Microscale Patterns of Tree Establishment near Upper Treeline, Snowy Range, Wyoming, U.S.A.

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Abstract

We report tree seedling (mostly *Picea engelmannii*, some *Abies lasiocarpa*, very infrequent *Pinus contorta*) invasion into meadows at upper timberline in the Snowy Range, Wyoming, from 1994 to 1996. We used gradient analysis to relate this to environmental patterns, particularly plant community structure (as aggregates of plant life-forms) and persistence of snowpack in 1995 and 1996. Tree seedlings established best at sites where snow melted earliest; the site with the shortest growing season had fewest seedlings. Microsites dominated by vascular plants admitted few or no seedlings; seedlings were most likely to be found where cryptogams dominated. These findings have implications for forest advance under some climate scenarios and successional hypotheses.

Introduction

Invasion of trees into high elevation meadows is an ongoing global happening (Kullman, 1993; Payette and Lavoie, 1994). In western North America, many studies have reported tree invasion in mountain landscapes during the past century and millennium. Since the 1940s tree regeneration has been active above the present tree limits at Niwot Ridge in the Front Range, Colorado (Daly and Shankman, 1985). Numerous reviews have discussed the sensitivity of the forest-alpine tundra ecotone (Löve, 1970) to climate change (Grant and French, 1990; Romme and Turner, 1991; Stevens and Fox, 1991; Slatyer and Noble, 1992; Noble, 1993; Walker et al., 1993; Woodward and Rugh, 1993). Do recent advances of trees into areas otherwise long-maintained as subalpine meadow or alpine tundra throughout the Rocky Mountain and Sierra Nevada/Cascadian Cordillera indicate the onset or continuance of global warming (Hasselman, 1997)? Some studies have tried to relate tree invasion chronologies to changing climates (Earle, 1993; Kullman, 1993; Lavoie and Payette, 1994; Moir and Huckaby, 1994; Hessl and Baker, 1997). Several generalized scenarios of both short- and long-term climate forcing upon tree seedling dynamics at upper timberline have been proposed (Fig. 1).

Landscape analyses were employed to partition the forest/alpine tundra ecotone into areas of varying climatic sensitivities. At nearby Rocky Mountain National Park, portions of this ecotone that are strongly structured by natural disturbances may be relatively insensitive to climatic change, while other portions may have climate changes reflected more by responses in krummholz leader growth than by seedling establishment (Baker and Weisberg, 1995; Weisberg and Baker, 1995a). Similarly, by using dendrochronology techniques, Earle (1993) reported that on gently sloping uplands in the Snowy Range, Wyoming, some past-climate intervals favored periods of tree seedling invasion while other intervals favored only krummholz growth. Tree-ring and leader growth studies relating tree growth to climatic patterns are useful and informative (LaMarche and Mooney, 1967; Hansen-Bristow et al., 1988), but they do not tell us how or why trees established. These and studies cited in Moir and Huckaby

(1994) concluded that tree invasion at a given site was controlled by factors such as microtopography, snow depths, surficial geology, soil types, wind patterns, spatial location and proximity of seed sources, and local disturbance regimes, including fire, snow avalanches, active talus and soil freeze-thaw processes, livestock grazing, and pocket gopher tunneling and soil casting; all of these are interactive and difficult to isolate experimentally or by tree-ring studies. In most studies the invading trees were usually established decades prior to measurement, by which time the larger trees at least (often referred to as "seedlings") may have already modified the microenvironment.

