



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 (Wilkerson 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 populations 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 I

Understory 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.

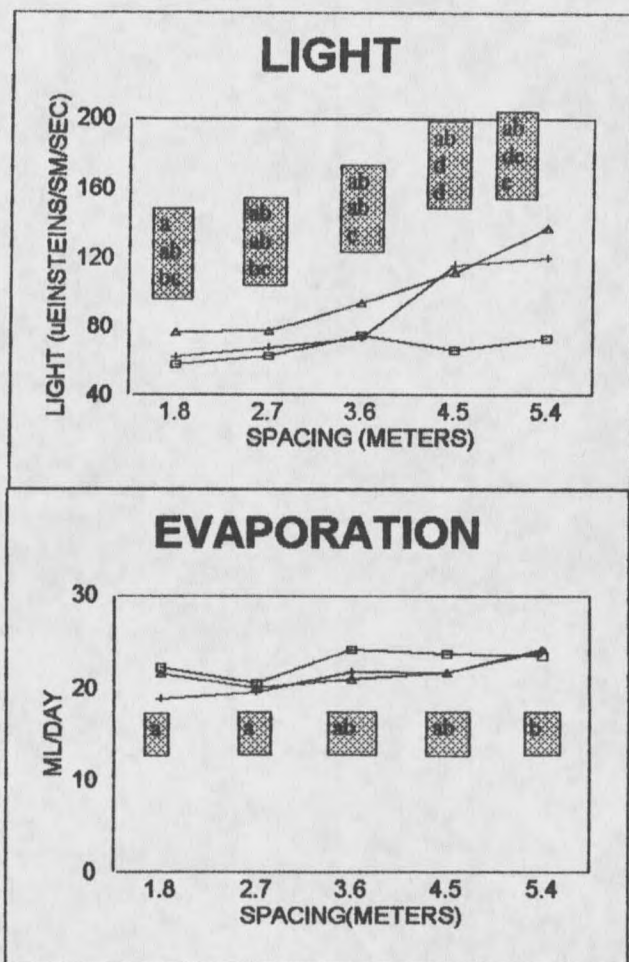


Fig 1. Average light ($\mu\text{Einstein}/\text{m}^2/\text{sec}$) and evaporation (ml/day) at five tree spacings and three positions. Each line is a position (under=squares, dripline=+, and between the trees=triangles). Shaded boxes indicate the significance of spacing and/or position. The same letters 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 ($p=0.05$) 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 ($p=0.05$).

Table 4. Total cover as influenced by spacing, position, & location.

A. Analysis of variance:

MODEL Total cover=mean+spacing+position+location+rep+error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	4	5834	1458	7.48	0.0001
POSITION	2	206	103	0.53	0.5908
LOCATION	3	23363	7788	39.96	0.0001
REP	1	320	320	1.64	0.2027
ERROR	109	21245	195		

B. Predicted values: effect of spacing on total cover.

spacing	mean	comparisons ¹	sd	sem
1.8	34	A	21	4
2.7	47	B	22	5
3.6	50	B	22	4
4.5	52	B	18	4
5.4	54	B	15	3

C. Predicted values: effect of position on total cover.

position	mean	comparisons ¹	sd	sem
UNDER	46	A	22	3
DRIP	48	A	21	3
OPEN	49	A	20	4

D. Predicted values: effect of location on total cover.

location	mean	comparisons ¹	sd	sem
TARGHEE	38	A	19	3
L & C(2)	40	A	17	3
GALLATIN	41	A	8	2
KOOTENAI	72	B	16	3

1. Test used was Tukey's test. Values followed by same letter not significant at the 0.05 level.

(2). L&C is Lewis and Clark site.

Table 5. Graminoid cover as influenced by spacing, position, & location.

A. Analysis of variance:

MODEL Graminoid cover= mean +spacing+position+location+rept+ error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	4	1103	278	5.50	0.0004
POSITION	2	91	45	0.91	0.4070
LOCATION	3	6600	2200	43.91	0.0001
REP	1	13	13	0.25	0.6160
ERROR	109	5461	50		

B. Predicted values: effect of spacing on graminoid cover.

spacing	mean	comparisons ¹	sd	sem
1.8	8	A	9	2
2.7	11	A	12	2
3.6	10	A	9	2
4.5	15	B	14	3
5.4	17	B	8	2

C. Predicted values: effect of position on graminoid cover.

position	mean	comparisons ¹	sd	sem
UNDER	11	A	11	2
DRIP	12	A	10	2
OPEN	13	A	11	2

D. Predicted values: effect of location on graminoid cover.

location	mean	comparisons ¹	sd	sem
TARGHEE	14	B	8	2
L&C(2)	4	A	6	1
GALLATIN	7	A	8	1
KOOTENAI	23	C	8	2

1. Test used was Tukey's test. Values followed by same letter not significant at the 0.05 level.

(2). L&C is Lewis and Clark site.

Table 6. Forb cover as influenced by spacing, position, & location.

A: Analysis of variance:

MODEL Forb cover=mean+spacing+position+location+rep+ error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	4	778	195	5.56	0.0004
POSITION	2	314	157	4.49	0.0134
LOCATION	3	8609	2870	81.96	0.0001
REP	1	1	1	0.03	0.8656
ERROR	109	3817	35		

B. Predicted values: effect of spacing on forb cover.

spacing	mean	comparisons ¹	sd	sem
1.8	11	A	9	2
2.7	15	AB	12	2
3.6	14	AB	9	2
4.5	18	B	13	3
5.4	18	B	10	2

C. Predicted values: effect of position on forb cover.

position	mean	comparisons ¹	sd	sem
UNDER	13	A	10	2
DRIP	17	B	12	2
OPEN	16	AB	10	2

D. Predicted values: effect of location on forb cover.

location	mean	comparisons ¹	sd	sem
TARGHEE	12	A	6	1
L&C(2)	11	A	8	1
GALLATIN	30	B	6	1
KOOTENAI	9	A	5	1

1. Test used was Tukey's test. Values followed by same letter not significant at the 0.05 level.

(2). L&C is Lewis and Clark site.

Table 7. Shrub cover as influenced by spacing, position, & location.

A. Analysis of variance:

MODEL Shrub cover=mean+spacing+position+location+ rep+error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	4	1938	485	3.21	0.0155
POSITION	2	86	43	3.21	0.7512
LOCATION	3	22484	7475	49.73	0.0001
REPL	1	261	261	1.72	0.1909
ERROR	109	16944	155		

B. Predicted values: effect of spacing on shrub cover.

spacing	mean	comparisons ¹	sd	sem
1.8	13	A	17	3
2.7	21	B	18	4
3.6	26	B	20	4
4.5	18	AB	16	3
5.4	21	B	21	4

C. Predicted values: effect of position on shrub cover.

position	mean	comparisons ¹	sd	sem
UNDER	21	A	21	3
DRIP	20	A	20	3
OPEN	19	A	17	3

D. Predicted values: effect of location on shrub cover.

location	mean	comparisons ¹	sd	sem
TARGHEE	15	B	17	3
L&C(2)	25	C	14	3
GALLATIN	3	A	5	1
KOOTENAI	40	D	13	2

1. Test used was Tukey's test. Values followed by same letter not significant at the 0.05 level.

(2). L&C is Lewis and Clark site.

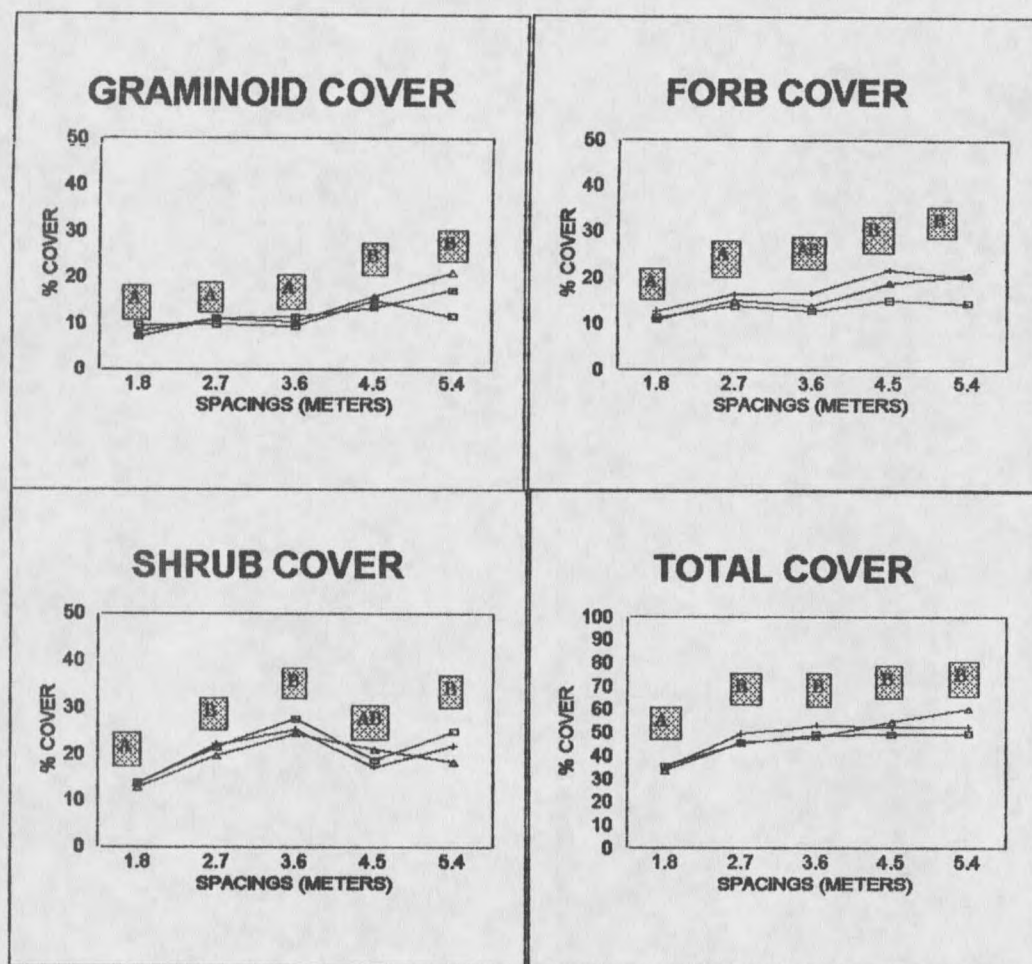


Fig 2. Plant cover by category, spacing, and position. Symbols used in the graph represent: squares (under the trees, + (at the dripline), and triangles (between the trees). Values are % cover. When spacings have significant differences ($\alpha=.05$ level) letters in shaded boxes are different.

