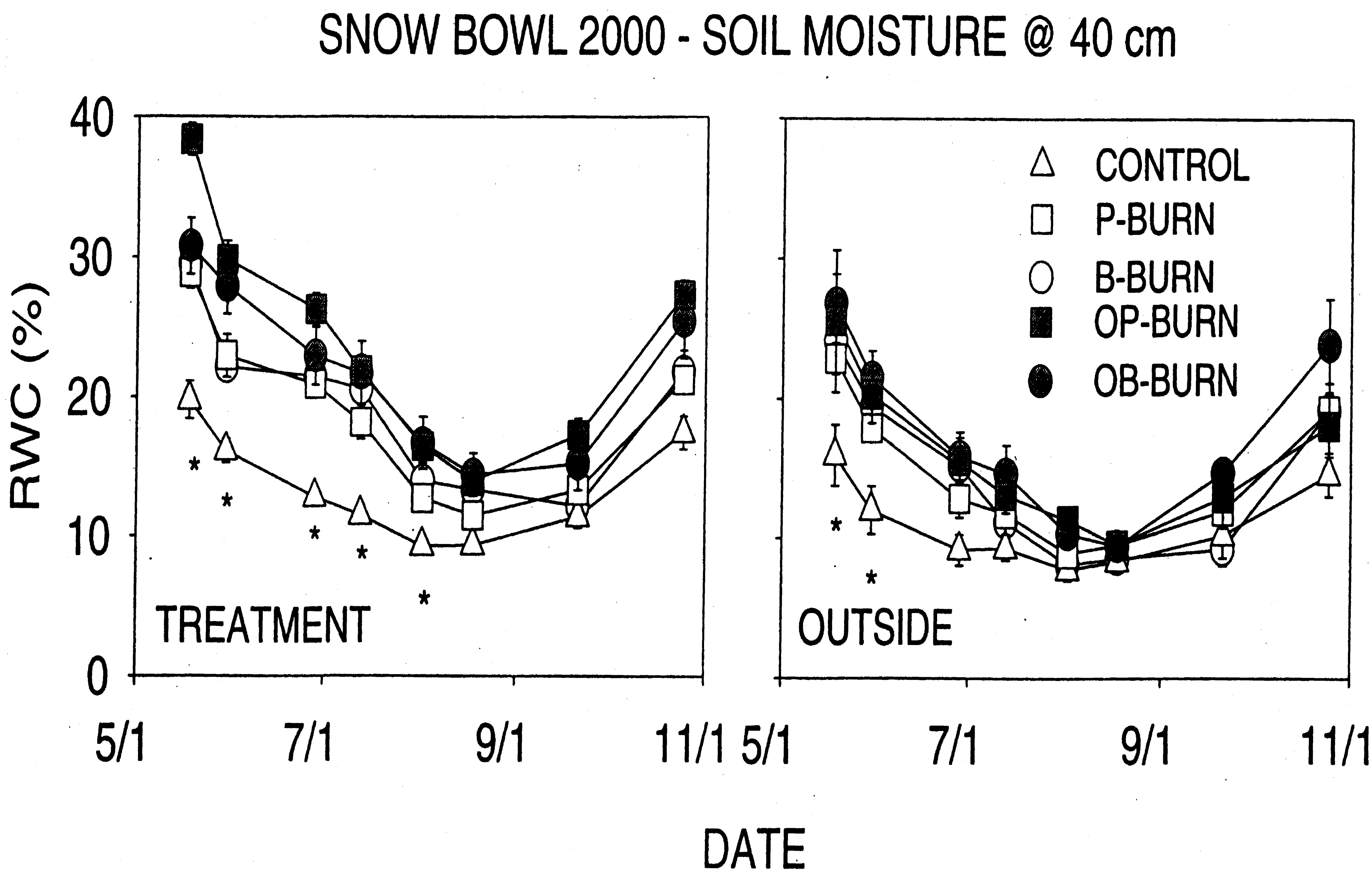

SNOW BOWL 2000 - SOIL MOISTURE @ 40 cm
RWC (%)
40
30
20
10
0
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
5/1
7/1
