



Effects of overstory thinning on lodgepole pine understories
by John Bernard Plaggemeyer

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Biological Science
Montana State University
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Abstract:

Young regrowth Lodgepole pine trees were thinned in the mid 1960's to spacings of 1.8, 2.7, 3.6, 4.5, and 5.4 meters between trees on four different National Forest sites in Montana and Idaho representing three different habitat types. These trees have been maintained at these spacings. The purpose of this study was to see if these spacing levels have affected the understory plants under these trees 25+ years later. I used two methods to measure the understory response. First, I estimated % cover. The second method was to measure the leaf area of all understory plants. Individual species and categories of plants, created by summing species, were analyzed.

Total understory density declined with increasing tree density.

The closest spacing had significantly less vegetation. Cover differences, among the four wider spacings was small. Total vegetation varied little between relative tree position. Different components of understory vegetation responded differently. Graminoid cover in the widest (4.5 & 5.4) spacing exceeded graminoids in the two narrower spacings (1.8, 2.7, & 3.6 meters). Forb vegetation also declined from the wide spacings to the narrowest spacing (1.8m). Shrub species were inhibited only at the narrowest spacing (1.8).

Multiple regression analysis was used to correlate environmental factors with vegetation measurement variables. Graminoid and forb species were correlated with light. Shrub species were unaffected. Graminoid, forb, and total vegetation was positively correlated with medium depth soil water (15-45 cm). Forb species were also correlated with deeper soil water (45-76 cm). Increasing evaporation on the soil surface correlated negatively with graminoid species and total understory vegetation. Average growing season temperature correlated positively with forb LAI and shrub vegetation. Forb cover decreased with increasing temperature. Litter cover correlated negatively with understory total vegetation. Regression models accounted for 50-70% of the variation in these understory plants.

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ABSTRACT

Young regrowth Lodgepole pine trees were thinned in the mid 1960's to spacings of 1.8, 2.7, 3.6, 4.5, and 5.4 meters between trees on four different National Forest sites in Montana and Idaho representing three different habitat types. These trees have been maintained at these spacings. The purpose of this study was to see if these spacing levels have affected the understory plants under these trees 25+ years later. I used two methods to measure the understory response. First, I estimated % cover. The second method was to measure the leaf area of all understory plants. Individual species and categories of plants, created by summing species, were analyzed.

Total understory density declined with increasing tree density. The closest spacing had significantly less vegetation. Cover differences among the four wider spacings was small. Total vegetation varied little between relative tree position. Different components of understory vegetation responded differently. Graminoid cover in the widest (4.5 & 5.4) spacing exceeded graminoids in the two narrower spacings (1.8, 2.7, & 3.6 meters). Forb vegetation also declined from the wide spacings to the narrowest spacing (1.8m). Shrub species were inhibited only at the narrowest spacing (1.8).

Multiple regression analysis was used to correlate environmental factors with vegetation measurement variables. Graminoid and forb species were correlated with light. Shrub species were unaffected. Graminoid, forb, and total vegetation was positively correlated with medium depth soil water (15-45 cm). Forb species were also correlated with deeper soil water (45-76 cm). Increasing evaporation on the soil surface correlated negatively with graminoid species and total understory vegetation. Average growing season temperature correlated positively with forb LAI and shrub vegetation. Forb cover decreased with increasing temperature. Litter cover correlated negatively with understory total vegetation. Regression models accounted for 50-70% of the variation in these understory plants.

INTRODUCTION

Plant growth is controlled by environmental factors (Fitter and Hay 1991; Kozlowski 1991) including availability of nutrients (carbon dioxide, water, oxygen, and minerals) and energy (light and temperature). Any plant will be stressed if given inadequate supplies of one or more of these materials.

Understory plants live in an environment in which light, water, and nutrients may be limited (Fitter & Hay 1991). For example, species growing under forest canopies must tolerate low light intensities; light readings on the forest floor may be 0.5 to 5% of full sunlight (Chazon & Pearcy 1991). Root competition for nutrients and water is also intense (Burrows 1990).

Thinning a forest stand is expected to increase the available supplies of light, water, and nutrients to understory plants until the canopy or "root canopy" closes again. In 1965-1966 study plots were installed on four locations in three different environmental types in Montana and Idaho to study the long term effects of different spacings on growth of lodgepole pine on recently logged sites (Cole 1976; Conway 1982). I re-examined these plots with a new objective. That is, to test our hypothesis that, in all environmental types, different levels of forest thinning releases resources to the understory .