Understory leaf area index response to
spacing, position, and location

The effects of spacing and position on four categories of plant LAIs are shown in Figure 3. Each category is treated individually in the following section.

Total LAI

Total understory leaf area index differed among spacings ($p=0.0008$, Table 8). The understory in the 1.8m spacing provided significantly less ($p=0.05$) LAI than either the 3.6 or 5.4 meter spaced plots (Table 8). Understory leaf area index was not significantly different as position changed from under trees to the open area between trees ($p=0.5396$). Location significantly affected total understory LAI ($p=0.0001$). The Kootenai produced the highest average LAI ($1.05 \text{ m}^2/\text{m}^2$). The Lewis and Clark understory had an LAI of $0.63 \text{ m}^2/\text{m}^2$. The Targhee location had the lowest LAI, $0.31 \text{ m}^2/\text{m}^2$ (Table 8). All locations were significantly different from each other ($p=0.05$).

Graminoid LAI

Spacing significantly affected graminoid leaf area ($p=0.0428$, Table 9). Graminoid leaf area on the 1.8m spacing was less than on the 5.4 meter spacing ($p=0.05$). The 3.6 meter spacing was not different ($p=0.05$) from either of the other two spacings (Figure 3). Position had no effect on graminoid leaf area ($p=0.5593$, Table 9). Location also affected leaf area ($p=0.0001$).

Forb LAI

Forb leaf area was significantly affected by spacing ($p=0.0028$, Table 10). The 1.8 meter spacing had significantly less forb leaf area than the other two spacings ($p=0.05$). Forb LAI was not significantly affected by position relative to the tree ($p=0.1272$). Locations significantly affected forb cover ($p=0.0414$, Table 10).

Shrub LAI

Tree spacing significantly affected shrub LAI ($p=0.0114$, Table 11). Tree spacings of 1.8 meters produced less shrub LAI than wider spacings ($p=0.05$). Position (under the tree, at the dripline, or between the trees) had no effect on shrub LAI ($p=0.2289$, Table 11). Location affected shrub LAI ($p=0.0001$, Table 11).

Overstory LAI

Overstory LAI declined significantly from the 1.8 meters spacing to the 5.4 meter spacing ($p=0.05$, Table 14). The 1.8 meter spacing had the highest tree LAI ($6.1 \text{ m}^2/\text{m}^2$); the 3.6 meter spaced trees produced significantly less LAI ($2.8 \text{ m}^2/\text{m}^2$); the 5.4 meter spaced trees produced the lowest tree LAI ($1.7 \text{ m}^2/\text{m}^2$). The Kootenai site is the youngest and has the smallest tree LAI ($2.5 \text{ m}^2/\text{m}^2$) at this time even though it is probably the most productive site (Table 13). The Targhee (4.4) and Kootenai (3.8) produced similar overstory LAI ($p=0.05$).

Understory and overstory LAI combined

Total stand LAI also fell significantly from 1.8 to 5.4 meters

spacings ($p=0.05$, Table 13). The densest spacing established a significantly higher LAI of 6.5; the intermediate spacing (3.6m) had an LAI of 3.7; and trees spaced at 5.4 meters had an LAI of 2.5 ($p=0.05$). Location did not make a difference in total in stand LAI ($p=0.0879$, Table 13).

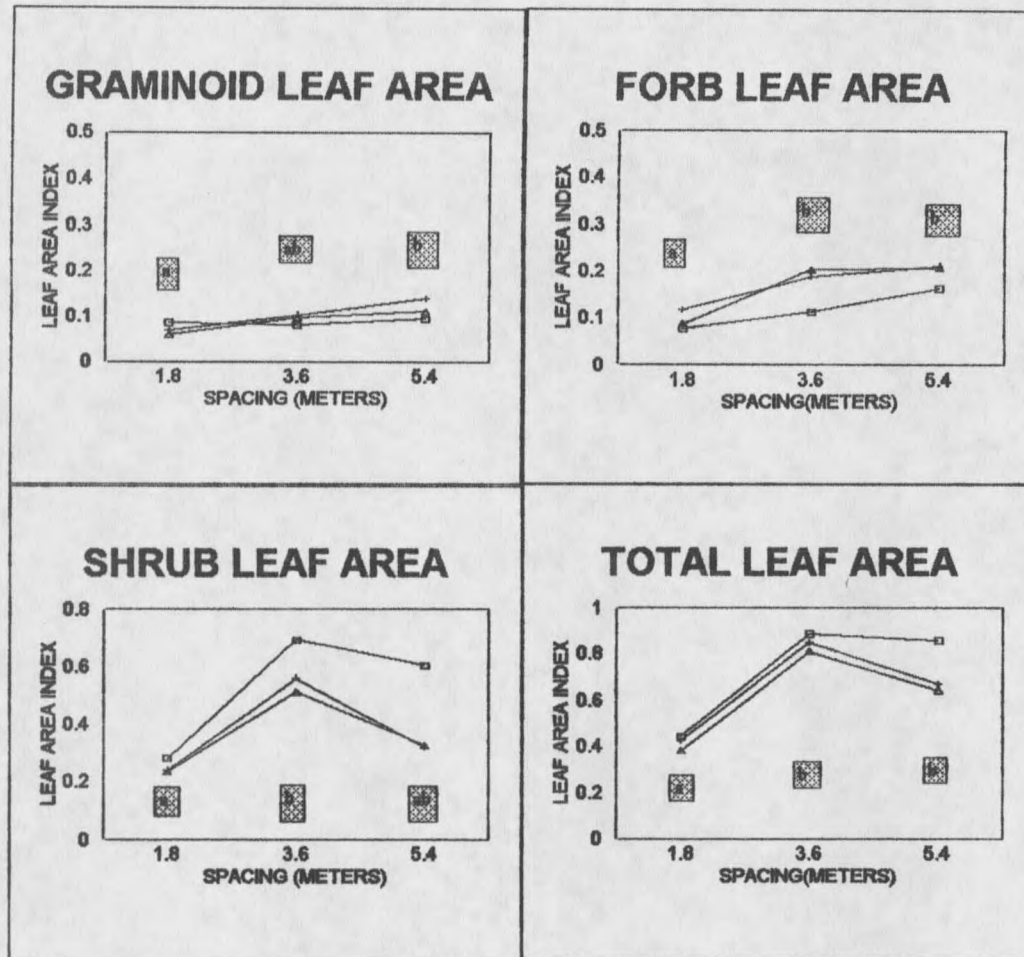


Fig 3. Leaf area index by category, spacing, and position. Separate lines in each graph represent different positions (under=squares, dripline=+, and between trees=triangles). Unit of measure is square meters of leaf area/ square meters of ground. Spacings are 1.8, 3.6, and 5.4 meters between trees. Shaded letters within graphs show the significance of spacing effects across positions (under, dripline, and between trees). Different letters indicate spacings are different at the $\alpha=0.05$ level; spacings with same letters are not significantly different.

Table 8. Total leaf area index as affected by spacing, position, & location.

A. Analysis of variance

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

Source	df	sum squares	mean square	F value	Pr>F
SPACING	2	1.78	0.89	7.77	0.0008
POSITION	2	0.13	0.07	0.58	0.5396
LOCATION	2	4.98	2.49	21.75	0.0001
REP	1	0.06	0.06	0.57	0.4382
ERROR	46	4.87	0.11		
LA GRAND MEAN		0.66			

B. Predicted values: effect of spacing on total LAI.

spacing	mean	comparisons	sd	sem
1.8	0.42	A	0.30	0.07
3.6	0.85	B	0.51	0.03
5.4	0.72	B	0.49	0.12

C. Predicted values: effect of position on total LAI.

position	mean	comparisons	sd	sem
UNDER	0.73	A	0.58	0.14
DRIP	0.65	A	0.37	0.09
OPEN	0.62	A	0.47	0.11

D. Predicted values: effect of location on total LAI.

location	mean	comparisons	sd	sem
TARGHEE	0.31	A	0.18	0.04
L & C(2)	0.63	B	0.36	0.08
KOOTENAI	1.05	C	0.49	0.11

1. Test used is Tukey's test. Value followed by same letter not significant at 0.05 level

(2). L&C is Lewis and Clark site.

