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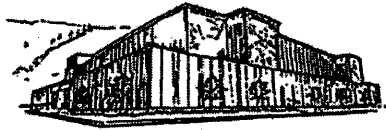
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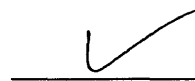
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**EFFECTS OF UNDERSTORY VEGETATION ON THE
PHOTOSYNTHESIS AND LEAF WATER POTENTIAL OF YOUNG
DOUGLAS-FIR TREES ON TWO CONTRASTING SITES IN
NORTHWESTERN MONTANA**

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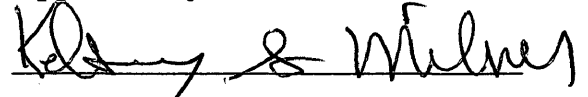
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2003

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Forestry

Effects of understory vegetation on the photosynthesis and leaf water potential of young Douglas-fir trees on two contrasting sites in northwestern Montana (60 pp.)

Committee Chair: Kelsey S. Milner, Ph.D.



Abstract

Competition between plants predominantly involves the struggle to obtain basic resources such as light, water, and nutrients, which control their overall carbon gain. In forest environments, understory vegetation has a strong competitive effect upon the growth of young conifers, especially during stand establishment. Little work has been done to quantify these competitive effects and the physiological response upon young conifer growth. Moreover, current modeling efforts forecasting forest growth are becoming increasingly reliant upon physiological processes to better explain the role of understory vegetation upon small tree growth through competitive interactions. Measurements of net photosynthesis, predawn leaf water potential, foliar nitrogen, carbon stable isotopes, microclimate, vegetation abundance, and tree growth on small naturally-regenerating Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) trees were taken at one dry and one wet site in northwestern Montana over a 12-week period from June until October of 2001. Treatment plots consisted of a reduction (10 to 90 percent) of understory vegetation by a photosynthesis inhibitor herbicide. Net photosynthesis, plant water status, and foliar nitrogen were significantly greater in treated plots throughout this period for both sites and extended the growing season at the dry site. Vegetation cover in several regression models was consistently correlated across site and season with both carbon gain and water availability in young Douglas-fir trees. Vegetation cover alone accounted for 10 to 20 percent of variation in both photosynthesis and predawn leaf water potential. After accounting for variation in measurement period and tree vigor attributes, the influence of understory vegetation upon small Douglas-fir carbon gain and water status was negative and varied according to site. As an important means of enhancing early stand productivity, reducing understory vegetation in young Douglas-fir stands will likely improve rates of net carbon gain through increasing water availability, plant nitrogen levels, and even extend growing season length.

Keywords: competition, leaf water potential, photosynthesis, conifer growth, Douglas-fir, understory vegetation, foliar nitrogen, carbon isotopes

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Introduction

Competition in forest communities has been long understood to play an important role in regulating plant growth and productivity as well as species diversity and community structure (Callaway and Walker 1997; Kozlowski et al. 1991). Competitive interactions among plants involve the differential acquisition and allocation of resources reflected through changes in physiological behavior that are largely determined by the proximity of neighboring plants (Bazzaz 1996). The effects of competition can also greatly impact stand development following disturbance, especially in early successional stages through changes in both structural and compositional characteristics that are largely determined by the initial conditions of a stand. Consequently, this sets the stage for subsequent forest development. These disturbance-induced changes in canopy-gap patterns are thought to play a critical role in regulating the dynamics and coexistence of species, yet little work has been done in assessing tree seedling responses across these smaller scales (Bazzaz and Wayne 1994). By examining the early life stages of naturally regenerating trees in response to varying levels of disturbance will likely reveal differences in resource acquisition by changes in resource availability and subsequent physiological performance and growth (Bazzaz 1996).

In addition, competition for similar resources is especially intense throughout the early stages of stand development and is likely having a significant effect upon tree growth rates and harvest periods by as much as several years. For example, in dry ponderosa pine forests, competition from shrubs alone can reduce growth and lengthen these rotation periods by as much as 10 years (Miller 1987). In a recent study, removal of understory vegetation in both ponderosa and lodgepole pine forests in western Montana

resulted in increased growth during the first 11 to 15 years after seedling establishment (Keyser and Milner 2003). In young Douglas-fir forests of the Pacific Northwest, release of understory vegetation has also positively affected tree growth and survivorship in many studies (McDonald 1994; McDonald 1986; Cole and Newton 1987; Monleon 1999). Conifer release from competing understory vegetation has become a popular tool by land managers to increase tree growth, and may be considered one of the most limiting factors affecting tree growth in the Inland Northwest (Uzoh 1999). By introducing vegetation removal treatments in newly developing stands to eliminate or mitigate vegetative competition, the likelihood of enhancing forest productivity will increase (Stewart et al. 1984).

Little work has been done that focus on the primary physiological responses of trees to competition in forest stands, especially as it concerns understory vegetation in western Montana (Wang et al. 1995; Milner and Coble 1995b). In many forests, thinning in order to reduce competition is an important management tool that results in increased growth of remaining trees through changes in individual tree physiology (Wang et al. 1995). The effects of thinning are discernible through modifications of environmental conditions within forest stands affecting physiological processes such as increased soil moisture (Gravatt et al. 1997). In lodgepole pine stands, the effects of thinning are seen through increased seasonal photosynthesis and decreased water stress (Donner and Running 1986). In red pine forests, the effects of thinning reduce both soil and needle water stress (Sucoff and Hong 1974). Generally, the growth response of individual trees to thinning is determined primarily by their photosynthetic capacity to acquire and assimilate carbon (Brix 1983).

In particular, increased knowledge of the physiological responses of small trees to competing vegetation is especially important since they play such a crucial role in stand development. Early tree size differences in northern forest ecosystems as a result of controlling competing vegetation can have significant long-term consequences in overall stand development and yield (Wagner et al. 1999). It is also critical to understand small tree function at this early stage in order to make sound management prescriptions that can potentially avoid substantial reductions in tree growth over time and wasted expenditures on vegetation control (Wagner 2000). With an increasing tendency of current forest management policy to encourage and promote natural stand regeneration, better understanding of these mechanisms will contribute to more thoughtful and effective silvicultural practices that are better equipped to identify thresholds of response in relation to natural site conditions and quality. To achieve this, successful forest management today requires a better understanding of the physiological effects of understory vegetation upon small tree growth as they compete for resources.

Furthermore, forest managers today also desire models of forest development that can accommodate all of the vegetation in a stand through a much more process-oriented approach. These models can serve an important role in managing for a multitude of age and structural conditions as well as explore the effects of a range of management options to resource managers before their implementation (Milner and Coble 1995a). Development of these models requires more precise knowledge of variation in factors affecting tree physiology and their responses (Gravatt et al. 1997). Physiologically based models also have the potential to be far more flexible in their ability to model responses to environmental stimuli which serve as the primary drivers for any ecological system

(Landsberg and Gower 1997). One important aspect of these process-modeling efforts focuses on the competition between understory plants and newly regenerating trees.

Better understanding of these competitive effects will also improve the ability of stand dynamic models to forecast early stand developmental processes and measure the success of competition removal treatments. Several of these currently existing models, developed to predict tree carbon uptake and growth are increasingly reliant upon physiological data for their proper calibration (Korol 2001). More study will also improve mechanistic understanding and quantification of the many important factors contributing to early growth in a competitive setting by revealing interactions and shifts in resource availability and utilization because of competitive interactions.

Objectives

This study hopes to integrate the physiological effects upon growth at different levels of understory competition through examination of these treatment effects upon photosynthesis, leaf water potential, and subsequently growth in young Douglas-fir trees. Specifically, we seek to determine 1) how much reduction in vegetation results in increasing net carbon gain (growth) and plant water status, and 2) what are the seasonal trends in response to competitive release from vegetation. Our working hypotheses supporting these objectives are as follows: 1) less competing vegetation will reduce water stress upon small Douglas-fir trees; 2) reduced water stress will lead to greater tree net photosynthesis, hence growth; 3) reduced water stress from less competing vegetation will lengthen the growing season and; 4) tree attributes will be important in explaining tree responses to competing vegetation.

Previous physiological work

Competition between plants can induce considerable changes in individual whole plant physiology (Bazzaz 1996). Net photosynthesis, leaf water potential, foliar nitrogen, and carbon isotopes are important physiological indicators of plant performance that can reveal differences in resource acquisition. The choice of these measurements reflects thinking based on considerable previous work.

Net photosynthesis represents a plant's ability to uptake carbon for the eventual production of necessary sugars to be used for all metabolic activities such as growth and reproduction. Since it is the net uptake of carbon that is being measured, it takes into account the offsetting effects of carbon efflux through respiration (Larcher 1995). The rate at which trees take up carbon is contingent upon many interrelated factors, including nutrient and water status, plant size and vigor, microclimate, and the extent of competition present in order to obtain these resources (Kozlowski et al. 1991).

Of these, plant water status is an important determinant of overall photosynthetic rates (Lambers et al. 1998). Gas-exchange occurs through leaf stomata, which open and close depending on microclimatic conditions and internal water stress, among other factors. Under conditions of less water stress, leaf stomata will remain open for a longer duration, permitting gas-exchange to occur. Since plant water potential equilibrates with soil water potential at night when leaf stomata are closed, measurements of internal water status are typically made before dawn. Predawn leaf water potential thus represents an important measure of overall plant water stress (Pallardy et al. 1991). Moreover, as a measure of overall water availability, predawn leaf water potential is a close surrogate of soil water potential, minus internal stem and root resistances, making it also good

measure of the overall amount of soil water that is available to plants (Kozlowski et al. 1991).

Foliar nitrogen concentrations also play an important role in determining the amount of photosynthesis in plants and are highly correlated with maximum photosynthetic capacity and carbon assimilation (Schoettle and Smith 1996; Aerts and Chapin 2000). Consequently, leaf nitrogen concentrations are highly correlated with annual carbon gain for many species (Zotz and Winter 1994). Since nitrogen is one of the most limiting nutrients in many forest ecosystems, leaf nitrogen levels are an important determinant of how trees compete with surrounding vegetation for this nutrient in the form of ammonium nitrate (Robinson et al. 2001). Quantifying this relationship under varying levels of vegetative competition will enable a clearer profile of overall photosynthetic response in small trees. More specifically, higher nitrogen content within foliage is related to a greater abundance of the carboxylating enzyme in C₃ plants called *Rubisco* (ribulose-biphosphate-carboxylase-oxygenase). The amount of *Rubisco* present in a leaf is largely responsible for the rate of carbon uptake and fixation in plants (Waring and Running 1998; Zotz and Winter 1994).

The use of carbon stable isotopes suggests a pattern of resource acquisition that is more integrated over time than instantaneous CO₂ gas-exchange measurements (Korol et al. 1999). Carbon isotope signatures are more useful than gas-exchange measurements since they integrate carbon assimilation over the entire period the leaf tissue was synthesized and are better integrators of plant carbon-water function (Dawson et al. 2002). In general, lower carbon isotope discrimination against ¹³C is typical for C₃ species in water-limited environments due to low intracellular CO₂ concentrations

resulting from more frequent stomatal closure (Ehleringer 1993). Conversely, high ratios of leaf mesophyll CO_2 to ambient concentrations reflect low water use efficiencies (high discrimination against ^{13}C) and may indicate higher productivity in plants (Ehleringer and Osmond 1989).

When considering the relationship between carbon uptake and its allocation to growth, the role of phenological development, maintenance respiration costs, and competing carbon source-sink relationships must be included (Gower et al. 1995). Although net gas-exchange measurements represent instantaneous estimates and take into account the offsetting effects of respiration, it does not account for carbon loss occurring at night when photosynthesis ceases. Nor does it account for respiration costs in non-photosynthetic plant tissues. Fortunately, these confounding factors are least pronounced in young conifer carbon budgets where there is little carbohydrate storage, with most assimilated carbon used for the production of new plant structures, especially roots (Luxmoore et al. 1995). In addition, growth in young trees is mostly limited by carbon assimilation since carbon sinks for growth are readily available to utilize incoming carbon for new structures. Thus, most carbon gain in immature conifers can be attributed to growth processes more than tissue maintenance activities, especially before sexual maturity where reproductive structures represent further carbon costs (Luxmoore et al. 1995).

Lastly, both tree size and vigor will partially determine carbon gain and growth in conifers. As trees grow in both size and vigor, their increased on-site establishment allows them greater access to basic resources. This, in turn, reduces the competitive effects of surrounding vegetation since other less competitive resources become

available. Much empirical evidence exists in conifer growth studies suggesting that many small conifers escape this zone of competition after reaching heights between 2 and 7 meters, depending on species and site conditions (Keyser 1999; Milner, personal communication).

Materials and methods

Site location and description

Two study sites were selected from a larger and already existing experimental study. The sites were chosen from the Small Tree-Competing Vegetation Study (STVC), an ongoing study examining the effects of competing understory vegetation upon small tree growth throughout the Pacific Northwest and sponsored by the Inland Growth and Yield Cooperative (INGY) (Inland Growth and Yield Cooperative 1998). Various stand level attributes were used to identify study areas of relatively homogeneous overstory density (basal area/hectare) and site quality (site index), as well as understory vegetation composition and density, for a given forest type.

Both sites are located in northwestern Montana on private cooperator lands. They were selected for measurement in 2001 and represented dry (Douglas-fir/dwarf huckleberry) and wet (western redcedar/queencup bead lily) conditions (Pfister et al. 1977) (Table 1). The wet site is located at 48.58 degrees N, 114.51 degrees W in the Whitefish Range, immediately southwest of Glacier National Park at an elevation of 1,200 meters and consists of a 15 to 20 year old east aspect clear-cut with no overstory present. The dry site is located almost 50 miles due south of the wet site at 47.94 degrees N, 114.72 degrees W, about 25 miles west of Flathead Lake. The dry site is west facing with a Douglas-fir/western larch overstory averaging 12.2 square meters/hectare.

Elevation is also 1,200 meters. Site indexes for the wet and dry sites are PSME 70 and PIPO 56, respectively, based on a breast-height age of 50 years (Table 1).

