



Response of understory vegetation to varied lodgepole pine (*Pinus contorta*) spacing intervals in western Montana  
by Terry Michael Conway

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Range Science  
Montana State University  
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**Abstract:**

During 1981, research was conducted on five forested sites in Montana and Idaho to determine the response of understory vegetation to five spacing intervals of lodgepole pine (*pinus contorta*). The sites were located on the Lewis and Clark, Gallatin, Bitterroot, and Kootenai National Forests in Montana and on the Targhee National Forest in Idaho. The five sites represented varied latitudes, elevations, and forest habitat types. Yield and canopy cover of understory vegetation were determined for each spacing interval on each site. Soil temperature and moisture, and vegetative crude protein content, with respect to the varied spacings, were also determined. Yield and canopy cover of understory vegetation on the five sites decreased from wide to narrow tree spacings. Tree canopy cover correlated with yield and canopy cover of understory vegetation showed significant negative linear relationships on all sites but the Kootenai. Although overstory/understory correlations were significant, tree canopy cover generally accounted for less than 60 percent of the variation in understory yield and canopy cover on the sites.

The responses of vegetative classes to the varied tree spacings differed, with grasses showing the greatest response followed by forbs and shrubs. Crude protein content of grass, forb, and shrub species did not vary significantly among the spacing intervals. The greatest difference between maximum and minimum soil temperatures occurred under the widest tree spacing, while the least difference occurred under the narrowest spacing. Soil moisture did not vary significantly among the varied tree spacings. The results of the study indicate that thinning lodgepole pine stands to wide spacing intervals may result in a significant increase of understory vegetation compared to unthinned or lightly thinned stands. Tree canopy cover may serve as a fairly good predictor of understory vegetation.

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RESPONSE OF UNDERSTORY VEGETATION TO VARIED LODGEPOLE PINE

(PINUS CONTORTA) SPACING INTERVALS IN WESTERN MONTANA

by

TERRY MICHAEL CONWAY

A thesis submitted in partial fulfillment  
of the requirements for the degree

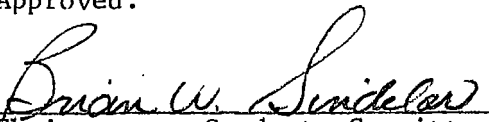
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## ABSTRACT

During 1981, research was conducted on five forested sites in Montana and Idaho to determine the response of understory vegetation to five spacing intervals of lodgepole pine (*Pinus contorta*). The sites were located on the Lewis and Clark, Gallatin, Bitterroot, and Kootenai National Forests in Montana and on the Targhee National Forest in Idaho. The five sites represented varied latitudes, elevations, and forest habitat types. Yield and canopy cover of understory vegetation were determined for each spacing interval on each site. Soil temperature and moisture, and vegetative crude protein content, with respect to the varied spacings, were also determined. Yield and canopy cover of understory vegetation on the five sites decreased from wide to narrow tree spacings. Tree canopy cover correlated with yield and canopy cover of understory vegetation showed significant negative linear relationships on all sites but the Kootenai. Although overstory/understory correlations were significant, tree canopy cover generally accounted for less than 60 percent of the variation in understory yield and canopy cover on the sites.

The responses of vegetative classes to the varied tree spacings differed, with grasses showing the greatest response followed by forbs and shrubs. Crude protein content of grass, forb, and shrub species did not vary significantly among the spacing intervals. The greatest difference between maximum and minimum soil temperatures occurred under the widest tree spacing, while the least difference occurred under the narrowest spacing. Soil moisture did not vary significantly among the varied tree spacings. The results of the study indicate that thinning lodgepole pine stands to wide spacing intervals may result in a significant increase of understory vegetation compared to unthinned or lightly thinned stands. Tree canopy cover may serve as a fairly good predictor of understory vegetation.

## Chapter 1

### INTRODUCTION

Natural regeneration of lodgepole pine (*Pinus contorta*) commonly results in overstocking and stagnation (Tackle 1959). Overly dense stands contribute little timber or understory vegetation. Most forest managers agree that if these stands are to make reasonable progress toward producing merchantable products they must be thinned.

While increased wood production on merchantable sized trees is the primary objective of thinning, this silvicultural practice also results in modification of the understory environment. Soil moisture, temperature, nutrients, and understory vegetative production, may be altered by stand manipulation (Kittredge 1948). This warrants an effort to more fully comprehend overstory/understory relationships. A more complete understanding may prove beneficial to management of forest resources, particularly if managers are trying to optimize product mix.

In 1964 the U.S.D.A. Intermountain Forest and Range Experiment Station at Bozeman, Montana, initiated a study to evaluate effects of spacing on growth of lodgepole pine. While the basic intent was to investigate effects of spacing on tree growth the study provided an opportunity to answer questions about modification in understory vegetation and environment which occur as a result of overstory

manipulation.

During 1981 the previously established Forest Service study plots were examined to determine the response of understory vegetation to varied spacing intervals of lodgepole pine. The primary objective was to measure and compare understory vegetative canopy cover and yield on five sites with five pine spacing intervals and ultimately determine overstory/understory relationships. An additional objective was to evaluate the effects of environmental factors, as modified by the overstory, on understory vegetation.

Data concerning litter, moss, lichen, and bare ground coverage, tree canopy cover and basal area, soil temperature and moisture, and understory vegetative crude protein content, with respect to spacing intervals, were also collected. With this combination of data, a better understanding of the effects of lodgepole pine overstory on understory vegetation may be provided. Such information may furnish insight into causes of understory responses and provide possible management implications.

## Chapter 2

### REVIEW OF LITERATURE

The manipulation of pine overstory results in the modification of understory environmental factors as well as vegetation. A number of studies have been conducted to determine these overstory/understory relationships.

#### Relationship of Pine Overstory to Understory Vegetation

Trappe and Harris (1958), in northeastern Oregon, reported approximately 280 kg/ha dry weight of understory vegetation produced under open stands of lodgepole pine (*Pinus contorta*). Dense stagnated stands had less than 56 kg/ha.

Basile and Jensen (1971) observed clearcutting of lodgepole pine in western Montana stimulated productivity of understory vegetation. Maximum production of 890-1120 kg/ha occurred 11 years after clearcutting.

In central Oregon, Dealy (1975) conducted a study to determine the response of understory vegetation to five spacing intervals of mature lodgepole pine. Spacing intervals of 8, 6, 4, 3 and 2 m were established by thinning. After nine years, the stands produced between 300 and 1000 percent more understory vegetative cover than before thinning, with 4 and 6 m pine spacings being more productive.

Dodd, McLean, and Brink (1972), in British Columbia, reported a

significant negative relationship between lodgepole pine overstory and understory vegetative production. Pine canopy cover accounted for 66 percent of the variation in understory yield. They determined that estimates of understory production may be made from estimates of tree canopy cover derived from aerial photographs.

Studies indicate understory vegetative production tends to decrease under other species of pine. Arnold (1950), in a study conducted on ponderosa pine (*Pinus ponderosa*) bunchgrass range in northern Arizona, reported herbaceous density declined under increasing amounts of pine canopy. Grass yield under 10 percent canopy was about five and one-half times as great as the yield under 100 percent canopy.

Gaines, Campbell, and Brasington (1954) observed forage production under longleaf pine (*Pinus palustris*) in southern Alabama. They reported a curvilinear overstory/understory relationship with 1120 kg/ha of forage produced under 0 basal area compared to 532 kg/ha under a basal area of 25 m<sup>2</sup>/ha.

In the forest of Georgia, Halls (1955) reported a curvilinear relationship between longleaf and slash pine (*Pinus elliottii*) crown cover and understory grass production. In open forests grass production of 1120 kg/ha declined consistently as pine canopy cover increased from 50 to 35 percent. After 35 percent canopy cover, less decline was noted.

Smith, Campbell, and Blount (1955) observed a curvilinear relationship between longleaf pine and understory herbage production in Georgia. Average grass yields for three years for open, moderate, and dense stands were 952, 504, and 448 kg/ha, respectively.

Pase (1958) noted a curvilinear relationship between mature stands of ponderosa pine and understory vegetation in the Black Hills of South Dakota. Total understory vegetation produced ranged from 45 kg/ha under 70 percent pine canopy cover to 2,419 kg/ha on clear-cut areas. Grasses, forbs, and shrubs produced 1,937, 342, and 140 kg/ha on clear-cut areas compared to 28, 6, and 10 kg/ha under unthinned stands, respectively.

In a study conducted in central Washington, McConnell and Smith (1965) observed a linear relationship between recently thinned ponderosa pine and understory vegetative production. Total yield ranged from 78 kg/ha under 80 percent pine canopy cover to 257 kg/ha under 10 percent canopy cover. Forbs produced more than grasses under a pine canopy cover greater than 45 percent, while below 45 percent grasses produced more than forbs.

In central Oregon, Barrett (1970) noted that eight years after thinning, understory vegetative cover was significantly greater under widely spaced ponderosa pine than under narrow spaced trees. Vegetative cover ranged from 42 percent under an 8 m pine spacing to 29 percent under a 2 m spacing.

Young, Hedrick, and Keniston (1967) in a mature, mixed forest in northeast Oregon discovered a significant negative association between pine crown cover and understory vegetative yield ( $r^2 = .25$ ). Pine crown cover accounted for more of the variation in vegetative yield than either tree basal area ( $r^2 = .10$ ) or stems per acre ( $r^2 = .09$ ).

#### Modification of Understory Environment by Pine Overstory

It has been widely recognized that understory environmental factors such as light quantity and quality, soil moisture, precipitation, and temperature may be altered by the overstory. These factors may be significant in determining relationships between pine overstory and understory vegetation.

Light. Studies generally indicate that light intensity in the understory is inversely related to pine canopy, spacing, basal area, and density. Shirley (1945), in jack pine (*Pinus banksiana*) forest of northern Minnesota observed a negative curvilinear relationship between stand density and light intensity. In an uncut stand, light intensity was 23 percent of full sunlight compared to 36 percent in a lightly thinned stand (20 percent of basal area removed). In a heavily thinned stand (70 percent of the basal area removed) light intensity was recorded at 80 percent. Surface soil temperatures were 6 to 9° C higher and air temperatures 3° C higher on the heavily thinned areas compared to the uncut stand.

In thinning plots of 25 year old red pine (*Pinus resinosa*)

plantation in Minnesota, Cheo (1946) found light intensity to increase with an increase of spacing intervals. A 1 by 1 m pine spacing (6,724 trees/ha) revealed a light intensity of approximately 15 percent of full sunlight. Under a 3 by 3 m spacing (1,329 trees/ha), light intensity had increased to approximately 60 percent.

Wellner (1948) related light intensity to stand basal area of small-crown trees, including lodgepole pine, and large-crown trees. He noted a greater reduction of light intensity by large-crown compared to small-crown trees for the same basal area. The basal areas of mature lodgepole pine and other small-crown species correlated with light intensity revealed negative curvilinear relationships. Under a heavily thinned stand (basal area of  $5 \text{ m}^2/\text{ha}$ ) light intensity was 94 percent of full sunlight. Under a moderately thinned stand ( $23 \text{ m}^2/\text{ha}$ ) light intensity was 63 percent, compared to an uncut stand ( $92 \text{ m}^2/\text{ha}$ ) where light intensity was reduced to 12 percent of full sunlight.