Table 9. Graminoid leaf area as influenced by spacing, position, & location.

A. Analysis of variance:

MODEL Graminoid LAI=mean+spacing+ position +location+ rep+error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	2	0.02	0.08	3.38	.0428
POSITION	2	0.00	0.00	.59	.5593
LOCATION	2	0.15	0.08	30.92	.0001
REP	1	0.02	0.02	7.90	.0072
ERROR	46	0.11	0.01		
TOTAL	53	0.30			
GRAND MEAN(54) = 0.09					

B. Predicted values: effect of spacing on graminoid LAI.

spacing	mean	comparisons	sd	sem
1.8	0.07	A	0.10	0.02
3.6	0.09	AB	0.10	0.02
5.4	0.11	B	0.10	0.02

C. Predicted values: effect of position on graminoid LAI.

position	mean	comparisons	sd	sem
UNDER	0.09	A	0.08	0.02
DRIP	0.10	A	0.08	0.02
OPEN	0.09	A	0.07	0.02

D. Predicted values: effect of location on graminoid LAI.

location	mean	comparisons	sd	sem
TARGHEE	0.08	B	0.07	0.02
L&C(2)	0.03	A	0.02	0.01
KOOTENAI	0.16	C	0.06	0.02

1. Test used is Tukey's test. Value followed by same letter not significantly different at 0.05 level.

(2). L & C is abbreviation for Lewis and Clark site.

Table 10. Forb leaf area as influenced by spacing, position, & location.

A. Analysis of variance:

MODEL Forb LAI= mean+spacing+position+ location +rep+ error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	2	0.10	0.05	6.68	.0028
POSITION	2	0.03	0.02	2.16	.1272
LOCATION	2	0.05	0.03	3.42	.0414
REP	1	0.00	0.00	.00	.9748
ERROR	46	0.34	0.01		
TOTAL	53	0.52			
GRAND MEAN(54) = 0.15					

B. Predicted values: effect of spacing on forb LAI.

spacing	mean	comparisons ¹	sd	sem
1.8	0.09	A	0.09	0.02
3.6	0.17	B	0.07	0.02
5.4	0.19	B	0.10	0.02

C. Predicted values: effect of position on forb LAI.

position	mean	comparisons ¹	sd	sem
UNDER	0.12	A	0.08	0.02
DRIP	0.17	A	0.10	0.02
OPEN	0.17	A	0.09	0.02

D. Predicted values: effect of location on forb LAI.

location	mean	comparisons ¹	sd	sem
TARGHEE	0.11	A	0.07	0.02
L&C(2)	0.19	B	0.12	0.03
KOOTENAI	0.16	AB	0.09	0.03

1. Test used is Tukey's test. Value followed by same letter not significantly different at 0.05 level.

(2). L & C is abbreviation for Lewis and Clark site.

Table 11. Shrub leaf area as influenced by spacing, position, & location.

A. Analysis of variance:

MODEL Shrub LAI=mean +spacing +position+location+rep+error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	2	1.01	0.51	4.94	.0114
POSITION	2	0.32	0.16	1.52	.2289
LOCATION	2	3.41	1.70	16.60	.0001
REP	1	0.15	0.15	1.48	.2305
ERROR	46	4.72	0.10		
TOTAL	53	9.60			
GRAND MEAN(54) = 0.42					

B. Predicted values: effect of spacing on shrub LAI.

spacing	mean	comparisons ¹	sd	sem
1.8	0.25	A	0.17	0.04
3.6	0.59	B	0.48	0.11
5.4	0.42	AB	0.49	0.11

C. Predicted values: effect of position on shrub LAI.

position	mean	comparisons ¹	sd	sem
UNDER	0.53	A	0.54	0.13
DRIP	0.37	A	0.30	0.07
OPEN	0.36	A	0.40	0.09

D. Predicted values: effect of location on shrub LAI.

location	mean	comparisons ¹	sd	sem
TARGHEE	0.12	A	0.13	0.03
L&C(2)	0.41	B	0.38	0.09
KOOTENAI	0.73	C	0.45	0.11

1. Test used is Tukey's test. Value followed by same letter not significantly different at 0.05 level.

2. L&C is abbreviation for Lewis and Clark site.

Table 12. Overstory LAI as influenced by spacing & location.

A. Analysis of variance:

MODEL Overstory LAI = mean + spacing + location + error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	2	63	31	55.56	.0001
LOCATION	2	11	6	9.84	.0025
ERROR	13	7	1		
TOTAL	17	81			
GRAND MEAN(18) = 3.5					

B. Predicted values: effect of spacing on Overstory LAI.

spacing	mean	comparisons ¹	sd
1.8	6.1	C	1.8
3.6	2.8	B	.7
5.4	1.7	A	.4

C. Predicted values: effect of location on overstory LAI.

location	mean	comparisons ¹	sd
TARGHEE	4.4	B	2.8
L&C(2)	3.8	B	2.1
KOOTENAI	2.5	A	1.3

1. Test used is Tukey's test. Value followed by same letter not significantly different at 0.05 level.

2. L&C is abbreviation for Lewis and Clark site.

Table 13. Overstory and understory LAI as influenced by spacing & location.

A. Analysis of variance:

MODEL Overstory LAI = mean + spacing + location + error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	2	53	26	36.38	0.0001
LOCATION	2	4	2	2.95	0.0879
ERROR	13	9	1		
TOTAL	17	67			
GRAND MEAN(18) = 4.3					

B. Predicted values: effect of spacing on Overstory LAI.

spacing	mean	comparisons ¹	sd
1.8	6.5	C	1.54
3.6	3.6	B	.49
5.4	2.4	A	.37

1. Test used is Tukey's test. Value followed by same letter not significantly different at 0.05 level.

2. L&C is abbreviation for Lewis and Clark site.

Table 14. Leaf area of understory and overstory. Tree height is measured in meters. LAI measurements are square meters leaf area/ square meters of ground. Total LAI is the sum of the overstory LAI and understory LAI(leaf area index). Spacings are 1.8, 3.6, and 5.4 meters between trees. Tree circumference is measured in centimeters.

SITE	SPACING	TREE ¹ CIRC. (cm)	TREE HEIGHT (m)	TREE ² LAI	UNDERSTORY LAI	TOTAL LAI
TARGHEE (REPLICATION 1)						
	1.8	42.2	8.1	8.61	0.18	8.79
	3.6	55.9	10.4	3.87	0.28	4.15
	5.4	63.8	10.3	2.27	0.36	2.62
TARGHEE (REPLICATION 2)						
	1.8	38.3	10.4	6.95	0.09	7.04
	3.6	47.1	8.9	2.70	0.60	3.31
	5.4	58.3	10.3	1.88	0.35	2.22
LEWIS AND CLARK (REPLICATION 1)						
	1.8	36.7	10.5	6.33	0.50	6.84
	3.6	47.9	9.1	2.80	0.44	3.24
	5.4	60.6	8.6	2.04	0.75	2.79
LEWIS AND CLARK (REPLICATION 2)						
	1.8	37.5	9.8	6.64	0.42	7.06
	3.6	51.9	10.3	3.32	1.12	4.43
	5.4	56.7	9.6	1.77	0.54	2.31
KOOTENAI (REPLICATION 1)						
	1.8	29.5	8.0	3.88	0.99	4.87
	3.6	40.7	8.2	1.98	1.40	3.38
	5.4	46.3	8.4	1.16	0.76	1.92
KOOTENAI (REPLICATION 2)						
	1.8	31.1	9.2	4.38	0.32	4.70
	3.6	43.9	8.9	2.33	1.25	3.58
	5.4	48.7	8.1	1.29	1.59	2.88

1. average tree circumference.