The climate at the wet site is largely affected by the mild and moist maritime influences from the Pacific Coast that predominate in northwestern Montana (Arno 1979). This is generally characterized by dry summers and wet winters. Consequently, annual precipitation averages about 580-mm per year with over 33 percent or 190-mm falling during the summer months (June through September). Mean annual snowfall is over 3,000-mm. Mean annual minimum and maximum temperatures are -2.5 and 12.6 degrees Celsius, respectively, with summertime means ranging from 4.4 to 24.4 degrees Celsius. The dry site is characterized as a rain shadow with annual precipitation approximating 300-mm per year with about 33 percent or 100-mm of it occurring during the summer months. Mean annual snowfall is between 900 and 1,000-mm. Mean annual minimum and maximum temperatures are 0.4 and 13.7 degrees Celsius, respectively, with summertime means ranging from 7.7 to 25.0 degrees Celsius (Western Regional Climate Center 2003).

Experimental design

Small tree-competing vegetation design

Each site consisted of seven treatment plots (0.2 hectares each), subjectively located to represent similar conditions of aspect, slope, site quality, overstory tree density, and understory plant composition and density. One-time understory removal treatments were randomly assigned to four or five plots and implemented during the 1999-growing season. The vegetation removal treatments consisted of a one-time application of the herbicide hexazinone (Pronone), a photosynthesis inhibitor that has

little to no affect upon Douglas-fir trees (Pro-Serve, Inc., Memphis, TN). The remaining untreated plots represented controls containing natural regeneration of both trees and understory vegetation (Figure 1).

Within each plot, six small tree subplots (0.003 hectares each), which are concentrically arranged around each plot center, were established to capture spatial variation and to serve as the basis for small tree sampling. Vegetation transects emanating from plot center and extending to each subplot (small tree plot) were previously established and served as the basis for estimates of understory vegetation and canopy volume (Figure 2).

Physiological study design

At the outset of the study, site selection was narrowed down from an existing database of STVC sites that contained information including accessibility, site moisture, inventoried small tree data, and treatment date information. Other criteria for site selection included slope, aspect, elevation, overstory density, and accessibility. Of the five treatment and two control plots present at each individual site, one control and one treatment plot were chosen that were sufficiently contrasted in understory vegetation and that met small tree sample size and height criteria. The selected treatment plots from both sites had vegetation removed in 1999. Based on pilot study results completed during the summer of 2000 in order to establish sample protocols and study methods, sample size estimates of small trees were determined and applied to site selection criteria. Both control and treatment plots selected from both sites were each within 100 meters of one another.

Tree measurements - Measurements were conducted during the summer of 2001, making this a two-year post-treatment study. We selected twenty-five small Douglas-fir trees per plot that were between 0.25 and 2.0 meters in height for physiological measurements. Current year foliage with a common crown position, orientation, and aspect were prepared and sampled for gas-exchange measurements and preliminary determination of projected leaf area. Gas-exchange was performed with a portable LICOR-6200 infrared gas-exchange analyzer (LI-COR, Inc., Lincoln, Nebraska). Photosynthesis was measured during midday between 10 am and 3 pm on a random selection of 24 to 36 trees, alternating every 6 trees between treatment and control plots for a given site. To the extent possible, all measurements were conducted under full ambient sunlight conditions on foliage to avoid the confounding problem of cloudy days (Dawson and Ehleringer 1993). Predawn leaf water potential was measured on a subsample of 6-10 trees per plot that morning prior to photosynthesis measurements using a standard pressure chamber (PMS Systems, Corvallis, OR) and established methods and sampling considerations (Waring and Cleary 1967; Boyer 1995).

Physiological measurements were made biweekly at each site beginning in late June (when new foliage was fully expanded) through September and early October. A total of 6 biweekly visits were made for each site spanning a 12-week measurement period. At the end of the season, foliage measured for gas-exchange was excised and a final projected leaf area determined by which to express photosynthesis and other physiological variables, using computer scanning, pixel image analysis, and established optical planimetric methods (Drew and Running 1975). After leaf area determination, a random sample of foliage from 40 trees (10 per plot) was selected and subsequently

analyzed for carbon and nitrogen content as well as carbon stable isotopes. Carbon isotope ratios ($\delta^{13}\text{C}_{\text{plant}}$) were analyzed relative to PeeDee Belemnite and expressed as discrimination against the heavier isotope (Δ) where: $\Delta = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}})$, where $\delta^{13}\text{C}_{\text{air}}$ was assumed to be -8‰ (Farquhar and Richards 1984). Lastly, diurnal minimum and maximum soil temperatures were recorded at a depth of 10 cm for each small tree plot within each large tree plot using digital thermometers (Taylor Environmental Instruments, Fletcher, NC).

Vegetation measurements - Measures of understory vegetation abundance for each site and plot were completed by two separate and independent methods. Overall vegetation volumes were estimated for each individual plot using single-dimension canopy-point methods (Inland Growth and Yield Cooperative 1998). A second method was employed to better capture variation in understory competition for each individual sample tree. This consisted of ocular estimates of vegetation cover and average height by life form (grasses, shrubs, forbs) and open soil (duff) for each sample tree. Sample tree height was used as the radius of a circular plot for estimating understory vegetation. Cover estimates were expressed on a percentage basis and, in conjunction with mean vegetation height, converted to a volume per area estimate for each tree. Vegetation cover was measured in late August at both sites during the estimated period of peak foliage (biomass).

Statistical analyses

All statistical procedures used the SPSS statistical software package (SPSS Inc.1999). Individual tree photosynthesis and leaf water potentials were treated as dependent variables in both analysis of variance (ANOVA) and linear regression models.

For each model developed, indicator variables representing the time period for each site visit were included to adjust for seasonal changes that influenced net photosynthesis.

Normality of residuals and constant variance in both procedures to validate model assumptions were performed through Kolmogorov-Smirnov test of normality and Levene's F-test, at the 5 percent significance level, respectively.

ANOVA - A two-way analysis of variance was performed to assess the overall effects of both time of measurement and treatment upon individual tree carbon gain and leaf water potential. Fisher's Least Significant Difference (LSD) procedures were used to assess factor level (period and treatment) differences between measurement visits for each site. Due to the unbalanced design resulting from both empty cells and different sample sizes across groups, Type IV Sums of Squares were used where possible to assess model and residual variation (Christenson 1996).

In addition, an individual means comparison of photosynthesis, leaf water potential, foliar nitrogen, vegetation level, tree growth, and other attributes were conducted using Student's t-tests. Means testing was performed to determine significance of variables contributing to observed differences in net carbon gain. In cases where equal variances could not be safely assumed, the more conservative significance values of differences between means were used to reflect this assumption. Both comparisons of mean differences between each individual site visit as well as on a seasonal basis were conducted.

Least Squares Regression - Differences in net carbon gain and leaf water potential between control and treatment plots were analyzed for each site using standard linear regression analysis procedures. Percent cover total vegetation, considered here the best-

integrated measurement of vegetation amount, was included as a continuous independent variable in order to estimate overall treatment effect upon photosynthesis and leaf water potential. To adjust for seasonal effects upon the dependent variables, times of measurement (period) were treated as indicator (“dummy”) variables for each site through procedures described in Kleinbaum and Kupper (1978). This resulted in five additional variables ($k-1$) representing the six measurements periods for each site and reducing the degrees of freedom for each model by five. For the wet site, no data transformations were necessary for the models produced since regression assumptions of constant variance and normality of residuals were entirely met. However, mild to severe first-order positive auto-correlation determined through Durbin-Watson tests of residuals ($P < 0.05$) was observed at the dry site in both photosynthesis and leaf water potential models. To correct for this, Prais-Winsten auto-regression procedures for parameter estimates were used for net carbon gain and plant water status, respectively, at the dry site (SPSS Inc. 1999). As with the analysis of variance described above, model assumptions of uniform variance and normality of error were tested at the 5 percent significance level using Levene’s and Kolmogorov-Smirnov tests, respectively.

Results

Treatment effects

Results from an analysis of variance indicated significant effects of treatment and time of measurement (period) (Tables 2 and 3). For each site, both factors were found to be highly significant effects upon both photosynthesis and leaf water potential ($P < 0.001$). The interaction between measurement period and treatment was not significant at the dry site ($P = 0.172$) but was moderately significant at the wet site ($P = 0.045$). Overall, the

effect of both period and treatment account for nearly 37 percent of the variation in net photosynthesis at the dry site while only accounting for 30 percent at the wet site (Table 2). Overall, significance of the treatment effect was greater at both sites than with period, when individual F-statistics are compared.

Similarly, both period and treatment factors were found to be highly significant upon predawn leaf water potential at both sites ($P < 0.001$) (Table 3). The effects of season and treatment accounted for over 59 percent of variation in leaf water potential explained at the dry site and over 43 percent at the wet site. No significant interaction was found between these factors at both sites ($P = 0.384$ dry site and $P = 0.124$ wet site). In comparing the relative effects of both factors upon leaf water potential using their F-statistics, the effect of treatment was greater than period for the wet site but less of an effect overall at the dry site.

Effects of treatment on physiological measurements

Net photosynthesis - For both sites, the effects of treatment upon overall carbon gain were apparent. Net photosynthesis was greater in both treatments than the control plots for each measurement period over the course of the growing season (Figures 3 and 4). Seasonal photosynthesis averages for each site showed highly significant differences ($P < 0.001$) from one another with both treatments fixing more carbon overall than the controls (Table 4). The dry site control plot assimilated an average of 0.79 micromoles/m²/sec of carbon over the entire season while the treatment averaged 2.17 micromoles/m²/sec of carbon assimilation. At the wet site, seasonal net photosynthesis for the control plot averaged 2.38 micromoles/m²/sec while the treatment plot averaged 3.8 micromoles/m²/sec. Overall, trees from the dry site treatment plot acquired, on

average, almost 3 times (274 percent) more carbon than the control over all measurement periods during the season. Similarly, wet site treatment trees acquired, on average, over one and half times (160 percent) more carbon than the controls for all measurement periods combined.

Mean net carbon gain differences between control and treatments at both sites for each biweekly measurement period were mostly statistically significant (Table 5). At the dry site, mean differences in photosynthesis were highly significant between plots throughout the season ($P < 0.003$) except for the late June and the late September measurement visits, which were moderately significant ($P = 0.041$ and $P = 0.037$, respectively). At the wet site, differences in seasonal mean photosynthesis for each plot were highly significant from late July until mid-September ($P < 0.001$). Measurements taken early July and early October at the wet site were not significant ($P = 0.696$ and 0.749 , respectively)

Leaf water potential – Similarly, treatment effects upon plant water status were also evident. Predawn leaf water potential in both treatment plots at each site exhibited lower water stress than the controls over the duration of the growing season (Figures 5 and 6). Overall mean differences in leaf water potential between plots at both sites are also highly significant ($P < 0.001$) on a seasonal basis with the dry site control and treatment averaging -1.97 and -1.63 MPa, respectively (Table 4). The wet site experienced relatively lower overall water stress with seasonal averages for the control and treatment of -1.32 and -1.05 MPa, respectively. At both sites overall, the treatment plots showed a higher absolute leaf water potential than the controls with all plots exhibiting a distinct downward trend as soils became progressively drier throughout the

summer. Mean leaf water potentials between plots for each biweekly measurement period at the dry site were mostly significant ($P < 0.05$) using one-tailed t-tests (Table 6) except for the late June measurement, which was moderately insignificant ($P = 0.055$). Most statistically significant differences were observed during late July ($P = 0.006$) and late August ($P < 0.001$).

At the wet site, differences in leaf water potential were not significantly different from one another ($P > 0.09$) from early July until early August. By mid-August and mid-September however, differences in leaf water potential were highly significant ($P < 0.001$). The last measurement period in early October indicated moderately insignificant differences in leaf water potential between control and treatment plots ($P = 0.074$).

Foliar nitrogen and carbon stable isotope measurements – Vegetation treatment differences also appeared to affect the relative nutrient status of sample trees and their relative water content differences through carbon isotope discrimination comparisons. Mean nitrogen content of sampled foliage, expressed on a percent dry weight basis, indicated significant differences between plots at the dry site ($P = 0.021$) but were not significant at the wet site ($P = 0.151$) (Table 4). Foliar nitrogen content at the dry site control plot averaged 0.86 percent of dry leaf weight while the treatment averaged nearly 1.0 percent. At the wet site, the control plot mean foliar nitrogen content was 1.05 percent of dry weight while the treatment mean content was 1.14 percent. Comparisons of carbon isotope ratios indicated highly significant differences between plots at the dry site ($P = 0.002$) but not significant at all for the wet site ($P = 0.629$) (Table 4). Across both sites, differences between control plots were also highly significant ($P = 0.014$) but not at all significant between the treatment plots.

Effects of treatment on understory vegetation

As a direct consequence of treatment effects, understory vegetation amounts between plots indicated statistically significant differences. In terms of average percent cover as estimated for each individual sample tree, the dry site control plot had an average of almost 39 percent total vegetation cover (Table 4). The treatment plot had nearly a 27 percent mean total vegetation cover. The wet site control plot had a mean total cover of almost 64 percent while the control had nearly 33 percent. Differences in mean vegetation cover between plots were very significant for the dry site ($P=0.012$) and highly significant for the wet site ($P<0.001$). At the plot-level, independent volume estimates of total vegetation differed similarly as with percent vegetation cover. However, since they represented single-value volume estimates scaled to the entire plot, no statistical tests could be performed for comparison.

Tree growth patterns

Average heights and relative growth rates of sampled trees taken at the end of the 2001-growing season were significantly greater at each site in both treatment plots than controls, suggesting a 2-year post-treatment effect. At the dry site, treatment plot trees on average were 0.3 meters taller than control trees (Table 4). Differences in height were highly significant ($P<0.001$). Similarly, treatment plot trees at the wet site were 0.18 meters taller than the control on average with moderately significant differences in height ($P=0.07$). Average height growth for the 2001-measurement year was 0.03 meters greater at the dry site treatment plot than the control. Treatment plot trees at the wet site grew 0.12 meters more than the control during the course of the growing season. Differences in height growth between plots at both dry and wet sites were highly significant ($P<0.001$).

Effects of treatment on soil temperature

Little to no consistent effect of treatment was found in regard to soil temperatures for both sites. Diurnal minimum and maximum soil temperatures varied little between plots throughout the summer season, never differing by more than 0.6 degrees Celsius between treatment and control. Overall, mean seasonal maximum temperatures for the dry site control were 16.7 degrees Celsius and 16.8 degrees Celsius for the treatment (Table 4). Mean seasonal minimum temperatures for the control and treatment plots were 13.9 and 13.6 degrees Celsius, respectively. At the wet site, control and treatment maximum seasonal averages were both 18 degrees Celsius while seasonal minimum averages were 13.1 and 13.3 degrees Celsius, respectively. Highly significant differences were found with minimum average temperatures between plots at the dry site ($P=0.006$) but were not significant at the wet site ($P=0.429$). At both sites, average maximum soil temperatures between plots did not differ significantly from one another ($P>0.510$).