Tisdale and McLean (1957) investigated the possibility of solar radiation limiting understory vegetation developed under mature stands of lodgepole pine. They reported that under a fairly dense stand (basal area of  $28 \text{ m}^2/\text{ha}$ ) light intensity averaged 38 percent of full sunlight and may not have been influential in limiting plant growth. Soil moisture may have been the more important controlling factor.

Similar relationships were reported by Miller (1959) who observed

negative curvilinear correlations of light intensity with mature lodgepole pine canopy closure and stem density. He noted canopy closure, in conjunction with canopy depth, was probably the more important factor influencing light intensity. Light intensity ranged from 5 percent of full sunlight under a 70 percent canopy to 30 percent under a 40 percent canopy to 80 percent under a 10 percent canopy.

In northwestern Washington, Moir (1966) reported that a decline in understory vegetation was partially due to increased light interception by ponderosa pine canopy. He noted under the densest canopy, light levels dropped as low as 20 percent of full daylight conditions. The linear relationship of light intensity with total understory vegetative cover ( $r = -.45$ ) was less than with glass inflorescence number ( $r = -.66$ ).

In northern Wisconsin, Anderson, Loucks, and Swain (1969) investigated the influence of red pine canopy cover on light intensity, precipitation, and understory vegetative responses. They observed positive curvilinear relationships of percent pine canopy opening with light intensity ( $r = .76$ ) and throughfall precipitation ( $r = .81$ ). Correlation of understory vegetative cover with light intensity ( $r = .70$ ) was less than with throughfall precipitation ( $r = .84$ ). They noted that light levels in the understory were above minimum threshold for understory species. This suggests correlation of vegetative cover with light intensity may have been due to the close association of

precipitation and light, as both depend on canopy opening.

McLaughlin (1978) studied the predictability of light and precipitation reaching the forest floor based on measurements of ponderosa pine canopy and basal area in northern Arizona. Overhead canopy cover accounted for most of the variation in light ( $r^2 = .55$ ) and throughfall precipitation ( $r^2 = .66$ ) compared with basal area ( $r^2 = .44$ ,  $r^2 = .34$ , respectively).

The pine overstory appears to have minimal effect on light quality. Freyman (1968) observed the spectral composition of light under mature stands of lodgepole pine in British Columbia. He reported minimal influence of light quality by overhead canopy and suggested the total amount of light rather than quality exerted the greater influence on understory vegetation.

Soil moisture. Studies generally indicate that following thinning soil moisture withdrawal is reduced until remaining trees and understory vegetation reoccupy the site. In southwestern Oregon, Hallin (1967) compared soil moisture depletion rates for clearcut and adjacent uncut stands of Douglas-fir (*Pseudotsuga menziesii*). The invading vegetation on the clearcut was shown to be as effective as the stand of Douglas-fir in depleting soil moisture at the 15 cm and 46 cm depths and nearly so at the 91 cm depth.

Barrett (1970) reported ponderosa pine spacing and understory vegetation had an effect on seasonal water use in pumice soils of

central Oregon. Total water use was 1.6 times greater on plots containing 2,471 trees/ha than on plots containing 153 trees/ha. Soil moisture use on plots which had allowed understory vegetation to develop naturally was 45 percent greater than on plots which had the vegetation removed. He also noted under thinned stands that as crowns and roots of remaining trees and invading vegetation reoccupied the site, an increasing amount of soil moisture was withdrawn.

In central Oregon, Dahms (1971) reported that immediately following thinning of mature lodgepole pine, soil moisture withdrawal was significantly greater from high density stands than from low density stands. Soil moisture withdrawn from the top 152 cm of soil was 20 cm for a low density stand with a basal area of  $10 \text{ m}^2/\text{ha}$ . Moisture withdrawn from a high density stand with a basal area of  $22 \text{ m}^2/\text{ha}$  was 28 cm. As roots and crowns of remaining trees on lower density stands expanded, soil moisture withdrawal increased relative to high density stands.

Dahms (1973), in central Oregon, observed soil moisture withdrawal was definitely less after thinning mature lodgepole pine. For a low density stand, with basal area of  $7 \text{ m}^2/\text{ha}$ , additional moisture left in the top 120 cm of soil after thinning averaged 13 cm compared to pre-thinning. For a high density stand, with basal area of  $27 \text{ m}^2/\text{ha}$ , additional moisture left after thinning averaged 2 cm compared to pre-thinning.

Johnston (1975), in northeastern Utah, compared soil water depletion by cut and uncut stands of lodgepole pine on glacial till. He noted soils on clearcut plots contained from 18 to 71 cm more water than uncut plots at the end of each summer after cutting. These changes in soil water content were restricted to the top 180 cm of soil. He also observed snow accumulation was greater in clearcut than in adjacent timbered sites. Average snow water equivalents on the clearcut plots was 264 cm compared to 147 cm under the uncut stand. Snow disappeared approximately at the same time from both cut and uncut plots.

Precipitation. Studies generally indicated throughfall precipitation varies inversely with pine canopy. Niederhof and Wilm (1941), in north central Colorado, reported net rainfall reaching the forest floor in mature stands of lodgepole pine was increased through thinning. They noted net rainfall should increase approximately .8 cm for each meter increase in radius of the canopy opening up to about 5 m.

Wilm and Dunford (1948), in north central Colorado, observed that net precipitation reaching the forest floor was strongly influenced by cutting of mature lodgepole pine. On the average 9 cm of rainfall reached the litter surface under an uncut stand compared to 11 cm under a heavily cut-over stand. Snow water equivalent under the uncut stand was 18 cm compared to 25 cm under the heavily cut stand. It was noted that timber cutting exerted no significant influence on the duration

of snowmelt. Snow disappeared at approximately the same time from under cut and uncut stands. While the melting of snow was considerably accelerated on cut-over areas, the accelerated rate was balanced by excess accumulation of snow.

In central Colorado, Goodell (1952) reported that thinning dense, young lodgepole pine stands increased net precipitation reaching the forest floor. Net summer rainfall under an unthinned stand with basal area of  $21 \text{ m}^2/\text{ha}$  was 8 cm compared to 11 cm under a thinned stand with basal area of  $8 \text{ m}^2/\text{ha}$ . Snow water equivalent under the unthinned stand was 25 cm compared to 30 cm under the thinned stand. Higher snow melt rates occurred under the thinned stand.

Berndt (1965), in southeastern Wyoming, investigated accumulation of snow in lodgepole pine clearcuts of varying sizes. Snow accumulation and rate of snow disappearance were similar for 2, 4, and 8 ha clearcut blocks. Snow persisted in the adjacent uncut stand approximately 10 days longer than in the cut-over area.

Temperature. In southeastern Wyoming, Bergen (1971) observed during summer months that lodgepole pine canopy affected windspeed and air temperature. Minimum windspeed and maximum air temperature occurred in the midcanopy region (6 m above the ground) where needle and branch weight were concentrated. Subcanopy windspeed near 3 m was greater than midcanopy due to lack of understory reproduction and vegetation.

Maximum windspeed for all levels occurred in early afternoon. Maximum air temperatures were always found near minimum level of windspeed.

Similar results were reported by Gary (1974). He noted in lodgepole pine forest of southeast Wyoming that subcanopy maximum windspeed was near 3 m in height and midcanopy minimum windspeed was near 6 m.

## Chapter 3

### STUDY AREAS

The original pine spacing experiment was replicated at several sites selected to represent varying productive capabilities, based upon site index, and geographic location (Figure 1). Physical characteristics of the study sites are summarized in Table 1.

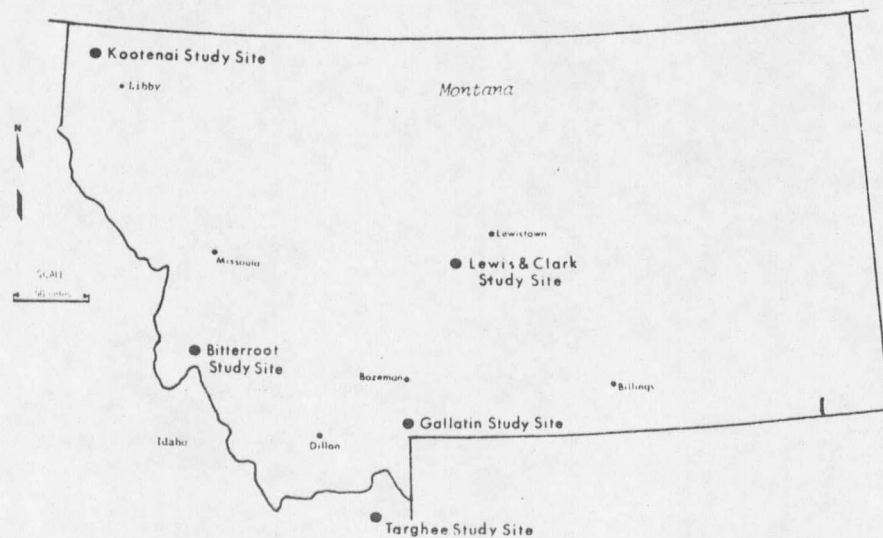


Figure 1. Location of Study Sites.

#### Targhee Study Site

Location. The site was located on the Island Park Ranger District of the Targhee National Forest, approximately 5 km north of Island Park, Idaho (SW one fourth of Section 10, T13N, R43E).

Table 1. Physical Characteristics of the Study Sites.

SITES	CHARACTERISTICS								
	Township Range Section	Elevation (m)	Slope	Aspect	Soils	Habitat Type <sup>1</sup>	Site Index	Mean Annual Temp (°C)/ Ppt (cm)	
Targhee	13N43ES10	1951	2	East	cryopsamment	PSME/CARU	75	7	78
Kootenai	37N30WS19	973	level	-	cryochrept	THPL/CLUN	110	6	90
Lewis and Clark	11N10ES16	1946	3	Southeast	cryoboralf	ABLA/VASC	55	5	42
Gallatin	8S9ES35	2408	2	West	cryochrept, cryoboralf	ABLA/VASC	65	5	68
Bitterroot	3N18WS21	2088	6	Southwest	cryochrept, cryorthent	ABLA/XETE	85	5	40

<sup>1</sup> PSME/CARU = *Pseudotsuga menziesii/Calamagrostis rubescens* h.t.; THPL/CLUN = *Thuja plicata/Clintonia uniflora* h.t.; ALBA/VASC = *Abies lasiocarpa/Vaccinium scoparium* h.t.; ABLA/XETE = *Abies lasiocarpa/Xerophyllum tenax* h.t. (Pfister et al. 1977).

The study area, elevation 1951 m, sloped gently toward the east at approximately 2 percent.

Vegetation. Forest vegetation was classified as *Pseudotsuga menziesii/Calamagrostis rubescens* habitat type (Pfister et al. 1977). The overstory was composed solely of lodgepole pine (*Pinus contorta*). Understory vegetation was dominated by pinegrass (*Calamagrostis rubescens*), elk sedge (*Carex geyeri*) silky lupine (*Lupinus sericeus*), and grouse whortleberry (*Vaccinium scoparium*).

A species list for the study sites is presented in Appendix A.

Soils. Soils were classified as cryopsamment (Stermitz et al. 1974). Cryopsamment soils are well drained sandy loams of moderate to deep depth commonly associated with cold, mountainous areas.