2. The regression equation used was: $LAI = -2.0 + 0.21(\text{basal area})$ (Hungerford 1987).

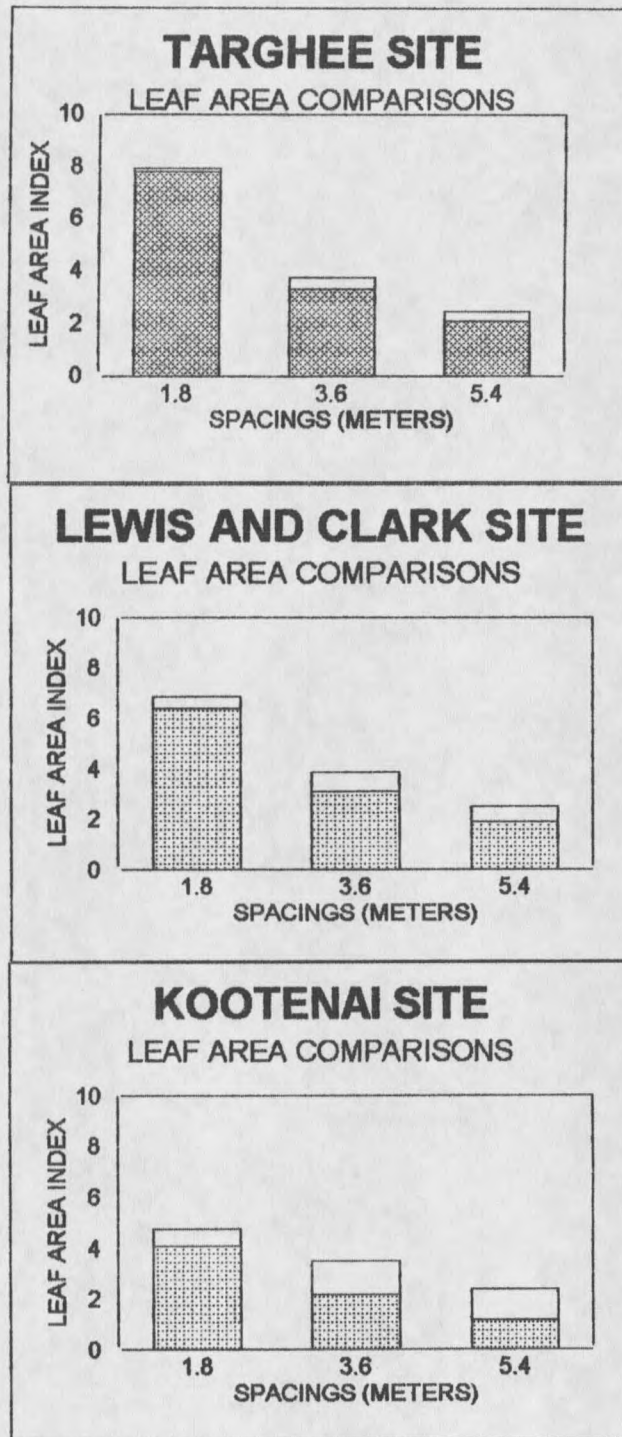


Fig 4. Leaf area comparisons of overstory, understory, and total leaf area on three sites (Targhee, Lewis & Clark, and Kootenai). The unit of measure is leaf area index (square meters of leaf area/square meters of ground). The bottom portion of each bar is the tree leaf area, and the top portion is the understory LAI. The total is the sum of overstory and understory LAI.

Species richness response to spacing, position
and location

Species richness was significantly affected by spacing ($p < 0.0001$, Table 15). The average number of species/plot (2x5 dm) at the 1.8m (8.75 species/plot) spacing distance was significantly less than the number of species/plot found in the four wider spacings ($p = 0.05$). Position did not significantly affect the number of species present on these plots ($p = 0.391$, Table 15). Location significantly affected the number of species per plot ($p = 0.0045$, Table 15).

Table 15. Number of species as affected by spacing, position, & location.

A. Analysis of variance:

MODEL number of species = mean + spacing + position + location + rep + error

Source	df	sum squares	mean square	F value	Pr>F
SPACING	4	254	64	7.33	0.0001
POSITION	2	16	8	0.94	0.3927
LOCATION	3	109	36	4.60	0.0045
REP	1	19	19	2.21	0.1396
ERROR	109	862	8		
GRAND MEAN=	11				

B. Predicted values: effect of spacing on number of species.

spacing	mean	comparisons ¹	sd	sem
1.8	8	A	2	0.5
2.7	11	B	3	0.7
3.6	11	B	2	0.4
4.5	11	B	3	0.7
5.4	13	B	4	0.7

C. Predicted values: effect of position on number of species.

position	mean	comparisons ¹	sd	sem
UNDER	11	A	3	0.5
DRIP	11	A	3	0.5
OPEN	12	A	4	0.6

1. Test used is Tukey's test. Value followed by same letter not significantly different at 0.05 level.

RESULTS II

Correlation of factors and vegetation variation

ANOVA's of "Results I" isolated environmental and vegetation quantities which vary with spacing, position, and location. The objective of "Results II" is to show if any relationships exist between the environmental factors and vegetation that may indicate causation. We have shown that differences in plant performance differ among tree spacings and locations. We speculate that light, evaporation, litter cover, and soil water might determine the understory vegetation. We therefore regressed cover and LAI against these environmental factors to find which are correlated with understory growth.

Factors correlated with plant cover

Total cover factors

The full transformed total cover model accounted for 59% of the variance ($r^2=0.59$, Table 16). A reduced model with evaporation, litter, medium depth soil water (15-45 cm), and deep soil water (45-76 cm) was equally as good ($r^2=0.588$, Table 16). A partial F-test of this reduced model against the full model gave an F-value of .258 with 4 and 113 degrees of freedom (Critical F value 3.05, p value=0.9030). Site index, light, shallow soil water, and average growing season temperature did not improve the regression prediction and probably are not correlated with total cover.

To measure relative value of the remaining independent variables I removed them one at a time and used a partial F test to determine how much removal reduced the model's prediction of total cover. Removing

litter reduced the model's r square about 31% ($r^2=0.305$). Removing medium depth soil water reduced the model's r square about 19% ($r^2=0.422$). Removing evaporation reduced the models predictability 9% ($r^2=.52$). Removing deep soil water reduced the model's r square about 5% ($r^2=0.559$). Coefficients for evaporation, litter, and deep soil moisture (45-76 cm) were negative. The medium soil water(15-45 cm) coefficient was positive.

Graminoid factors

The best graminoid cover model included light, evaporation, site index, and the medium depth soil water. Light, site index and soil water coefficients were positive (Table 16). R square for this model was 0.471. Graminoids therefore grow better with more light, higher medium depth water, and on sites with higher site indexes.

Forb factors

The best forb cover reduced model included light, evaporation, average growing season temperature, site index, and deeper soil water (45-76 cm, Table 16). Coefficients for light, evaporation, site index, and deep soil water were positive. Forbs on these plots grow less when temperature increases. Forbs seem to take moisture from deeper in the soil with evaporation at the soil surface having little effect on them. Forb species on these plots seem to be higher elevation species negatively affected by increasing average temperature. R square for the best forb model was 0.693(Table 16).

Shrub factors

Important factors for shrub's best cover model for the transformed shrub cover variable (shrub cover taken to the 0.2 power) included average growing season temperature, site index, medium depth soil water, and litter cover (Table 16). All coefficients except the % litter cover were positive. Litter cover slightly negatively affected these shrub species. R square for this best model was 0.640 (Table 16).

Factors correlated with leaf area

Total LAI

The reduced model (Table 17) that best predicted the transformed total LAI(log of LAI) included medium (+) and deep soil water(+), average temperature(+), and litter(-). The litter coefficient was negative in the best model; the other coefficients were positive. R square for the full model was 0.526 (Table 17). The reduced model gave a r square of 0.522. A partial F-test gave an F of 0.0872 compared to a critical F value 2.95(with 3 and 28df.). Evaporation, shallow soil water, and light were not significant factors in explaining variation in LAI.

Removing the average temperature predictor from the model reduced its predictability 31% ($r^2=0.211$). Removing litter reduced the model 15%. Removing medium depth soil water from the reduced model reduced the r square 4%. Removing deep soil water reduced the model 1%.

Graminoid LAI

Best regression analysis (Table 17) shows graminoid species present respond to light (+) and average temperature (-). Increasing

shallow soil water (+) and medium depth soil water(+) and site index (+) increases total graminoid leaf area. This model explained 59% of the graminoid LAI (Table 17).

Forb LAI

Forb LAI increased as average temperature, light, and medium depth soil water increased (Table 17). Increasing litter cover reduced forb leaf area. Forb species LAI on these study sites increased with distance from the trees (Table 17). Forb LAI increased as I moved to warmer sites (lower elevation); this is opposite to the effect of increasing temperature on forb cover. Increasing litter cover under the tree inhibits understory forb growth. The effect of medium depth soil water (15-45 cm) suggests that it is the water factor supporting forb LAI.

Shrub LAI

Shrub LAI increases as litter(-) and light intensity (-) decreases (Table 17). Shrub LAI increases as average temperature (+) increases, and increases very slightly with increasing evaporation (+). Shrub species on these three locations grow better on warmer locations.

Table 16. Cover regression models. Values are % cover. The full model includes all the factors listed. Coefficients shown are for predictors used in the best reduced models. Blank spaces are coefficients not significantly different from 0 and they are emitted from the reduced model.

COEFFICIENTS										
VAR(1)	RSQ	CONT	LIGHT	EVAP	%LTR	TEMP	SITE	SOIL WATER		
							INDEX	SHALL	MED	DEEP
TC(2)	0.59	206		-6.6	-3.3				22.4	-6.0
GM(3)	0.47	-27	0.13	-0.8			0.3		1.10	
FORBS	0.69	169	0.10			-2.8	0.3			0.5
SB(4)	0.64	-4.8			-0.01	0.1	0.01		0.10	

(1). Abbreviations are var (variable), rsq (r square), cont (constant), evap (evaporation), %ltr (% litter), temp (average growing season temperature), shall (shallow soil water), med (medium soil water), deep (deep soil water).

(2). The term TC is an abbreviation for total cover transformed by taking it to 1.4 power.

(3). The term GM is the abbreviation for graminoids.

(4). The term SB is the abbreviation for shrub cover transformed by taking it to .2 power.

Table 17. Leaf area regression models. Measure used is square meters of leaf area/square meters of ground. Full model includes all the factors listed. Coefficients shown are for predictors used in the best reduced models. Blank spaces are coefficients not significantly different from 0 and are omitted from the model.