In the following pages we test the hypotheses:

I expected the effects of level of thinning (spacing) to vary with position with respect to the tree; that is under the tree, at the dripline, or out between the trees. 1) I expected no difference in understory cover and leaf area under the trees regardless of tree

spacing treatment. 2) I expected that cover and leaf area at the dripline may increase with thinning due to increases in light, but without increases in water and nutrients. 3) Outside the tree canopy I expected understory cover and LAI to be positively correlated with increase in light, water, and nutrients.

LITERATURE REVIEW

Physiological ecology of thinning

Nutrients are an important control of vegetation development (Burrows 1990). In a fully stocked forest resources are limited for understory species. Overstory cover generally reduces understory production (Pase 1958; McConnell & Smith 1965, 1967; Jameson 1967; Riegel et al 1992). Clearings in forests appear to produce much more herbaceous material than areas with dense tree cover (Jameson 1967). As spacing between Ponderosa pine trees increased the understory biomass increased significantly (McConnell and Smith 1970). Eight years after thinning understory biomass increased 79% under 13 foot spacings and 246% under a 26 foot spacing.

A tree canopy may limit understory species by control of light, mineral nutrients, water, and/or antagonistic chemical effects (Anderson 1964; Jameson 1967; Anderson et al. 1969; Riegel and Miller 1991).

Water and nutrients

Ditching experiments have shown that competition for water and nutrients may be as important as light in governing understory species composition and production (Watt and Fraser 1933; Weaver 1974; Christy 1986; Riegel et al. 1991). Belowground resources were primary factors limiting understory growth in *Pinus ponderosa* forests (Riegel et al. 1992). Light level had little effect on understory vegetation (Riegel et al. 1992). Two years after cutting tree roots understory biomass was 53-94% higher in root-reduction treatments than in control treatments. In previously stressed Western hemlock (*Tsuga heterophylla*), production was increased by minimizing root competition and to a lesser extent by

altering the canopy (Christy 1986).

Water and nitrogen were environmental factors controlling understory production in Pinus ponderosa forests of northeastern Oregon (Riegel et al. 1992). Light had very little effect on understory production. The amount of nitrogen circulating in litterfall is a predictor of the potential for nitrogen loss following disturbance (Vitousek et al. 1982). If so, litter probably is an important supply of understory plant nitrogen.

Light

Light can also affect understory performance. The overstory canopy intercepts light energy first. Leaves absorb blue and red light reducing the ratio of red/far-red light quality. Thus light available to understory plants is lower in intensity and richer in red light than direct sunlight (Fitter & Hay 1987; Young and Smith 1980). Light in usable wave lengths available for plants under forest canopies can be reduced 95-99.5% by the canopy vegetation (Pearcy 1990; Chazon & Pearcy 1991).

Leaf area is a key characteristic of ecosystems because it sets upper limits on water use by transpiration and carbon fixation through photosynthesis (Gholz 1982). In natural lodgepole pine stands maximum LAI occurs early in stand life (40-45 years)(Long & Smith 1992); maximum LAI on these sites was approximately 4.0. Leaf area index in lodgepole pine stands can range from 4.5 to 14.0 (Peet 1988).

Adaptations to shade include thin leaves with few palisade parenchyma cells per unit area, dense veins, and densely packed chloroplast (Fitter & Hay 1987; Begon et al 1990; Kozłowski 1991). As

Light decreases plants produce leaves with a greater surface area per unit of weight than plants growing in more lighted areas (Jackson 1967; Fitter & Hay 1987). Some plant species have evolved lower photosynthetic rates to use this light richer in red wave lengths (Fitter & Hay 1987; Begon et al. 1990). Sun plants usually display leaves in a multilayered canopy contrasted to the single layered canopy common in shade plants (Begon et al. 1990). Shade plants are more efficient in using the available light of passing sunflecks (Begon et al 1990; Chazdon & Pearcy 1991). Understory plants of forests may receive substantial amounts of solar radiation in the form of sunflecks which vary with time of day (Young et al. 1980; Christy 1986; Pearcy 1990) .

