INFLUENCES OF SNOW PERSISTENCE ON SUBALPINE FOREST REGENERATION IN SMALL GAPS, COLORADO FRONT RANGE

by

Christopher Daly[1]

INTRODUCTION

Areas that experience appreciable snow accumulation are characterized by a wide range of vegetational communities that are often related to the depth and duration of snowcover. A deep, continuous cover during winter provides protection from the rigors of the non-snowpack environment (i.e. desiccation and temperature and radiation extremes), but exerts physical pressure on vegetation (Shaw, 1909; Sakai, 1970; Lindsay, 1971). In spring and summer, snow persistence can influence growth by controlling the timing of soil temperature increase and soil moisture decrease, the duration and severity of light attenuation under the pack, and the likelihood of infection by snow fungi (Geiger, 1965; Wardle, 1968; Tranquillini, 1979). Responses of vegetation to these snow-related factors help determine community structure by favoring the establishment and survival of some species over others.

Relationships between tree seedling establishment and the duration of snowcover are not well-documented. Griggs (1938), Wardle (1968) and Billings (1969) reported some of the effects of snowcover, but did not perform intensive, quantitative investigations. Dix and Richards (1976) addressed the possible effects of snow augmentation on spruce-fir forests in southwestern Colorado, but relied on low-resolution, small-scale data. Major contributions to the understanding of the physical responses of tree seedlings to snowcover were made by Tranquillini (1979), but were not directly related to the success of seedling establishment. Ronco (1970), Noble and Alexander (1977), and Alexander (1983) conducted experiments to assess the influences of factors indirectly related to snow persistence (i.e. drought and solar radiation) on the seedling establishment of Engelmann spruce.

Objectives

The purpose of this investigation is to provide a preliminary assessment of the possible impacts of snow persistence on the regeneration of Engelmann spruce (*Picea engelmannii* (Parry) Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) on the eastern slope of the Colorado Front Range. This study is the first part of a long-term investigation of forest dynamics in the Front Range. The results of this preliminary study will be used to determine whether the influences of snowcover on forest regeneration should be pursued, and if so, what direction future research should follow.

The focus of this study is on small gaps within the contiguous subalpine forest, where variations in direct solar radiation exposure (e.g. sunny gap borders vs. shady gap borders) produce distinct patterns of snow persistence over small areas. Initial observations did not reveal any clear-cut patterns of spruce or fir regeneration within small gaps. Therefore, the null hypothesis to be tested is:

> Variation in snow persistence within small gaps is not a major influence on the seedling establishment patterns of Engelmann spruce and subalpine fir.

Seedling density is considered to be an indicator of germination and establishment success. Only seedlings at least a year old were included in the analysis; cotyledons that may become established during the first year do not normally appear until August in these forests, and were not yet visible during data collection in

---

Presented at the Western Snow Conference, April 17-19, 1984, Sun Valley, Idaho.

[1] Department of Geography, University of Colorado, Boulder, Colorado.

July. Vulnerability to environmental stress is greatest during the establishment stage (Dix and Richards, 1976; Spurr and Barnes, 1980). According to Noble and Ronco (1978), mortality rates of spruce and fir are fives times higher during the first year than the following six years combined.

Recent increases in the silvicultural management intensity of Engelmann spruce have prompted research directed at isolating the variables that influence seedling establishment and survival (e.g. Alexander, 1969; Ronco, 1970; Noble and Alexander, 1977), and determining cutting methods that optimize these variables (Alexander, 1974; 1977; 1983). Alexander (1977; 1983) recommended cutting openings of 1-2 ha, 5-6 tree heights wide, for an optimum combination of seed dispersal, snow retention, radiation exposure, wildlife food supply, and economy. Clear cuts on southerly aspects were discouraged because of excessive radiation exposure, which can lead to premature drought and solarization damage. Subalpine fir has been of little commercial value and has been largely ignored in silvicultural investigations. The present study examines the effects of small openings up to 2 tree heights wide on snow persistence and regeneration patterns of both Engelmann spruce and subalpine fir.