Climate. Climate data were derived from the closest recording weather station at Island Park, Idaho. Mean annual temperature and precipitation, based on an 11 year average from 1970-1980, was 7° C and 78 cm. Precipitation and mean temperature from April through August 1981 was 29 cm and 11° C compared to 24 cm and 9° C for the 11 year average over the same period.

Past History. The even-aged original stand was approximately 67 years old at the time of harvest in 1956. The following year slash was broadcast burned. Regeneration was thinned in 1966 when the pine spacing study was established. Stocking density prior to thinning averaged 16,556 trees per hectare.

## Kootenai Study Site

Location. The site was located on the Yaak Ranger District of the Kootenai National Forest, approximately 12 km northeast of Yaak, Montana (S one-half of Section 19, T37N, R30W).

The study area, elevation 973 m, was relatively level.

Vegetation. Forest vegetation was classified as a *Thuja plicata*/*Clintonia uniflora* habitat type (Pfister et al. 1977). The dominant overstory species was western redcedar (*Thuja plicata*), accompanied by grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*). Understory vegetation was dominated by pinegrass, elk sedge, bearberry (*Arctostaphylos uva-ursi*), and whortleberry (*Vaccinium globulare*).

Soils. Soils were classified as cryochrept (USDA Soil Conservation Service 1978). Cryochrept soils are well drained gravelly loams to silts of deep depth. Parent material, deposited by glacial action, consists of clayey alluvium and colluvium.

Climate. Climate data were derived from the closest recording weather station at Troy, Montana. Mean annual temperature and precipitation, based on an 11 year average from 1970-1980, was 6° C and 90 cm. Precipitation and mean temperature from April through August 1981 was 40 cm and 13° C compared to 25 cm and 13° C for the 11 year average over the same period.

Past History. The original stand was harvested in 1962. The site was prepared for planting by dozer piling and slash burning in 1965. In 1968 the area was stocked with 80 percent lodgepole pine, 18 percent western larch (*Larix occidentalis*), and 2 percent subalpine fir. The spacing study was established in 1971 by planting of lodgepole pine seedlings.

#### Lewis and Clark Study Site

Location. The site was located on the Judith Ranger District of the Lewis and Clark National Forest, approximately 35 km west of Utica, Montana (SE one-fourth of Section 16, T11N, R10E).

The study area, elevation 1946 m, sloped gently toward the southeast at approximately 3 percent.

Vegetation. Forest vegetation was classified as an *Abies lasiocarpa/Vaccinium scoparium* habitat type (Pfister et al. 1977). The dominant overstory species was lodgepole pine, accompanied by Engleman spruce (*Picea engelmannii*), subalpine fir, and whitebark pine (*Pinus albicaulis*). Undergrowth was dominated by elk sedge, silky lupine, showy aster (*Aster conspicuus*), and whortleberry.

Soils. Soils were classified as cryoboralf (USDA Soil Conservation Service 1978). Cryoboralf soils are well drained stony loam to sandy loam of moderate to deep depth formed over granitic parent

material.

Climate. Climate data were derived from the closest recording weather station at Utica, Montana. Mean annual temperature and precipitation, based on an 11 year average from 1970-1980, was 5° C and 42 cm. Precipitation and mean temperature from April through August 1981 was 38 cm and 11° C compared to 28 cm and 11° C for the 11 year average over the same period.

Past History. The original stand was approximately 150 years old at the time of harvest in 1954. Slash was dozer piled and burned the same year. Regeneration was thinned in 1965 when the pine spacing study was established. Stocking density prior to thinning averaged 36,793 trees per hectare.

#### Gallatin Study Site

Location. The site was located in the Gardiner Ranger District of the Gallatin National Forest, approximately 10 km north of Jardine, Montana (SW one-fourth of Section 35, T8S, R9E).

The study area, elevation 2408 m, was located on a flat ridge top that sloped gently to the west at approximately 2 percent.

Vegetation. Forest vegetation was classified as an *Abies lasiocarpa/Vaccinium scoparium* habitat type (Pfister et al. 1977). The dominant overstory species was lodgepole pine, accompanied by subalpine fir, Douglas-fir, and limber pine (*Pinus flexilis*).

Understory vegetation was dominated by elk sedge, showy aster, and whortleberry.

Soils. Soils were classified as cryochrepts and cryoboralfs (USDA Soil Conservation Service 1978). These soils are well drained gravelly sandy loam to silts of moderate to deep depth, associated with high mountainous areas. Parent material consisted of loess, colluvium, alluvium, and sedimentary rock.

Climate. Climate data were derived from the closest recording weather station at Mystic Lake, Montana. Mean annual temperature and precipitation, based on an 11 year average from 1970-1980, was 5° C and 68 cm. Precipitation and mean temperature from April through August 1981 was 39 cm and 12° C, compared to 35 cm and 12° C for the 11 year average over the same period.

Past History. The even-aged original stand was approximately 108 years old at time of harvest in 1953. Slash was dozer piled and burned the same year. Regeneration was thinned in 1967 when the spacing study was established. Stocking density prior to thinning average 11,663 trees per hectare.

#### Bitterroot Study Site

Location. The site was located on the Sula Ranger District of the Bitterroot National Forest, approximately 16 km northeast of Sula,

Montana (S one-half of Section 21, T3N, R18W).

The study area, elevation 2088 m, sloped rather steeply to the southwest at approximately 6 percent.

Vegetation. The forest vegetation was classified as an *Abies lasiocarpa/Xerophyllum tenax* habitat type (Pfister et al. 1977). The dominant overstory species was lodgepole pine. Understory vegetation was dominated by pinegrass, elk sedge, lupine (*Lupinus sulphureus*), beargrass (*Xerophyllum tenax*), and whortleberry.

Soils. Soils were classified as cryochrepts and cryothents (USDA Soil Conservation Service 1978). These soils are well drained gravelly sandy loam to silts of shallow to deep depth.

Climate. Climate data were derived from the closest recording weather station at Sula, Montana. Mean annual temperature and precipitation, based on an 11 year average from 1970-1980, was 5° C and 40 cm. Precipitation and mean temperature from April through August 1981 was 30 cm and 14° C, compared to 23 cm and 12° C for the 11 year average over the same period.

Past History. The study area was included in the Sleeping Child Fire of 1961. The lightning caused blaze consumed 28,000 acres on the Bitterroot National Forest. In 1962, 180 tons of a mixture of smooth brome (*Bromus inermis*), annual rye (*Secale cereale*), timothy (*Phleum pratense*), and dutch white clover (*Trifolium repens*) were

applied to the burned area for watershed protection (Lyon 1976).  
Chemical thinning of regeneration was conducted from 1966 through  
1969. The spacing study was established in 1967 by mechanical  
thinning of regeneration.

## Chapter 4

### METHODS AND PROCEDURES

The complete spacing experiment was replicated at five locations; four sites were in Montana and one was in Idaho. Sites were selected to represent varying productive capabilities and geographic locations.

#### Sampling

Each experimental site included a randomized complete-block of two replications of five treatments. Treatments consisted of thinning lodgepole pine to five spacing intervals: 1.8 by 1.8 m (260 trees/treatment plot), 2.7 by 2.7 m (176 trees/treatment plot), 3.6 by 3.6 m (114 trees/treatment plot), 4.5 by 4.5 m (98 trees/treatment plot), and 5.4 by 5.4 m (98 trees/treatment plot). Treatment plot dimensions from the narrowest to the widest spacing level were: 18 by 47 m, 22 by 60 m, 22 by 68 m, 32 by 64 m, and 37 by 77 m, respectively. Each experimental area covered 1.7 hectares.

Each site was sampled at approximately the time of peak standing crop. The sample schedule was based upon latitude, elevation, and accessibility. Sample dates were: Targhee site June 29-July 5, Kootenai site July 9-July 14, Lewis and Clark July 18-July 24, Gallatin site July 27-August 2, and Bitterroot site August 6-August 12.

Vegetative Sampling. To determine herbaceous and shrub species yield, 25 concentric circular quadrats of 0.45 and 0.90 m<sup>2</sup> were used. Yield quadrats were located systematically from a randomly selected starting point. Individual species yields from four harvested and 21 estimated quadrats were combined in double sampling. Regression analysis was performed to adjust estimates from non-harvested quadrats. Vegetative samples were oven-dried at 60° C for 24 hours and weighed to the nearest 0.1 g.

Understory herbage and shrub canopy cover, litter, moss, lichen, rock, and bare ground were estimated from 40 systematically located 2 by 5 dm quadrats along a line transect (Daubenmire 1959). To prevent overestimation of low coverage species, an additional cover class (0-1%) was used. Canopy cover estimates were: class 1 = 0-1 percent; class 2 = 2-5 percent; class 3 = 6-25 percent; class 4 = 26-50 percent; class 5 = 51-75 percent; class 6 = 76-95 percent; class 7 = 96-100 percent.

Tree basal area was derived from circumference measurements taken 1.5 m above the ground. Tree canopy was measured by the crown-diameter method as described by Mueller-Dombois and Ellenberg (1974). From each treatment plot, 12 estimates of tree canopy cover and basal area were made.

Crude protein analyses were performed on herbage and shrub.

samples collected August 2 from the Gallatin site and August 11 from the Bitterroot site. Three samples of a selected grass, forb, and shrub species along with a composite sample were collected from four treatment plots (1.8 by 1.8 m, 3.6 by 3.6m, 5.4 by 5.4 m, and control). Composite samples were provided by harvesting three 0.45 m<sup>2</sup> quadrats. Crude protein analyses were performed by the Montana State University Livestock Nutrition Center.

Measurement of physical characteristics. Limited soil temperature and soil moisture data were collected on the Gallatin site. Soil temperatures, using stem mercury thermometers, were recorded at a depth of 20 cm from 10 randomly selected sample points. Maximum temperatures were measured between 12 and 2 p.m.; minimum temperatures were recorded between 6 and 8 a.m.

Soil moisture determinations were made for samples collected at a depth of 25 cm from 10 randomly located sample points. Samples were weighed, oven-dried at 105° C for 24 hours, and percent moisture of each sample was determined. Water content at 15 atmospheres tension was determined by the pressure membrane method. Soil temperature and moisture data were collected July 27, August 16, and September 18.

#### Statistical Analyses

Analysis of variance and Duncan's New Multiple Range Test

(Duncan 1955) were used to compare understory vegetative canopy cover and yield, tree canopy cover and basal area, and vegetative crude protein content values among the five spacing treatments. Linear regression and correlation analyses were used to determine the relationship between understory vegetative canopy cover and yield (dependent variables) and tree canopy cover and basal area (independent variables). The term "significant" in the study means  $P \leq .05$ . Statistical procedures follows Steel and Torrie (1960).

## Chapter 5

### RESULTS AND DISCUSSION

A lodgepole pine spacing experiment was established by the USDA Forest and Range Experiment Station to investigate the effects of spacing on tree growth. The experiment also provided an opportunity to answer the question of what effects do varied tree spacing intervals have on understory vegetation. Therefore, the primary objective of the present research was to determine the response of understory vegetative canopy cover and yield to five spacing intervals of lodgepole pine. An additional objective was to examine the effects of light, soil moisture, precipitation, soil temperature, and litter accumulation on understory vegetation.

#### Response of Understory Vegetation to Varied Tree Spacing Intervals

To determine the response of understory vegetation to varied spacing intervals of lodgepole pine five study sites were examined. The sites differed in latitude, elevation, soil, and forest habitat type. To aid in the interpretation of the results of the study, the five sites were compared.