Temperature and humidity

Extremes of temperature or relative humidity in the understory environment influenced by light gradients and uneven heating of soil and vegetation surfaces may also limit growth of an individual species (Samoilov 1990; Riegel et al. 1992). Leaves in the shade have temperatures close to ambient air temperature, but as they are illuminated by a passing sunfleck leaf temperatures can increase 8-20 degrees C (Smith 1981; Pearcy 1990).

Litter

Litter alters the physical and chemical characteristics of the soil surface (Berg & Agren 1984; Facelli & Picket 1991; Berg et al 1993). Nutrients and phytotoxic substances may be released by forest litter which tends to decay slowly affecting other plants in the community (Facelli & Picket 1991; Harborne 1988; Sinsabaugh et al.). Accumulating litter intercepts light, shades seeds and seedlings, and

may change the temperature of the soil (Facelli & Pickett 1991; Carreiro & Koske 1992). Seeds of other plants may be prevented from sprouting by litter and duff by preventing them from reaching nutrients and water. Water may also be intercepted by litter preventing understory plants from using it (Facelli & Pickett 1991).

Ecotypes

Ecotypes of plants of a single species may grow in different sites and access different pools of resources (Field 1991; Grime & Campbell 1991). Some species are adapted to photosynthesize over a wide range of light levels, but many have very narrow tolerances for light (Burrows 1990). In low light conditions a species should increase investment in light harvesting (Field 1991). Interspecific differences in photosynthetic investment may restrict different species to different regions of a resource gradient (Fitter & Hay 1987; Burrows 1990; Field 1991; Grime & Campbell 1991; Riegel et al. 1992).

Plant species adapted to this understory environment may not be able to cope with other environments and may be restricted to the understory environment (Grime & Campbell 1991).

Response of understory plants species to shade

Arnica cordifolia, a common Douglas fir understory species, appeared to produce sun leaves and shade leaves according to the amount of sunlight in its environments (Young & Smith 1980). Thus, Arnica has the physiological plasticity to grow either in shade or full sunlight.

The evergreen graminoid, Carex geyeri, and the deciduous graminoid Calamagrostis rubescens, survive relatively dry soil conditions which

may aid them in survival under tree canopies (Svejcar 1986).

Calamagrostis rubescens made its maximum contribution to understory composition in Ponderosa stands thinned to narrow spacing (13 feet) and in unthinned stands (McConnell & Smith 1980).

Lupinus sericeus responded to thinning with increased production of 1,100% in the widest spacing (26 feet) (McConnell & Smith 1980). Lupinus is an early colonizing species after herbicide removal of lodgepole pine understory plants (Cole 1976).

Epilobium angustifolium was present in 5 year old stands but nearly absent in 10 year old stands (Petersen et al. 1988). Epilobium angustifolium establishes from immigrant seeds rather than from rootstocks present in the soil (Burrows 1990).

METHODS AND STUDY SITES

General environment

Lodgepole Pine (*Pinus contorta* var *latifolia* Englm.) is a seral species maintained by fire over a broad environmental gradient ranging from habitat types dominated, at climax, by Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), Subalpine fir (*Abies lasiocarpa*), and Western redcedar (*Thuja plicata*) (Pfister et al 1977; Despain 1983; Romme 1982). Lodgepole pine also appears as a climax dominant in some environments (Despain 1983; Pfister and Daubenmire 1975).

Three of the study sites lie within 200 km of Yellowstone Park so its climate may represent the general climate of our sites. Lodgepole pine dominates 80% of the forested areas of Yellowstone National Park. The mean January temperature in Yellowstone National Park is -10 degrees C and the mean July temperature is 15.3 degrees C (Despain 1983). The Park's mean annual precipitation is 582 mm. Romme (1982) describes winters in Yellowstone National Park as long and cold with minimum daytime temperatures often below freezing. Summers are short and mild with maximum daytime temperatures around 21 degrees C. and occasional nighttime frosts. Snow covers the ground throughout most winters.

Site descriptions

The four locations chosen for this study represent the range of productive potentials for lodgepole pine in the northern Rocky Mountains (Conway 1982). Three environmental (habitat) types are represented by the four locations. Table 1 compares the four locations with respect to average temperature, average rainfall, elevation, aspect, and habitat

type.