Patterns of variation in microclimate

No consistent or discernible effect of treatment was apparent in microclimate conditions present at each site throughout the summer season. Patterns of variation encountered were likely due instead to naturally varying conditions. During each of the measurement periods, measurements of light, relative humidity, and air temperature for all gas-exchange measurements were moderately to highly variable (Table 7). Levels of Photosynthetically Active Radiation (PAR) were the most variable for nearly all of the periods for each site. Typical ranges were between 1,700 and nearly 2,000 micromoles/m²/sec for the dry site and between 1,700 and nearly 2,300 micromoles/m²/sec for the wet site. Consequently, standard errors of the mean were relatively high, especially

during the first period at each site with the smallest sample sizes. Mean PAR for each measurement period at the dry site ranged from 600 to 1,100 micromoles/m²/sec while at the wet site it ranged from about 100 to almost 1,300 micromoles/m²/sec.

Both air temperatures and relative humidities throughout the season varied far less for both sites. Mean air temperatures for the dry site had a range of 10 degrees Celsius (23 to 33 degrees Celsius) from late June until mid-September. The wet site had seasonal mean temperatures ranging 24 degrees (12 to 36 degrees Celsius). Standard errors for air temperature measurements from both sites were mostly small and below 0.5 degrees. Similarly, mean relative humidities for the dry site ranged from 15 to 25 percent over the season and at the wet site from 21 to 45 percent. Standard errors were notably small, falling well below 0.6 percent during all measurement periods except for one (early July at the wet site).

Overall, seasonal mean differences in temperature and relative humidity between control and treatment plots over all measurement periods for both sites indicated highly insignificant differences ($P > 0.400$). For light, differences at the dry site for all periods were also insignificant ($P = 0.421$) but were significant at the wet site ($P = 0.042$) (not shown). In general, differences in microclimate between plots within each period for each site indicated mostly insignificant differences in their means. Significant mean differences between plots at the 5 percent level are indicated by period for each site (Table 7).

Although precipitation was not measured as part of this study, records compiled for western Montana indicated that both sites experienced between 50 and 70 percent of normal precipitation for the 2001 Water Year (October 2000 through September 2001).

Montana was in its 5th year of cumulative drought and considered extreme by standard measures. Surface water supply indices (SWSI) for proximal drainages were considered extremely dry throughout most of the entire 2001-growing season. Palmer Drought Severity Indices (PDSI) also indicate moderate to extreme drought conditions for both site areas throughout the summer of 2001 (Montana Natural Resource Information Center 2001).

Models of vegetation effects on tree carbon gain and water status

Net photosynthesis - Regression analyses of net photosynthesis yielded varying results using percent total vegetation cover as a predictor variable. Various models were produced in an attempt to further discern the significant treatment effect of reduced competing vegetation upon photosynthesis indicated through the analysis of variance. Of the two independent estimates of vegetation measured, percent total vegetation cover was considered the best measure since it alone captured individual sample tree variation (versus the single plot-level estimate) and was more integrated than the individual percent cover estimates also collected by life form. It also avoided the potential for propagated error from other derived measures of vegetation amount, including estimated vegetation volume per individual tree plot and vegetation volume on a per-meter² basis. Consequently, it was decided that percent total vegetation cover (referred to as percent cover from this point onward) should be the primary predictor variable of interest for all models examined.

For both sites, several models were considered to assess the relative effect of vegetation upon net photosynthesis. The simplest models included examining the influence of percent cover by itself and after accounting for other highly significant

predictor variables, such as initial tree height for the dry site and crown ratio for the wet site. The latter predictors were considered measures of tree vigor that would most likely be differentially affected by competing vegetation. More complex models considered measurement period as a factor by inclusion of “dummy” variables in conjunction with the aforementioned predictors. This was done to account for the inherent seasonal variation upon net carbon gain. All predictor variables were first-order with one exception. A quadratic percent cover term for the dry site was found significant and included in the above combinations since it best fit the data. Given the varying extent of positive serial correlation of the error terms found at the dry site, auto-regression methods described earlier were employed. Generalized Least Squares regression was appropriate for the wet site since all error assumptions were met.

In all models examined for the dry site, the slope coefficients for percent cover were highly significant and remained very stable for each model. Given this stability, representative models depicting this consistency are presented (Tables 8a-d). Considering all models summarily, slope coefficients for percent cover without a quadratic term and with and without height ranged from -0.0246 to -0.0286. With the quadratic term the percent cover partial slope range was -0.0779 to -0.0829 (not shown). Both lower-order terms throughout were highly significant ($P < 0.001$) and of the highest relative importance when standardized Beta coefficients are compared. The quadratic term showed similar stability in all models where it was included. Initial tree height was also highly significant in all models ($P < 0.001$). Beta coefficients for each model estimated percent cover of highest importance relative to other all other predictors included. The

interaction between percent cover and height was highly insignificant in the presence of the lower order terms ($P=0.593$) but highly significant alone ($P=0.001$) (not shown).

Similarly, the effect of percent cover at the wet site showed considerable stability throughout all models tested. Given this consistency, representative models are depicted (Tables 9a-d). In other models with and without the indicator variables, initial tree height was insignificant but crown ratio was significant ($P<0.006$). Slope coefficients for percent cover ranged from -0.0180 to -0.0254 with all estimates highly significant ($P<0.002$). All Beta coefficients for percent cover were among the highest in comparison with other predictor variables. The interaction of percent cover and crown ratio was highly insignificant in the presence of the lower order terms ($P=0.916$) but highly significant alone ($P=0.011$) (not shown).

For both sites overall, inclusion of other significant variables such as crown ratio and initial height only slightly impacted the partial slopes of percent cover, indicating only additive effects of these predictors. At the dry site nearly 26 percent of the variation in net photosynthesis was explained after accounting for period and initial tree height (Table 8d). Considered alone, percent cover accounted for only about 11 percent of the variation in net carbon gain (Table 8a). At the wet site, percent cover explained nearly 17 percent of the variation after accounting for period (Table 9c). Without accounting for period, percent cover alone explained only 8 percent of photosynthesis variation (Table 9a). All of the period indicator variables were moderately to highly significant for both sites with the exception of Period 5 (late summer), which was highly insignificant at each site ($P>0.376$).

While partial slope coefficients for percent cover from each site were highly significant and negative, regardless of which model was chosen, their relative stability in the presence of other variables can be used to portray an overall estimated effect of understory vegetation upon photosynthesis. Using the slope coefficients from the simplest models with estimated values that best approximate the range of data observed (Tables 8a and 9a), the estimated effect of vegetation upon photosynthesis is negative for both sites over the range of percent vegetation cover observed at each site (Figures 7 and 8). Expressed on a percent reduction basis using the slopes from these models, photosynthesis at the dry site declined nearly 75 percent as cover increases from 0 to 70 percent (Figure 9). At the wet site, carbon gain declined almost 45 percent over the same range of vegetation cover. These estimated declines are based on an observed range of photosynthesis at both sites.

Incorporating tree height and crown ratio in models along with percent cover also resulted in declines in net carbon gain for both sites (Figures 10 and 11). Net photosynthesis declined at the dry site over a range of observed tree heights but more dramatically for smaller trees on a percentage basis. For trees 0.25 meters tall, estimated mean decline in carbon uptake over the range of observed vegetation cover was from 1.57 micromoles/m²/sec to -0.35 micromoles/m²/sec or 122 percent. Declines in carbon uptake for 1-meter tall trees were from 2.3 to 0.38 micromoles/m²/sec or 83 percent. The range of decline for 2-meter tall trees was from 3.26 to 1.35 micromoles/m²/sec or 59 percent.

Similar effects upon carbon gain were evident across a typical range of crown ratios at the wet site (Figure 11). The estimated decline in photosynthesis over the range

of vegetation cover for trees with 80 percent crown ratio was from 4.19 to 2.75 micromoles/m²/sec or 34 percent. Trees with 60 percent crown ratio declined from 3.73 to 2.29 micromoles/m²/sec or 39 percent. The estimated mean decline of carbon gain for trees with 40 percent crown ratio was 49 percent or from 3.6 to 1.83 micromoles/m²/sec.

Leaf water potential – A similar analytical approach was adopted for plant water status. Various models were developed and their slope coefficients compared with and without other variables. Model fit and adequacy were also evaluated, especially for auto-correlation. For the dry site, auto-regression methods (Prais-Winsten) were used to correct for positive serial correlation in the error terms for models not including indicator variables for period. The wet site required only standard least-squares procedures since no auto-correlation was present. Models tested for both sites included leaf water potential against percent cover alone and with initial tree height, as well as with the five indicator variables adjusting for measurement period.

For the dry site, slope coefficients for percent cover were stable and varied little with the particular model. A quadratic term for percent cover was included for all models tested since it provided the best fit for the observed data. Given this stability, the simplest and most adequate models without and with accounting for period are presented (Tables 10a-b). Slope coefficients for these models were -0.0198 and -0.0245, respectively. Percent cover was highly significant ($P < 0.001$) in both models.

In other dry site models examined using standard least-squares procedures, models with initial tree height with and without indicator variables produced slope coefficients of -0.0216 and -0.0186, respectively (not shown). In the former model containing tree height, all variables were highly significant ($P < 0.01$) except for Period 5

(late summer), which was highly insignificant ($P=0.671$). After removing the indicator variables, all variables of the model were significant at the 1 percent level except for height which was highly insignificant ($P=0.382$).

Models containing percent cover without and with initial tree height (not shown) both explained nearly 9 percent of the total variation in leaf water potential, respectively (Table 10a). Accounting for measurement period with only percent cover explained over 52 percent of the variation (Table 10b). Further accounting of tree height explained 55 percent of the variation in leaf water potential (not shown). Inclusion of crown ratio was insignificant in all models examined ($P>0.065$).

Similarly, the wet site models also showed relative stability in their partial slopes for percent cover. The simplest and most adequate models without and with an adjustment for period are presented (Tables 11a-b). Percent cover slopes of these models are -0.00551 and -0.00572, respectively, and are both highly significant ($P<0.001$). Accounting for measurement period with tree height produced cover slope coefficients of -0.00570 (not shown). All variables for all models examined were significant ($P<0.05$) including percent cover ($P<0.03$) but with the exception of Period 5 ($P>0.10$). For all models except one, percent cover was highly significant ($P=0.001$). Models containing percent cover without and with initial tree height explained 11 percent and over 16 percent of the total variation in leaf water potential, respectively. Accounting for measurement period with only percent cover explained almost 34 percent of the variation (Table 11b). Further accounting of tree height explained over 39 percent of the variation in leaf water potential (not shown). Inclusion of crown ratio was highly insignificant in all models examined ($P>0.22$).

While partial slope coefficients for percent cover for each site were significant and negative, almost regardless of which model was chosen, their relative stability in the presence of other variables portray an overall estimated effect of understory vegetation upon predawn leaf water potential. For both sites, the slope coefficients from the simplest model above, which predict within the range of observed values, are used to estimate the effects (Tables 10a and 11a). The overall effect of vegetation upon leaf water potential is mostly negative for the range of percent cover observed at each site (Figures 12 and 13). Expressed on a percent reduction basis using the slopes from above, predawn leaf water potential at the dry site declined nearly 20 percent as cover increased from 0 to 50 percent (Figure 14). Despite the positive relationship above 50 percent due to the quadratic term for the dry site, these upper points nonetheless represent a relatively small number of observations when compared with the remaining data below a cover of 50 percent (Figure 14). Consequently, the relationship depicted is mostly negative over most of the observed range of percent cover. At the wet site, leaf water potential declined almost 45 percent over the same range of vegetation cover. These estimated declines are based on an observed range of plant water potentials at both sites.

Discussion

It is well established that understory vegetation plays a considerable role in affecting the early growth of trees (Stewart et al. 1984). The availability of the basic resources that drive individual plant growth such as water, nutrients, and light can be largely determined by the extent of competition present. Consequently, such competitive effects upon growth must be manifested at the physiological level.

For each of the sites studied, the effects of treatment on vegetation differed significantly from one another. Both treatment plots had significantly less vegetation than the controls and the overall treatment effect on net photosynthesis and leaf water potential was considerable. Sample trees from both treatment plots exhibited significantly greater photosynthesis and reduced water stress than controls for most of the summer growing season. Foliar nitrogen levels in both treatment plots were also greater than in control plots.

The differences in predawn leaf water potential between plots throughout the course of the season are likely explained by differences in understory vegetation amounts competing for water and the possible subsequent effects of solar heating of soils that would consequently experience higher rates of evaporation. However, the insignificant differences in maximum soil temperatures between the plots for each site do not support the latter. A much more plausible interpretation explaining these differences in plant water status is that trees are taking up more water in the absence of vegetation than not (Newton and Preest 1988).

The observed differences in foliar nitrogen suggest greater nutrient acquisition in treatment plots than controls very likely due to the absence of vegetation otherwise competing for soil nitrogen (Robinson et al. 2001). The higher nitrogen content also suggests a greater amount of the carboxylating enzyme *Rubisco* that is positively correlated with photosynthetic capacity and annual carbon gain. Considered together, both the higher foliar nitrogen content and lower water stress strongly support the greater photosynthetic rates occurring in both treatment plots for each site.

In addition, there is an extension of growing season that is especially evident at the dry site. Peak net photosynthesis for both plots occurred in mid-July with a steady decline until September. The treatment plot consistently showed greater carbon assimilation than the control over the entire season. By mid-September this was still the case while trees in the control plot were losing carbon through respiration.

Examination of the seasonal trend in leaf water potential largely corroborates this pattern of carbon gain. Stomatal closure in Douglas-fir has been thought to occur between -2.0 and -2.4 MPa, with no loss in hydraulic conductivity below -2.5 MPa. However, values as low as -3.0 MPa have been reported in Douglas-fir in very dry soils, especially with seedlings (Bond and Kavanagh 1999). By late August, the control plot for the dry site had averaged over -2.7 MPa, theoretically preventing any further gas-exchange from occurring. This is supported by the negligible photosynthesis occurring during this period. Conversely, the treatment plot during this same period experienced an average predawn leaf water potential of -2.1 MPa, and appreciably greater gas-exchange than the control. By mid-September, with little change in average leaf water potential, photosynthesis of control trees had fallen to where there was net carbon loss through leaf respiration. The treatment plot, with also little change in leaf water potential, still showed appreciable yet declining net carbon gains, resulting in an extension of the growing season (Figure 3).