9/1
11/1
DATE

FIGURE 3

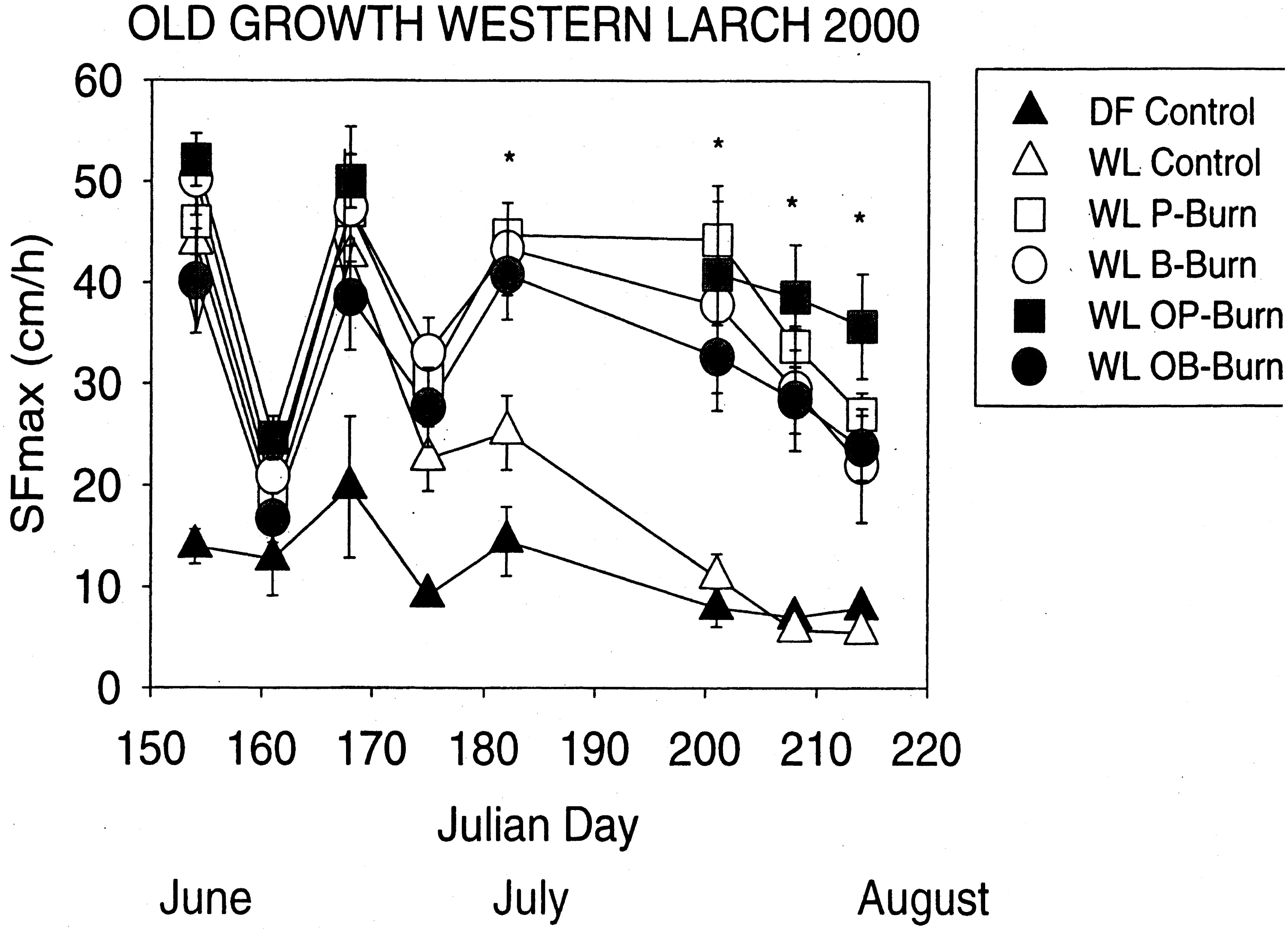
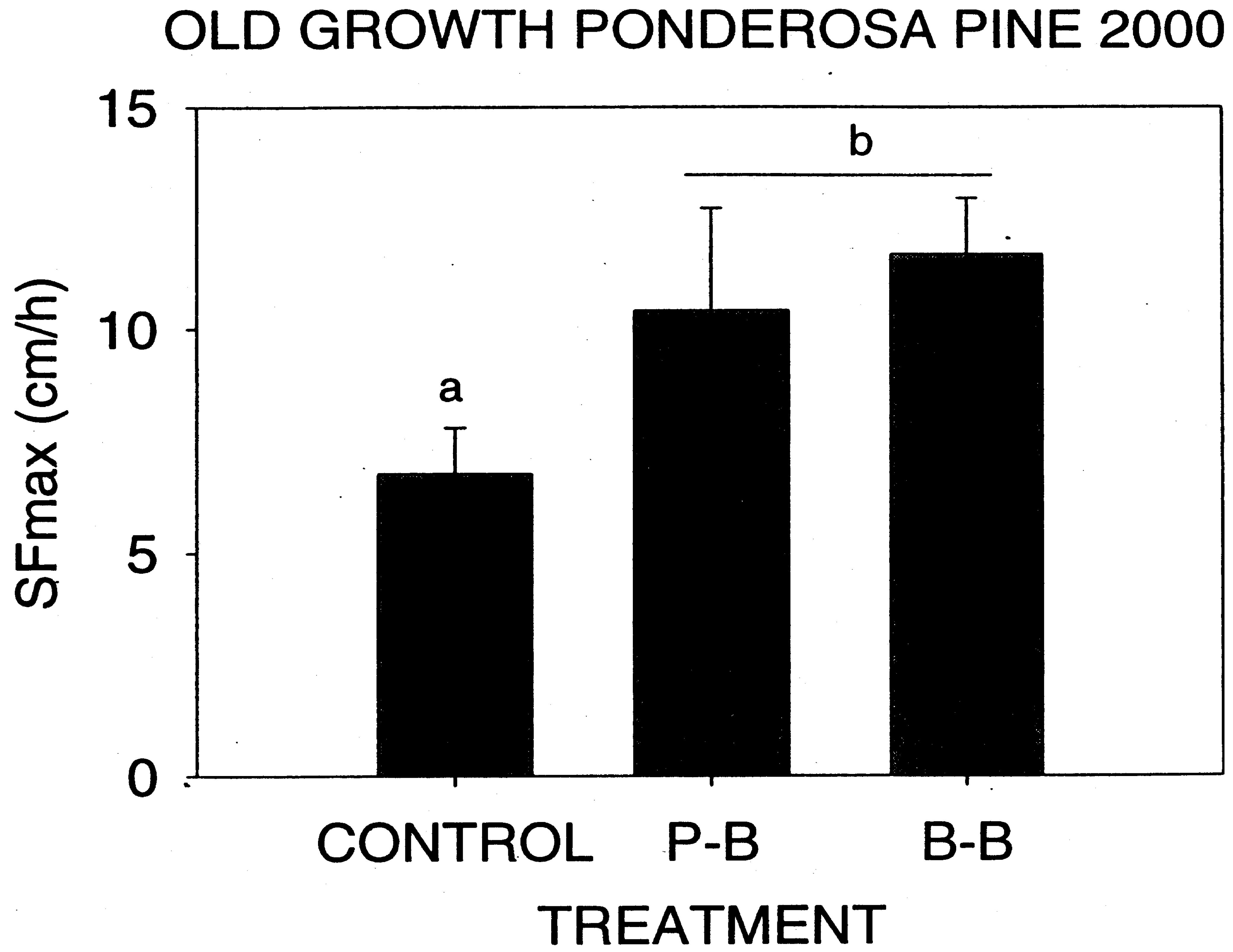
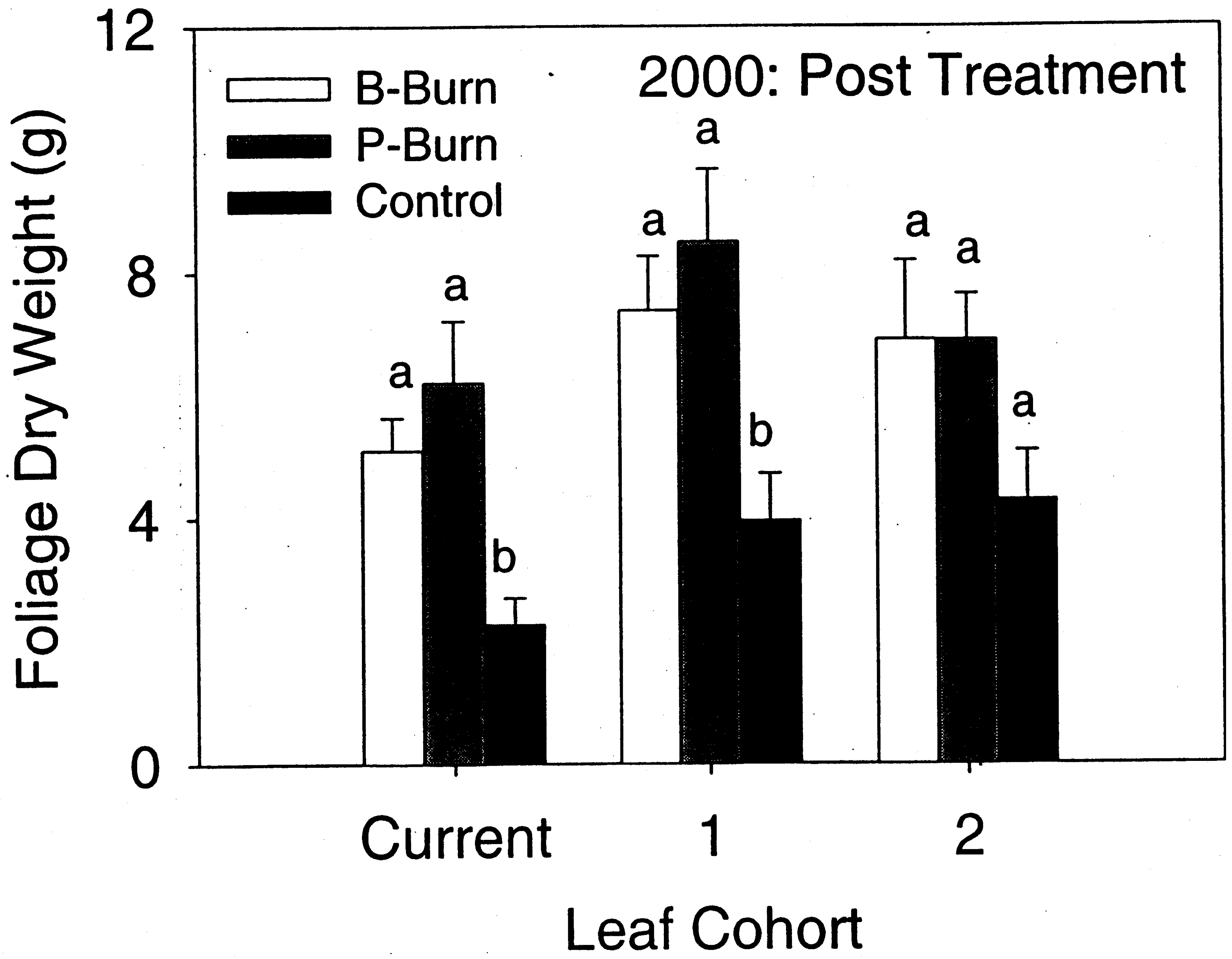