The Targhee site is located on the Island Park Ranger District approximately 5 km north of Island Park, Idaho. The Kootenai site is located on the Yaak Ranger District of the Kootenai National Forest approximately 12 km northeast of Yaak, Montana. The Lewis and Clark site is on the Judith Ranger District of the Lewis and Clark National Forest approximately 35 km. west of Utica, Montana. The Gallatin site is located on the Gardiner Ranger District approximately 15 km northeast of Gardiner Montana .

Each site consisted of two sub-sites. On each sub-site there were five randomly chosen plots thinned to 1.8, 2.7, 3.6, 4.5, and 5.4 meters between trees.

Table 1. Physical characteristics of study sites (Conway 1982)

SITE	MEAN ANNUAL T(C) ²	MEAN ANNUAL PPTN ² (cm)	ELEVATION (m)	SLOPE	ASPECT	HABITAT TYPE ³
Targhee	7	78	1951	2%	East	PSME/CARU
Kootenai	6	90	973	0%	level	THPL/CLUN
L & C(1)	5	42	1946	3%	SE	ABLA/VASC
Gallatin	5	68	2408	2%	W	ABLA/VASC

(1). Lewis and Clark National Forest

2. Average temperature measured in degrees Celsius and average precipitation measured in centimeters.

3. Habitat types and species names are PSME/CARU= Pseudotsuga mensiesii/Calamagrostis rubescens h.t.; THPL/CLUN= Thuja plicata/Clintonia uniflora h.t.; ALBA/VASC= Abies lasiocarpa/Vaccinium scoparium h.t. (Pfister et al. 1977).

Measurements of environmental factors

Air temperature

Minimum and maximum temperatures were recorded periodically throughout several growing seasons (Cole pers communication) at each location with duplicate Taylor 6's thermometers. I averaged these periodic readings to find the mean growing season temperature for each site.

Light

To compare the understory environment under different thinning levels I measured light levels associated with three randomly chosen trees in each plot. At each tree measurements were made at three positions (under the tree, at the dripline, and midway between the tree and a neighboring tree). Light was measured over one day (24 hours) with

the ozalid method (Friend 1961). It was recorded in micro-Einstein per square meter per sec. The instruments were calibrated by exposing them to light of constant output for various times.

Evaporation

Evaporation rates at each of the positions (described above) were indexed with a 11 cm (Watman number 4 qualitative) filter paper placed on a glass plate lying on the ground and supplied with water from a glass bottle inverted over it. The quantity of water evaporated from the saturated filter paper in 24 hours was measured to the nearest ml/day.

Water

Soil water (% volume) was measured in the soil profile with a neutron probe from May 1 to September 15 for three years (Cole pers communication). Soil water was measured at nine depths at three locations (Targhee, Lewis and Clark, and Gallatin). I used data from the 0-15, 15-45, 45-76 centimeter depths in my analysis.

Understory cover measurements

I estimated cover in each spacing treatment with 2X5 dm plots (Daubenmire 1959). Percent cover of each species was estimated separately. Measurements were made at three positions under nine trees in each plot. Species nomenclature follows Hitchcock et al. (1973) and Studdendieck et al (1992). The spacing treatments were replicated twice in each study site. The nine quadrats in each treatment plot were averaged to estimate the cover of each species in each spaced plot.

Separate measurements were made at each relative tree position. These averages provided the data points used in analysis. Cover data were summarized by individual species and classes of species (graminoid, forb, shrub, and total cover) created by summing species in each category.

Understory leaf area measurements

To estimate specific leaf areas and thus LAIs leaves of all classes of plants in the understory were collected randomly from the 1.8m, 3.6m, and 5.4m plots on all study locations. Graminoids were pooled. Shrub and forb were separated by species. Shrub and forb species collection included the above ground stems as well. While the leaves were still moist and green, leaf area of each species was measured. All leaves were then oven dried and weighed. From these data I calculated a leaf area/gram of leaf weight factor for each species. Shrub and forb "leaf area" also included the area of photosynthesizing stems. Hagler(1992) weighed all graminoids, forbs, and shrub standing crop in the previous year on the Targhee, Lewis and Clark, and Kootenai study plots. By multiplying his standing crop data by my leaf area factors I calculated leaf area indexes by species and species classes for the three spacings at three positions (under, dripline, and between).