COEFFICIENTS									
VAR(1)	RSQ	CONT	LIGHT	EVAP	%LTR	TEMP	SOIL WATER		
							SH	MED	DEEP
LAI(2)	0.52	-9.0			-0.03	0.1		0.02	0.01
GM(3)	0.59	0.4	0.004		0.01	-0.01		0.04	0.04
FB(4)	0.70	-7.2	0.003		-0.008	0.10		0.03	
SB(5)	0.35	-3.7	-0.001	0.004	-0.002	0.08			

(1). Abbreviations are var (variable), rsq (r square), cont (constant), evap (evaporation), ltr (litter), temp (average growing season temperature), sh (shallow soil water), med (medium soil water), deep (deep soil water).

(2). Total leaf area is transformed by taking the log of LAI.

(3). This is the abbreviation for graminoid LAI and it was transformed by taking it to 1.2 power.

(4). The forb (FB) variable was transformed by taking its log.

(5). The shrub LAI (SB) was transformed by taking it to its log.

Factors correlated with distribution of major species

I used regressions to predict performance of individual species by regressing cover against environmental factors. The next paragraphs expand on the contributions of each factor in individual species distribution in these understories using these regressions. Coefficients values are not important because this data is not coded to standardize

them. Sign is important, and the coefficients have been tested to see if they are significantly different from zero. The signs in the following text are based on the signs of the factor coefficients.

Carex geyeri produces more cover away from the trees (-litter) and on sites with lower site indexes (-). Increasing light (+) increases Carex geyeri. Increasing evaporation(+) reduces its cover (Table 18). It seems to be favored by poorer sites.

Calamagrostis rubescens does much better away from the trees and on warmer sites(+temp). It responds positively to more soil water at medium depths (15-45 cm) and on sites with a higher site index (Table 18).

The forb species (Solidago multiradiata) earlier cited as a light requiring species (Petersen et al. 1988) benefitted from increasing light (+) and was negatively affected by litter cover (-). Solidago was also negatively affected by rising temperatures (-) and medium depth soil water (-). These effects might be the direct result of competition from other species (Table 18).

Epilobium angustifolium was very slightly affected by light(-), and increasing litter (-). Epilobium grows better on better sites (+) with higher soil water at medium soil depth (+).

Campanula rotundifolia cover increased with increasing light (+). Increasing average temperature (+), higher site index(+), and more medium depth water (+) also positively affected this species (Table 18).

The shrub Vaccinium scoparium does well in low light conditions under the tree (-). Its cover also increases with increasing deep water

(Table 18).

Arctostaphylos uva-ursi is another understory shrub which increases with increasing litter indicating that it grows well under trees. The cover of Arctostaphylos increases as deep water decreases. It responds positively to increases in shallow water(+). A possible explanation is that under the tree the trees consume the deep water, and Arctostaphylos responds to whatever shallow water is available.(Table 18).

Factors correlated with species number

The number of species present in a plot increases with increasing light(+). Species number declines with increasing litter cover(-), increasing temperatures(-), higher site index (-), and medium depth soil water (-). While they suggest some factors controlling the major species, the models only accounted for about half of the variability found on these plots.

Table 18. Species regression analysis. Values are % cover. The full model includes all the factors listed. Coefficients shown are for predictors used in the best reduced models. Blank spaces are coefficients not significantly different from 0 and are omitted from the reduced model.

VAR(1)	RSQ	CONT	LIGHT	EVAP	%LTR	TEMP	Coefficients			
							SITE	SOIL	WATER	
							INDEX	SH	MED	DEEP
CARO(3)	0.56	-9	0.010			0.07	0.06		0.1	
CARU	0.53	-68	0.028	-0.4		0.58	0.59		0.6	
CAGE	0.31	14	0.015	-0.2	-0.3		-0.01			
SOMU	0.41	14	0.034		-0.02	-0.2			-0.1	
LUSE	0.33	32	0.022		-0.56		-0.09			0.2
EPAN	0.37	-7	-0.002		-0.03		0.09		0.6	
VASC	0.58	11	-0.196		-0.17				-1.6	2.5
ARUV(2)	0.59	2		-0.02	-0.01			0.1		-0.02
ARCO	0.23	5			0.02	-0.14	0.04			
SP#(4)	0.48	49	0.041		-0.03	-0.6	-0.22		-0.03	

(1). Abbreviations are var (variable), rsq (r square), cont (constant), evap (evaporation), %ltr (% litter), temp (average growing season temperature), sh (shallow soil water), med (medium soil water), deep (deep soil water).

(2). ARUV transformed to .2 power.

(3). Species names are: CAGE= Carex geyeri, ARCO= Arnica cordifolia, CARO= Campanula rotundifolia, CARU= Calamagrostis rubescens, SOMU= Solidago multiradiata, EPAN= Epilobium angustifolium, ARUV= Arctostaphylos uva-ursi, LUSE= Lupinus sericeus, VASC= Vaccinium scoparium.

(4). SP# is an abbreviation used for number of species.

DISCUSSION

Understory response to overstory thinning

Young lodgepole pine stands were thinned to spacings of 1.8, 2.7, 3.6, 4.5, and 5.4 meters. Overstory trees have average LAI's of 6.1 (1.8 spacing), 2.8 (3.6 spacing), and 1.7 (5.4 spacing) on the study plots. The objective of this paper is to determine understory response to this thinning. This discussion ties together understory plant responses as measured by the two different methods (cover estimation or leaf area measurements).

Vegetation response was measured by observing total cover and leaf area index (LAI) at different tree spacings. Leaf area is probably the most useful measure of each species' importance in the community (Marshall & Waring 1986; Kozłowski 1991).

The total understory vegetation under trees declined with increasing density (Table 4). The closest spacing (1.8m) had significantly less cover and LAI than wider spacings. Cover differences among 2.7, 3.6, 4.5, and 5.4 meter spacings were surprisingly small.

Within stands, even open ones, total understory vegetation varied little with position relative to the tree (ie. under, at the dripline, or between the tree; Table 4).

Different components of understory vegetation responded differently. 1) Graminoid cover in the widest spacings (4.5 & 5.4m) exceeded graminoid cover in the narrower spacings (1.8, 2.7, and 3.6 meters; Fig 2 & Table 5). Tree position did not affect graminoid cover. 2) Forb cover also declined from wide spacings (4.5 and 5.4 meters) to narrow spacings (1.8) (Fig 2 & Table 6). Unlike graminoids forbs did

best at the dripline position. The between and under tree positions produced lower and similar forb cover (Fig 2 & Table 6). 3) While shrub cover was inhibited by the densest tree spacings (1.8m), they were otherwise unaffected (Table 7).

Species richness was increased significantly ($p=0.05$) by widening the spacing of trees (Table 12). In the understory the narrowest (1.8m) spacing had fewer species than the 3.6m, 4.5m, and 5.4m spaced trees. Position with respect to the trees had no effect on species number.

Species responded uniquely as spacing distance changed. Most common graminoid and forb species were positively affected by light (Table 18). The most common understory shrubs were indifferent to increasing light. The forb species responded positively to medium depth soil water (15-45 cm) (Table 18). *Lupinus* and *Solidago* responded the most positively to increased light (Table 18).

Correlation of environmental factors with understory vegetation

Thinning is expected to reduce competition from the trees for resources. More resources should be available for the understory plants. As the canopy re-closes these resources will be pre-empted by the trees and become unavailable again to the understory plants. I examined these stands about 25 years after they were thinned.

I used multiple regression analysis to determine which factors may be important. I realize that this is a hypothesis generating process, and that experimentation will be required to test these hypotheses. Spacing is the experimental manipulation under study, therefore we

looked at environmental factors that may be influenced by spacing manipulation. Presumptive factors we measured were light, ground level evaporation, and the amount of litter cover. Soil water and growing season data from the same sites was available (Cole pers communication). To reduce location effect, we also included site index and average temperature in our regressions.

Light

Light levels increased significantly ($p=0.05$) as tree spacing increased from 1.8 meters to 5.4 meters and as one moved from tree trunk to between the trees at all spacings (Table 2). In no case did light levels reach levels that could be classified as sunny (Young & Smith 1980).

Increasing light increased the number of species (Table 16). Graminoid and forb species found on these plots responded positively to increasing light (Table 14 & 15). Shrub species did not respond to increasing light, and so seemed well adapted to living under trees in relatively low light (Table 18).

Soil water

Soil water integrated precipitation input and plant consumption of the water. Different plant types and species appeared to use water from different levels of the soil.

Shallow soil water (0-15 cm) did not correlate with any life-form (Tables 16 & 17). One species, Arctostaphylos uva-ursi, was positively correlated with shallow water (Table 18).

Medium depth soil water (15-45 cm) availability accounted for 19% of the variation in total cover (page 45), but affected total LAI by only 4% (page 47). Increasing medium depth soil water (15-45 cm) positively affected both graminoid cover and graminoid LAI (Tables 14 & 15).

Forb species cover increased as deep (45-76 cm) soil water increased (Table 16). *Lupinus*, especially, benefitted from increased deep soil water (Table 18). A shrub species, *Vaccinium scoparium*, was also positively affected by deep soil water (Table 18).

Evaporation

Evaporation at the soil surface generally differed little among spacings or position (Table 3). An exception was the 5.4 meters spacing which had significantly ($p=0.05$) higher rates of evaporation than the other four spacings (Table 3). This suggests that air circulation in the understory is general rather than local.