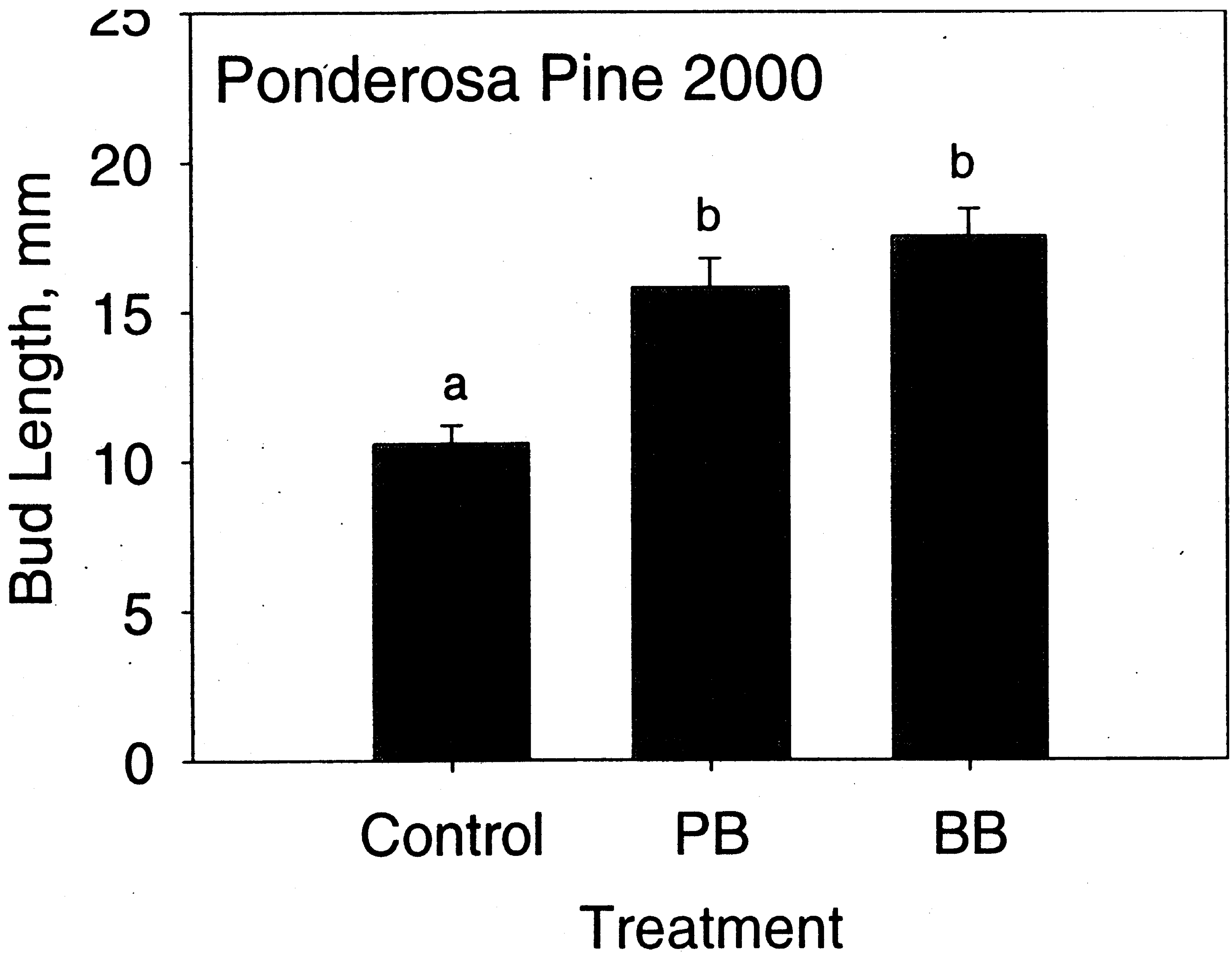

OLD GROWTH WESTERN LARCH 2000
SFmax (cm/h)
60
50
40
30
20
10
0
150
160
170
180
190
200
210
220
Julian Day
June
July
August
DF Control