Overstory leaf area measurements

The overstory trees have been regularly measured to record their growth since the spacing study was initiated (Cole pers communication). Measurements recorded included diameter at breast height (dbh) and tree

height. I used the 1993 dbh data to calculate a cross-sectional area of the average tree in each tree plot. Then, using a regression equation (Hungerford 1987) which uses cross sectional area as the independent variable I calculated the total leaf area on each tree. I divided the total leaf area by the square of the spacing distance of each plot to get a leaf area index (m^2 of leaf area / m^2 of ground) contributed by the trees. The tree LAI and understory LAI were summed to obtain the total LAI for each spacing for three locations (Targhee, Lewis & Clark, and Kootenai).

Species number

The species richness variable is defined as the average of the maximum number of species I found in the nine 2X5 dm understory plots in treatment plot at each position. This value can be used in this study as a measure of richness (diversity) across spacings, positions, and locations because the quadrats in each location, spacing, and position are equal in size and number (Pielou 1977,1984; Ludwig & Reynolds 1988).

Statistical analysis

First I used an analysis of variance (SAS GLM 1987) to compare all locations at all spacing and all measurement positions (e.g. under the tree, dripline, and out in between the trees). After differences were found I used MSUSTAT's stepwise/ backwards multiple regression analysis procedure (Lund 1992) to select a model to predict cover with environmental factors I measured (light, % litter ground cover, and

evaporation) or factors obtained from other sources (average soil water at three soil depths (Cole pers communication), average growing season temperature, and site index (Cole 1976; Conway 1982)). Data was analyzed using computer software programs including SYSTAT (Wilkinson 1990), MSUSTAT (Lund 1992), and SAS (SAS Institute 1987).

All variables used in the ANOVA's and multiple regression analysis were tested for normality and equality of variances of dependent variables in all independent variable ranges to meet the assumptions necessary to obtain valid results (Kershaw 1973; Neter et al. 1990). Variables were transformed when necessary to meet statistical assumptions of normality and equal variances.

The Central Limit Theorem states that as the number of means taken from a population becomes larger, the distribution of the means approaches normality. Most data points used in my analysis were means of nine observations. The number of means involved in each cover variable is 120. The number of means in each leaf area variable is 54. Using this theorem I could assume that the cover data was normal, and the LAI data was close to normal.

Soil water data (Cole pers communication) were only available for three locations (L&C, Gallatin, and Targhee) and in three spacings (1.8, 3.6, & 5.4). Since soil water undoubtedly affects understory vegetation, I reduced my field data to match these variables.

I removed all environmental factors that were highly correlated with each other (Neter et al 1990). For example, since July soil water variables were highly correlated with the growing season average water variables, I removed the July soil water variables from the analysis.

Similarly, since the temperature variables are positively correlated with each other, and very negatively correlated with elevation, I chose to use average temperature in my regression analysis to represent their combined effect.

Next I compared each dependent variable (e.g. total cover, graminoid cover, forb cover, shrub cover, and LAI categories) to each remaining independent variable (light, evaporation, % cover of litter, site index, growing season soil water at the depths of 0-15, 15-45, and 45-76 centimeters soil depths, and average growing season temperature). Variances across spacings and positions were not equal for all the dependent variables; so I used the Box-Cox method (Neter et al.1991) to get the best approximate transformations for each dependent variable (Table 13). All dependent variables then met the assumptions necessary to use multivariate regression analysis.

In my full model I regressed all the independent variables simultaneously against each dependent variable. Then I used MSUSTAT's stepwise/backwards procedure (Lund 1992) to find the best reduced model for each dependent variable. Lastly, I jackknifed the best regression model for each variable (Potvin & Roff 1993). This procedure removes observations one at a time and computes a regression line without that observation. Values reported are means of all the regression lines calculated for each variable.

RESULTS IUnderstory environmental variables response
to spacing, position, and location

As noted above analysis was performed in two steps. First, ANOVA was used to identify understory differences in environmental factors and understory vegetation due to location, thinning treatment, and position. Second, after differences were identified we used regression analysis to correlate differences in understory vegetation with understory environmental factors. Results I reports the results of the ANOVA's.