Total understory cover decreased as evaporation increased accounting for about 9% of the variation of total cover (page 45). Graminoid species were negatively affected by increasing evaporation (Table 16). Most species present in these understories were unaffected by evaporation rates observed on these plots (Table 18).

Litter

Litter cover was well correlated with understory cover and LAI (Table 16 & 17). Litter cover accounted for 31% of the variation in total cover (page 45); high litter cover reduced total cover and total

LAI (Table 16 & 17). Increasing litter reduced forb LAI (Table 17). Litter decreased the amount of shrub cover and shrub LAI (Table 16 & 17). In contrast, graminoid species seemed immune to the effects of litter (Tables 16 & 17). The mechanism for litter cover effects was not isolated in this study.

Temperature

On these study sites average growing season temperature decreased as elevation increased (Table 1). Average temperature had the largest effect on total LAI (31%). High average temperature reduced graminoid LAI and forb cover; however, forb LAI increased with increasing average temperature (Tables 16 & 17). Increasing average temperature increased shrub cover and shrub LAI.

Site index

Site index may be a measure of long term climate and nutrient availability (Kozlowski et al. 1991). On our study sites site index decreased as elevation increased (Table 1). Higher site indexes increased production of most life-forms of understory plants on these plots (Table 16 & 17). In contrast Carex geyeri and Lupinus sericeus were negatively affected by high site indexes (Table 18). These negative responses to site are probably not direct; other species may be better competitors on the more productive sites and may exclude these two species.

Model adequacy

Our models account for 50 to 70% of the observed variability in understory plants. For example, our total cover model accounted for 59% of variability found. The total LAI model had an r^2 of 0.522.

Underground factors may account for much of the remaining variability of the understory vegetation. Soil fertility may affect the overstory-understory relationship (Bennett et al. 1987; Moore & Deiter 1992). Adding a soil fertility predictor variable improved prediction models of yield of understory plants of Ponderosa pine in South Dakota (Bennett et al 1987). A more descriptive model could perhaps be derived if soil fertility data were also incorporated into the model.

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APPENDIX

VEGETATION SUMMARY DATA SHOWING DIFFERENCES

BETWEEN REPLICATIONS

Table 19. TARGHEE SITE
Under Tree

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
Graminoids										
Calamagrostis rubescens	4	4	3	17	16	11	25	7	15	13
Carex geyeri		0	1				1			1
Danthonia intermedia			1		1	1	1	1	3	1
Total cover graminoids	4	4	6	17	17	11	26	9	18	14
Forbs										
Arnica cordifolia	3	1	1	1	6	3	2	0		
Antennaria racemosa	2	2	1	1	1	2	2	2	1	3
Campanula rotundifolia	1	1	1	3	3	1	2	2	2	2
Solidago multiradiata		1	2	1	1	3	1	5	0	3
Lupinus sericeus		0	0	1	1	2	1	0	2	1
Epilobium angustifolium	1	0	1	0	1	2	1	0	2	1
Potentilla arguta			1	1	2		1	1	1	6
Fragaria virginiana			1			1				
Agoseris glauca			1				1		1	1
Taraxicum officinale				1				1		
Geranium viscosissimum										1
Achillea millifolium						1				
Total cover forbs	8	4	7	8	18	11	8	11	14	12
Shrubs										
Vaccinium scoparium	8		28		8	48				
Arctostaphylos uva-ursi			1	4	4	12	8	2	2	3
Spiraea betulifolia							1			
Total cover shrubs			30	4	12	68	8	2	2	3
Total cover all	21	7	43	29	47	86	42	22	35	29
Bare ground	3	2	1		1				2	
Litter	81	96	68	95	91	39	91	96	93	81

Table 20. TARGHEE SITE
Dripline

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens	4	7	3	22	19	7	26	6	17	14
Carex geyeri			1				1		1	
Danthonia intermedia			1	1	1	1	6		3	4
Trisetum spicatum							1			
Stipa columbiana					2					
Deschampsia caespitosa					1		1		1	1
Sitanian hystrix							5		1	
Total cover graminoids	4	7	3	23	20	10	26	15	20	20
FORBS										
Arnica cordifolia	3	1	2	0	1	1	1	0	4	1
Lupinus sericeus		2		1	2		2	8	2	4
Epilobium angustifolium	1		1		3	11	2		4	
Campanula rotundifolia	1	1	1	2	4	2	3	3	2	1
Potentilla argula	2		1		1		1		1	1
Agoseris glauca	1		1		1		1	1	1	2
Antenaria racemosa	2	1	1	1	1	1	2	1	2	4
Solidago multiradiata			1	1	2	2	1	11	2	7
Hieracium umbelli		1		2						
Fagaria virginiana			1		1	2				
Achillea millifolium			1		1					
Total cover forbs	9	4	6	8	15	18	10	26	18	19
SHRUBS										
Vaccinium scoparium	7		22		43					
Arctostaphylos uva-ursi	1		4	3	5	5	13	2	9	3
Spirea betulifolia							4			
Total cover shrubs	8		26	4	6	54	18	4	9	3
Total cover all	21	11	43	31	44	76	55	45	35	41
Bare ground	1	1	1				4		1	4
Litter	71	87	72	95	93	40	85	91	92	81

Table 21. TARGHEE SITE
Open

Spacing(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens	11	5	3	14	20	10	38	9	15	12
Danthonia intermedia		1	1	1	3	3	3	2	4	1
Carex geyseri			1		3		1			
Stipa columbiana					2					
Deschampsia caespitosa					2				1	1
Sitanian hystrix										1
Trisetum spicata										1
Total cover graminoids	6	6	7	14	22	16	42	11	20	14
FORBS										
Arnica cordifolia	5	1			1		1	1	1	
Aster conspicuus					1				1	
Fagaria virginiana			1		1				1	
Lupinus sericeus		1	1	1	1		2	13	8	8
Epilobium angustifolia	1		2		8		4		2	
Campanula rotundifolia		1		1	3	3	4	2	4	3
Antennaria racemosa	1	1	1		1	1	2	0	1	2
Solidago multiradiata		1	1	3	1		4		3	14
Chimaphila umbellata			1		1					
Achillea millefolium			1		1	1				
Agoseris glauca			1		1	1				1
Potentilla arguta			1		1		3	1	2	2
Total cover forbs	5	6	8	5	8	15	12	23	23	24
SHRUBS										
Vaccinium scoparium	1		23		3	27	1		5	
Spiraea betulifolia	1		2	7						
Arctostaphylos uva-ursi					8	6	8	6	1	5
Populus tremuloides							3			
Total cover shrubs	5	0	25	7	11	34	8	14	6	5
Total cover all	15	11	40	26	38	61	63	47	50	46
Bare ground	2		1		1		4	3	2	18
Litter	70	87	70	95	85	50	85	87	82	67

Table 22. LEWIS & CLARK SITE
Under Tree

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens	5									
Carex geyseri					1	1	1	1	1	5
Danthonia intermedia							1	1	1	1
Trisetum spicatum					1					
Elymus glaucus							1			
Deschampsia caespitosa							1			
Festuca idahoensis							1			
Agropyron canium									1	
Total cover graminoids	0	5	0	0	1	1	2	2	3	8
FORBS										
Arnica cordifolia	1	1	1	1	1		1	2	1	
Aster conspicuus	1	1	1	1	4		1	2	4	1
Saxifrage	2									
Pyrola secunda	1		1	2	1	1				
Lupinus sericeus	1		1				1	2	1	1
Epilobium angustifolium	1		1		1	1			3	1
Campanula rotundifolia		1						1	2	2
Hieracium umbelli			1	1	1		1		1	1
Fagaria virginiana	1		1				1		1	1
Trifolium pratense		1								
Chimaphila umbellata			2		5					
Antennaria racemosa					1		1	1		
Agoseris glauca					1					
Taraxicum officinale										1
Geranium viscosissimum										1
Penstemon procerus									2	1
Total cover forbs	3	6	6	5	8	8	4	10	13	9
SHRUBS										
Vaccinium scoparium	46	1	42		15	3	4	2	3	36
Vaccinium globare	3	6	1	12	12	3	18	14	24	
Symphoricarpus albus	4									
Spiraea betulifolia		4			2		9		3	4
Rosa woodsii	2		1							1
Berberis repens	1		1							
Juniperus cummunis					2					
Arctostaphylos uva-ursi							1	4	1	7
Total cover shrubs	53	12	44	13	31	5	22	31	32	55
Total cover all	57	22	50	18	39	14	28	43	48	72
Bare ground	1				2	3				
Litter	64	96	65	94	77	91	88	95	82	73