The wet site showed a similar but less pronounced trend. Peak photosynthesis for both plots occurred in early to mid-August with a steady decline thereafter. Minimum water stress coincided with the periods of peak photosynthesis (Figures 4 and 6). Maximum water stress for both plots occurred in late September and October but still

well below the threshold for complete stomatal closure. Prior to mid-August, average leaf water potential for both plots remained relatively stable but declined slightly. By mid-August however, differences in plant water status were clear with the control experiencing significantly higher stress than the treatment. Consequently, net photosynthesis was considerably greater throughout the season on the treatment plot.

However, it is not clear at the wet site that any possible extension of the growing season through continued carbon gain was due to treatment effects. The last measurement day indicated no differences in net photosynthesis but still a considerable difference in leaf water potential (Figures 4 and 6). This accounts for the significant interaction effect between period and treatment found through the analysis of variance (Table 2). The interaction was predominately due to the low light, low vapor pressure differences, and low temperature conditions for gas-exchange measurement where leaf stomata were largely closed and relatively unresponsive to allow for differences in gas-exchange to occur. Removing this last measurement period from the analysis resulted in a highly non-significant interaction ($P= 0.408$) with both period and treatment still remaining highly significant ($P<0.001$) (not shown).

Had microclimatic conditions at the wet site been more favorable for photosynthesis at this time, carbon gain for treatment trees would have likely been greater than the control, especially considering the lower water stress present. The increase in carbon gain for control trees from the previous measurement period suggests a temporary recovery from water stress due to a combination of recent moisture, low light and vapor pressure deficits, and air temperatures that permitted greater stomatal conductance and consequently greater photosynthesis. Given the continued differences in leaf water

potential between plots, photosynthesis would likely have been appreciably greater in the treated plot than in the control. Extrapolating this trend would plausibly extend the growing season in the treatment than the control but unfortunately, these data do not support this as they do at the dry site.

The differences in carbon isotope discrimination between plots for both sites appear to corroborate the relative differences in soil water availability found through predawn leaf water potentials. The significantly lower discrimination values determined for the dry site indicate the higher water stress found overall when compared with the wet site. Leaf stomata remain closed for a longer period under conditions of higher water stress resulting in less discrimination (i.e. greater abundance, diffusion, and assimilation of the heavier isotope) and greater water-use efficiency. Conversely, the higher average discrimination at the wet site is indicative of less water stress since leaf stomata remained open longer to permit greater discrimination against the heavier isotope.

For both sites, the control plots discriminated less overall, owing to their relatively greater water stress than the treatments (Table 4). The relatively greater on-site establishment of treatment trees due to their taller height and vigor may partly explain the statistically significant differences in discrimination between plots at the dry site. Trees at the wet site plots were more similar in height and vigor, which may, in part, account for the insignificant differences in carbon stable isotope discrimination. Considered together, both the statistically significant differences between plots at the dry site and the insignificant differences at the wet site help corroborate real differences in soil water content for each plot that were observed by the predawn leaf water potential measurements.

Further explanation of differences in net carbon gain between control and treatment plots for each site must also consider the role of microclimate. In conjunction with the mostly insignificant differences between plots of light, air temperature, and relative humidity, which all affect photosynthetic rates (Table 7), the random sampling scheme designed and implemented for gas-exchange measurements likely reflect true treatment differences between young Douglas-fir. To a certain extent, the patchy underlying vegetation present in each plot likely produced shaded conditions that affected sample tree microclimate through changes in light levels, air temperature, relative humidity, and even soil moisture. Such an effect would have been most likely prevalent at the wet site control plot, where the greatest vegetation volume and cover was present. However, these effects upon photosynthesis overall are seen here as minimal.

Regression analyses estimating the overall influence of competing vegetation upon photosynthesis seem to indicate a stable and consistently negative effect across sites using percent cover as a predictor (Tables 8a-d and 9a-d). Even after accounting for the time of measurement and measures of relative tree status and vigor such as tree height and crown ratio, the effect of vegetation cover remained very consistent for all model combinations tested. Both sites exhibit very similar negative effects when the relative magnitudes of the various model slope coefficients for percent cover are compared. The seemingly greater impact of vegetation upon carbon gain at the dry site may be largely due to the comparatively greater water stress present (Figure 9). Trees seeking to maximize carbon gain and minimize water loss while already operating at relatively low water thresholds would exhibit greater stomatal control to water stress. The greater water use efficiency observed in trees at the dry site would result in more frequent full and

partial stomatal closures, making carbon uptake more strongly reduced than transpiration (Larcher 1995). This may account for the more dramatic estimated effect of vegetation upon photosynthesis than at the wet site.

The effects of tree height and crown ratio in conjunction with vegetation cover at both sites did not display any differential effect upon net photosynthesis. At the dry site, taller trees took up more carbon but were similarly and adversely affected by increasing vegetation levels (Figure 10). Throughout the observed range of tree heights, estimated carbon gain varied equally by vegetation cover. Similarly, trees with higher observed crown ratios took up more carbon but were equally and adversely affected by increasing vegetation cover. This suggests that the population of trees measured over this range of observed heights and crown ratios is competing more or less equally for resources in the presence of varying vegetation amounts.

Regression analyses estimating the overall influence of competing vegetation upon leaf water potential also seem to indicate similar negative effects across sites representing varying understory vegetation amounts even after accounting for time of measurement (Tables 10a-b and 11a-b). A greater impact upon leaf water potential at the wet site is seen when the different partial slopes for percent cover are expressed on a percent change basis (Figure 14). The greater impact of understory vegetation upon leaf water potential at the wet site may simply be a function of the greater amount of water present potentially producing a smaller gradient of vaporization (i.e. greater rate of water loss) for a given vapor pressure difference. Conversely, the smaller impact of vegetation upon leaf water potential at the dry site may simply be due to its higher inherent water

limitation and consequently larger gradient of vaporization of site moisture for a given vapor pressure difference.

Although total carbon gains through photosynthesis do not necessarily translate to increases in tree biomass, this argument is better made with smaller trees than with larger ones. As trees age, net productivity increases to a point but tends to decline after peak leaf area is reached (Binkley et al. 2002). This is due to an interplay of many age-related changes including reduced nutrition, growth efficiency, and hydraulic limitations that all tend to reduce carbon assimilation and consequently biomass production. Thus, the highest growth efficiencies are typically found in younger trees (Ryan et al. 1997). Moreover, in the presence of competition and the onset of sexual maturity, carbon is also allocated to defensive compounds and reproductive structures. In small, immature trees however, proportionately greater amounts of carbon gain are allocated to the growth of roots, branches, and ultimately stems. Given the significant differences in overall growth between control and treatment trees and the physiological differences observed between them, net photosynthetic rates are reasonably good surrogates for comparing relative growth rates, since they are both highly correlated in some conifers (Tjoelker et al. 1998).

Lastly, some important caveats must be made with the interpretation of these consistent effects from the various regression models examined and the overall treatment effect. Despite the stability of the slope coefficients from each of the models, the total amount of variation explained for net carbon gain was typically between 10 and 30 percent. For plant water status, between 10 and 55 percent of the variation in leaf water potential was accounted for. Removing the effects of season in both cases greatly reduced the amount of explained variation to between 10 and 20 percent. It was these simpler

models that were used to estimate the overall effects of vegetation since they alone estimated over the observed ranges of the dependent variables. Given the highly significant effect of treatment found for both photosynthesis and leaf water potential (Tables 2 and 3), the actual measures of vegetation cover may not have been adequate enough to better discern the treatment effects upon both variables. Assuming that the true treatment effects represent differences in vegetation levels between plots, other measures of vegetation such as biomass may be better suited to portray treatment differences.

In addition, vegetation cover was only measured once during the entire season, not for each measurement period. An important but unlikely assumption implicit in these models is that vegetation was relatively constant for all measurement periods, which permitted the use of all the data collected over the summer season. Despite this limitation however, percent vegetation cover may be a more consistent one-time measure over the season than biomass, making this comparatively a better assumption under the circumstances.

Conclusions

In summary, there does appear to be a discernible and even substantial effect of competing vegetation upon both photosynthesis and plant water status in small Douglas-fir trees at these sites. By making less water and nutrients available for tree carbon gain and growth, understory vegetation can potentially play a significant role in determining the rate of biomass accumulation in young conifers by reducing plant water potentials and reducing the uptake of important nutrients such as nitrogen. Reduced levels of either or both of these basic resources lower the photosynthetic capacity of small trees and consequently relative growth rates.

Although competing vegetation for a given site may have a relatively lesser influence upon carbon gain when compared to other environmental drivers such as microclimate or site quality, it nonetheless offers land managers a controllable means of enhancing growth and overall productivity in many young forest stands. This is achieved by promoting acquisition of resources needed for biomass production and accelerating on-site tree establishment. For silviculturalists, relatively small reductions in competing vegetation may have more profound effects upon eventual tree growth, especially for small trees in water-limited environments, than sites with greater available moisture. A better understanding of these responses may contribute to a more efficient implementation of vegetation treatments in order to control costs and to account for site quality conditions. Based on these data, the 10 to 20 percent of variation in carbon gain and plant water status accounted for by vegetation alone at both sites may otherwise improve tree carbon gain by a like amount in the relative absence of vegetation. For young forest stands, this is likely of considerable importance in hastening their eventual establishment on a site by escaping the competitive effects of understory vegetation.

Finally, this study is consistent with many empirical studies that have documented the role of competing vegetation upon basic tree resource availability such as water and nitrogen, and its positive effects upon tree growth. Beyond contributing to this general area in forestry, it is hoped that this study will serve as a useful aid to silviculturalists interested in the basic physiological impacts of vegetation management upon small trees when devising prescriptions for young forest stands. Of like importance, this study will hopefully contribute to a growing interest in forest growth models that incorporate

physiological principles in their predictions through their improved quantification and further calibration, especially for young conifer trees during early stand development.

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Appendix A: Tables

Table 1. Site summary characteristics for small tree competing vegetation study.

| Site | Elevation (m) | Slope (%) | Aspect | Habitat Type | Overstory BA (m ² /ha) | Site Index | Treatment Year |
|------|---------------|-----------|--------|---------------|-----------------------------------|------------|----------------|
| Dry | 1,200 | 14 | W | PSME/ VACA | 12.2 | PIPO 56 | 1999 |
| Wet | 1,200 | 14 | NE | THPL/ CLUN | 0.0 | PSME 70 | 1999 |

Table 2. Analysis of variance for factor effects of treatment and measurement period upon net photosynthesis.

| Site | Source | Type IV Sum of Squares | df | Mean Square | F | Sig. | R ² | Adj. R ² |
|------|--------------------|------------------------|-----|-------------|--------|-------|----------------|---------------------|
| Dry | Corrected Model | 283.42 | 11 | 25.77 | 16.04 | 0.000 | 0.393 | 0.368 |
| | Intercept | 358.89 | 1 | 358.89 | 223.35 | 0.000 | | |
| | Treatment | 79.40 | 1 | 79.40 | 49.42 | 0.000 | | |
| | Period | 127.64 | 5 | 25.53 | 15.89 | 0.000 | | |
| | Treatment * Period | 12.52 | 5 | 2.51 | 1.56 | 0.172 | | |
| | Error | 438.67 | 273 | 1.61 | | | | |
| | Total | 1,379.89 | 285 | | | | | |
| | Corrected Total | 722.09 | 284 | | | | | |
| Wet | Corrected Model | 203.67 | 11 | 18.52 | 10.20 | 0.000 | 0.333 | 0.300 |
| | Intercept | 1,431.79 | 1 | 1,431.79 | 788.56 | 0.000 | | |
| | Treatment | 59.49 | 1 | 59.49 | 32.77 | 0.000 | | |
| | Period | 58.77 | 5 | 11.75 | 6.47 | 0.000 | | |
| | Treatment * Period | 20.94 | 5 | 4.19 | 2.30 | 0.045 | | |
| | Error | 408.53 | 225 | 1.82 | | | | |
| | Total | 2,891.47 | 237 | | | | | |
| | Corrected Total | 612.20 | 236 | | | | | |

Table 3. Analysis of variance for factor effects of treatment and measurement period upon predawn leaf water potential.

| Site | Source | Type IV Sum of Squares | df | Mean Square | F | Sig. | R ² | Adj. R ² |
|------|--------------------|------------------------|-----|-------------|----------|-------|----------------|---------------------|
| Dry | Corrected Model | 27.77 | 11 | 2.53 | 18.03 | 0.000 | 0.627 | 0.592 |
| | Intercept | 321.58 | 1 | 321.58 | 2,296.22 | 0.000 | | |
| | Treatment | 3.80 | 1 | 3.80 | 27.15 | 0.000 | | |
| | Period | 22.45 | 5 | 4.49 | 32.06 | 0.000 | | |
| | Treatment * Period | 0.75 | 5 | 0.15 | 1.06 | 0.384 | | |
| | Error | 16.53 | 118 | 0.14 | | | | |
| | Total | 467.75 | 130 | | | | | |
| | Corrected Total | 44.30 | 129 | | | | | |
| Wet | Corrected Model | 5.86 | 11 | 0.53 | 8.30 | 0.000 | 0.493 | 0.433 |
| | Intercept | 129.87 | 1 | 129.87 | 2,021.82 | 0.000 | | |
| | Treatment | 1.68 | 1 | 1.68 | 26.19 | 0.000 | | |
| | Period | 3.28 | 5 | 0.66 | 10.22 | 0.000 | | |
| | Treatment * Period | 0.57 | 5 | 0.11 | 1.78 | 0.124 | | |
| | Error | 6.04 | 94 | 0.06 | | | | |
| | Total | 158.95 | 106 | | | | | |
| | Corrected Total | 11.90 | 105 | | | | | |

Table 4. Seasonal summary of plot and sample tree characteristics for both sites in 2001.

| Site | Plot | Mean % Veg. Cover | Veg. Volume (m ³ /ha) | Mean Height Growth (m) | Mean Height (m) | Seasonal Mean LWP (MPa) | Seasonal Mean PSN (micromoles/m ² /sec) |
|------|-----------|-------------------|----------------------------------|------------------------|-----------------|-------------------------|--|
| Dry | Control | 38.5 | 725 | 0.04 | 0.92 | -1.97 | 0.79 |
| | Treatment | 26.9* | 433 | 0.07** | 1.22** | -1.63** | 2.17** |
| Wet | Control | 63.5 | 1,463 | 0.17 | 1.32 | -1.32 | 2.38 |
| | Treatment | 32.9** | 592 | 0.29** | 1.54 | -1.05** | 3.80** |

Table 4 (continued).

| Site | Plot | Mean Seasonal Maximum Soil Temperature (Celsius) | Mean Seasonal Minimum Soil Temperature (Celsius) | Mean Foliar Nitrogen (% dry wt.) | Mean Carbon Isotope Discrimination (‰) |
|------|-----------|--|--|----------------------------------|--|
| Dry | Control | 16.7 | 13.9 | 0.86 | 18.02 |
| | Treatment | 16.8 | 13.6* | 0.99* | 19.39* |
| Wet | Control | 18.0 | 13.1 | 1.05 | 18.97 |
| | Treatment | 18.0 | 13.3 | 1.14 | 19.16 |

**Differences between plots are significant at $p \leq 0.001$ (two-tailed) using t-tests.

* Differences between plots are significant at $p < 0.05$ (two-tailed) using t-tests.