Light

To examine the effect of spacing and position on understory light levels I treated each combination of spacing and position as a treatment. This was necessary due to the significant interaction between the two factors ($p < 0.0001$). Light intensity increased both as tree spacings became wider and as we moved out from under the tree (Table 2). First, at all spacings light intensity ($\mu\text{Einstein} / \text{m}^2 / \text{sec}$) increased as one moved from trunk to dripline to between tree positions (Table 2). Second, understory light at the trunk did not vary significantly with tree spacing (Table 2, Figure 1). The light in the understory became significantly brighter when spacing distance reached 4.5 meters (Figure 1). The most intense light observed in the understory (mean $136.9 \mu\text{E}$) was in the open among the 5.4m spaced trees .

I recorded higher light levels on the Targhee location than the other three locations ($p = 0.05$); however this is meaningless because location differences are due to differences in season and daily weather

conditions.

Evaporation

Evaporation in the understory increased significantly ($p=0.05$) as tree spacings increased (Table 3). Surprisingly, however, we observed no significant effect of position (trunk, dripline, and between trees) on ground level evaporation ($p=0.1304$). Slight differences in air movement may cause the observed evaporation differences between spacings.

Evaporation rates differed significantly among forests ($p=0.0001$, Table 3), but without replication of the location effect I could not isolate the cause of this difference.

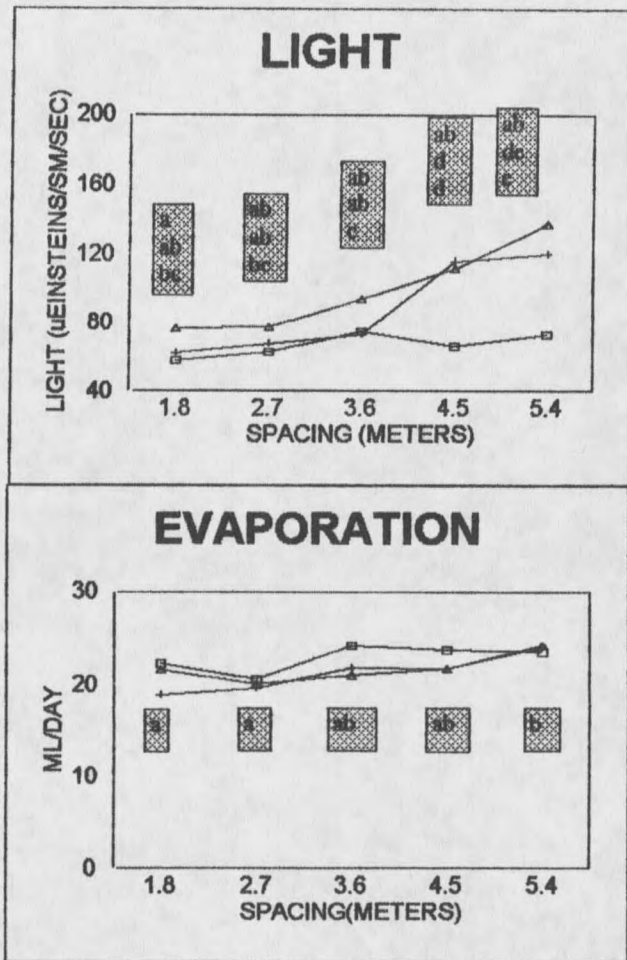


Fig 1. Average light ($\mu\text{Einstein}/\text{m}^2/\text{sec}$) and evaporation (ml/day) at five tree spacings and three positions. Each line is a position (under=squares, dripline=+, and between the trees=triangles). Shaded boxes indicate the significance of spacing and/or position. The same letters above spacings indicate no significant difference at $\alpha=0.05$ level. Different letters indicate significant difference at that level.

Table 2. Understory light as affected by spacing, position & location.

A. Analysis of variance:

MODEL Light=mean+spacing/position+location+rep+error

Source	df	sum squares	mean square	F value	Pr>F
SPAC/POS(1)	14	68638	4903	15.70	0.0001
LOCATION	3	28484	9495	30.40	0.0001
REP	1	1555	1555	4.98	0.0279
ERROR	101	31546	312		

B. Predicted values: effect of spacing and position on light.

spacing	position	mean	comparisons	sd	sem
1.8	UNDER	58	A	25	9
2.7	UNDER	63	AB	20	7
3.6	UNDER	75	AB	19	7
4.5	UNDER	66	AB	27	9
5.4	UNDER	73	AB	14	5
1.8	DRIPLINE	62	AB	21	7
2.7	DRIPLINE	68	AB	19	7
3.6	DRIPLINE	73	AB	20	7
4.5	DRIPLINE	116	D	26	9
5.4	DRIPLINE	120	DE	22	8
1.8	OPEN	77	BC	36	13
2.7	OPEN	77	BC	26	9
3.6	OPEN	94	C	26	9
4.5	OPEN	112	D	26	9
5.4	OPEN	137	E	29	10

(1). SPAC/POS means that each combination of spacing and position was treated as a treatment.