DESCRIPTION OF STUDY AREA

The Front Range is the easternmost range of the Rocky Mountain chain, and extends northward from the Arkansas River area in southern Colorado to the Medicine Bow and Laramie Mountains in southeastern Wyoming (Marr, 1961). The crest of the Front Range forms the Continental Divide in northern Colorado. The two study sites (Site 1 and Site 2) are located in the subalpine forest (Marr, 1961), 5-6 km east of the Continental Divide and about 25 km west of Boulder.

Site 1 is located at an elevation of 3170 m, 2.5 km west of the University of Colorado Mountain Research Station. The site is on the southeastern flank of Niwot Ridge, a prominant glacial interfluve. The forest at Site 1 is co-dominated by Engelmann spruce and subalpine fir. Lodgepole pine (*Pinus contorta* Dougl.) also occurs in substantial numbers, usually in the larger size classes. An occasional dead or dying limber pine (*Pinus flexilis* James) can also be found. Soils are thin and rocky, with only a thin layer of litter. Most are well-drained sandy loams (Marr, 1961).

The 15 gaps studied here range from 22 to 75 m^2 in area, with a mean of 58 m^2 (tree bole-to-tree bole) and are on slopes of 0 to 15^o with southern to eastern exposures. Some show evidence of logging, but most appear to have been created by windthrow. The gaps are adjacent to a 36 x 54 m (0.19 ha) permanent plot established by Dr. Thomas Veblen in 1982. Descriptive statistics from this plot show subalpine fir dominating the seedling and sapling classes (< 4 cm dbh), Engelmann spruce predominating in the small and intermediate tree sizes (4-25 cm dbh), and lodgepole pine dominating (and largely restricted to) the large tree population (> 26 cm dbh). Understory cover averages 10-25 percent and usually consists of the shrub *Vaccinium myrtillus* L. (Veblen, personal communication). Lodgepole pine is typically replaced by spruce-fir in this area (Peet, 1981) and shows only limited regeneration.

Site 2 is located 0.6 km southwest of Brainard Lake, just inside the Indian Peaks Wilderness Area and about 4.3 km northwest of Site 1. The site is at an elevation of 3220 m, near the top of a small ridge on the northern flank of Niwot Ridge. The forest at Site 2 is co-dominated by Engelmann spruce and subalpine fir. The forest floor is extensively covered by broken and upturned logs, possibly toppled by strong westerly winds. Soils are well-drained sandy loams and have a much thicker layer of humus than those at Site 1 (Marr, 1961). The incidence of rocky outcrops is very low in comparison to Site 1.

The 9 gaps studied at Site 2 range from 32 to 204 m^2, but most are less than 60 m^2 and the mean area is 49 m^2. Exposures are generally northerly, and vary from west-northwesterly to east-northeasterly. Slopes are gentle, and all are less than 10^o. Most gaps were apparently created by windthrow; six cut stumps were found, but cutting did not contribute greatly to the formation of the gaps. These gaps are also near a permanent 36 x 54 m plot established in 1982 by Dr. Thomas Veblen. Subalpine fir is more numerous than Engelmann spruce in all but the largest size class (> 35 cm dbh). Understory coverage averages 20 to 30 percent, with *Vaccinium myrtillus* L.

predominating. A long period of time has apparently passed since a major disturbance here, allowing the forest to become dense in places. Light levels at the forest floor are consequently relatively low. Spruce seedlings prefer partial shade (Ronco, 1970), but fir appears to have greater reproductive success in the shade (Peet, 1981).

Climate

The climate of the subalpine zone east of the Continental Divide is highly continental, characterized by extreme weather changes from hour to hour as well as season to season (Marr, 1961). Summers are cool and short, and convective precipitation occurs almost daily. Winters are cold, dry and windy; strong westerly winds cause appreciable blowing and drifting snow in exposed areas. Spring is the wettest season, and heavy snows in April and May are common. Weather observations have been taken at climate station C-1, 120 m lower and 1.7 km east of Site 1, since 1952. Meteorological statistics for C-1 compiled by Barry (1973) provide a useful climatic summary.