Table 5. Biweekly plot means comparisons of net photosynthesis for dry and wet sites.

| Site | Period | t | df | Sig. (2-tailed) | Mean Difference | Std. Error Difference | 95% Confidence Interval of the Difference | |
|------|---------------|--------|----|--------------------|--------------------|--------------------------|---|--------|
| | | | | | | | Lower | Upper |
| Dry | Late June | -2.214 | 12 | 0.047 | -0.733 | 0.331 | -1.454 | -0.011 |
| | Mid-July | -5.681 | 56 | 0.000 | -2.126 | 0.374 | -2.875 | -1.376 |
| | Late July | -4.489 | 68 | 0.000 | -1.456 | 0.324 | -2.102 | -0.808 |
| | Early August | -4.433 | 68 | 0.000 | -1.392 | 0.314 | -2.018 | -0.765 |
| | Late August | -3.124 | 47 | 0.003 | -0.992 | 0.317 | -1.630 | -0.353 |
| | Mid-September | -2.217 | 22 | 0.037 | -0.916 | 0.413 | -1.772 | -0.059 |
| Wet | Early July | -0.399 | 13 | 0.696 | -0.403 | 1.009 | -2.583 | 1.777 |
| | Mid-July | -4.438 | 52 | 0.000 | -1.463 | 0.329 | -2.124 | -0.801 |
| | Early August | -4.883 | 64 | 0.000 | -1.741 | 0.356 | -2.453 | -1.028 |
| | Mid-August | -4.925 | 58 | 0.000 | -1.649 | 0.335 | -2.320 | -0.979 |
| | Mid-September | -4.788 | 21 | 0.000 | -2.087 | 0.436 | -2.993 | -1.180 |
| | Early October | 0.325 | 17 | 0.749 | 0.194 | 0.596 | -1.064 | 1.452 |

Table 6. Biweekly plot means comparisons of predawn leaf water potential for dry and wet sites.

| Site | Period | t | df | Sig. (1-tailed) | Mean Difference | Std. Error Difference | 95% Confidence Interval of the Difference | |
|------|---------------|--------|----|--------------------|--------------------|--------------------------|---|--------|
| | | | | | | | Lower | Upper |
| Dry | Late June | -1.832 | 7 | 0.055 | -0.283 | 0.155 | -0.649 | 0.082 |
| | Mid-July | -1.707 | 23 | 0.051 | -0.323 | 0.189 | -0.714 | 0.068 |
| | Late July | -3.012 | 24 | 0.003 | -0.381 | 0.126 | -0.642 | -0.120 |
| | Early August | -1.938 | 26 | 0.032 | -0.205 | 0.106 | -0.423 | 0.012 |
| | Late August | -4.073 | 25 | 0.000 | -0.647 | 0.159 | -0.973 | -0.320 |
| | Mid-September | -2.038 | 13 | 0.031 | -0.448 | 0.220 | -0.923 | 0.026 |
| Wet | Early July | -1.384 | 7 | 0.105 | -0.208 | 0.150 | -.0562 | 0.147 |
| | Mid-July | -1.398 | 16 | 0.091 | -0.221 | 0.158 | -0.556 | 0.114 |
| | Early August | -0.471 | 18 | 0.322 | -0.050 | 0.106 | -0.273 | 0.173 |
| | Mid-August | -5.517 | 28 | 0.000 | -0.437 | 0.079 | -0.599 | -0.275 |
| | Mid-September | -4.707 | 13 | 0.000 | -0.453 | 0.096 | -0.660 | -0.245 |
| | Early October | -1.549 | 12 | 0.074 | -0.295 | 0.190 | -0.710 | 0.120 |

Table 7. Seasonal summary of microclimate conditions for gas-exchange measurements.

| | | | N | Minimum | Maximum | Mean | Std. Error | Std. Deviation |
|------|---------------|-------------|----|---------|----------|----------|------------|----------------|
| Site | Period | | | | | | | |
| Dry | Late June | Light | 14 | 155.73 | 1,997.66 | 624.36 | 163.78 | 612.82 |
| | | Air temp. | 14 | 26.36 | 32.43 | 27.97 | 0.52 | 1.95 |
| | | Humidity | 14 | 22.78 | 28.60 | 25.16 | 0.43 | 1.61 |
| | Mid-July | Light | 58 | 112.70 | 1,999.00 | 621.06 | 64.54 | 491.57 |
| | | Air temp. | 58 | 27.42 | 36.24 | 31.35 | 0.23 | 1.78 |
| | | Humidity | 58 | 15.71 | 37.35 | 24.35 | 0.89 | 6.83 |
| | Late July | Light | 70 | 64.36 | 2,193.33 | 1,059.09 | 94.66 | 791.98 |
| | | Air temp.* | 70 | 26.49 | 40.62 | 33.53 | 0.39 | 3.27 |
| | | Humidity | 70 | 11.58 | 24.26 | 15.58 | 0.37 | 3.11 |
| | Early August | Light | 70 | 67.49 | 2,012.66 | 983.02 | 89.02 | 744.79 |
| | | Air temp. | 70 | 25.40 | 39.46 | 33.09 | 0.42 | 3.53 |
| | | Humidity | 70 | 11.99 | 28.29 | 20.08 | 0.43 | 3.65 |
| | Late August | Light | 49 | 70.64 | 2,061.33 | 762.34 | 99.76 | 698.35 |
| | | Air temp. | 49 | 23.30 | 31.61 | 27.29 | 0.32 | 2.28 |
| | | Humidity | 49 | 16.70 | 27.28 | 20.58 | 0.38 | 2.66 |
| | Mid-September | Light | 24 | 62.27 | 1,943.50 | 845.43 | 117.49 | 575.61 |
| | | Air temp. | 24 | 20.28 | 26.54 | 23.32 | 0.34 | 1.67 |
| | | Humidity | 24 | 17.95 | 25.75 | 20.82 | 0.42 | 2.09 |
| Wet | Early July | Light ** | 15 | 118.13 | 2,146.00 | 791.54 | 153.69 | 595.26 |
| | | Air temp.* | 15 | 20.07 | 32.58 | 27.14 | 1.06 | 4.11 |
| | | Humidity ** | 15 | 15.86 | 44.60 | 24.50 | 1.96 | 7.61 |
| | Mid-July | Light | 54 | 167.76 | 2,437.00 | 1013.62 | 94.13 | 691.75 |
| | | Air temp. | 54 | 21.32 | 36.87 | 29.03 | 0.55 | 4.05 |
| | | Humidity | 54 | 18.08 | 32.44 | 25.10 | .51 | 3.80 |
| | Early August | Light | 66 | 57.42 | 2,085.33 | 1,272.76 | 89.64 | 728.24 |
| | | Air temp. * | 66 | 27.95 | 40.24 | 34.68 | 0.31 | 2.59 |
| | | Humidity | 66 | 17.39 | 30.86 | 23.80 | 0.39 | 3.18 |
| | Mid-August | Light ** | 60 | 63.85 | 1,999.00 | 1,257.61 | 83.47 | 646.57 |
| | | Air temp.* | 60 | 30.31 | 41.44 | 35.84 | 0.40 | 3.10 |
| | | Humidity | 60 | 14.52 | 29.40 | 21.47 | 0.43 | 3.38 |
| | Mid-September | Light | 23 | 89.20 | 1,815.00 | 939.65 | 109.52 | 525.28 |
| | | Air temp. | 23 | 26.87 | 34.10 | 31.11 | 0.39 | 1.90 |
| | | Humidity * | 23 | 17.24 | 26.05 | 20.78 | 0.44 | 2.11 |
| | Early October | Light | 19 | 56.54 | 250.30 | 118.83 | 10.94 | 47.70 |
| | | Air temp. | 19 | 9.92 | 13.11 | 11.85 | 0.21 | 0.93 |
| | | Humidity | 19 | 41.59 | 52.65 | 45.72 | 0.64 | 2.82 |

**Mean differences between plots are significant at $p \leq 0.001$ (two-tailed) using t-tests.

* Mean differences between plots are significant at $p < 0.05$ (two-tailed) using t-tests.

Note – units: 1) light – micromoles/m²/sec, 2) temperature – Celsius, and 3) relative humidity – percent.

Tables 8a-d. Regression models used to assess vegetation effects upon net photosynthesis for the dry site.

a)

| Model | Prais-Winsten Estimates | | | | | |
|---------------------|--------------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.344 | 0.118 | 0.112 | 1.346 | 2.145 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 69.00 | 1 | 69.00 | 38.121 | 0.000 |
| | Residual | 512.44 | 283 | 1.81 | | |
| | Total | 581.44 | 284 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | 2.297 | 0.1905 | | 12.062 | 0.000 |
| | % Cover | -0.0246 | 0.00398 | -0.3444 | -6.173 | 0.000 |

b)

| Model | Prais-Winsten Estimates | | | | | |
|---------------------|--------------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.428 | 0.184 | 0.175 | 1.294 | 2.15 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 106.11 | 2 | 53.06 | 31.58 | 0.000 |
| | Residual | 470.85 | 281 | 1.68 | | |
| | Total | 576.96 | 283 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | 1.3240 | 0.2790 | | 4.746 | 0.000 |
| | % Cover | -0.0273 | 0.00385 | -0.3873 | -7.103 | 0.000 |
| | Height | 0.9692 | 0.2095 | 0.2522 | 4.625 | 0.000 |

Tables 8a-d (continued).

c)

| Model | Prais-Winsten Estimates | | | | | |
|--------------|-------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.471 | 0.222 | 0.202 | 1.290 | 2.04 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 131.59 | 6 | 21.93 | 13.21 | 0.000 |
| | Residual | 460.99 | 277 | 1.66 | | |
| | Total | 592.58 | 283 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | 1.304 | 0.3933 | | 3.315 | 0.001 |
| | % Cover | -0.0263 | 0.004014 | -0.3480 | -6.559 | 0.000 |
| | Period 1 | 1.1215 | 0.6019 | 0.1219 | 1.863 | 0.063 |
| | Period 2 | 2.0147 | 0.4399 | 0.3987 | 4.579 | 0.000 |
| | Period 3 | 1.3552 | 0.4288 | 0.2863 | 3.161 | 0.002 |
| | Period 4 | 0.7931 | 0.4288 | 0.1675 | 1.849 | 0.065 |
| | Period 5 | 0.2530 | 0.4482 | 0.0470 | 0.565 | 0.573 |

d)

| Model | Prais-Winsten Estimates | | | | | |
|-----------------|-------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.529 | 0.280 | 0.259 | 1.242 | 2.03 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 165.96 | 7 | 23.71 | 15.396 | 0.000 |
| | Residual | 426.06 | 276 | 1.54 | | |
| | Total | 592.02 | 283 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | 0.2829 | 0.4363 | | 0.649 | 0.517 |
| | % Cover | -0.0286 | 0.00389 | -0.3790 | -7.354 | 0.000 |
| | Height | 0.9967 | 0.2096 | 0.2452 | 4.757 | 0.000 |
| | Period 1 | 1.2372 | 0.5822 | 0.1341 | 2.125 | 0.034 |
| | Period 2 | 2.0362 | 0.4252 | 0.4017 | 4.788 | 0.000 |
| | Period 3 | 1.3660 | 0.4144 | 0.2877 | 3.296 | 0.001 |
| | Period 4 | 0.8154 | 0.4144 | 0.1717 | 1.967 | 0.050 |
| Period 5 | 0.2570 | 0.4331 | 0.0476 | 0.594 | 0.553 | |

Tables 9a-d. Regression models used to assess vegetation effects upon net photosynthesis for the wet site.

a)

| Model | Generalized Least Squares | | | | | |
|---------------------|----------------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.293 | 0.086 | 0.082 | 1.554 | 1.73 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 52.39 | 1 | 52.39 | 21.682 | 0.000 |
| | Residual | 558.17 | 231 | 2.42 | | |
| | Total | 610.56 | 232 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | t | Sig. |
| | Intercept | 4.214 | 0.260 | | 16.224 | 0.000 |
| | % Cover | -0.0234 | 0.005 | -.293 | -4.656 | 0.000 |

b)

| Model | Generalized Least Squares | | | | | |
|---------------------|----------------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.339 | 0.115 | 0.107 | 1.550 | 1.73 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 68.19 | 2 | 34.01 | 14.19 | 0.000 |
| | Residual | 526.40 | 219 | 2.40 | | |
| | Total | 594.59 | 221 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | t | Sig. |
| | Intercept | 2.337 | 0.736 | | 3.176 | 0.002 |
| | % Cover | -0.0180 | 0.006 | -0.219 | -3.195 | 0.002 |
| | Crown Ratio | 2.320 | 0.843 | 0.189 | 2.752 | 0.006 |

Tables 9a-d (continued).