Comparison of study sites. Understory vegetation of the five sites was compared using Sorensen's index of similarity based on

species constancy values (Sorensen 1948). The similarity matrix revealed that no two sites were more than 50 percent similar to one another (Table 2). The Lewis and Clark site was 50 percent similar to the Targhee, Gallatin, and Bitterroot sites. The Kootenai was the least similar site. The dominant understory species constancy values are presented in Table 3.

Table 2. Indices of Stand Similarity (Numbers in Percent)

Sites	T	K	L&C	G	B
T	-	.34	.50	.40	.44
K		-	.25	.15	.18
L&C			-	.50	.50
G				-	.35
B					-

Although a habitat type supports a particular plant community at climax, it may also support a variety of disturbance induced seral communities (Daubenmire 1968). The four habitat types of the study were in various stages of succession. The predominant overstory species on each site was lodgepole pine, which is considered a major seral species in each habitat type except for the *Thuja plicata*/*Clintonia uniflora* type (Kootenai site) where it is considered a

Table 3. Percent Constancy of Dominant Understory Species on the Five Sites.

Species	T	K	L&C	G	B
<i>Calamagrostis canadensis</i>			25		
<i>Carex geyeri</i>	44	76	59	70	45
<i>Calamagrostis rubescens</i>	67	92	16		9
<i>Danthonia intermedia</i>	15				
<i>Poa pratensis</i>				53	
<i>Sitanion hystrix</i>				52	
<i>Trisetum spicatum</i>	19		18		
<i>Achillea millefolium</i>			10	27	7
<i>Agoseris glauca</i>			10		
<i>Anaphalis margaritacea</i>					12
<i>Antennaria racemosa</i>	46		12		
<i>Arnica cordifolia</i>	8		28	28	16
<i>Aster conspicuus</i>	13		42	61	
<i>Astragalus</i> sp.				26	
<i>Epilobium angustifolium</i>	15		43	23	10
<i>Fragaria glauca</i>		76			
<i>Fragaria virginiana</i>	24		18	30	
<i>Lupinus sericeus</i>	36		50	65	36
<i>Pentstemon gracilis</i>			19		
<i>Potentilla arguta</i>	24			30	
<i>Pyrola secunda</i>					12
<i>Senecio integerrimus</i>	18				
<i>Solidago multiradiata</i>				45	
<i>Trifolium pratense</i>		23			
<i>Xerophyllum tenax</i>					6
<i>Amelanchier alnifolia</i>		12			
<i>Arctostaphylos uva-ursi</i>	18	68			
<i>Rosa woodsii</i>		10			
<i>Spiraea betulifolia</i>	4		37		
<i>Vaccinium globulare</i>		38	30		
<i>Vaccinium scoparium</i>	16		36	12	36

minor seral species (Pfister et al. 1977). Barring any disturbance, lodgepole pine may be eventually replaced by more shade tolerant species such as Douglas-fir, redcedar, or subalpine fir.

While overstory succession generally moves towards more shade tolerant species, the accompanying change in understory vegetation may not be that evident (Table 4). Comparison of seral and climax understory vegetation showed similar dominant species in both communities. The seral communities did contain several dominant species, such as fireweed, showy aster, clover (*Trifolium pratense*), and goldenrod (*Solidago multiradiata*) which were not present in the climax forest. These species, as with lodgepole pine, may be disturbance dependent and may be eventually lost as the stand proceeds towards climax.

Although the five study sites differed in various aspects, the response of understory vegetation to varied tree spacings were relatively similar. The response of understory vegetation was considered in terms of both canopy cover and yield.

Understory vegetative yield. Understory yield of the study sites tended to decrease from wide to narrow tree spacings (Table 5). Statistical comparison of vegetative yield values among the varied spacings generally revealed significant differences only between wide and narrow spacings. Similar results were observed when tree

Table 4. Percent Canopy Cover of Dominant Understory Species Associated with Climax and Seral Communities.

Species	Habitat Type			
	PMSE/CARU Climax/Seral	ABLA/VASC Climax/Seral	ABLA/XETA Climax/Seral	THPL/CLUN Climax/Seral
<u>Grass</u>				
<i>Carex geyeri</i>	13 <sup>1</sup> /3	11/3	2/2	/2
<i>Calamagrostis rubescens</i>	45/4		5/2	/5
<u>Forb</u>				
<i>Arnica cordifolia</i>	16/	4/	6/2	12/
<i>Aster conspicuus</i>	/2	/5		
<i>Clintonia uniflora</i>				3/
<i>Coptis occidentalis</i>				11/
<i>Epilobium angustifolium</i>	/2	/2	/2	
<i>Fragaria glauca</i>				11/
<i>Lupinus sericeus</i>	/4	/6	/4	
<i>Solidago multiradiata</i>		/2		
<i>Thalictrum occidentale</i>	7/			
<i>Trifolium pratense</i>				/4
<i>Xerophyllum tenax</i>			20/2	
<u>Shrub</u>				
<i>Arctostaphylos uva-ursi</i>	11/2			/19
<i>Linnaea borealis</i>				4/
<i>Prunus virginiana</i>	16/			
<i>Spiraea betulifolia</i>	4/			
<i>Vaccinium globulare</i>				8/4
<i>Vaccinium Scoparium</i>	/2	/58	58/4	

<sup>1</sup> Climax canopy cover values from Pfister et al. (1977).

Table 5. Yield (kg/ha) of Understory Vegetation Among the Tree Spacing Intervals.

Sites	Tree Spacing Interval (m)					C
	5.4	4.5	3.6	2.7	1.8	
<u>Targ.</u>						
Grass	165a <sup>1</sup>	123a	73b	101ab	56b	-
Forb	163a	109a	129ab	80bc	51c	-
Shrub	35a	18a	65a	34a	26a	-
Total	363a	250a	267ab	215b	133c	-
<u>Koot.</u>						
Grass	245ab	375a	250ab	223b	243ab	-
Forb	147a	105a	171a	164a	114a	-
Shrub	444a	377a	440a	464a	295a	-
Total	836ab	857a	861a	851a	652b	-
<u>L&amp;C</u>						
Grass	374a	166b	83b	66c	47c	20c
Forb	257a	181bc	210ab	145c	76d	72d
Shrub	124ab	185ab	88a	79a	189b	166ab
Total	755a	532b	381bc	290c	312c	258c
<u>Gall.</u>						
Grass	335a	203b	106bc	134bc	74c	-
Forb	429bc	598a	506ab	370c	465bc	-
Shrub	2a	6a	34a	12a	5a	-
Total	766ab	807a	646bc	516c	544c	-
<u>Bitt.</u>						
Grass	136a	69b	56b	80b	69b	39c
Forb	335a	165b	115b	190b	113b	68b
Shrub	203ab	264a	82ab	80ab	110ab	51b
Total	674a	498ab	253bc	350b	292bc	158c

<sup>1</sup>Means in rows not followed by the same letter are significantly different at the .05 level.

canopy cover and basal area values were statistically compared (Appendix B). The range of the five spacing intervals, from 1.8 m to 5.4 m, may not have allowed sufficient variation of the overstory to cause significant differences of understory vegetation among the varied spacings.

Individual species responses to varied tree spacings may also partially explain the lack of significant difference of yield values among the spacings. Grass yield tended to decrease from wide to narrow spacings, while forb yield, depending on the species, either decreased, first increased then decreased, or remained relatively constant. Shrub yield responded somewhat independently of spacing. The overall outcome of species responses may have reduced the difference of yield values among the varied spacings. The response of individual species to varied tree spacings will be discussed later in the text.

Understory vegetative yield on the Kootenai site did not differ among the varied tree spacings except for a significant decrease under the 1.8 m spacing. The lack of response by understory vegetation may be attributed to the age of the stand. The Kootenai stand was established in 1971 by planting lodgepole seedlings at designated spacings (Figure 2). In contrast, the other four sites were established in 1965-67 by thinning 10-12 year old lodgepole pine regeneration to designated spacings (Figure 3). On the Kootenai,



Figure 2. The 5.4 m (above) and 1.8 m (below) Tree Spacing Plot on the Kootenai Site.



Figure 3. The 5.4 m (above) and 1.8 m (below) Tree Spacing Plot on the Lewis and Clark Site.

tree canopies had not yet thickened nor had root systems expanded sufficiently, at least under wide and intermediate spacings, to adversely affect understory vegetation. This is substantiated by statistically similar vegetative yield and canopy cover values reported for varied tree spacings.

Understory yield values on the Targhee study site were relatively low compared with the other sites. This may have been a reflection of an early sample data (June 29-July 5) or coarse texture of the soil. Cryopsamment soils have high infiltration rates but low water holding capacity (Stermitz et al. 1974). Soil moisture may then become unavailable for plant use early in the growing season.

Understory canopy cover. Understory canopy cover among the four similar sites generally decreased from wide to narrow tree spacings (Table 6). As with yield values, statistical comparison of canopy cover values among the varied spacings showed significant differences only between wide and narrow spacings. This may be attributed to the design of the study and/or to varied species responses to the overstory.

Species respond differently to various environmental gradients due to its own physiological and ecological tolerances (Whittaker 1970). The responses of dominant understory species to increasing tree canopy cover is presented in Table 7.

Pinegrass (*Calamagrostis rubescens*) and elk sedge (*Carex geyeri*),

Table 6. Percent Canopy Cover of Understory Vegetation Among the Tree Spacing Intervals.

Sites	Tree Spacing Interval (m)					
	5.4	4.5	3.6	2.7	1.8	C
<u>Targ.</u>						
Grass	14.8a <sup>1</sup>	9.9ab	6.9b	6.3b	4.3b	-
Forb	24.1a	14.0ab	23.3ab	14.4ab	7.5b	-
Shrub	2.2a	2.4a	8.3a	4.8a	1.5a	-
Total	41.1a	26.3b	38.5ab	25.5b	13.3c	-
<u>Koot.</u>						
Grass	8.5a	9.5a	7.7a	8.0a	6.9a	-
Forb	24.3ab	11.5b	19.3ab	28.5a	18.7ab	-
Shrub	25.3a	27.6a	28.5a	30.0a	23.1a	-
Total	58.1a	48.6a	55.5a	66.5a	48.7a	-
<u>L&amp;C</u>						
Grass	11.2a	8.3a	3.0b	3.2b	2.0b	1.2b
Forb	23.3a	17.7ab	20.3ab	16.2ab	12.5b	10.3b
Shrub	6.7a	10.6a	10.1a	13.6a	15.7a	13.5a
Total	41.2a	36.6ab	33.4ab	33.0ab	30.2ab	25.0b
<u>Gall.</u>						
Grass	11.0a	5.0ab	3.0b	3.0b	2.4b	-
Forb	22.0a	28.0a	27.7ab	26.0ab	27.0a	-
Shrub	0.5a	0.6a	2.3a	0.9a	0.4a	-
Total	33.5a	33.6a	33.0a	29.9a	29.8a	-
<u>Bitt.</u>						
Grass	5.0a	2.9b	2.3b	2.7b	2.7b	2.2b
Forb	12.1a	10.6ab	6.8ab	9.3ab	5.0ab	4.0b
Shrub	5.7a	4.2a	2.8a	2.9a	2.8a	2.6a
Total	22.8a	17.7ab	11.9ab	14.9ab	10.58b	8.8b

<sup>1</sup>Means in rows not followed by the same letter are significantly different at the .05 level.