Since 1955, snow depth and water content for December through May have been measured along the University Camp snow course, at the same elevation, but 2.2 km southwest of climate station C-1. These measurements indicate that maximum depth usually occurs at the end of March or early April, and is on the order of 1.4 m. Water storage in the pack does not reach a maximum until late April or early May, when it averages about 47 cm (Platt; personal communication). Records from a nearby United States Soil Conservation Service Snotel, in operation since 1979, indicate that snow disappeared by 1 July in all years (United States Soil Conservation Service; unpublished data). However, snow persists longer at Site 1 and Site 2, because of cooler temperatures and higher precipitation at higher elevations (Barry, 1973).

METHODOLOGY

Gap Demarcation and Snow Persistence Measurements

At each site, gaps were selected by establishing a transect approximately 0.3 km long along a constant compass direction. Gaps visible from the transect were considered for study. The forests had many small openings and irregularities, making the demarcation of individual gaps difficult. A number of gaps had discontinuous perimeters. Specific size criteria were not used in the selection process, but gaps had to be large enough to possess marked differences in direct solar radiation exposure (Dietrich and Meiman, 1974; Gary, 1974b) and small enough to avoid snow redistribution by wind (Gary, 1974c). Openings that were smaller than about 5 m in diameter did not have distinct sunny and shady sides because of continuous shading by surrounding trees; gaps larger than about 25 m in diameter were large enough to allow snow drifting by wind. Selections were made in the early spring, when at least 1 m of snow remained on the ground. This was done to avoid choosing gaps on the basis of preconceived seedling distribution patterns. Gap shapes varied widely, but were considered to approximate ellipses for the sake of consistency. Intermediate or main canopy trees nearest to the ends of the major and minor axes were tagged.

Observations of snow persistence were made weekly at 1-m intervals along the major and minor axes during the 1983 melt period (Figure 1). Observations began at a given site with the appearance of bare ground, and ended when all snow had disappeared. The measurement period at Site 1 ran from 15 June to 13 July 1983, for a total of five observations. Records at Site 2 started on 22 June and ended on 20 July 1983, also five observations. Measurements along the major and minor axes are representative of only small portions of a gap, and sizable snow patches can be missed, so wide-angle photographs of snow patches were taken to supplement the records. Gaps were mapped during the summer, after all snow had disappeared. The main purpose of mapping was to provide baseline data in small gaps for a long-term study of forest dynamics. A rectangular grid was laid out in the field to include a gap and surrounding trees, and all tree species were mapped. Seedlings were defined as any individuals less than 1.3 m in height. Two gaps selected at Site 1 were found to be unsuitable for analyses involving seedlings. One was situated on an abandoned logging road, and supported little regeneration because of soil compaction. In the other, a thick cover of the grass Poa nervosa apparently restricted tree seedlings to higher ground, namely around tree bases, distorting their potential response to snow persistence.

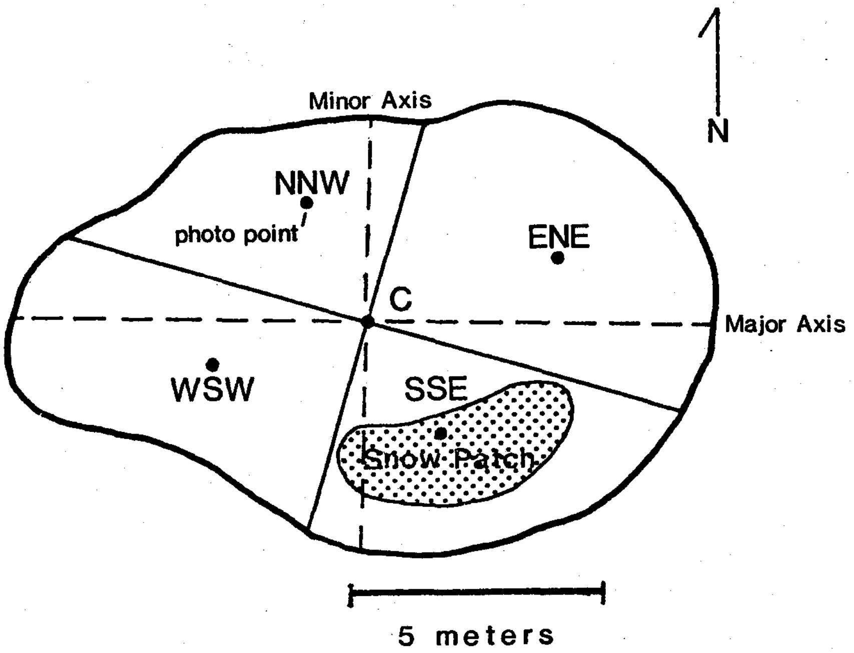

Figure 1: A typical gap with major and minor axes. The four sections are based on snow persistence observations. There are five photograph points, one in the center and one inside each of the sections.