The major objective of this study was to determine microenvironmental patterns of tree seedling establishment. We reasoned that the influx of viable seeds, followed by seed germination and seedling survival were sensitive, "weak link" tree life-history traits in this high-elevation environment. Numerous studies in the subalpine forest region have shown that tree regeneration depends upon many biotic and abiotic factors (summarized by Alexander et al., 1985; Cui and Smith, 1991; Little et al., 1994; Rochefort et al., 1994; Anderson and Winterton, 1996; Kuuluvainen et al., 1996; Rochefort and Peterson, 1996). The most important of these were the size of the viable seed influx, ambient diurnal growing season temperatures, precipitation during the growing season, light intensity, sky exposure and photoinhibition, substrate (especially litter depth), infiltration and drainage of the mineral soil seedbed, freezing soil activities, persistence of late-lying snow, seedling root depths at the end of season, presence of snow molds, density of vegetative cover, and intensity of seedling predation (especially by birds and small mammals). It seems reasonable that conditions limiting tree seedling establishment in clearcuts and forest edges at lower elevations, where the above studies were conducted, would be even more limiting at upper timberline and within the forest/alpine tundra ecotone. This hypothesis is supported by few *in situ* studies on the occurrence and survival of seedling *Picea engelmannii* or *Abies lasiocarpa* within the forest/alpine tundra ecotone (Daly and Shankman, 1985; Germino and Smith, 1999).

Meadow or tundra openings limit tree invasions through mechanisms of plant competition from herbaceous or shrubby

Dry climate →	longer growing season →	ample carbon assimilation by seedlings
	shallow snowpack →	more drought stress
Wet climate →	shorter growing season →	low cargbon assimilation by seedlings
	deep snowpack →	less drought stress
Cold climate →	shorter growing season →	poor, infrequent seed crops
	long-duration snowpack →	low carbon assimilation
	→	slow seedling growth
Warm climate →	longer growing season →	good seed crop
	short-duration snowpack →	more drought stress
	→	ample carbon assimilation
	→	fast seedling growth

FIGURE 1 Climate change scenarios and implications for tree seedling establishment (modified from Franklin et al., 1971 and Romme and Turner, 1991). Dry, cold climates and wet, warm climates have offsetting consequences, and both dry, warm and wet, cold climates have reinforcing adverse consequences on tree seedling establishment.

species adapted to the openings (del Moral, 1983), and by microenvironmental factors mentioned above. But plants of the subalpine meadows and tundra are themselves affected by climatic variations and various kinds of animal and soil disturbances. Having suggested that regional climate variations set the stage for meadow/tundra invasions by trees (Moir and Lee, 1990; Moir and Huckaby, 1994), we were interested in detailed vegetation patterns where tree seedlings successfully established. Plant composition and life-form architecture at tree seedling microsites reflect the multifactor complexity mentioned above, and the seedlings themselves point to microsite conditions that admit forest advance into otherwise hostile meadow/tundra environments. After measuring tree seedlings densities along with plant composition and structure, we then used gradient analysis to reveal gradients of environmental factors along which these plant communities differentiated (ter Braak and Prentice, 1988). If major gradients (measured by their eigenvalues) emerged, they would help provide a basis for field experiments to test hypotheses about causes or thresholds affecting seedling survival.

The Study Area

The study area in the Snowy Range, Medicine Bow Mountains, southeastern Wyoming (41°15'N, 106°18'W) is near upper timberline, which is about 3200 m elevation. The area has short, but variable, growing seasons, determined mostly by snowpack characteristics (Sommerfeld et al., 1990). The terrain has complex glacial-fill and bedrock topography, and other features which result in strong patterns of tree seedlings, plant communities, persisting snowfields, coniferous krummholz "islands," and forest edges (Baker and Weisberg, 1995).

The general environmental features of the study area are described by Musselman (1994), and are briefly summarized. The climate is cold: mean winter months (December through February) minimum temperatures range from −23 to −1°C, and summer (June through August) minimum temperatures range from −7 to 21°C. The mean July temperature is 11.1°C. The soil temperature regime is at the Cryic/Pergelic boundary. Precipitation averages about 1.08 m yr⁻¹, mostly as snow, and average June–October precipitation is low, varying from year to year around 50 mm yr⁻¹. Meadows and forests use snowmelt as an important source of growing season water. The depth and water