Table 7. Percent Canopy Cover of Dominant Species Arranged in Order of Increasing Tree Canopy Cover

Species	Tree Canopy Cover (%)											
	10-30				30-50				50-70			
	T <sup>1</sup>	G	L&C	B	T	G	T&S	B	T	G	L&C	B
AGGL			2				+ <sup>2</sup>				+	
CACA			2				+				+	
CAGE	5	5	5	2	2	+	2	2	+	+	+	+
CARU	5			+	3			+	3			2
FRVI	2	3	2		2	2			+	+		
PEGR			4				+				+	
SEIN	3				+				+			
SIHY		2				+				+		
SOMU		4				2				2		
TRSP	2		2		+		+		+		+	
XETA				2				+				
ANRA	3				3				+			
AS.SP.		+				2				+		
EPAN	+	+	+	+	2	2	2	2	+	2	+	+
POAR	2				3				+			
SPBE			2				2				5	
ARCO	+	+	+	2	+	2	+	+	+	2	2	2
ARUV	+				2				+			
ASCO	+	3	3		2	5	5		+	5	3	
LUSE	3	4	6		6	9	6		5	7	3	
LUSU				4				4				2
VAGL			3				4				3	
VASC	+	+	3	5	4	+	5	3	+	+	5	3

<sup>1</sup>T = Targhee site, G = Gallatin site, L&C = Lewis and Clark site, and B = Bitterroot site.

<sup>2</sup>+ = less than 2 percent canopy cover.

although tolerant of semi-closed and closed canopies, were most abundant under more open canopies. Since both species are fairly drought tolerant (Sampson 1917) the decrease under closed canopies may have been due to reduced light intensity.

Lupine and showy aster were the dominant species under semi-closed and closed tree canopies. The dominance of these species may be related to their ability to quickly invade a disturbed area through producing an abundant supply of wind born seed (McLean 1968). The capability of a species to invade and hold space may limit establishment of later arriving species (Cavers and Harper 1967).

Fireweed and heartleaf arnica were most abundant under semi-closed and closed canopies. Fireweed has a fairly wide range of tolerance to light, moisture, and soil ph, but requires an abundant supply of nitrates for normal growth (Moss 1936). Brenchley and Heintze (1933) concluded competition with grasses was chiefly responsible for fireweed distribution. Grasses may be more efficient at absorbing nitrates thereby limiting the supply for fireweed. The ability of arnica to effectively use sunflecks, which commonly occur under dense tree canopy for photosynthesis, may explain its abundance under closed canopies (Young and Smith 1979).

Whortleberry (*Vaccinium scoparium*) was relatively abundant among the range of tree canopies. This suggests, as with lupine and aster, that whortleberry has a fairly wide ecological tolerance.

Percent bare ground, litter, moss, and lichen cover also showed a response to varied tree spacings (Table 8). Litter cover tended to increase from wide to narrow spacings while moss and lichen cover, and bare ground generally decreased.

The response of understory vegetation to varied tree spacing intervals in terms of quantity was significant. To determine if the tree spacings also affected the quality of understory vegetation crude protein content was measured.

Understory vegetative crude protein content. Crude protein content of selected species collected July 28 from the Gallatin site and August 15 from the Bitterroot site did not differ significantly among varied tree spacing intervals (Table 9). Composite samples, collected by clipping all species within three  $0.45 \text{ m}^2$  quadrats, differed significantly between the 5.4 m and 1.8 m tree spacing on both sites. This difference may simply reflect the dominance of *Lupinus sp.* found on narrow tree spacings. An average protein value of 18 percent has been reported for lupine growing on similar forested sites (Hammond 1980).

A higher protein level was noted for fireweed than for either bluegrass or elk sedge. This is to be expected as grasses experience a greater reduction in protein and phosphorus content over the growing season than do forbs (Cook and Harris 1950). Grouse whortleberry

Table 8. Percent Bare Ground, Litter, Moss, and Lichen Cover among the Tree Spacing Intervals.

Sites	Tree Spacing Interval (m)					
	5.4	4.5	3.6	2.7	1.8	C
<u>Targhee</u>						
Bare grd.	32	24	12	7	3	-
Litter	42	56	71	78	91	-
Moss-lich.	18	13	11	6	2	-
<u>Kootenai</u>						
Bare grd.	3	3	2	3	1	-
Litter	63	71	58	70	76	-
Moss-lich.	5	6	4	4	3	-
<u>Lewis-Clark</u>						
Bare grd.	32	27	21	20	4	3
Litter	54	49	63	65	85	90
Moss-lich.	10	17	11	12	6	3
<u>Gallatin</u>						
Bare grd.	48	43	41	29	12	-
Litter	43	48	44	63	76	-
Moss-lich.	6	2	4	3	3	-
<u>Bitterroot</u>						
Bare grd.	60	61	60	58	64	47
Litter	30	28	30	30	29	43
Moss-Lich.	4	5	3	5	3	2

Table 9. Percent Crude Protein of Selected Species Among the Tree Spacing Intervals.

Sites	Tree Spacing Interval (m)			
	5.4	3.6	1.8	C
<u>Gallatin Site</u>				
Cage	6.2a <sup>1</sup>	5.8a	6.0a	-
Popr	5.0a	6.0a	5.0a	-
Epan	13.8a	12.1a	12.5a	-
Composite	11.5a	13.5a	14.5b	-
<u>Bitterroot Site</u>				
Cage	5.3a	6.3a	7.6a	5.6a
Epan	11.3a	12.6a	11.6a	13.0a
Vasc	7.2a	7.3a	6.8a	7.0a
Composite	10.3a	12.2ab	14.3b	13.6ab

<sup>1</sup>Means in rows not followed by the same letter are significantly different at the .05 level.

revealed protein values midway between grasses and forbs.

Cook and Harris (1950) noted that differing soil moisture affected plant nutrients, particularly protein and phosphorous levels. They reported that a reduction in soil moisture may accelerate plant maturity, thereby influencing protein content. Similar soil moisture values between varied tree spacings reported in the present study may explain similarity of species protein content among the different species.

The relationship of tree canopy cover and understory vegetation have been described as both linear and curvilinear. Previous studies which described overstory/understory relationships as curvilinear were

conducted in mature unlogged forest (Pase 1958; Clary and Ffolliott 1966; Jameson 1967; Dodd et al. 1972). Studies which examined understory response to various thinning intensities have also described the relationship as linear (McConnell and Smith 1965; Grelan et al. 1971; Wolters 1973). Following thinning, roots and crowns of remaining trees eventually expand into the unoccupied area left by tree removal and the linear overstory/understory relationship gradually changes to curvilinear (Krueger 1981). In the present study the relationship between tree canopy cover and understory vegetation was determined using regression and correlation analyses.

Overstory/understory relationships. The correlation of tree canopy cover with understory yield and canopy cover revealed significant negative linear relationships among all sites except for the Kootenai (Figure 4). All correlation coefficients and coefficients of determination for each site are presented in Appendix C.

Overstory/understory relationships, across the range of tree spacings of 5.4 m to 1.8 m, were best described as linear. However, a curvilinear description of overstory/understory relationships may have been more appropriate if a wider range of spacings had been examined. Relations between two variables appear linear when viewed over a limited range but actually may be curvilinear when considered over a broader range (Steele and Torrie 1960).

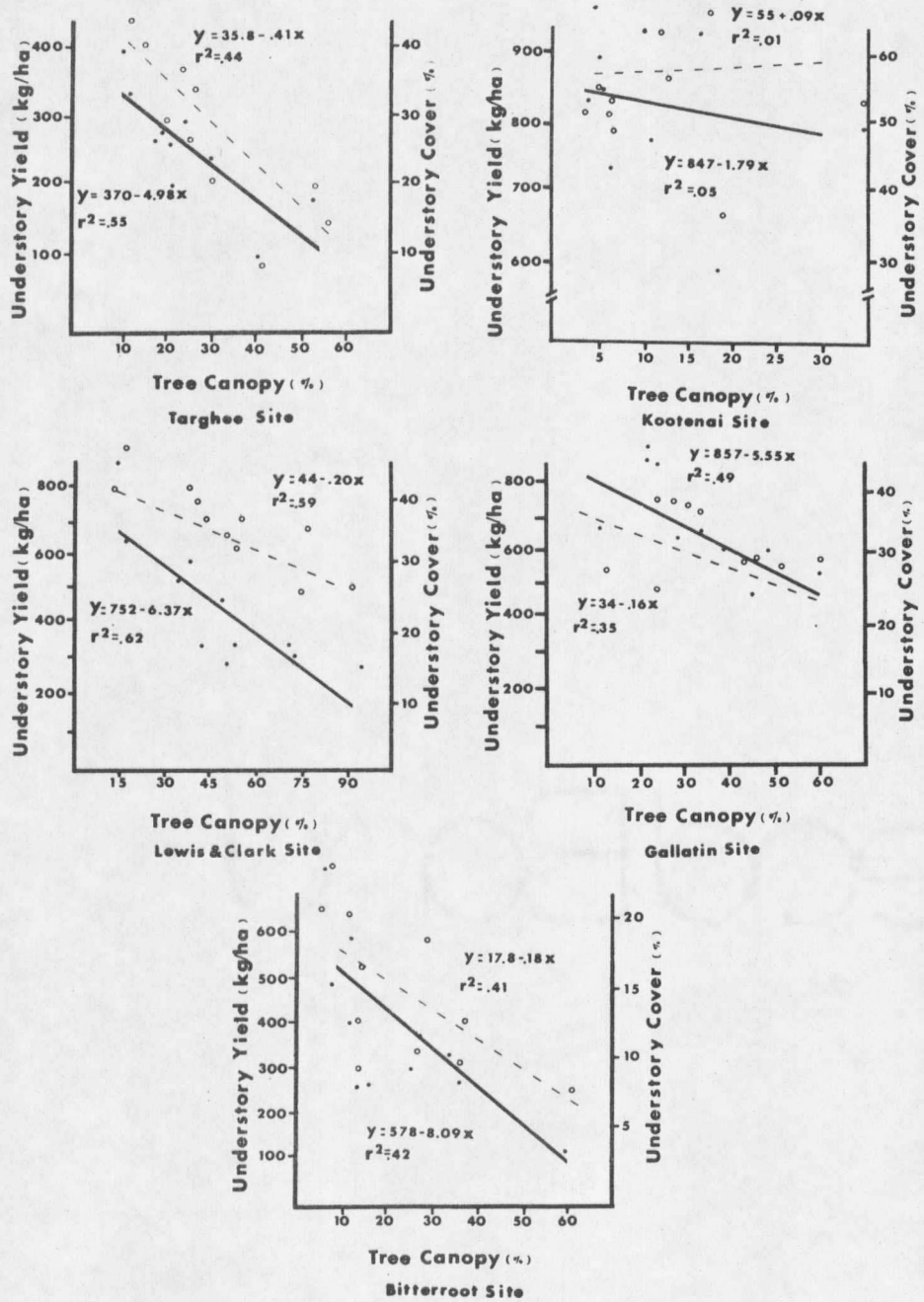


Figure 4. The Relationship of Tree Canopy Cover with Understory Vegetation Canopy Cover (---) and Yield (—).