Direct Solar Radiation

Direct solar radiation within the gaps was assessed by hemispherical photography. Instantaneous radiation measuring devices were not appropriate, given the large number of locations to be considered and the need to assess direct radiation regimes over a period of months (Anderson, 1964). An 8-mm Nikon lens, giving equidistant coverage of 180°, was used with a Nikon 35-mm camera body. Photographs were taken from a standing position and were oriented with a compass so that geographic north was always at the top of the picture. Leveling was accomplished by observing a plumb bob attached to the camera body.

The photographs were not taken until the fall, so snow persistence maps constructed during the summer were used to help locate the photograph points. The center of each gap was found on the maps, and the average position of latest snow persistence determined. The quarter of the gap containing this position was considered to be the shadiest. The quarter of the gap opposite the shady portion was considered the sunniest. The remaining two quarters were thought to be exposed to moderate amounts of direct radiation. Photographs were taken at the center of the gap and inside each of the four quarters, for a total of five photos in each gap (Figure 1). The dates of snow disappearance at these five points were used to characterize snow persistence in the five gap positions (see Table 1). Kodak Plus-X panchromatic negative film (ASA 100) was exposed and developed for maximum contrast. The negatives were cut and mounted in plastic slide holders. When projected, the sky looked dark grey or black and the trees appeared white or light grey.

The shady and sunny sides of the gaps did not correspond to the southern and northern sides, respectively, as might be expected. Instead, the directions were shifted counterclockwise 30° (Figure 1). The shady direction was south-southeast (150°) rather than south (180°), and the sunny direction was north-northwest (330°) rather than north (360°). It is suspected that this discrepancy was caused by typically cloudy afternoons during the months of June and July. Solar radiation was more likely to be attenuated by clouds after the noon hour, causing less melt on southwesterly exposures than southeasterly exposures (Olyphant, 1983). Therefore, persistence in a gap was greatest in areas a little east of south, where snow was shaded from the morning sun.

Sun track diagrams for 40° north latitude (List, 1951) were placed over the projections described above to determine the position of the sun in relation to the forest canopy for any month of the year. Spring and summer were the seasons in which solar radiation was of interest, so sun tracks for March through August were used. Sun tracks for July are similar to June's, and tracks for August are similar to May's, so the months of March through August could be lumped into March, April, May/August, and June/July. The average duration of direct radiation for each month was determined by assessing the percentage of unobstructed sky visible along each sun track.

A computer program was written to calculate hourly and daily radiation totals for each of the months considered. Instead of attempting to calculate absolute energy, energy was expressed as a fraction of the energy that would reach the ground if the sun was at the summer solstice (June 22), the sky unobstructed by foliage or clouds, and the ground level. Details on this program are available from Daly (1984).

RESULTS AND DISCUSSION

Descriptive Statistics

On the average, snow persisted through the last week of June at Site 1 and into the second week of July at Site 2 in 1983 (Table 1). Snow lasted longest in the SSE (south-southeasterly) gap position at both sites. The average difference between the NNW (sunny) and SSE (shady) positions is nearly two weeks at Site 1, but only one week at Site 2. This may be due to two factors: 1) snow persisted longer into July at Site 2, the warmest month of the year, so when snow finally began to disappear, it did so quickly because of higher melt rates; and 2) differences in direct radiation between NNW and SSE positions are lower at Site 2, resulting in less difference in melt rate. In the months of March through August, daily direct radiation at Site 2 averages about half that of Site 1. Site 1 radiation for June/July ranges from 0.4 of the summer solstice maximum in the central and NNW postions, to about 0.2 in the SSE. Site 2 radiation is much less, ranging from 0.3 in the NNW to 0.156 in the SSE. The radiation discrepancies are partially explained by the fact that Site 2 gaps are on southerly exposures and average gap size is larger.