content of snowpack is highly variable over the landscape. Typical depths are 1 to 3 m, but extremes outside this range are common. Most snow melts in June; however, some snowfields persist from one year to the next, and elsewhere shallow snowpack (<1 m) results in snow-free areas by early June (Sommerfeld, 1994). Most of the study area is snow-free by early July (but see our discussion on snowpack duration below). The study area is windy with mean wind speeds from 3 to 11 m s⁻¹ (overall average 7.4 m s⁻¹). Both wind direction (mostly westerly) and speed near the ground have been related to topographic factors and tree forms (Wooldridge et al., 1996). The soil parent materials are glacial tills of Proterozoic quartzite, mafic rocks, and eolian deposits, and are likely of late Pinedale age (Rochette, 1994). Drought can occur in the uppermost soil by late August or September, as evidenced by cracking soil surfaces and dead tree seedlings. Shallow ponds in the general study area became dry in late August or September 1995 and 1996. Soils having spring meltwater near the surface may show diurnal freeze-thaw activity in the form of puffy soil surface, vertical icing, and weak gravel sorting.

Methods

FIELD PROCEDURES

In late summer 1994, we searched openings in the study region for tree seedlings, but found few areas where they occurred in sufficient densities needed for this study. Three areas were found and named TL1, TL2, and GL. The first two areas were in a patch forest environment, and the latter in patch krummholz (Weisberg and Baker, 1995b). Impacts of sheep grazing may have triggered earlier tree establishment at TL1 and TL2 (Moir and Lee, 1990). In each area we located a 25 × 25 m macroplot which contained large numbers of tree seedlings. Each macroplot was divided into 5 × 5 m sectors, and each sector was divided into 1 × 1 m plots referred in this report as square-meter plots.

A tree seedling was defined to be any Picea engelmannii, Abies lasiocarpa, or (rarely) Pinus contorta ssp. latifolia less than about 3 cm in height. High-magnification ring counts (Moir and Huckaby, 1994) and bud scale scars (years of zero growth will cause underestimation of actual age) show that these were usually 1 to 9 yr in age. Most seedlings had epicotyl development well past the cotyledon stage (we found only 4–5 cotyledon seedlings) but without lateral branches. All seedlings found in each macroplot in 1994 were numbered and their location noted by a small stake. Additional seedlings were also noted when found during sampling in 1995 and 1996 but were not numbered or marked. Seedlings were mapped in 1996, providing information about the number of seedlings in each square-meter plot. Some of the marked and unmarked tree seedlings died during the time of our measurements. In addition, a very few seedlings were about 3 to 6 cm tall and over about 9 yr of age. These tree seedlings were called "established seedlings." Microenvironmental features of the four kinds of tree seedlings—marked, new, dead, and established—were analyzed separately but were too few in each category to yield interpretable results. Therefore, we pooled these seedlings into a single tree seedling category. Our use of the term "seedling(s)" in the rest of this report refers to the pooled values (even though some were dead).

In late spring, 1995 and 1996, snow melt over each macroplot was mapped approximately every other day using the 5 × 5 m grids as guides. The map lines were the boundaries of exposed soil at the edge of melting snow. During August, 1995

and 1996, vegetation and soil surface features were measured in four square-meter plots located at random in each sector (depending on visual vegetation homogeneity in a sector, we sometimes measured more or less than four square-meter plots).

Vegetation and soil features in each selected square-meter plot were measured in three 2 × 5 dm quadrats that had fixed geometric positions from plot to plot. Plant names follow Weber (1987). Vegetation was measured by the canopy coverage method (Daubenmire, 1959). The canopy coverage of all vascular plants was measured by species. The canopy coverage of cryptogams was differentiated into mosses and lichens. We did not measure saxicolous lichens (lichens on rocks). Tree seedlings were counted in each quadrat and later converted to square-meter density. If there was discrepancy between the density based on mapping data and the density computed from the three quadrats, the larger value was used for analysis. Soil surface features were also estimated by the canopy coverage method. We defined rocks to be exposed mineral particles with a maximum dimension >1 dm; gravels were exposed mineral particles of dimension 2 mm to 1 dm; and mineral soil were exposed soil particles <2 mm. Many of these properties are difficult to measure into cover classes. Different workers were calibrated (adjusted to some common bias) by methods described by Pfister and Arno (1980), and calibration was checked throughout the measurement period.