Table 23. LEWIS AND CLARK SITE
Dripline

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens		2					1	1	1	
Carex geyseri	1				2	1		2	2	5
Danthonia intermedia					1		1	2	2	7
Trisetum spicatum										1
Agropyron canium					1					5
Deschampsia caespitosa							1	1		
Festuca idahoensis								1		
Trisetum spicata										1
Total Cover Graminoids	1	2	0	0	2	5	3	7	5	19
FORBS										
Arnica cordifolia	1	1	1	1	2		1	2	1	
Aster conspicuus	1		2		4		2	2	10	1
Pyrola secunda	1		2	2						2
Lupinus sericeus			2	4	1	6	10	13	7	2
Epilobium angustifolium			1		1		1	2	3	
Campanula rotundifolia								2	2	
Hieracium umbelli		1	1	2	1	2	1			1
Fagaria virginiana			1		2			4	3	7
Agoseris glauca									1	1
Antennaria racemosa							1	4	6	
Chimaphila umbellata				1		2				
Achillea millefolium										1
Taraxicum officinale					1		1		1	
Penstemon procerus									1	2
Potentilla argula									1	
Solidago multiradiata					1				2	
Saxifrage spp.				3						
Total cover forbs	5	4	8	9	9	12	14	30	36	16
SHRUBS										
Vaccinium scoparium	27	6	36	1	15	7	4	2	3	28
Vaccinium globare	5		1	10	3	2	16	9	2	
Rosa woodsii	2									1
Symphoricarpos alba	4		1				1			
Spiraea betulifolia		3			5			1	4	1
Berberis repens				1						1
Juniperis communis						1				
Total cover shrubs	37	10	37	12	26	8	17	13	8	34
Total cover all	43	17	45	21	37	22	33	50	50	68
Litter	71	97	64	89	75	87	85	83	77	63

Table 24. LEWIS AND CLARK SITE
Open

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens		1			1		1	4	2	
Carex geyeri				3	1	1		2	9	6
Danthonia intermedia			5		1		4	1	5	7
Deschampsia caespitosa									2	
Festuca idahoensis	1									
Agropyron canium	0								1	6
Calamagrostis canadensis		1							1	
Stipa columbiana							2			
Total cover graminoids	0	3	1	3	2	1	3	8	16	21
FORBS										
Arnica cordifolia	1	2		1			1	1		
Aster conspicuus	1		3	1	6	1	1	6	5	2
Saxifrage		1								
Pyrola secunda		2			1	1				1
Hieracium umbella	1	2		2	1		1	1		
Epilobium angustifolia	1				1	2			2	1
Campanula rotundifolia						2			1	1
Antennaria racemosa	1				1	1	1	3	4	
Fragaria virginiana		1	1				1	4	5	5
Agoseris glauca						1		3	1	
Lupinus sericeus			1	4	2	3	4	2	5	2
Chimaphila umbellata				1		1				
Achillea millifolium								1	1	
Taraxicum officinale								1	1	
Geranium viscosissimum										1
Penstemon procerus								2	3	
Solidago multiradiata		1							1	1
Total cover forbs	5	7	7	7	11	7	10	19	28	13
SHRUBS										
Vaccinium scoparium	21	4	32		18	6	3	7	11	37
Vaccinium globare	5		2	8	15	11	17	7	4	
Symphoricarpos alba	4						1			
Berberis repens				1				1		1
Spirea betufofia		4			5			2	2	2
Total cover shrubs	35	8	34	9	36	17	21	21	17	40
Total cover all	40	20	42	21	49	25	34	42	62	74
Bare ground				2						
Litter	68	94	66	89	68	88	63	71	53	54

Table 25. GALLATIN SITE
Under Tree

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens	3	1	1	2	2		1	3	1	12
Carex geyseri		4	2	2	1	2	1			6
Elymus glaucus	1									
Trisetum spicatum					1					
Poa pratensis				1	1				1	
Deschampsia caespitosa							1			
Setarian hystrich					1	1			1	1
Danthonia intermedia									1	
Total cover graminoids	3	7	3	4	3	3	1	4	2	18
FORBS										
Astragalus spp.	17	11	16	11	7		24		13	5
Arnica cordifolia	3	1	7	2	1	2	2	3	3	3
Aster conspicuus	2	2	1	4	3	5	1	3	5	3
Lupinus sericeus	1	6	6	2	4	6		9		6
Pyrola secunda	2					6	9		3	13
Fagaria virginiana		3	1	1				1	3	1
Epilobium angustifolium	2			1				3	1	1
Solidago multiradiata	2	7	1	6	1	2	1	4	1	1
Hieracium umbelli			1	1		2	1			
Senecio spp.				1	1	1				
Antennaria racemosa					2	1	1			1
Campanula rotundifolia									1	
Taraxicum officinale				1						
Agoseris glaucus							1	1		1
Geranium viscosissimum										3
Penstemon procerus		1							2	1
Total cover forbs	27	25	32	30	25	21	39	37	32	25
SHRUBS										
Vaccinium scoparium						8		9		
Spiraea betulifolia						2		2		
Total cover shrubs	0	0	0	0	0	10	0	11	0	0
Total cover all	30	38	36	34	28	34	40	58	35	43
Bare ground			7				2		7	6
Litter	100	97	73	100	95	93	98	92	92	100

Table 26. GALLATIN SITE
Dripline

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens	1		2	1	4		1	2		11
Carex geeyeri	1	4	3	3		4	2		3	14
Poa pratensis		1		2						
Trisetum spicatum						2	1	1		
Deschampsia caespitosa						1				
Danthonia intermedia									1	
Poa nervosa									1	
Total Graminoids	3	4	5	6	4	7	3	5	5	26
FORBS										
Astragalus spp.	11	10	3	8	14		17		4	4
Arnica cordifolia	6	3	3		1	2	2	1	1	2
Aster conspicuus	7	7	11	4	7	6		1	11	4
Pyrola secunda					3				4	11
Lupinus sericeus	3	2	4	2	8	11		12	4	2
Epilobium angustifolium		2		1	2		1	1		
Campanula rotundifolia									1	
Hieracium umbellii		1	1		1	2		1	1	1
Fragaria virginiana	1	2	2	4	1		2	8	5	3
Penstemon procerus		2								
Antennaria racemosa				1	1				1	1
Taraxicum officinale	1			1						
Achillea millefolium			1						1	1
Agoseris glauca				1					1	1
Galium boreale										1
Geranium viscosissimum										1
Potentilla arguta										1
Solidago multiradiata	1	2	2	13	1	4	2	8	2	1
Agoseris glauca					1			2		1
Senecio spp.			1	1		2		2		
Total cover forbs	30	25	29	38	39	27	39	40	32	22
SHRUBS										
Vaccinium scoparium						14		6		
Spiraea betulifolia				1		3			1	
Juniperus communis			3							
Total cover shrubs	0	0	3	1	0	17	0	7	1	0
Total cover all	33	37	36	45	43	51	42	51	32	47
Bare ground	10	2	14	9	11	17	29	22	21	21
Litter	86	86	72	76	73	51	63	64	58	63

Table 27. GALLATIN SITE
Open

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
<i>Calamagrostis rubescens</i>	1	1	3		1	1	1	2	1	28
<i>Carex geyeri</i>		6	3	2	2		3	2	10	7
<i>Sitanian hystrix</i>	1			1	1	2		1	1	2
<i>Poa pratensis</i>				2						
<i>Elymus glaucus</i>	1									
<i>Agropyron canium</i>							1			
<i>Danthonia intermedia</i>									1	
<i>Trisetum spicatum</i>					1					
Total cover graminoids	3	7	6	4	3	4	5	4	14	37
FORBS										
<i>Astragalus</i> spp.	3	13	1	8	7		13		2	3
<i>Arnica cordifolia</i>	1	1	3		1	1	1		4	2
<i>Aster conspicuus</i>	8	2	8	2	5	6		1	8	2
<i>Senecio</i> spp.				3		2	3	1	1	1
<i>Pyrola secunda</i>					4			1		
<i>Hieracium umbellata</i>								1		
<i>Epilobium angustifolium</i>	1	2	1	1	1			2	1	1
<i>Campanula rotundifolia</i>							1		1	1
<i>Antennaria racemosa</i>			1					1	4	3
<i>Fragaria virginiana</i>	1	4		2	1		3	8	6	8
<i>Agoseris glauca</i>				1			1	1	1	3
<i>Lupinus sericeus</i>	11	6	10	6	3	8		9	1	
<i>Castilleja miniata</i>		1						2		
<i>Achillea millefolium</i>			1					1	4	3
<i>Epilobium angustifolium</i>	1	2	1	1	1			2	1	1
<i>Campanula rotundifolia</i>								1	1	1
<i>Penstemon procerus</i>		3								
<i>Solidago multiradiata</i>	3	4	3	11	3	6	2	6	6	1
<i>Potentilla arguta</i>		3								
<i>Trifolium pratense</i>					1					
Total cover forbs	28	20	29	36	23	25	36	35	33	23
SHRUBS										
<i>Vaccinium scoparium</i>					11		3			
<i>Symphoricarpos alba</i>	1						2		2	
<i>Spiraea betulifolia</i>					5		3			
<i>Juniperis communis</i>							1			
Total cover shrubs	1	0	0	0	0	16	3	6	2	0
Total cover all	31	43	35	40	26	45	44	45	52	60
Bare ground	23	13	32	14	52	53	47	38	38	29
Litter	76	87	56	65	32	28	44	49	39	44