2. Comparison procedure used was Tukey's test. Significance is to alpha=0.05 level.

Table 3. Evaporation as affected by spacing, position, & location.

A. Analysis of variance:

MODEL Evaporation= mean+spacing+position+location+rep+error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	4	212	53	3.83	0.0059
POSITION	2	57	29	2.08	0.1304
LOCATION	3	4573	1524	110.50	0.0001
REP	1	106	106	7.71	0.0065
ERROR	109	1503	14		

B. Predicted values: effect of spacing on evaporation.

spacing	mean	comparisons ¹	sd	sem
1.8	21	A	8	1.5
2.7	20	A	8	1.6
3.6	22	AB	7	1.4
4.5	22	AB	8	1.5
5.4	24	B	7	1.4

C. Predicted values: effect of position on evaporation.

position	mean	comparison ¹	sd	sem
UNDER	23	A	7	1.1
DRIP	21	A	8	1.2
OPEN	21	A	8	1.2

1. Comparison procedure used is Tukey's test. Values followed by same letter not significantly different at 0.05.

Understory cover response to spacing, position
and location

Figure 2 shows the effect spacing and position had on four plant cover categories (total cover, graminoid, forb, and shrubs) in four understories. The following paragraphs treat each category of plants individually.

Total cover

Tree density significantly affected understory cover ($p=0.0001$, Table 4). The ground layer under the closest spacing (1.8m) had significantly less cover than the others ($p=0.05$). Within stands, position had no significant effect on total understory cover ($p=0.5908$, Table 4). Location did affect cover ($p=0.0001$); Kootenai plots had much higher total cover than other sites ($p=0.05$).

Graminoid cover

Graminoid cover increased slightly as tree density decreased; graminoid cover under the two widest spacings was significantly greater than under the three narrower spacings ($p=0.05$, Table 5). Position relative to the tree had no significant effect on grass cover ($p=0.4070$). Location did effect graminoid cover ($p=0.0001$). The Kootenai plots had significantly higher ($p=0.05$) graminoid cover (mean=23%) than the other three locations; Targhee plots had intermediate graminoid cover (mean=15%); Lewis & Clark (mean=4%) and Gallatin plots (mean=7%) had fewer graminoids than the other locations and were like one another ($p=0.05$, Table 5).

Forb cover

Forb cover was significantly affected by tree density ($p=0.0004$, Table 6). The narrowest spacing of 1.8m supported significantly fewer forbs ($=-0.05$) than the two widest spacings (4.5m & 5.4m). Position affected forb cover ($p=0.0134$). Areas at the tree dripline had higher forb cover (17%) than areas under or between the trees ($p=0.05$). The other two positions (under and between the trees) were alike (13% and 16%, $p=0.05$) (Table 6). The Gallatin had significantly more forb cover than the other three locations ($p=0.05$). Gallatin understory vegetation was dominated by forbs (mean cover=30%). Lewis & Clark and Targhee locations produced 11% and 12% average forb cover and were not significantly different ($p=0.05$). Forbs provided an even smaller part of the Kootenai vegetation with an average cover of 9% and was not significantly different from the Lewis and Clark or the Targhee locations ($p=0.05$).

Shrub cover

Shrubs were inhibited at the densest tree spacing, but were unaffected by more open spacings ($p=0.05$) (Table 7). Position had no significant effect on shrub cover ($p=0.7512$). Shrub cover differed significantly ($p=0.0001$) among locations (Table 7). Kootenai mean shrub cover equaled 40%; Lewis and Clark mean shrub cover equaled 25%; Targhee mean shrub cover equaled 15%; and Gallatin mean shrub cover was 3%. All locations were significantly different from each other ($p=0.05$).