GRADIENT ANALYSIS

We performed gradient analysis on the three macroplots using program CANOCO (ter Braak, 1988). We used canonical correspondence analysis (CCA, cf. Nieppola and Carleton, 1991) in direct gradient analysis and correspondence analysis (CA) for indirect gradient analysis. Interpretations of the ordination results were facilitated by referring to Gauch (1982), ter Braak (1986, 1987, 1988), ter Braak and Prentice (1988), and Palmer (1993). The deficiencies pointed out by McCune (1997) did not apply, because we were more interested in the relationships between seedlings and environmental variables than we were in defining community structure, which already had been reported by Regan et al. (1998). Nevertheless, we verified our results by performing the same analyses using PCORD version 3.14 (MJM Software Design).

Plant life-forms over the square-meter plots varied widely. For CA analysis we used life-form variables: graminoid dominance (summed grasses and sedges as canopy coverage), vascular plant dominance (graminoids + forbs = total herbaceous canopy coverage), lichen dominance, total cryptogam dominance (canopy coverage of both mosses and lichens), and coverage by substrate factors such as bare soil, gravel, or rocks. We were interested in these variables as plant competition factors in relation to seedling density (number/square-meter). In addition each square-meter plot had a snow duration variable—the number of days (averaged over 2 yr) from earliest melt date in the macroplot to the last melt date in each square-meter plot. Snow duration limits the seedling growing season, and is not a plant competition factor although it may intensify plant competition. In this paper we refer to seedling density, snow, substrate, and life-form data as the life-form data set. Although seedling density was a covariable in the life-form data set, we were especially interested in its relationship to the other covariables and regarded it as a kind of "dependent" variable. Our life-form data set is the same as "species" data in CANOCO and PCORD.

At each macroplot we also chose plant species for CCA analysis. A different set of species was used for each macroplot. We were interested in canonical correlations between seedling density and cover of dominant or frequent plants as well as seedling relationship to the other variables in the life-form data set. The plant species used in direct gradient analysis are the same as the "species" data in CANOCO, and the life-form data set described above, now becomes the "environmental" data in CANOCO.

Results

PLANT COMMUNITIES

Macroplot TL1 had a plant community similar to the *Solidago spathulata–Danthonia intermedia* Association described in the lower alpine and krummholz zone of the Indian Peaks, Colorado by Komárková (1979). It distantly resembled the *Danthonia intermedia–Potentilla diversifolia* community of Regan et al. (1998). Our community was a meadow with high frequency and high cover of *Danthonia intermedia, Artemisia scopulorum,* and *Acomastylis rossii.* Other frequent species, but with variable cover, included *Erigeron peregrinus, Sibbaldia procumbens,* and *Potentilla diversifolia.* Frequent species with low cover included *Chlorocrepis tristis, Bistorta bistortoides,* and *Oreobroma pygmaea.* The low shrubs, *Vaccinium scoparium* and *V. cespitosum,* occurred in patches; another low, infrequent shrub was *Salix planifolia.* A common moss was *Polytrichum piliferum.* Except for species of *Vaccinium,* there was no clear patchiness caused by different combinations of associated vascular plants.

The most striking feature of TL1 was the massive tree invasion taking place, primarily by *Picea engelmannii.* Major invasion periods were 1948–1951 and 1960–1963 (Moir and Lee, 1990). These trees varied in height from 1 to 35 dm, and predated the seedlings of this study. In addition, layered branches of large *Abies lasiocarpa* almost completely covered the northern corner of the plot, and large *Abies lasiocarpa* occurred just outside the plot on the southeast and northeast edges.