WL Control
WL P-Burn
WL B-Burn
WL OP-Burn
WL OB-Burn

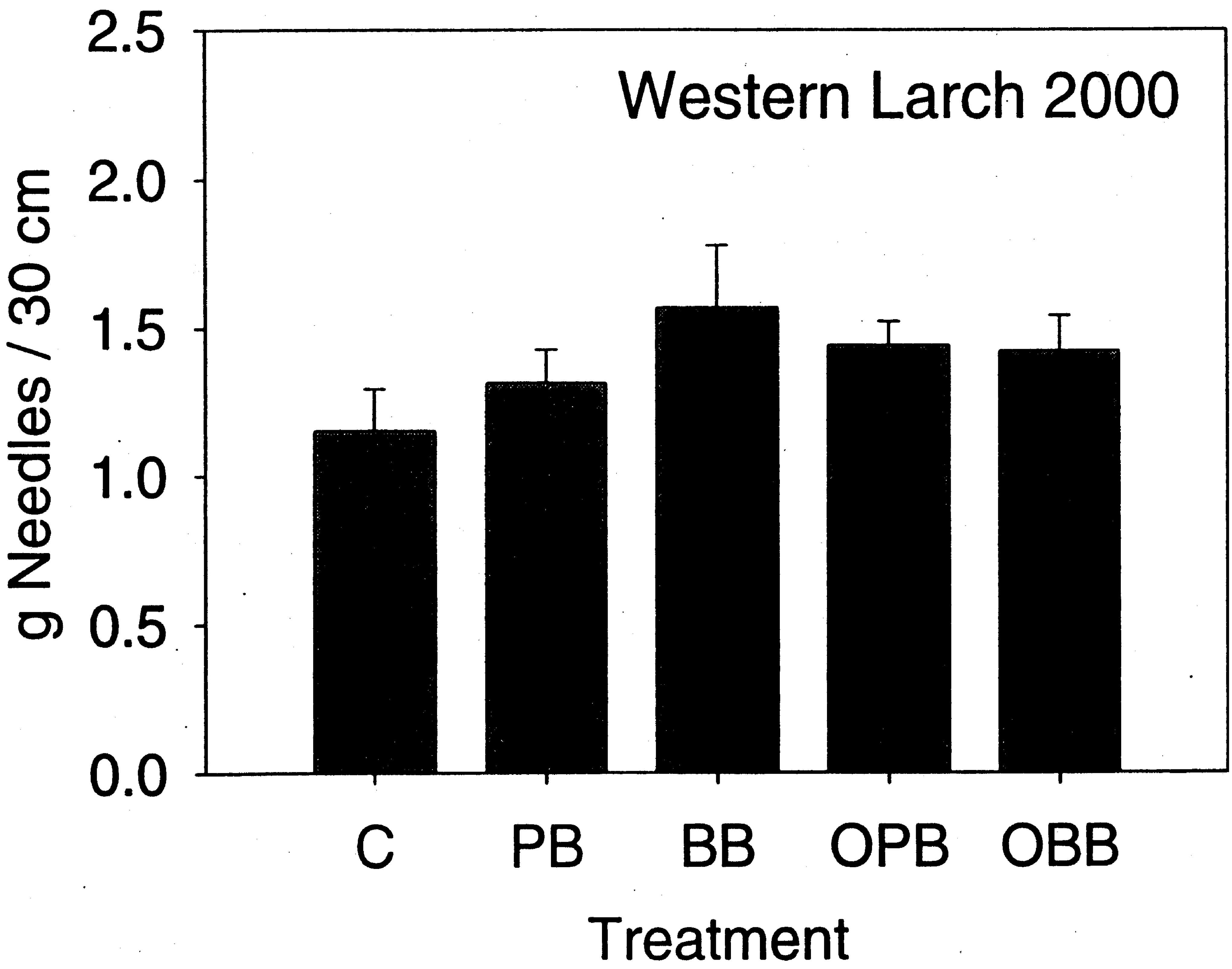
FIGURE 4

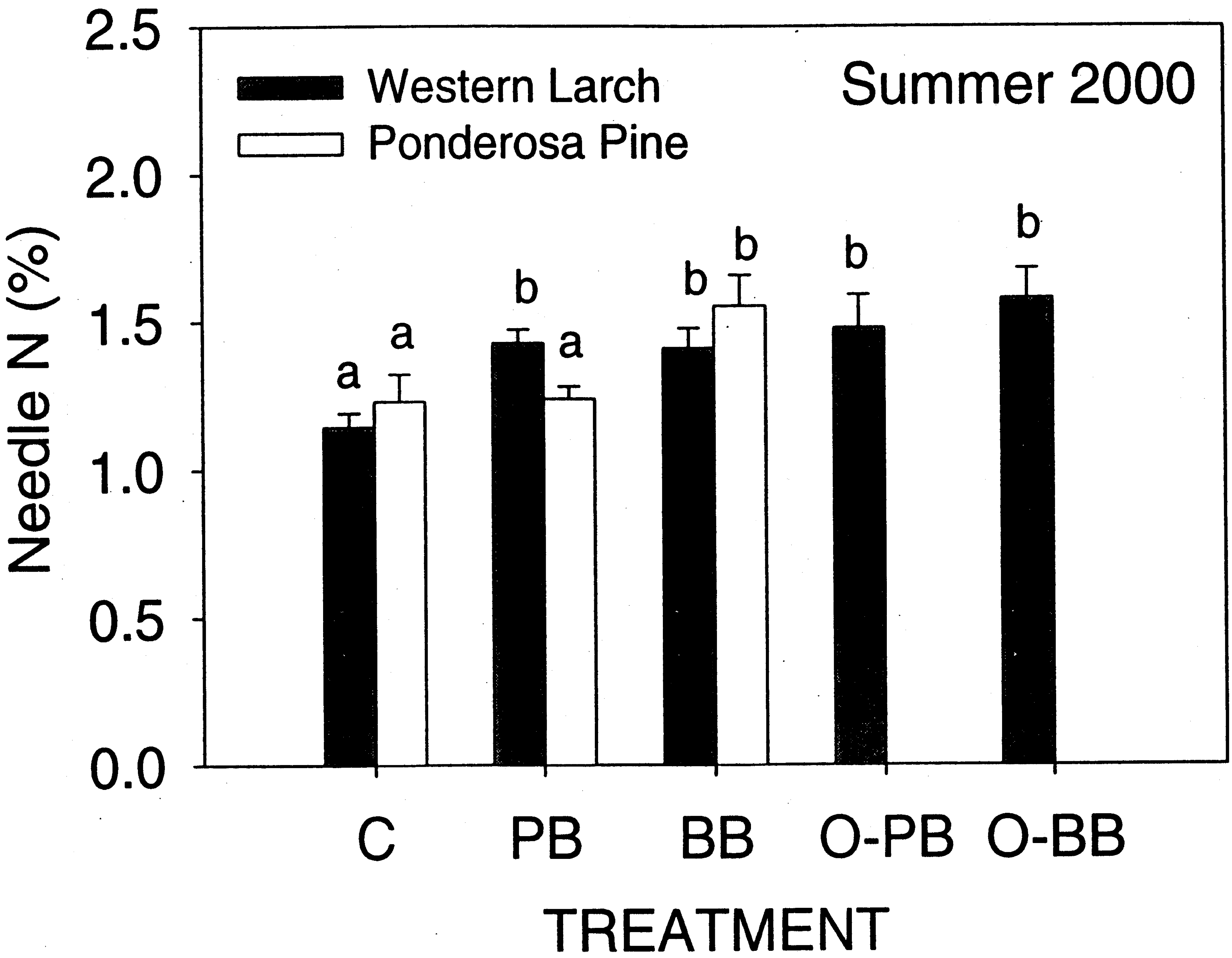


OLD GROWTH PONDEROSA PINE 2000