c)

| Model | Generalized Least Squares | | | | | |
|--------------|---------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.436 | 0.190 | 0.169 | 1.479 | 1.947 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 116.12 | 6 | 19.35 | 8.846 | 0.000 |
| | Residual | 494.45 | 226 | 2.19 | | |
| | Total | 610.57 | 232 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | t | Sig. |
| | Intercept | 3.262 | 0.394 | | 8.287 | 0.000 |
| | % Cover | -0.0254 | 0.005 | -0.312 | -5.185 | 0.000 |
| | Period 1 | 1.000 | 0.512 | 0.152 | 1.953 | 0.052 |
| | Period 2 | 1.673 | 0.398 | 0.430 | 4.200 | 0.000 |
| | Period 3 | 1.329 | 0.387 | 0.368 | 3.438 | 0.001 |
| | Period 4 | 0.715 | 0.391 | 0.192 | 1.826 | 0.069 |
| | Period 5 | 0.350 | 0.460 | 0.065 | 0.762 | 0.447 |

d)

| Model | Generalized Least Squares | | | | | |
|-----------------|---------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.480 | 0.231 | 0.206 | 1.462 | 1.97 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 137.27 | 7 | 19.61 | 9.177 | 0.000 |
| | Residual | 457.32 | 214 | 2.14 | | |
| | Total | 594.59 | 221 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | t | Sig. |
| | Intercept | 1.242 | 0.768 | | 1.617 | 0.107 |
| | % Cover | -0.0198 | 0.005 | -0.240 | -3.698 | 0.000 |
| | Crown Ratio | 2.407 | 0.797 | 0.196 | 3.019 | 0.003 |
| | Period 1 | 0.998 | 0.523 | 0.148 | 1.910 | 0.057 |
| | Period 2 | 1.779 | 0.405 | 0.454 | 4.398 | 0.000 |
| | Period 3 | 1.473 | 0.393 | 0.404 | 3.750 | 0.000 |
| | Period 4 | 0.786 | 0.398 | 0.209 | 1.975 | 0.050 |
| Period 5 | 0.414 | 0.467 | 0.076 | 0.887 | 0.376 | |

Tables 10a-b. Regression models used to assess vegetation effects upon predawn leaf water potential for the dry site.

a)

| Model | Prais-Winsten Estimates | | | | | |
|---------------------|--------------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.328 | 0.108 | 0.087 | 0.367 | 2.08 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 2.054 | 2 | 1.027 | 7.61 | <0.01 |
| | Residual | 17.012 | 126 | 0.135 | | |
| | Total | 19.066 | 128 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | -1.5222 | 0.1424 | | -10.684 | 0.000 |
| | % Cover | -0.0198 | 0.0055 | -1.2319 | -3.618 | 0.000 |
| | % Cover² | 0.00025 | 0.00008 | 1.0709 | 3.146 | 0.002 |

b)

| Model | Generalized Least Squares | | | | | |
|---------------------|----------------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.741 | 0.549 | 0.524 | 0.404 | 1.54 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 24.31 | 7 | 3.477 | 21.26 | 0.000 |
| | Residual | 19.96 | 122 | 0.164 | | |
| | Total | 44.27 | 129 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | -2.044 | 0.144 | | -14.21 | 0.000 |
| | % Cover | -0.0245 | 0.007 | -0.781 | -3.58 | 0.000 |
| | % Cover² | -0.000329 | 0.000 | 0.708 | 3.24 | 0.002 |
| | Period 1 | 1.243 | 0.175 | 0.541 | 7.10 | 0.000 |
| | Period 2 | 0.866 | 0.133 | 0.585 | 6.54 | 0.000 |
| | Period 3 | 0.814 | 0.133 | 0.558 | 6.13 | 0.000 |
| | Period 4 | 0.680 | 0.130 | 0.479 | 5.22 | 0.000 |
| Period 5 | 0.0445 | 0.130 | 0.031 | 0.34 | 0.734 | |

Tables 11a-b. Regression models used to assess vegetation effects upon predawn leaf water potential for the wet site.

a)

| Model | Generalized Least Squares | | | | | |
|--------------|---------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.344 | 0.118 | 0.110 | 0.318 | 1.60 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 1.401 | 1 | 1.401 | 13.817 | 0.000 |
| | Residual | 10.45 | 103 | 0.101 | | |
| | Total | 11.848 | 104 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | -0.934 | 0.073 | | -12.748 | 0.000 |
| | % Cover | -0.00551 | 0.001 | -0.344 | -3.717 | 0.000 |

b)

| Model | Generalized Least Squares | | | | | |
|-----------------|---------------------------|-----------------------|------------------------|---------------------------|-------------------|----------------------|
| Summary | | R | R² | Adj. R² | Std. Error | Durbin-Watson |
| | | 0.614 | 0.377 | 0.338 | 0.275 | 2.257 |
| ANOVA | | Sum of Squares | Degrees Freedom | Mean Square | F | Sig. |
| | Regression | 4.463 | 6 | 0.744 | 9.869 | 0.000 |
| | Residual | 7.385 | 98 | 0.0754 | | |
| | Total | 11.848 | 104 | | | |
| Coefficients | | Beta | Std. Error | Std. Beta | T | Sig. |
| | Intercept | -1.252 | 0.088 | | -14.156 | 0.000 |
| | % Cover | -0.00572 | 0.001 | -0.357 | -4.303 | 0.000 |
| | Period 1 | 0.266 | 0.119 | 0.221 | 2.241 | 0.027 |
| | Period 2 | 0.466 | 0.101 | 0.511 | 4.608 | 0.000 |
| | Period 3 | 0.518 | 0.096 | 0.606 | 5.42 | 0.000 |
| | Period 4 | 0.376 | 0.090 | 0.506 | 4.202 | 0.000 |
| Period 5 | 0.164 | 0.103 | 0.171 | 1.588 | 0.116 | |

Appendix B: Figures

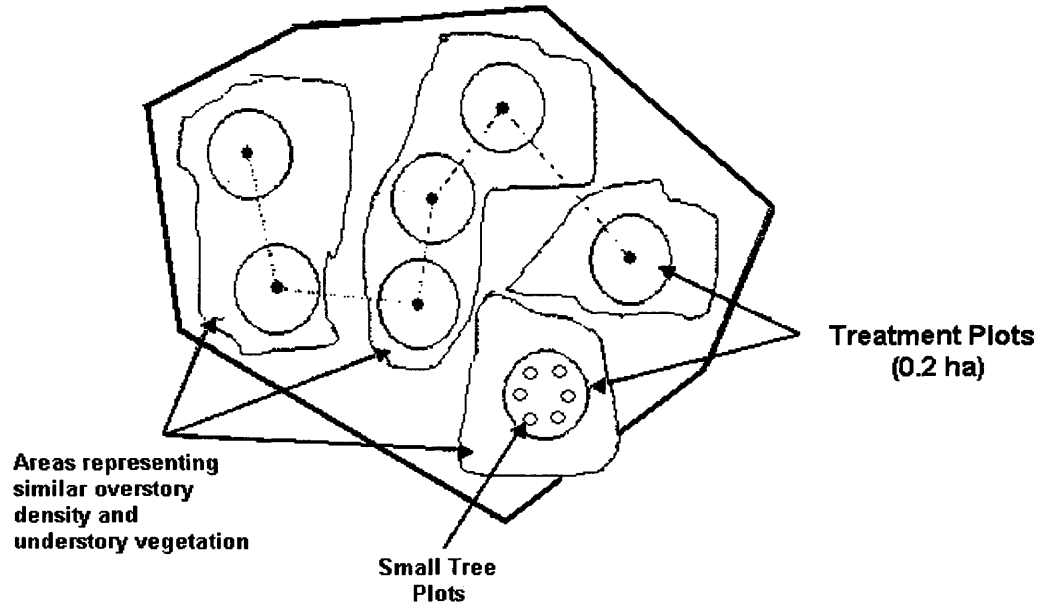


Figure 1. Plot layout of small tree and competing vegetation study.

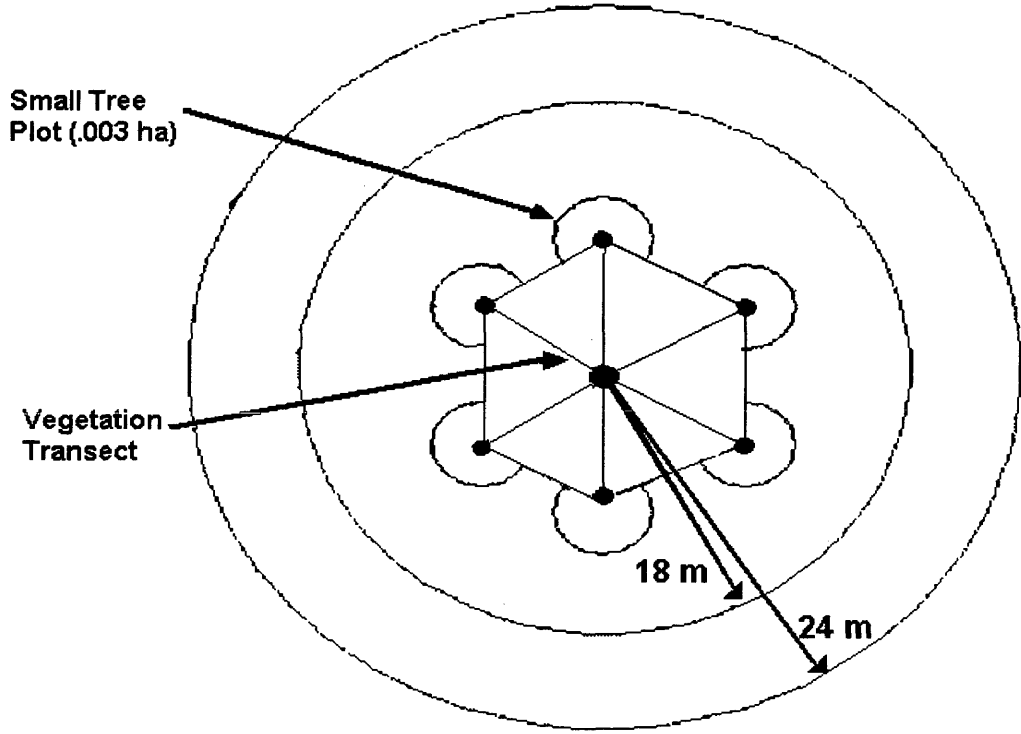


Figure 2. Individual plot and transect layout for sampling small trees and vegetation.

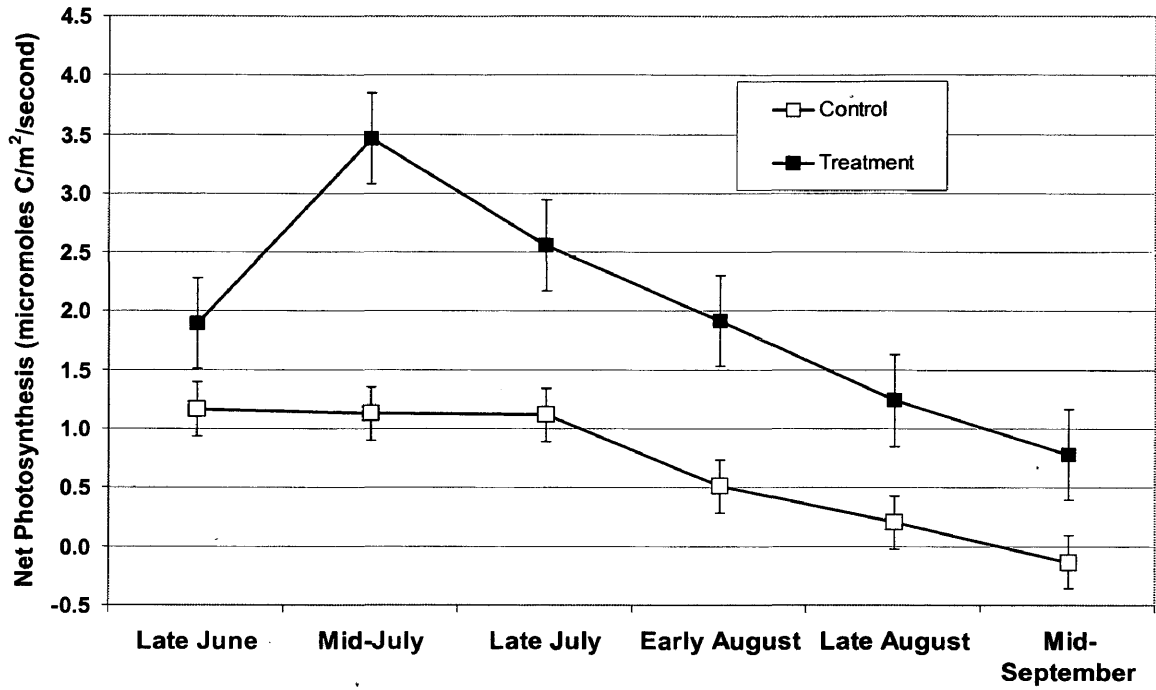


Figure 3. Summer net photosynthesis for the dry site (bars indicate one standard error).

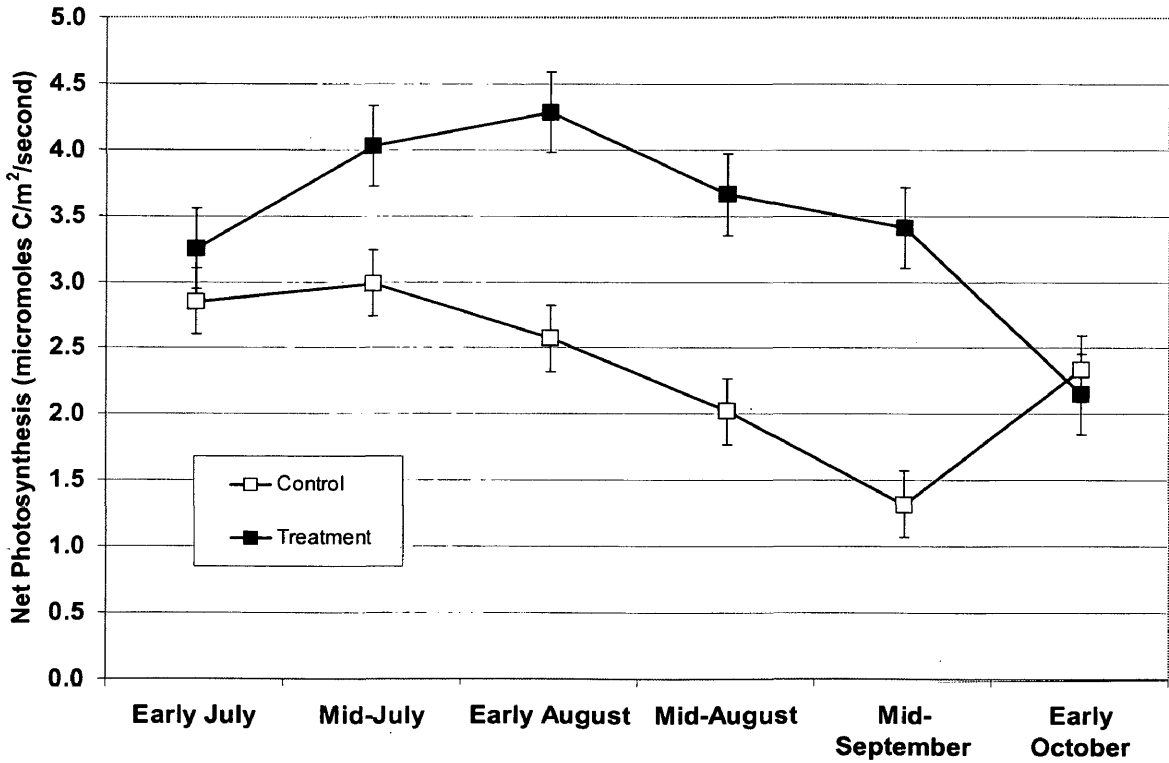


Figure 4. Summer net photosynthesis for the wet site (bars indicate one standard error).