Although the overstory/understory correlations presented in Figure 4 were significant, tree canopy cover generally accounted for less than 60 percent of the variation in understory yield and canopy cover across the sites. Tree canopy cover accounted for 5 and 1 percent of the variation in yield and canopy cover, respectively, on the Kootenai site, 49 and 35 percent on the Gallatin site, 41 and 42 percent on the Bitterroot site, 55 and 44 percent on the Targhee site, and 62 and 59 percent on the Lewis and Clark site.

The relatively weak coefficients of determination may be partially due to experimental design of the study. As previously suggested, the range of tree spacing intervals, from 1.8m to 5.4 m, may not have allowed sufficient variation in pine canopy and basal area to cause a significant response of understory vegetation. Krueger (1981) noted no significant relationships existed between pine canopy and understory vegetation when canopy coverage was restricted to a range between 20-50 percent. Stronger statistical correlations between tree canopy cover and understory vegetation may have resulted if a wider range of spacing intervals had been examined.

The responses of grasses, forbs, and shrubs to varied tree spacings differed among species and sites (Figure 5). As previously discussed, the varied species responses may possibly explain the relatively weak coefficients of determination.

Grass species showed a similar tendency among the sites to

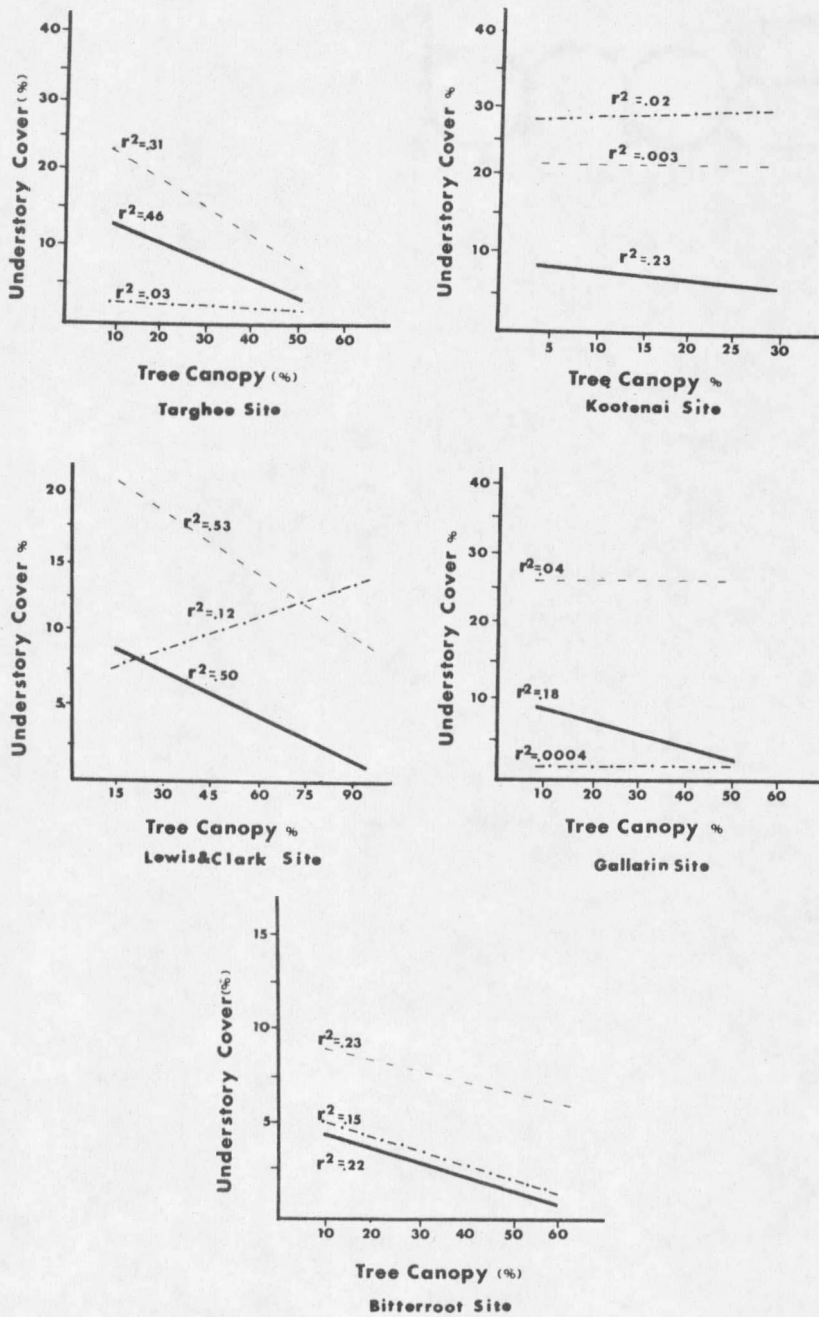


Figure 5. The Relationship of Tree Canopy Cover with Grass (—), Forb (----), and Shrub (-·-·) Canopy Cover.

decrease in yield and cover from wide to narrow tree spacings. The significant influence of tree canopy cover on grass abundance is indicated by the consistently high correlation coefficients. The correlation of tree canopy cover with grass canopy cover ranged from  $r = -.71$  at the Lewis and Clark site to  $r = -.43$  at the Gallatin site.

Grass canopy cover and yield not only decreased as tree canopy cover increased, but also comprised a smaller percentage of total understory vegetation. The decline of grasses may have been due to lowering of light intensity as overhead canopy thickened. Shading reduces the relative growth rate of grasses giving associated forbs and shrubs a competitive edge (Black 1957).

Because of less leaf area, compared to forbs or shrubs, grasses tend to produce more leaves at the expense of root development to maintain photosynthetic rates under reduced light (Blackman and Templeman 1938). This adaptive response along with increased tree root density under intermediate and narrow tree spacings may severely limit growth by restricting moisture and nutrient availability and uptake.

Forb canopy cover and yield among the sites also showed a tendency to decrease from wide to narrow tree spacings. The influence of tree canopy cover on forb abundance was less than with grasses as indicated by the lower and more variable correlation coefficients. The correlation of tree canopy cover with forb canopy cover ranged

from  $r = -.73$  at the Lewis and Clark site to  $r = .20$  at the Gallatin site.

The lower and more variable correlation coefficients were due to varied individual forb species responses to the spacing intervals. While the majority of forb species decreased from wide to narrow tree spacings, lupine (*Lupinus sericeus*), heartleaf arnica (*Arnica cordifolia*), fireweed (*Epilobium angustifolium*), and showy aster (*Aster conspicuus*) either increased, first increased then decreased, or remained fairly constant. The influence of these four dominant understory species on total forb as well as total vegetative response to varied tree spacings was quite significant.

In contrast to grasses, forbs tended to comprise a larger percentage of total understory vegetation as tree canopy cover increased. The dominance of forbs under semi-closed and closed canopies may be related to leaf characteristics of size, shape, thickness, and orientation which allow for more efficient use of low light intensity (Donald and Black 1958).

Shrub canopy cover and yield responded independently of tree spacings. The correlation of tree canopy cover with shrub canopy cover ranged from  $r = +.34$  at the Lewis and Clark site to  $r = -.39$  at the Bitterroot site.

Effect of Environmental Factors, as Modified by the  
Overstory, on Understory Vegetation

Overstory/understory correlations found in the study indirectly reflect relationships between understory vegetation and various environmental factors as modified by the overstory. Of these factors, light, soil moisture, temperature, and nutrients appear to be principle elements influencing understory herbage response (Moir 1966; Anderson et al. 1969); McLaughlin 1978). More precise interpretation of overstory/understory relationships would have been possible if direct measures of these environmental factors had been made. However, collection of soil moisture and temperature data was possible only on the Gallatin site.

Light. Light, as modified by tree canopy, may have been an important factor limiting understory vegetation particularly under the narrower tree spacings. Miller (1959) found that light intensity ranged from 5 percent of full sunlight under a lodgepole pine canopy cover of 70 percent to 75 percent under a canopy of 10 percent. Shirley (1945) pointed out that understory vegetation develops poorly under light intensities of less than 4 percent of full sunlight and if no other factors such as soil moisture are limiting, photosynthesis is directly proportional to an increase of light from 1 to 15 percent.

Low light intensity also increases plant susceptibility to

summer drought by stimulating top growth at the expense of root growth and leaf area development at the expense of strength and sturdiness (Shirley 1929).

The influence of light intensity on understory vegetation in the present study is suggested not only by the decrease of understory vegetation as tree canopy cover increased but also by the change in species composition. Grasses continually comprised a smaller percentage and forbs a larger percentage of total understory vegetation as tree canopy cover increased. Forbs are efficient at low light intensities because their horizontally exposed leaves enable them to achieve a full canopy of foliage and full exploitation of light, even at reduced intensities. In contrast, grass leaves are smaller and exposed at such angles and levels that a continuous cover of foliage is not formed.

Side-illumination is an important source of light for understory vegetation beneath an otherwise dense canopy cover (Anderson et al. 1969). Because of elevation and topography of the Gallatin site, side-illumination may have been responsible for the high understory yield values recorded under the narrower tree spacings.

Soil moisture. Soil moisture recorded during the period of July 25 to September 16 revealed similar soil moisture depletion rates for varied tree spacing intervals (Figure 6). Percent soil moisture measured July 25 ranged from 10 percent under the 1.8 m tree spacing.

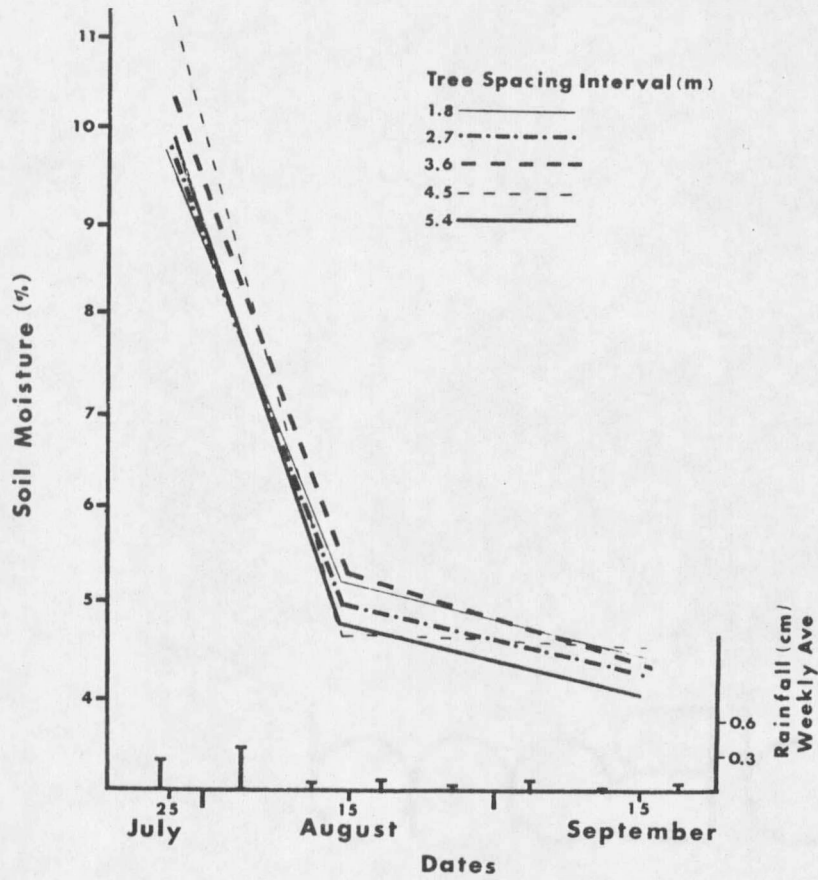


Figure 6. Percent Soil Moisture for Each Tree Spacing Treatment.

to 11 percent under the 4.5 m spacing. Soil moisture values for all spacings decreased to approximately 5 percent and then generally leveled off.