Table 1: Descriptive statistics for gaps used in the analysis. Snow persistence is given in weeks after 1 June and represents the date of snow disappearance at the hemispherical photograph point in a given gap position. Daily radiation is a decimal part of the hypothetical summer solstice radiation, and seedling density is seedlings/m^2 in each gap section; all are expressed as means.

gap	snow	direct solar radiation				seedling density	
position	persistence	March	April	May/Aug	Jun/Jul	fir	spruce
SITE 1							
No. of gaps	15	15	15	15	15	13	13
C	4.1	0.154	0.243	0.353	0.445	*	*
NNW	3.4	0.191	0.291	0.391	0.445	0.237	0.172
ENE	3.8	0.133	0.215	0.339	0.399	0.249	0.129
SSE	5.3	0.115	0.133	0.197	0.233	0.548	0.115
WSW	4.0	0.135	0.213	0.316	0.381	0.316	0.142
SITE 2							
No. of gaps	9	9	9	9	9	9	9
C	5.7	0.078	0.118	0.173	0.223	*	*
NNW	4.9	0.080	0.128	0.210	0.300	0.694	0.073
ENE	5.5	0.078	0.116	0.187	0.249	0.667	0.109
SSE	6.0	0.048	0.090	0.127	0.156	1.000	0.089
WSW	5.3	0.058	0.097	0.128	0.178	0.696	0.248

* The center position represents only a point in a gap, not an area, so seedling density cannot be calculated.

Subalpine fir seedling densities at Site 2 are double that at Site 1, while Engelmann spruce densities vary minimally. Fir seedlings outnumber spruce by almost six-to-one at Site 2, reflecting fir's relatively high regeneration rates. At both sites, fir seedling density is highest in the SSE gap position and lowest in the NNE position. Spruce seedling density does not show any discernible patterns.

Snow Persistence and Direct Radiation vs. Gap Position

Statistical analysis is restricted to the Kruskal-Wallis one-way analysis of variance by ranks and the Kendall correlation by ranks, both of which are nonparametric (Nie *et al.*, 1975; Hull and Nie, 1981). Direct solar radiation varies significantly with position within a gap at the 0.05 level for all months tested (March - August) at Site 1, and all months except April at Site 2 ($p = 0.575$). Sun tracks during April fall below the level of the crowns of trees surrounding many Site 2 gaps, so that direct radiation varies more randomly with position. This effect is minimized at Site 1, where gaps are larger and the forest more open. The reason why March radiation varies significantly at Site 2 and April does not may be due in part to the presence of a forest 'clear story' that allows some direct light to penetrate the canopy at low zenith angles. Forest trees often have few branches below the main canopy, a result of self-pruning and die-back caused by low light levels (Baig, 1972).

Snow persistence correlates strongly with direct solar radiation for March - August at Site 1, affirming that exposure to direct sunlight during the spring and summer is an important factor in the rate of snow melt (e.g. $t = -0.5363$; $p = 0.001$ for June/July radiation vs. snow persistence). Negative correlation coefficients indicate decreased snow persistence as radiation exposure increases. Site 2 also shows consistent negative correlations, but except for June/July ($p = 0.029$), they are not significant at the 0.05 level. This again is probably due to the small and shady charateristics of these gaps and the relatively late (and fast) snowmelt during June and July.

Seedling Density vs. Snow Persistence

A Kruskal-Wallis analysis of variance is used to test whether densities of Engelmann spruce and subalpine fir seedlings vary with the date of snow persistence. Only four positions in a gap represent actual areas, so the fifth, the center point, is not used.

Table 2: Kruskal-Wallis analysis of variance results for spruce and fir seedling densities (dependent variables) and snow persistence (independent variable).