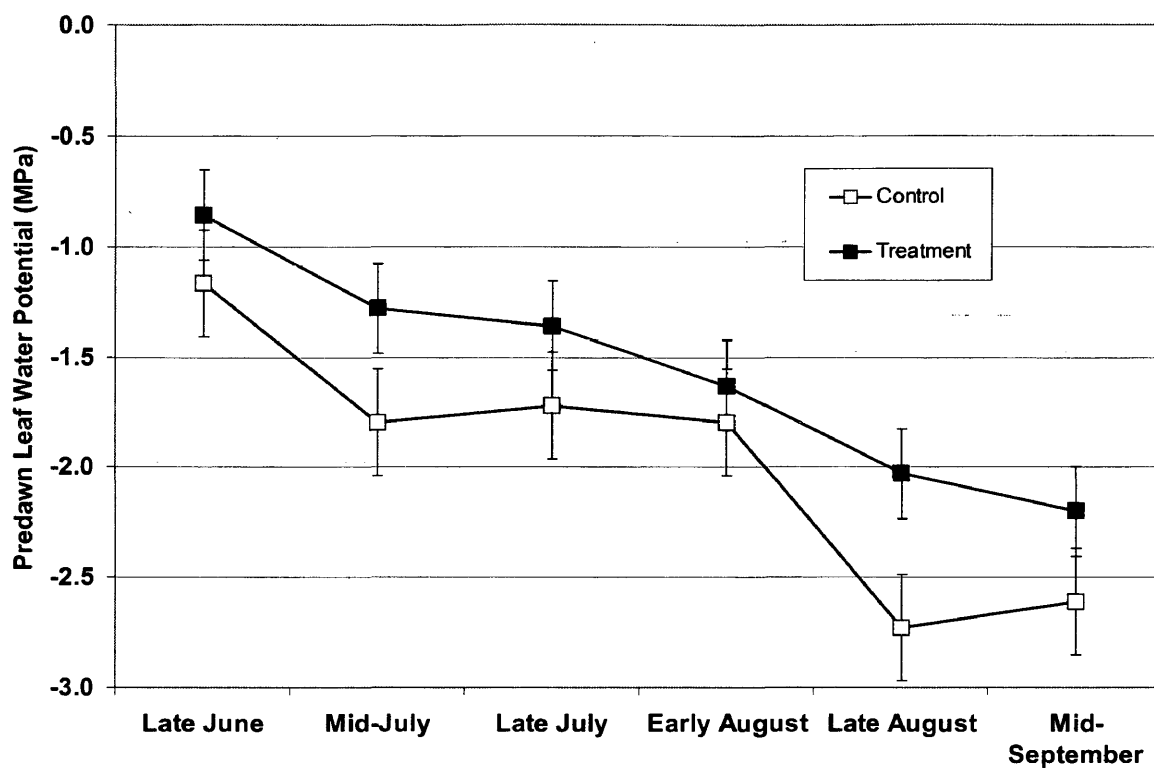


Figure 5. Summer predawn leaf water potential for the dry site (bars indicate one standard error).

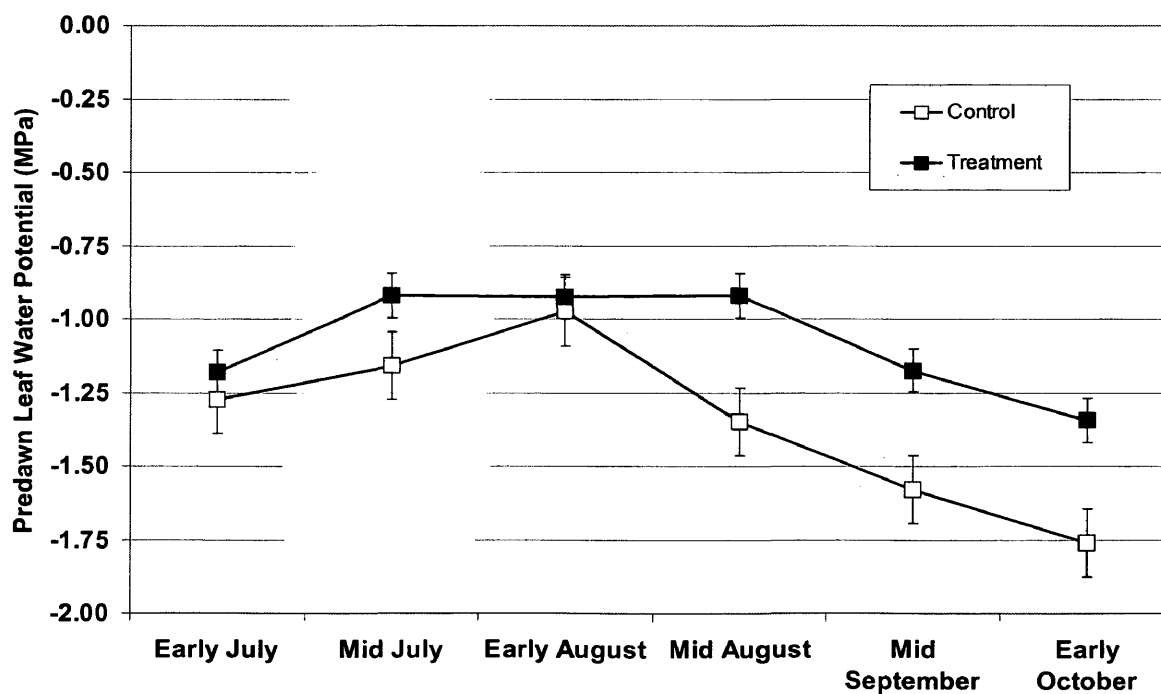


Figure 6. Summer predawn leaf water potential for the wet site (bars indicate one standard error).

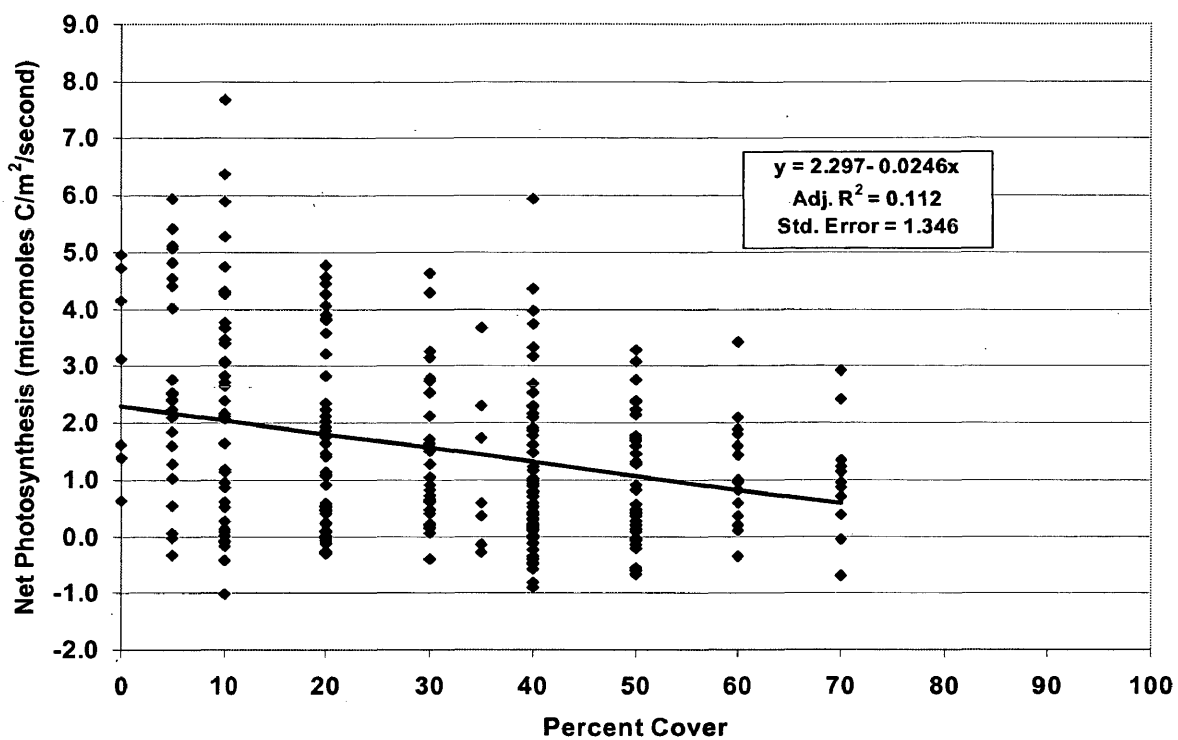


Figure 7. Estimated mean effect of vegetation cover upon net photosynthesis for the dry site.

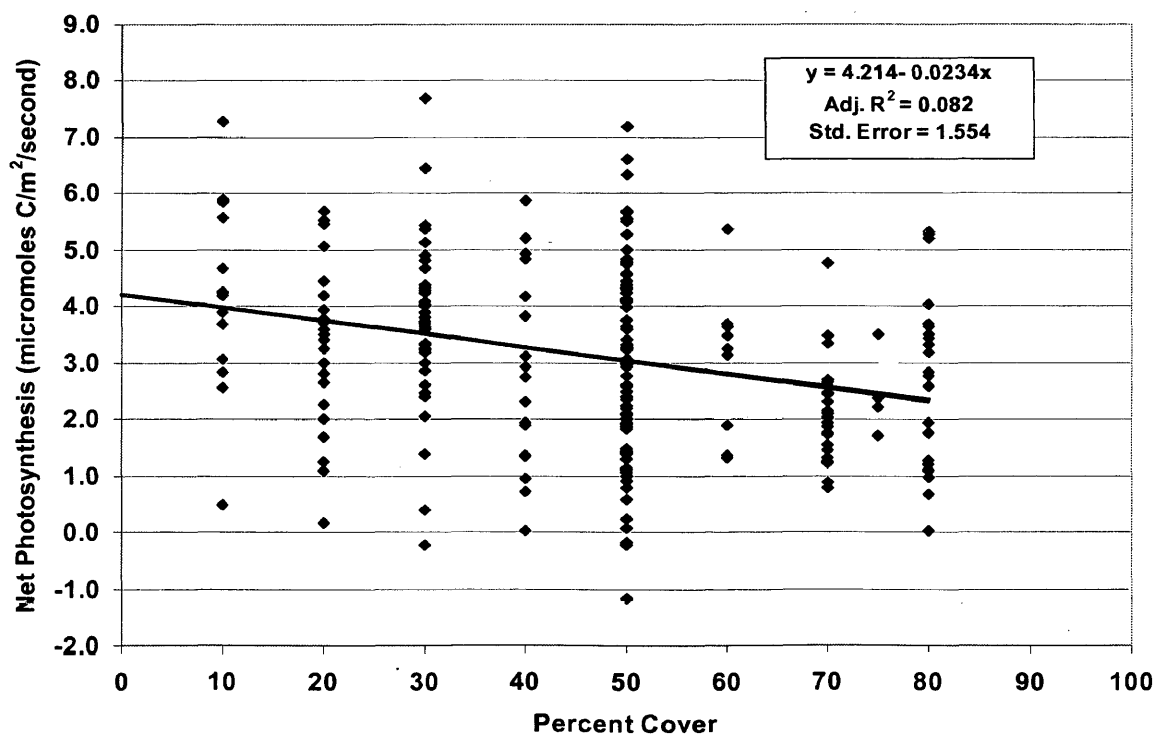


Figure 8. Estimated mean effect of vegetation cover upon net photosynthesis for the wet site.

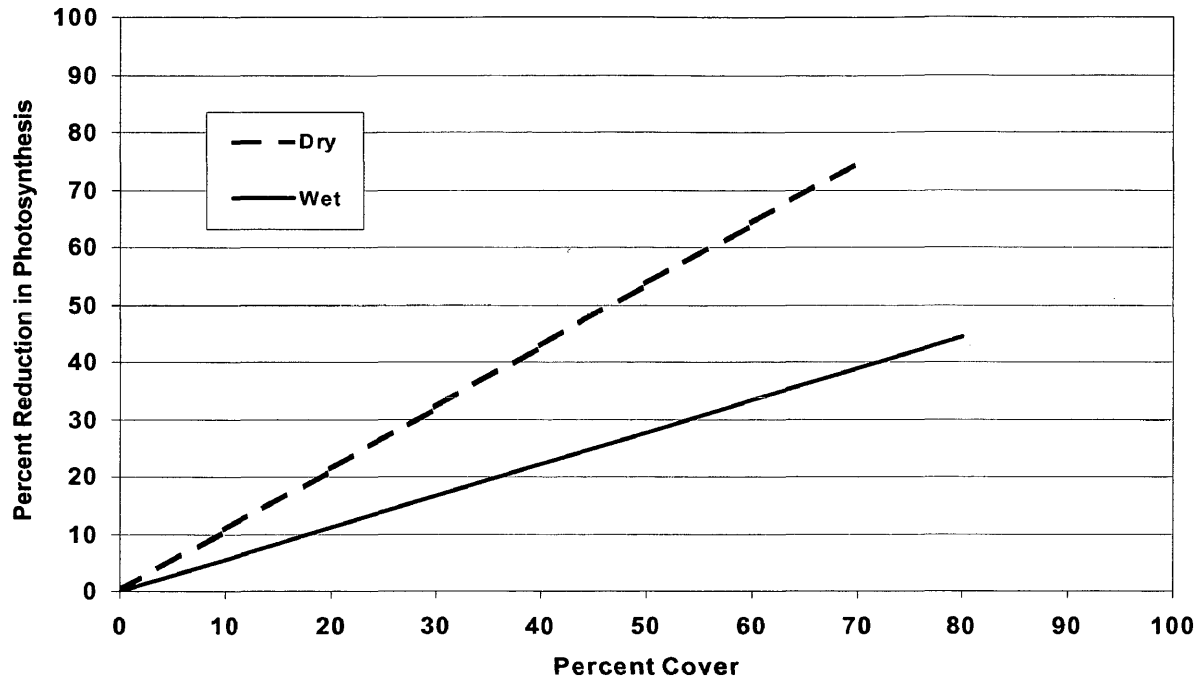


Figure 9. Estimated percent reduction in net photosynthesis by vegetation cover for dry and wet sites.