By late July soil moisture was below 15 bars at a depth of 25 cm on all tree spacing plots and remained below 15 bars well into September. Water held in the soil at greater than 15 bars is usually unavailable for plant use (Brady 1974). The fact that soil moisture near the surface reached 15 bars by late July may have limited the survival of shallow rooted species.

Following thinning of lodgepole pine, available soil moisture is increased until the remaining trees and understory vegetation reoccupy the site (Dahms 1971; 1973). In the present study similarity of soil moisture depletion rates for the varied tree spacing intervals suggest that abundant understory vegetation under wider tree spacings is as water demanding as trees under narrower spacings.

The heavy demand on soil moisture caused by understory vegetation under more open tree canopy may severely limit tree regeneration or restrict growth of existing trees. Barrett (1970) noted in a ponderosa pine thinning study that trees grew much more rapidly on plots where understory vegetation was removed compared to where vegetation was allowed to develop naturally.

Precipitation. Weather data from the closest recording station near the Gallatin site showed that over 60 percent of total

precipitation received during the growing season normally occurred in May and June (U.S. Dept. of Commerce, Weather Bureau. 1970-1980). Precipitation generally diminished in July and both July and August were fairly dry with only sporadic rainfall.

The Gallatin site during the summer of 1981 received a normal amount of precipitation based on an 11 year average. The limited soil moisture data collected did not reveal any significant increase in soil moisture content under wider tree spacings. This suggests that summer rainfall may not be especially effective in promoting soil moisture recharge and ultimately influencing vegetative growth. Summer growth may rely mostly on stored soil moisture provided by snowmelt and spring precipitation. Mueggler (1967) suggested precipitation during the period of most active growth may contribute more to total production than that which occurs at other times.

Lack of soil moisture recharge through summer precipitation under the narrower tree spacings may have been due to canopy and litter interception (Wilm and Dunford 1948; Goodell, 1952). Reynolds and Knight (1973) noted that lodgepole pine litter has a maximum water storage capacity of approximately 130 percent of its dry weight. This storage capacity must be satisfied before any infiltration of moisture into the mineral soil occurs. The influence of canopy and litter on rainfall interception may vary with storm intensity, duration, periodicity, and antecedent litter moisture (Ovington 1954; Reynolds

Knight, 1973).

Under wide tree spacings, lack of soil moisture recharge through summer precipitation may have been due to increased soil surface evaporation. High soil temperatures and bare ground percentages recorded under the wider spacings may have increased surface evaporative rates. Patten (1963) reported that due to increased isolation and soil temperature evaporation was 50 percent greater under open areas than occurred under relatively closed canopies of lodgepole pine.

No effort was made in the present study to assess the effects of varied tree spacings on snow interception or storage. It was assumed, however, that following snowmelt in the spring no significant difference in soil moisture content existed among the varied tree spacings. This assumption was based on the belief snowfall was adequate, at least on the five sites in the study, to replenish soil moisture regardless of tree spacing (U.S. Dept. of Commerce, Weather Bureau 1970-1980). The earliest soil moisture sample date of July 25 revealed similar moisture content between wide and narrow tree spacings which supports this assumption.

Soil temperature. Soil temperature recorded at a depth of 20 cm during the period of July 25 to September 16 revealed substantial differences between maximum temperatures recorded under varied tree spacing intervals (Figure 7). The highest maximum soil temperature

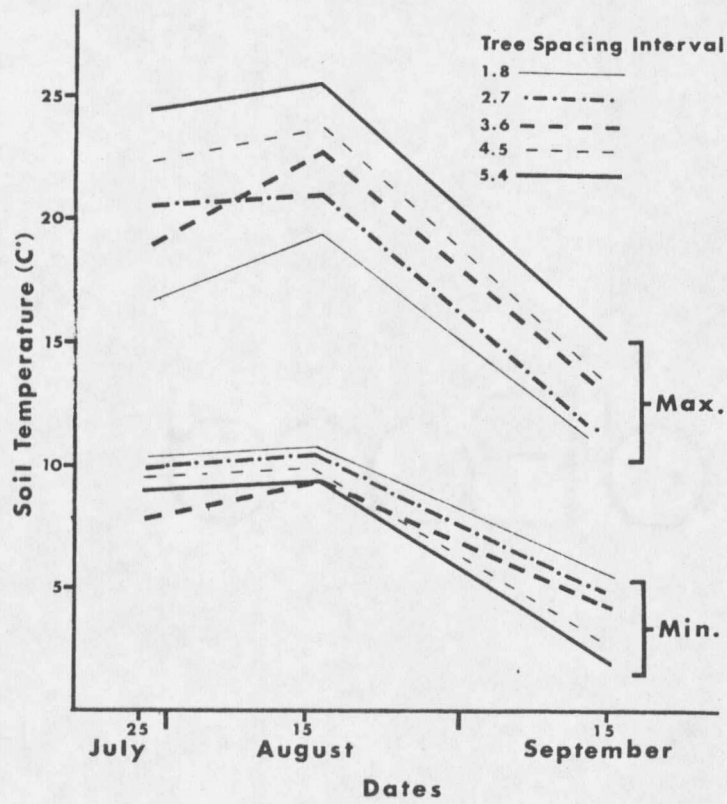


Figure 7. Maximum and Minimum Soil Temperature for Each Tree Spacing Treatment.

was recorded for the 5.4 m spacing following in decreasing order by the 4.5 m, 3.6 m, 2.7 m, and 1.8 m spacings.

Minimum temperatures recorded under varied tree spacings were much more closely grouped than were maximum readings. The 1.8 m tree spacing had the highest minimum temperature, followed in decreasing order by the 2.7 m, 3.6 m, 4.5 m, and 5.4 m spacing.

The greatest range between maximum and minimum temperatures occurred under the 5.4 m tree spacing, while the least difference was observed under the 1.8 m spacing. Soil temperatures under narrow tree spacings were cooler during the day and warmer at night compared to wider spacings where the reverse was observed.

Soil temperature may be effective in controlling seed germination. Daubenmire (1968) noted low soil temperature under forest canopies may limit germination of certain understory species. Higher and more variable soil temperatures under the more open canopies may be more suitable for species germination.

Litter accumulation. The gradual increase of litter cover as tree canopy cover increased may have had an adverse effect on understory vegetation, particularly under narrow spacings. As previously indicated, litter may intercept rainfall thereby reducing available soil moisture for herbage growth. Surface litter has a tendency to dry out quickly and allow dessication of developing seedlings before their radicles are able to reach available moisture

in mineral soil (Daubenmire 1968). Germinating seedlings may have difficulty in penetrating deep litter layers before food reserves are depleted (McConnell 1971).

Difficulty of germination and seedling establishment may partially explain why species capable of vegetative reproduction dominated under the narrower tree spacings. These species obviously have a competitive edge over species which reproduce entirely from seed. Litter accumulation may not only affect understory vegetative production, but may exert a strong influence on species composition.

#### Management Implication

Besides providing basic ecological information, the data in this study may have possible management implications. The influence of pine canopy cover on total understory vegetative yield varies with species. Pine canopy cover significantly reduced grass yield and to a lesser extent forb yield. Shrub species responded relatively independent of pine canopy. Varying responses of grasses, forbs, and shrubs may lessen the predictability of total understory vegetative yield at different thinning intensities, particularly if shrubs comprise a large percentage of the understory.

While exact response of understory vegetation to thinning was difficult to predict, generalizations, based on data from the present

study, may be made. Basile and Jensen (1971) reported understory vegetation reached peak production of 890-1120 kg/ha approximately 11 years after clearcutting lodgepole pine. Results from the present study indicate similar understory production values may be achieved approximately 30 years after clearcutting if immature stands are thinned to at least a 5.4 by 5.4 m spacing.

As revealed by the present study, thinning lodgepole pine to a 5.4 m spacing resulted 15 years later, in a significant increase of understory vegetative yield over stands which were unthinned or thinned to a 1.8 m spacing. Thinning to intermediate spacings of 4.5 m or 3.6 m, may or may not result in a significant yield increase. Grasses generally comprised a greater percentage of understory vegetation under wide and intermediate tree spacings than under narrow spacings. Forbs generally comprised a larger percentage of understory vegetation under intermediate and narrow tree spacings.

The significant correlation of pine canopy and basal area with understory vegetative yield may benefit management. Such relationships may allow gross field estimates of potential understory production in advance of varied thinning intensities. Such relationships may also provide quick estimates of understory yield based on tree canopy or basal area measurements.

Significant overstory/understory relationships may not hold true

for sites which were recently clearcut or planted, as on the Kootenai site. In these cases, the field moisture capacity of A and B soil horizons may serve as a better predictor of herbage yield (Basile and Jensen 1971).

The predictive equations presented in Table 10, although statistically significant, may have limited applicability. The equations need to be applied to areas of similar environmental conditions and tree stand characteristics as found on the study sites. The linear overstory/understory relationship expressed by the predictive equations apply to recently thinned stands of logdepole pine and therefore may not be representative of mature stands.

Table 10. Linear Regression Equations, Correlation Coefficients, and Coefficients of Determination of Understory Yield Related to Tree Factors.

Forest Habitat Type	Site	Equation	r	r <sup>2</sup>
ABLA/VASC	Gallatin	Y <sup>1</sup> = 857-5.55X	-.70*	.49
		Y = 796-15.81Z	-.68*	.46
ABLA/VASC	Lewis & Clark	Y = 752-6.37X	-.79**	.62
		Y = 708-21.15Z	-.82**	.67
PSME/CARU	Targhee	Y = 370-4.98X	-.74*	.55
		Y = 331-8.71Z	-.76*	.58
ABLE/XETE	Bitterroot	Y = 578-8.09X	-.65*	.42
		Y = 513-25.38Z	-.59*	.35
	Sites Combined	Y = 540-3.27X	-.36*	.13
		Y = 555-13.90Z	-.39*	.15

<sup>1</sup>Y = yield (kg/ha), X = tree canopy cover (%), Z = basal area (m<sup>2</sup>/ha).

\* Correlation coefficient significant at the .05 level.

\*\*Correlation coefficient significant at the .01 level.

## Chapter 6

### SUMMARY

In 1964 the USDA Forest and Range Experiment Station initiated a study to evaluate effects of spacing on growth of lodgepole pine (*Pinus contorta*). The study provided an opportunity to investigate modifications which occur in the understory environment as a result of overstory manipulation.

In 1981 research was conducted in conjunction with the previously established Forest Service study to determine the response of understory vegetation to varied spacing intervals of lodgepole pine. The primary objective was to measure and compare understory vegetation yield and canopy cover of five sites with five pine spacing intervals and ultimately determine overstory/understory relationships.

The complete spacing experiment was replicated at five sites, four were in Montana and one was in Idaho. Each experiment included a randomized complete-block of two replications of five treatments. Treatments consisted of thinning lodgepole pine to five spacing intervals: 1.8 by 1.8 m, 2.7 by 2.7 m, 3.6 by 3.6 m, 4.5 by 4.5 m, and 5.4 by 5.4 m.