Test	number of observations	H-statistic	significance
SITE 1			
fir seedlings vs. snow persistence	52	0.401	0.940
spruce seedlings vs. snow persistence	52	2.983	0.394
SITE 2			
fir seedlings vs. snow persistence	36	2.278	0.517
spruce seedlings vs. snow persistence	36	0.901	0.825

Significance values are low in all cases, indicating that neither spruce nor fir seedling densities vary appreciably with changes in snow persistence. Mean fir seedling densities do show consistent patterns with snow persistence (Table 1), but the variances are so high that they are statistically insignificant. These findings are confirmed by similar results from an analysis of variance on seedling densities with gap position.

The outcomes of these tests suggest that the establishment of spruce and fir seedlings is not significantly affected by one to three weeks difference in snow persistence. Site 1 and Site 2 are approximately 250 m and 150 m below timberline, respectively, and growing seasons are apparently long enough to mask the effects of any delays in growth caused by snowcover.

Gary (1974a) arrived at a similar conclusion for mature Engelmann spruce trees growing 150 m below timberline in New Mexico, where snow persisted into late July and early August. However, Billings (1969) observed in Wyoming that snow persisting into July and August excluded spruce and fir. Billings' site was 300 to 400 m below timberline, relatively low compared to Gary's site. The difference may lie in the topographic and edaphic characteristics of the sites. On relatively flat sites, such as Billings', where drainage can be poor, an indirect effect of late-lying snow may be continual flooding of the soil by meltwater (Griggs, 1938; Klikoff, 1965; Wardle, 1968). Even if the snow-free period is sufficiently long to allow seedlings to successfully complete their growth and maturation, the cold, leached, water-logged soil would be a detriment to growth. In contrast, hillslope areas, such as that in Gary's study, tend to be relatively well-drained and not as prone to waterlogging by snowmelt.

Long-term snow conditions are important in assessing the response of tree seedling establishment to snow persistence. Any effects of changes in snow persistence on herbaceous plant growth can be seen in just a few years (Knight _et al._, 1979), while tree species, which are slow-growing perennials, respond much more slowly (Dix and Richards, 1976).

It is not precisely known how the 1983 snow disappearance dates at Site 1 and Site 2 compare with previous years, but an approximation can be made by considering Snotel and University Camp snow course observations, and summer temperature and precipitation at climate station C-1. At the end of May, 1983, the snowpack at the University Camp snow course was above the mean, but within one standard deviation. The Snotel recorded 3.2 cm of moisture on the ground by the last week in June, 1983. In a normal year, such as 1979, 1.3 cm remained, but snow disappeared within the same week in both years. The mean of the average monthly temperatures during the summer of 1983 was the coldest of the 31-year record. Precipitation was above average, though within one standard deviation (Losleben, personal communication). Low temperatures probably decreased the rate of snow melt at high elevation sites such as Site 1 and Site 2, although rains during June and July may have increased melt in some areas. From the evidence presented here, it may be surmised that snow persisted longer than usual at the study sites in 1983, but probably not by more than a week.

Another consideration is the variability of snow persistence from year to year. The University Camp snow course observations reveal that the late-spring snowpack varied widely in depth and moisture content. It is possible that if seedlings can become established during a period of favorable snow years, they may be able to survive subsequent years that are less than optimum (Franklin, _et al._, 1971). The quality and quantity of Engelmann spruce and subalpine fir seed crops also varies widely (Alexander, 1969; Noble and Ronco, 1978), so establishment would be most likely in years when both seed availability and climate are optimal.

Seedling Density vs. Direct Radiation

Snow persistence is highly dependent on direct radiation exposure, so the possible effects of solar radiation on seedling density are examined separately. Only May/August and June/July radiation values are considered, because they include the months of July and August, which normally represent that part of the growing season when seedlings are not directly affected by snow.

Kendall correlation results show very strong positive relationships between spruce seedling density and May/August and June/July radiation at Site 1 ($p = 0.007$ and 0.006, respectively), while all Site 2 correlations are not significant. Further inspection of the data reveals that a large number of zeros in the seedling density population dominates the correlation, decreasing the contributions of nonzero values.