Table 28. KOOTENAI SITE
Under Tree

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens	28	26	33	16	29	10	46	30	16	13
Elymus glaucus						1				
Total cover graminoids	28	26	33	16	29	10	46	30	16	13
FORBS										
Lupinus sericeus	7		2				1			
Arnica cordifolia		2		2			2			
Mintha spp.	1			1						
Achillea millifolium	1			1	2	1	1	1		
Epilobium angustifolium	1		1		1	1		1	3	1
Fagaria virginiana	4	3	2	4	4	2	2	3		
Viola spp.				1						
Aster conspicuus				1			2			
Smilacina stellata				6						
Chimaphila umbellata				2		5				
Thalictrum occidentale				2						
Agoseris glauca				1						
Galium boreale					1		1			
Clintonia uniflora							1			
Total cover forbs	12	6	4	18	5	6	7	4	1	9
SHRUBS										
Vaccinium scoparium		1								
Vaccinium globare	12		5	3	11	6	8	1	10	2
Arctostaphylos uva-ursi	7	8	23	34	39	31	17	41	33	52
Berberis repens	7	2	3	1			2			3
Spiraea betulifolia	1		2	3		6				5
Rosa woodsii	2		1	2	3	1				1
Symphoricarpus albus				2						
Salix spp.				1						
Total cover shrubs	32	12	34	46	50	44	27	48	41	64
Total cover all	72	44	71	81	84	60	79	82	58	76
Bare ground	3	1	1		6		6		3	1
Litter	97	99	99	90	98	70	100	79	98	76

Table 29. KOOTENAI SITE
Dripline

Spacings	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINIOIDS										
Calamagrostis rubescens	27	9	34	14	24	20	18	21	19	12
Carex geeyeri			2				9		4	3
Elymus glaucus				1		1				
Deschampsia caespitosa										3
Phleum pratense										1
Total Cover Graminoids	27	9	36	15	24	21	18	30	23	19
FORBS										
Arnica cordifolia		5		6			1		1	
Aster conspicuus		1		1	2		2		1	
Pyrola secunda				2						
Lupinus serecius	11		2		2		2			3
Fagaria virginiana	3	3	5	10	4	2	7	2	4	6
Mentha spp.	1				1					
Hieracium umbelli		1		2			1			1
Trifolium pratense				1						
Thalictrum occidentale				2						
Antennaria racemosa			1				1	4		1
Viola spp.				1			1			
Achillea millefolium			1		1	1	1			1
Smilacina stellata				1						
Taraxicum officinale						1				
Total cover forbs	15	10	7	25	8	4	8	6	8	8
SHRUBS										
Arctostaphylus uva-ursi	11	9	25	29	44	30	28	24	26	35
Vaccinium globare	14		16	1	7	2	17	1	19	6
Berberis repens	9	1	6	2	1	2	3	3	2	
Rosa woodsii	4	2	1	7		1			1	2
Spiraea betulifolia	1			6	2	1				1
Total cover shrubs	41	12	46	46	54	36	47	31	48	44
Total cover all	83	30	89	85	90	62	76	67	75	71
Bare ground	19		3				6	29	25	20
Litter	80	100	99	96	85	73	85	86	75	52

Table 30. KOOTENAI SITE
Open

Spacings(meters)	1.8		2.7		3.6		4.5		5.4	
Replication	1	2	1	2	1	2	1	2	1	2
GRAMINOIDS										
Calamagrostis rubescens	25	14	29	22	21	9	23	27	22	14
Elymus glaucus				1		2				
Carex geyseri						3		3	8	5
Deschampsia caespitosa									1	1
Total cover graminoids	26	14	29	24	21	13	23	30	23	22
FORBS										
Lupinus sericeus	8	0	2		7		2		1	
Fagaria virginiana	5	1	5	9	4	7	5	2	8	4
Arnica cordifolia	0	1		2			1	1	1	1
Mentha	1									
Achillea millifolium	1			1			1		0	1
Pyrola secunda		1								
Hieracium umbella	1	2		2	1		1	1		
Aster conspicuus				3			1		1	1
Viola spp.				2			1			
Xerophyllum tenax				2						
Thalictrum occidentale				1						
Taraxicum officinale					1					
Penstemon procerus							1			
Antennaria racemosa									1	
Total cover forbs	14	2	6	21	11	10	9	6	13	6
SHRUBS										
Arctostaphylos uva-ursi	13	7	22	17	32	16	32	46	9	28
Vaccinium scoparium		2								1
Rosa woodsii	2	1		3		2		1		
Vaccinium globare	12		16	1	14	10	7		21	10
Symphoricarpos alba	2			3						
Berberis repens	6	1	3	7	1	2	3	3	1	6
Spiraea betulifolia		1	2	5	2	3				1
Total cover shrubs	41	12	47	34	49	31	42	52	31	44
Total cover all	81	28	82	80	83	58	75	88	67	72
Litter	76	100	97	96	74	64	82	61	54	46
Bare ground	24		3		11	21	18	21	67	72

Table 31. LEAF AREA COMPARISONS
1.8 METER SPACING

REPLICATION	TARG ¹		L&C ²		Koot ³		Gall ⁴	
	1	2	1	2	1	2	1	2
GRAMINOIDS								
ALL TOGETHER	47	61.2	93.2	87.9	81.2	79	38	54
FORBS								
Agoseris glauca	11.1						85.7	
Arnica cordifolia	118	200	213	161		146	127	187
Campanula rotundifolia	91	133		88.6			145	
Epilobium angustifolium	106			181			154	134
Lupinus sericeus	107	84.9	105	72.1	150		105	79.5
Solidago multiradiata				204			82	97.4
Aster conspicuus		175	185				158	155
Chimaphila umbellata			57			163		
Hieracium umbellata			265	73.5				
Fagaria virginiana				144	175	95	157	138
Achillea millifolium					125			
Pyrola secunda					147			
Astragalus spp.							151	98
average	77	103	125	117	153	128	131	110
SHRUBS								
Arctostaphylos uva-ursi	58.9							
Spiraea betulifolia	101		118	137	49.2	124		
Vaccinium scoparium	37.2	36.8	53.7	46.7	51.7			
Vaccinium globare			56	62.7		38.3		
Shepherdia canadensis			57.9				32	
Berberis repens				85.9	91	65.2		
Symphoricarpos albus							95	121
Rosa woodsii						147		
average	68.8	36.8	64.4	75.5	65.4	57.6	71.4	121

1. Targ is abbreviation for Targhee National Forest.

2. L&C is abbreviation for Lewis and Clark National Forest.

3. Koot is abbreviation for Kootenai National Forest.

4. Gall is abbreviation for Gallatin National Forest.

Table 32. LEAF AREA COMPARISONS
3.6 METER SPACING

REPLICATION	TARG ¹		L&C ²		Koot ³		Gall ⁴	
	1	2	1	2	1	2	1	2
GRAMINOIDS								
ALL TOGETHER	82	40.6	68.6	73	78.3	90	57	51
FORBS								
Agoseris glauca							161	
Arnica cordifolia	187		148		130	232	181	145
Campanula rotundifolia	81.8	81.8						
Epilobium angustifolium	124	102		141			81.2	128
Lupinus sericeus			77.4	62.5	96.2		82.9	90
Solidago multiradiata		150					106	101
Aster conspicuus	142		149		126	267	139	133
Fagaria virginiana		120			116	160		
Hieracium umbellata			114	75				
Pyrola secunda			103	121				
Antennaria racemosa			84.4					
Chimaphila umbellata				50.1		181		
Taraxicum officinale				244		303		
Achillea millefolium					86	97		100
Polygonatum biflorum						207		
Potentilla arguta							140	
average	144	124	95.5	111	101	176	113	113
SHRUBS								
Arctostaphylos uva-ursi	46.2	46.2		40.5	30	32.8		64
Spiraea betulifolia	12.6		162	90.5	152	100		
Vaccinium scoparium	37.2	37.9	52.7	36.7				53.4
Vaccinium globare			64	113	59.3		77.2	
Berberis repens					81.2	82.9		
Rosa woodsii					149	63.8		
Symphoricarpos							143	101
Shepherdia canadensis							172	113
Sambucus canadensis							72	205
average	32	30.2	93	80	94	70	68.3	107

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Table 33. LEAF AREA COMPARISONS
5.4 METER SPACING

REPLICATION	TARG ¹		L&C ²		Koot ³		Gall ⁴	
	1	2	1	2	1	2	1	2
GRAMINOIDS								
ALL TOGETHER	107	45.4	39.4	59.6	77	57	49	49
FORBS								
Agoseris glauca			129	210				
Arnica cordifolia	111	141		144	186	154		125
Campanula rotundifolia	65		56.8				60.9	56.4
Epilobium angustifolium	123	101	95.1	111				125
Lupinus sericeus	60.6	40.2	53.4	79.5	83.4			81.6
Solidago multiradiata	79.3	111					62.7	
Aster conspicuus	118						86	107
Fragaria virginiana		120	132	136	121	134	126	123
Potentilla arguta	135	101					58.8	
Antennaria racemosa		76.7	61.8					
Taraxicum officinale			225	225				
Penstemon procerus			46.8			85.2		
Pyrola secunda				117				
Hieracium umbellatum					155			
Achillea millefolium					77	76	33	
Trifolium pratense						144		
Astragalus spp.							62	108
average	98.9	98.7	100	117	137	132	70	103
SHRUBS								
Arctostaphylos uva-ursi	51.1	46.2	107		31.5	35.3		
Spiraea betulifolia			115	85.9		93.9		
Vaccinium scoparium	37.6	44.9	48.6	41.2			58.8	
Vaccinium globare			52.1	51.9				
Berberis repens			91.9	72.1	64.3	84.2		76.9
Rosa woodsii				104				
Shepherdia canadensis						33.9	165	
Artemisia tridentata								30.3
Symphoricarpos albus						14.8	68	30
Sambucus canadensis							103	
average	44.4	47.9	83	71	32	52	98.8	45.7

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