To meet the objectives of the study, understory vegetative canopy cover, yield, tree canopy cover, and basal area data were collected among the varied tree spacing intervals. Additional information

collected included soil moisture, soil temperature, and understory species crude protein content with regard to the varied spacings.

The response of understory vegetation to varied spacing intervals of lodgepole pine was similar on Bitterroot, Gallatin, Targhee, and Lewis and Clark sites. From wide to narrow tree spacings understory vegetative yield and canopy cover, along with bare ground, moss, and lichen cover decreased while litter cover increased. The correlation of tree canopy cover with understory vegetative yield and canopy cover across the four sites revealed significant negative linear relationships.

Understory vegetative yield and canopy cover on the Kootenai site did not differ significantly among the varied tree spacings. The Kootenai stand was established in 1971 by planting of lodgepole pine seedlings at designated spacing intervals. Ten years later the roots and crowns of the planted trees had not yet expanded sufficiently, at least on intermediate and wide spacings, to adversely affect understory growth.

The responses of grasses, forbs, and shrubs to varied tree spacings differed among species and sites. Grass species tended to decrease in abundance from wide to narrow tree spacings, while forbs, depending on the species, either decreased, increased, or remained relatively constant. Shrub species appeared to respond somewhat independently

of tree spacing.

The correlation of tree canopy cover with grass yield and canopy cover across the sites generally revealed significant negative linear relationships. The correlation of tree canopy cover with forb and shrub canopy cover and yield generally revealed weaker and more variable relationships. Grasses tended to comprise a larger percentage of understory vegetation under wide and intermediate tree spacings than under narrow spacings. Forbs comprised a larger percentage of understory vegetation under intermediate and narrow spacings than under wide spacings.

Tree canopy cover had no influence on crude protein content of understory species. The crude protein content of selected grass, forb, and shrub species did not differ significantly among the varied tree spacings. Forb species contained the highest amount of protein followed by shrubs, then grasses.

Environmental factors altered by the overstory which may have affected understory vegetative response were reviewed. The following were considered significant in influencing understory vegetation:

- (a) Reduction of light intensity by tree canopy may have influenced understory vegetative production as well as species composition. Grasses comprised a small percentage and forbs a larger percentage of declining total understory vegetation as tree canopy cover increased.

- (b) Available soil moisture following thinning normally will increase. Surplus soil moisture allows understory vegetation to invade and occupy the space left by tree removal. Once established, abundant understory vegetation may reduce the initial increase of soil moisture created by thinning. The heavy demand on soil moisture by understory vegetation, particularly in the upper surface layers, may then limit tree regeneration.
- (c) Higher and more variable surface temperatures under open tree canopies may favor species germination. High temperatures may also increase surface evaporative rates and reduce moisture available for vegetative use.
- (d) Summer precipitation may not be especially significant in influencing understory growth. During the growing season the greatest amount of precipitation received by the study sites occurs in May and June. During July and August little precipitation is received, the majority of which is probably intercepted or lost through evaporation.
- (e) Excessive litter accumulation under semi-closed and closed tree canopies may influence understory vegetative production as well as species composition. Surface litter may limit soil moisture available for plant usage through

interception of throughfall precipitation. Surface litter may also restrict germination and development of seedlings. Species which reproduce vegetatively may have a competitive edge over species that reproduce entirely from seed.

Data provided by the study have possible management implications. The significant correlation of pine canopy and basal area with understory vegetation may provide gross estimates of yield in advance of varied thinning intensities. Quick estimates of understory vegetative yield based on tree canopy or basal area measurements may be made. Varying responses of grasses, forbs, and shrubs may lessen the predictability of total vegetative yield to different thinning intensities, particularly if shrubs comprise a large percentage of understory vegetation. The predictive equations presented in the study may have limited applicability.

APPENDIX

APPENDIX TABLE A. List of Plant Species Recorded on the Study Sites.

Scientific Name	Code	Study Sites				
		K	T	B	G	L&C
<u>Grass Species</u>						
<i>Agropyron trachycaulum</i> (Link)	AGTR				x	x
<i>agrostis scabra</i> Willd.	AGSC	x	x		x	x
<i>Bromus inermis</i> Nees.	BRMA		x	x		
<i>Calamagrostis canadensis</i> (Michx.) Beau.	CACA					x
<i>Calamagrostis rubescens</i> Buckl.	CARU	x	x	x	x	x
<i>Carex filifolia</i> Nutt.	CAFI	x				
<i>Carex geyseri</i> Boot.	CAGE	x	x	x	x	x
<i>Dactylis glomerata</i> L.	DAGL			x		
<i>Danthonia intermedia</i> Vasey	DAIN		x		x	x
<i>Festuca idahoensis</i> Elmer.	FEID			x	x	x
<i>Phleum pratense</i> L.	PHPR	x		x		x
<i>Poa nervosa</i> (Hook.) Vasey.	PONE		x			
<i>Poa pratensis</i> L.	POPR	x			x	x
<i>Sitanion hystrix</i> (Nutt.) J.G.Smith	SIHY		x		x	
<i>Stipa columbiana</i> Macoun.	STCO		x		x	x
<i>Trisetum spicatum</i> (L) Richt.	TRSP		x	x	x	x
<u>Forb Species</u>						
<i>Achillea millefolium</i> (L.)	ACMI	x	x	x	x	x
<i>Agoseris glauca</i> (Pursh) Raf.	AGGL		x		x	x
<i>Anaphalis margaritacea</i> (L.) B. & H.	ANMA			x		
<i>Antennaria luzuloides</i> T. & G.	ANLU				x	
<i>Antennaria racemosa</i> Hook.	ANRA	x	x	x	x	x
<i>Arnica cordifolia</i> Hook.	ARCO		x	x	x	x
<i>Aster conspicuus</i> Lindl.	ASCO	x	x		x	x
<i>Astragalus</i> sp. L.	AS SP				y	
<i>Campanula rotundifolia</i> L.	CARO	x	x		x	x
<i>Castilleja miniata</i> Dougl.	CAMI				x	
<i>Epilobium angustifolium</i> L.	EPAN	x	x	x	x	x
<i>Fragaria glauca</i> Wats.	FRGL	x				
<i>Fragaria virginiana</i> Duchesne	FRVI		x	x	x	x
<i>Gentiana amarella</i> L.	GEOM	x				
<i>Geranium viscosissimum</i> Fish. & Mey.	GEVI				x	
<i>Lupinus sericeus</i> Pursh	LUSE	x	x	x	x	x
<i>Lupinus sulphureus</i> Dougl.	LUPA			x		
<i>Pentstemon gracilis</i> Nutt.	PEGR	x	x			x
<i>Potentilla arguta</i> Pursh.	POAR		x		x	x
<i>Pyrola secunda</i> L.	PYSE	x	x	x	x	x
<i>Sedum lanceolatum</i> Torr.	SELA				x	
<i>Senecio canus</i> Hook.	SECA		x		x	
<i>Senecio integerrimus</i> Nutt.	SETN		x		x	x
<i>Solidago multiradiata</i> Ait.	SOMU		x		x	
<i>Taraxacum officinale</i> Weber.	TAOF		x	x	x	x
<i>Trifolium pratense</i> L.	TRPR	x				x
<i>Viola nuttallii</i> Pursh.	VINU		x		x	x
<i>Xerophyllum tenax</i> (Pursh) Nutt.	XETE			x		
<u>Shrub Species</u>						
<i>Amelanchier alnifolia</i> Nutt.	AMAL	x				
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	ARUV	x	x			
<i>Berberis repens</i> Lindl.	BERE	x				x
<i>Rosa woodsii</i> Lindl.	ROWO	x				x
<i>Spiraea betulifolia</i> Pall.	SPBE	x	x		x	x
<i>Symphoricarpos occidentalis</i> Hook.	SYOC	x				
<i>Vaccinium globulare</i> Rydb.	VAGL	x		x		x
<i>Vaccinium scoparium</i> Leiberger.	VASC	x	x	x	x	x
<u>Tree Species</u>						
<i>Pinus contorta</i> Dougl.	PICO	x	x	x	x	x

APPENDIX TABLE B. Percent Tree Canopy Cover and Basal Area ( $m^2/ha$ )  
Among the Tree Spacing Intervals

Sites	Tree Spacing Interval (m)					C
	5.4	4.5	3.6	2.7	1.8	
<u>Targ.</u>						
Cover	13a <sup>1/</sup>	17ab	24b	29b	52c	-
B.A.	3.9a	5.5a	7.3a	9.9a	23.4b	-
<u>Koot.</u>						
Cover	5a	5a	8a	11a	31b	-
B.A.	1.1a	1.4a	2.1a	2.8ab	4.2b	-
<u>L&amp;C</u>						
Cover	18a	42ab	44ab	61b	62b	93c
B.A.	3.9a	8.1ab	10.2b	15.1c	21.9d	23.3d
<u>Gall.</u>						
Cover	18a	26ab	33ab	42ab	60c	-
B.A.	3.1a	5.2ab	6.5b	9.8c	18.7d	-
<u>Bitt.</u>						
Cover	9a	14ab	16ab	29bc	36c	60d
B.A.	1.7a	2.6ab	2.4ab	5.2ab	8.2b	16.3c

<sup>1</sup>Means in rows not followed by the same letter are significantly different at the .05 level.

APPENDIX TABLE C. Simple Correlation Coefficients and Coefficients of Overstory Variables With Understory Vegetation.

Site	Tree Cover <sub>1</sub>		Basal Area <sub>2</sub>	
	r	r <sup>2</sup>	r	r <sup>2</sup>
<u>Targ.</u>				
Grass Yield	-.76*	.58		
Forb Yield	-.70*	.49		
Shrub Yield	-.05	.003		
Total Yield	-.74*	.55	-.76*	.58
Grass Cover	-.68*	.46		
Forb Cover	-.56	.31		
Shrub Cover	-.17	.03		
Total Cover	-.66*	.44	.68*	.46
<u>Koot.</u>				
Grass Yield	-.15			
Forb Yield	-.05			
Shrub Yield	-.35			
Total Yield	-.22	.05	-.16	.03
Grass Cover	-.48			
Forb Cover	+.05			
Shrub Cover	+.14			
Total Cover	+.11	.01	+.07	.005
<u>L&amp;C</u>				
Grass Yield	-.81**	.66		
Forb Yield	-.79**	.62		
Shrub Yield	+.23	.05		
Total Yield	-.79**	.62	-.82 **	.67
Grass Cover	-.71**	.50		
Forb Cover	-.73**	.53		
Shrub Cover	+.34	.12		
Total Cover	-.77**	.59	-.65*	.42
<u>Gall.</u>				
Grass Yield	-.65*	.42		
Forb Yield	-.18	.03		
Shrub Yield	-.08	.006		
Total Yield	-.70*	.49	-.68*	.46
Grass Cover	-.43	.18		
Forb Cover	+.20	.04		
Shrub Cover	-.02	.0004		
Total Cover	-.59	.35	-.20	.04
<u>Bitt.</u>				
Grass Yield	-.53	.28		
Forb Yield	-.54	.29		
Shrub Yield	-.51	.26		
Total Yield	-.65*	.42	-.59	.35
Grass Cover	-.47	.22		
Forb Cover	-.48	.23		
Shrub Cover	-.39	.15		
Total Cover	-.64*	.41	-.61*	.37

\* Correlation coefficient significant at the .05 level.

\*\*Correlation coefficient significant at the .01 level.

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