The number of zeros can be reduced by considering only two gap positions, NNW and SSE, which represent the widest differences in radiation exposure (see Table 1). Only those Site 1 gaps in which at least one of the two density values is nonzero are used. The means and variances of seedling density and radiation of this sample are very similar to the rest of the Site 1 gaps, assuring comparable results. A Kendall correlation is again used to assess the relationships. Correlations are not significant at the 0.05 level, though they are fairly high (p = 0.178 and 0.132 for May/August and June/July, respectively) and the number of observations is low (n = 18). Correlation coefficients are positive, indicating positive relationships.

Ronco (1970) measured the photosynthetic rate of Engelmann spruce seedlings under full sun, partial shade and full shade. Photosynthesis increased as average light intensity rose from near zero to one-third full sunlight (about 4000 foot-candles), then leveled-off in a manner suggesting light saturation at higher intensities. Wide-spread chlorosis, an indication of solarization damage, appeared on the needles of unshaded seedlings.

Daily radiation averages at the study sites range from near zero to 0.64 of the summer solstice maximum. The highest seedling density is found at 0.26 of maximum for June/July radiation, but most high density points cluster at 0.4 to 0.5 of maximum. If radiation values greater than 0.64 had been measured, it is possible that seedling density would have shown a decrease because of mortality by solarization.

An interesting question to raise is: why isn't the density of spruce seedlings more strongly related to radiation at Site 2? The answer is not clear. At Site 1, radiation levels, precipitation, snow persistence, elevation, and soil composition differ from Site 1. Roe et al. (1970), Ronco (1970) and Noble and Alexander (1977), among others, recognized that seedling establishment and survival are influenced by a combination of these environmental factors, plus biotic factors such as seed and seedling damage by rodents and birds (Noble and Alexander, 1977; Alexander, 1983). Even in carefully controlled experiments, the effects of radiation alone are difficult to isolate.

SUMMARY AND CONCLUSIONS

This investigation has provided a preliminary assessment of the impacts of snow persistence on the regeneration of Engelmann spruce and subalpine fir on the eastern slope of the Colorado Front Range. Study was focused on seedling density within small forest gaps, where snow persistence varied appreciably over small areas. The hypothesis tested was stated as follows:

> Variation in snow persistence within small gaps is not a major influence on the seedling establishment patterns of Engelmann spruce and subalpine fir.

The hypothesis was subsequently accepted. Results of the analysis are summarized below.

1) Neither spruce nor fir seedling densities varied appreciably with snow persistence. This lack of variation applied to position within a gap as well.

2) Spruce seedling density was intially found to be significantly related to May/August and June/July radiation, but further analysis revealed that a large number of zero values in the seedling density population had strengthened the relationships. Subsequent reduction of the number of zeros produced positive relationships that were not well-defined and not significant.

3) Exposure to direct radiation was highly dependent upon gap position, especially during the summer months. Exposure was greatest on northern gap borders and least on southern borders.

4) Snow persistence varied significantly with position within a gap. Snow disappeared earliest in the north-northwest and latest in the south-southeast, rather than in the north and south, respectively. This was thought to be a result of afternoon cloudiness that occurred regularly during the summer. Persistence was found to vary negatively with radiation exposure, confirming that snow disappears earlier on sunny sites.

Billings, W.D. 1969: Vegetational patterns near alpine timberline as affected by fire-snowdrift interactions. Vegetatio 19, 192-207.

Daly, C. 1984: Influences of snow persistence on the regeneration of Engelmann spruce and subalpine fir, Colorado Front Range. University of Colorado, Boulder, unpublished M.A. thesis.

Dietrich, T.L. and J.R. Meiman 1974: Hydrological effects of patch cutting of lodgepole pine. Colorado State University Hydrology Paper 66, Fort Collins (31 pp.).

Dix, R.L. and J.D. Richards 1976: Possible changes in species structure of the subalpine forest induced by increased snowpack. In H.W. Steinhoff and J.D. Ives (editors), Ecological impacts of snowpack augmentation in the San Juan Mountians, Colorado. San Juan Ecology Project, Final Report, Colorado State University Publication, Fort Collins, 311-322.

Franklin, J.F., Moir, W.H., Douglas, G.W. and C. Wiberg 1971: Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic and Alpine Research 3, 215-224.