SFmax (cm/h)
15
10
5
0
a
b
CONTROL
P-B
B-B
TREATMENT


2000: Post Treatment
B-Burn
P-Burn
Control
Foliage Dry Weight (g)
12
8
4
0
a
a
b
a
a
b
a
a
a
Current
1
2
Leaf Cohort


Ponderosa Pine 2000
Bud Length, mm
25
20
15
10
5
0
a
b
b
Control
PB
BB
Treatment


Western Larch 2000
g Needles / 30 cm
2.5
2.0
1.5
1.0
0.5
0.0
C
PB
BB
OPB
OBB
Treatment


Western Larch
Ponderosa Pine
Summer 2000
Needle N (%)
2.5
2.0
1.5
1.0
0.5
0.0
a
a
b
a
b
b
b
b
C
PB
BB
O-PB
O-BB
TREATMENT

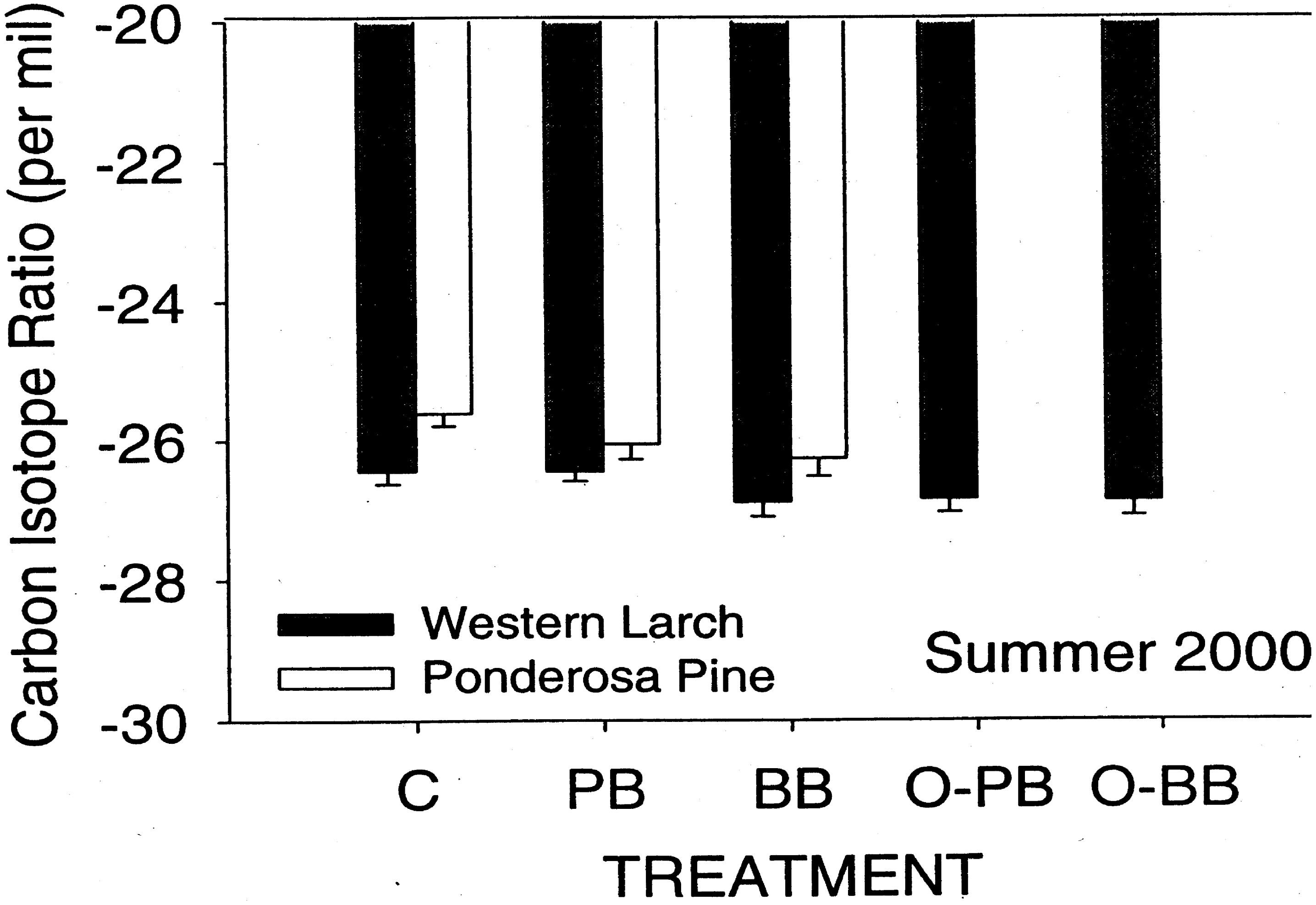

Carbon Isotope Ratio (per mil)
-20
-22
-24
-26
-28
-30
Western Larch
Ponderosa Pine
Summer 2000
C
PB
BB
O-PB
O-BB
TREATMENT

FIGURE 10