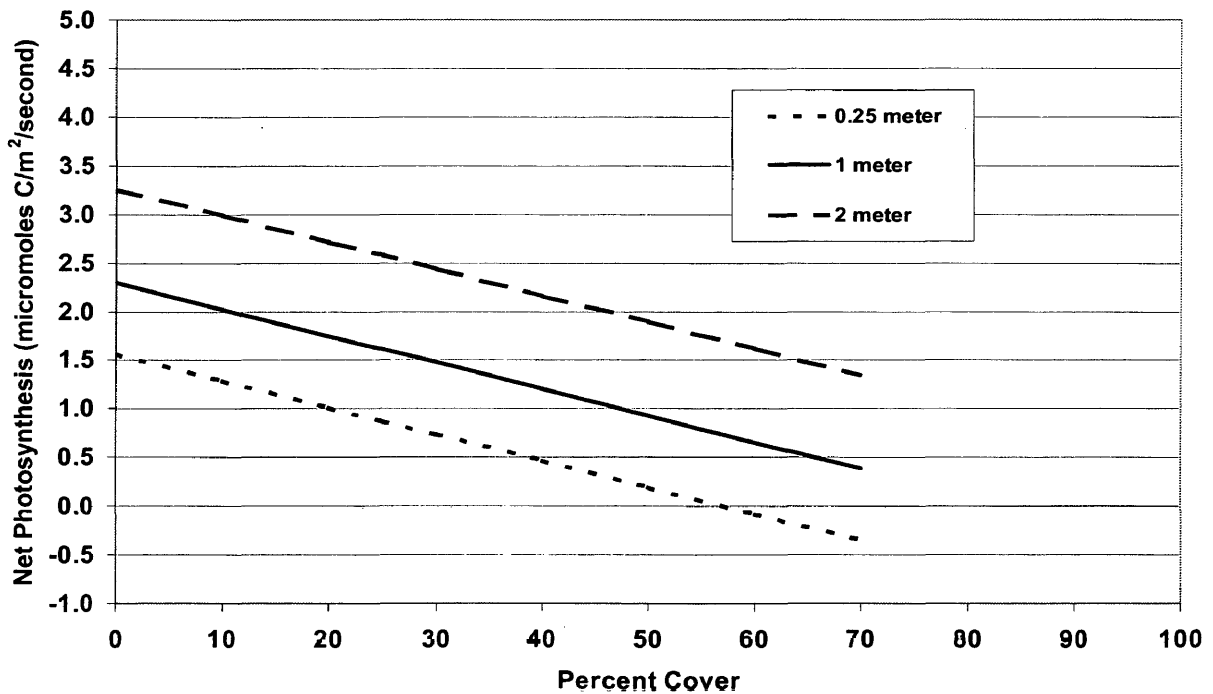


Figure 10. Estimated mean effect of vegetation cover upon net photosynthesis of young Douglas-fir at three different heights for the dry site (standard error = 1.294).

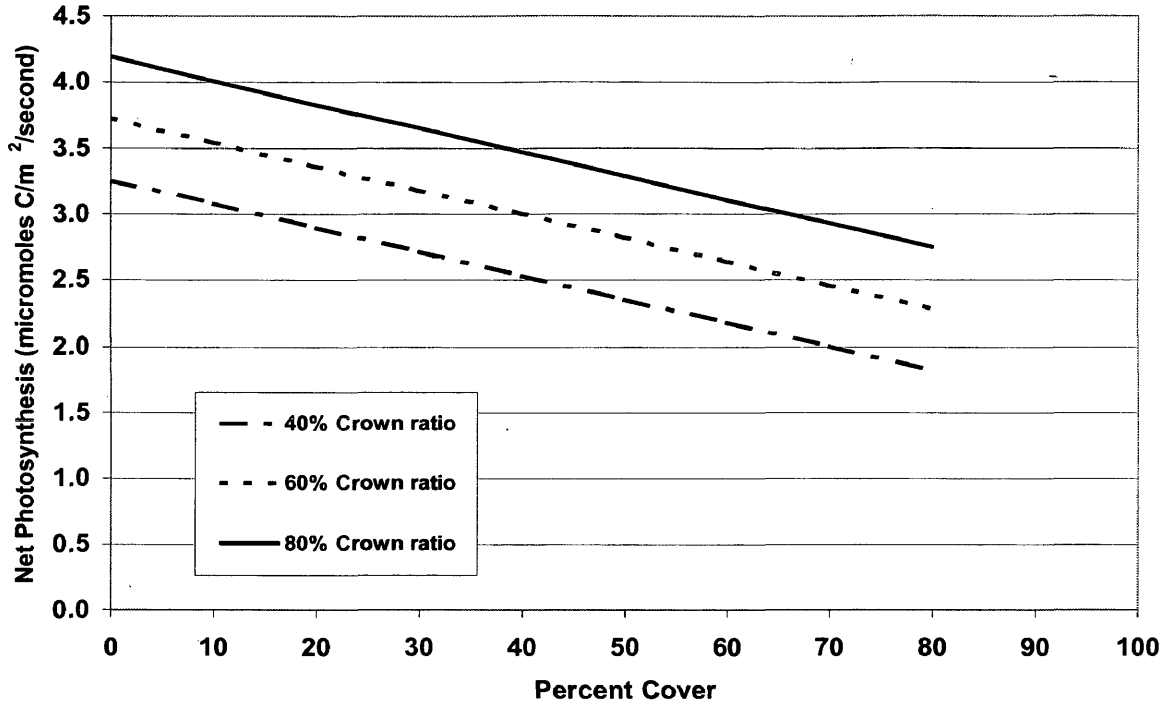


Figure 11. Estimated mean effect of vegetation cover upon net photosynthesis of young Douglas-fir at three different crown ratios for the wet site (standard error = 1.550).

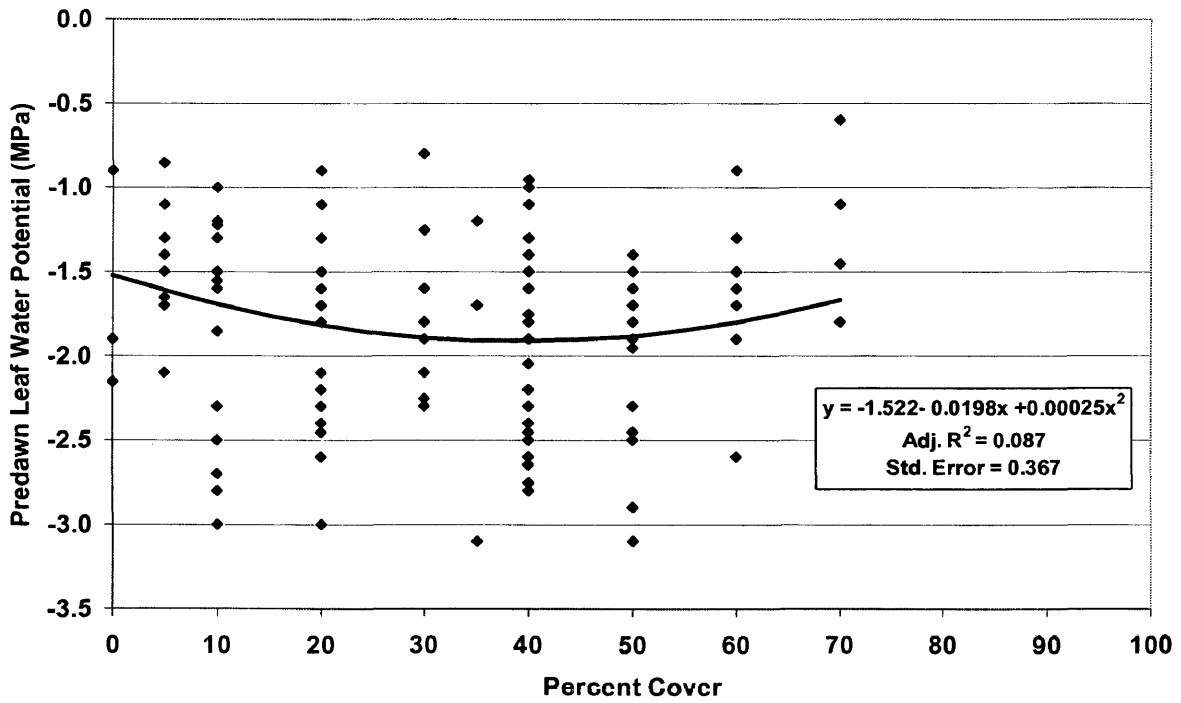


Figure 12. Estimated mean effect of vegetation cover upon predawn leaf water potential for the dry site.

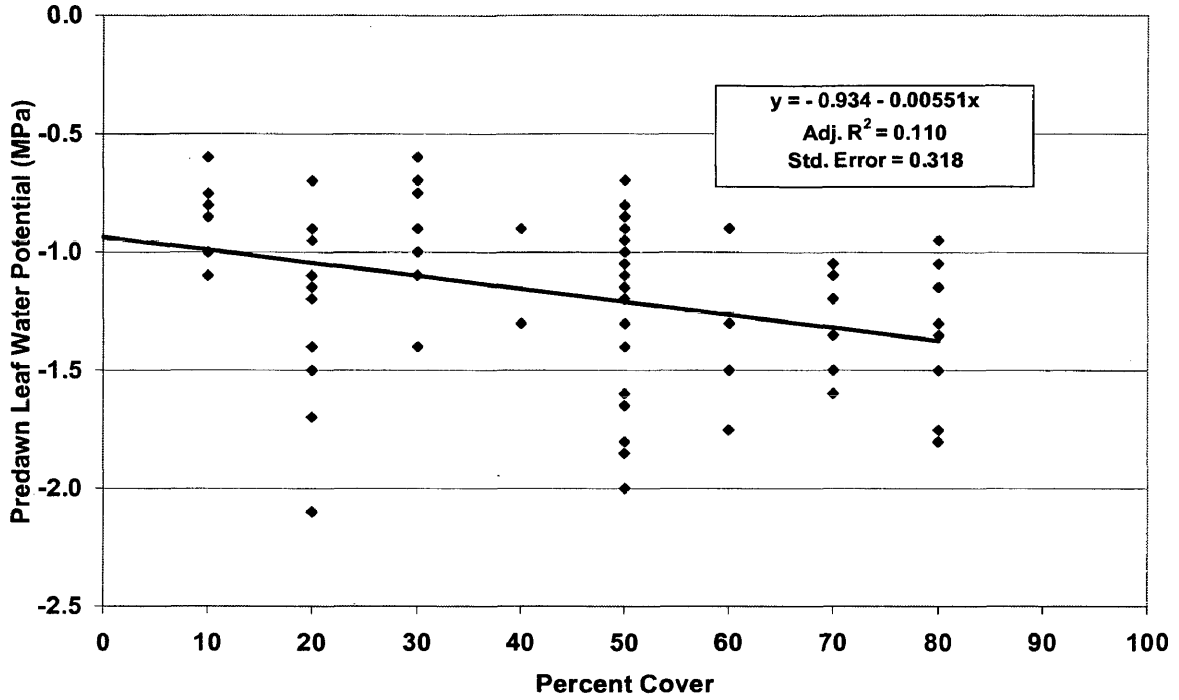


Figure 13. Estimated mean effect of vegetation cover upon predawn leaf water potential for the wet site.

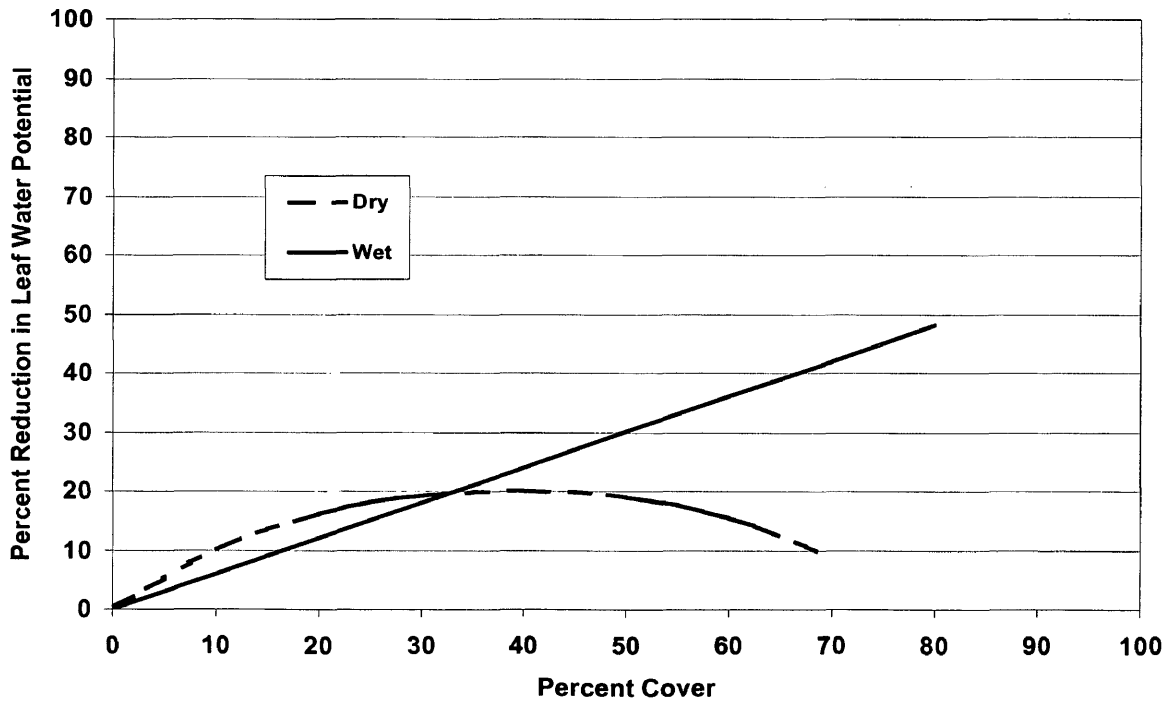


Figure 14. Estimated percent reduction in predawn leaf water potential by vegetation cover for dry and wet sites.