Gary, H.L. 1974a: Growth of Engelmann spruce (Picea engelmannii) unaffected by increased snowpack. Arctic and Alpine Research 6, 29-36.

----- 1974b: Snow accumulation and melt along borders of a strip cut in New Mexico. USDA Forest Service Research Note RM-279, Rocky Mountain Forest and Range Experiment Station, Fort Collins (8 pp.).

----- 1974c: Snow accumulation and snowmelt as influenced by a small clearing in a lodgepole pine forest. Water Resources Research 10, 348-353.

Geiger, R. 1965: The climate near the ground. Cambridge: Harvard University Press (611 pp.).

Griggs, R.F. 1938: Timberlines in the northern Rocky Mountains. Ecology 19, 548-564.

Hull, C.H. and N.H. Nie (editors) 1981: SPSS update 7-9. New York: McGraw-Hill (402 pp.).

Klikoff, L.G. 1965: Microenvironmental influence on vegetational pattern near timberline in central Sierra Nevada. Ecological Monographs 35, 187-211.

Knight, D.H., Weaver, S.W., Starr, C.R. and W.H. Romme 1979: Differential response of subalpine meadow vegetation to snow augmentation. Journal of Range Management 32, 356-359.

Lindsay, J.H. 1971: Annual cycle of leaf water potential in Picea engelmannii and Abies lasiocarpa at timberline in Wyoming. Arctic and Alpine Research 3, 131-138.

List, R.J. 1951: Smithsonian meteorological tables (6th edition). Smithsonian Miscellaneous Collections 114, Washington: Smithsonian Institute (527 pp.).

Losleben, M. 1984: Personal communication. University of Colorado Mountain Research Station, Nederland, Colorado.

Marr, J.W. 1961: Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies, Series in Biology 8 (134 pp.).

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. and D.H. Bent 1975: SPSS - Statistical Package for the Social Sciences (2nd edition). New York: McGraw-Hill (675 pp.).

Noble, D.L. and R.R. Alexander 1977: Environmental factors affecting natural regeneration of Engelmann spruce in the central Rocky Moutains. Forest Science 23, 420-429.

Noble, D.L. and F.R. Ronco 1978: Seedfall and establishment of Engelmann spruce and subalpine fir in clearcut openings in Colorado. USDA Forest Service Research Paper RM-200, Rocky Mountain Forest and Range Experiment Station, Fort Collins (12 pp.).

Olyphant, G. 1983: Direct insolation to Indian Peaks cirques during the snowmelt season. American Association of Geographers Program Abstracts, Annual Meeting, Denver, Colorado.

Peet, R.K. 1981: Forest vegetation of the Colorado Front Range. Vegetatio 45, 3-75.

Platt, T. 1984: Personal communication, Boulder Water Utility, 1739 Broadway, Boulder, Colorado. (University Camp snow course measurements for 1955-1984).

Roe, A.L, Alexander, R.R., and M.D. Andrews 1970: Engelmann spruce regeneration practices in the Rocky Mountains. USDA Forest Service Products Research Report 115, Washington, D.C. (32 pp.).

Ronco, F. 1970: Influence of high light intensity on survival of planted Engelmann spruce. Forest Science 16, 331-339.

Sakai, A. 1970: Mechanism of desiccation damage to forest trees wintering in soil-frozen areas. Ecology 51, 657-664.

Shaw, C.H. 1909: The causes of timberline in mountains; the role of snow. Plant World 12, 169-181.

Spurr, S.H. and B.V. Barnes 1980: Forest ecology (3rd edition). New York: John Wiley and Sons (687 pp.).

Tranquillini, W. 1979: Physiological ecology of the alpine timberline: tree existance at high altitudes with special reference to the European Alps. Ecological Studies 31, New York: Springer-Verlag (137 pp.).

United States Soil Conservation Service 1984: University Camp Snotel data for 1979-84. Unpublished data.

Veblen, T.T. 1984: Personal communication, Department of Geography, Boulder, Colorado.

Wardle, P. 1968: Engelmann spruce (Picea engelmannii ENGEL) at its upper limits in the Front Range, Colorado. Ecology 49, 483-495.