Macroplot TL2 featured a meadow generally differentiated into plant communities across a gradient perpendicular to a strip of trees (ribbon forest, cf. Billings, 1969; Earle, 1993) extending along the south side of the plot about 5 to 10 m from its edge. Mosses and forbs dominated along the south edge of the plot, and cover by grasses and sedges was usually sparse. *Erigeron melanocephalus* was a common, mat-forming species. The center and northwestern corner of the plot had high cover of herbaceous species. Here *Danthonia intermedia* was the dominant turf-forming grass usually associated with *Trifolium dasyphyllum.* The north-center and northeastern portions of the plot were dominated by various forbs and had much exposed soil; *Deschampsia cespitosa* and *Sibbaldia procumbens* were common species. Species common throughout TL2 included *Potentilla diversifolia, Bistorta bistortoides, Senecio dimorphophylla,* and the moss, *Polytrichum piliferum.*

A large portion of macroplot GL has a plant community in which *Sibbaldia procumbens* was common with cover varying from high to sparse. Frequent associated plants were *Chlorocrepis tristis, Juncus drummondii, Antennaria umbrinella, Oreobroma pygmaea,* and several species of *Carex.* A moss-lichen layer contained *Polytrichum piliferum, Cladonia* sp., and *Lecidea alpina.* This community was similar to the *Sibbaldia procumbens–Oreobroma pygmaea* plant association of Komárková (1979). Small drainages ran through portions of the southeastern quarter of the plot. Several tree saplings of vintages described in TL1 occurred along interfluves of these drainages and in southern portions of the plot. We did not describe plant communities at these locations.

SNOW DURATION

The recession of snow fronts in macroplot TL1 began on 5 July 1995 and continued until all of the plot was snowfree on 19 July 1995. In 1996, the recession of snow fronts occurred between 22 June and 12 July. On macroplot TL2, the snow front receded from 7 to 21 July 1995, and from 24 June to 8 July 1996. The ground became snow-free at the GL macroplot from 10 to 27 July 1995 and from 28 June to 18 July 1996.

With the above information we compare the three macroplots as follows:

Earliest snowmelt (both years)		TL1 <	TL2 <	GL
Snow-free dates	1995:	TL1 <	TL2 <	GL
	1996:	TL2 <	TL1 <	GL
Snowmelt duration (days)		TL1	TL2	GL
	1995:	14	14	17
	1996:	20	14	20

Averaged over both years, it required 14 d to become snow-free in plot TL2, about 17 d in plot TL1, and about 18.5 d for plot GL. These intervals are determined mostly by the amount of snowpack in the plots and the temperature or heat load (degree-days) on these plots (Rango and Martinec, 1995). On the basis of snowpack duration, macroplot TL2 was the warmest and driest, and macroplot GL was the coldest and wettest of the three macroplots.

GRADIENT ANALYSIS

CANOCO and PCORD yielded identical results in CA; for CCA the latter yielded slightly higher eigenvalues for each macroplot and slightly higher correspondences between species and life-form axes for TL1 and TL2. The differences were so minor that our interpretations would be the same in either case. We report results from the more conservative CANOCO.

Inertia (Table 1) is a measure of the overall variability among the square-meter plots of the pooled multivariate data, whether as life-form or species data (ter Braak, 1988). The biplot arrows (e.g. Fig. 2B) are vectors in the direction of maximum variation of environmental (life-form) variables and whose length (i.e., the distance from the origin to the arrowhead) gives the relative importance of those variables. The importance of any ordination axis is given by its eigenvalue. Other values were entered in Table 1 or Figures 2 to 4 only if they had high weighted correlations or cumulative fits above 12% of variance. Blanks indicated that variables made little or no contribution to the ordination axis, or had little or no correlative relationship to other variables. In direct ordination (CCA), the first axis and overall ordination results were significant at $P < 0.01$ by Monte Carlo permutation (99 replicates) tests provided by the program CANOCO.

TL1

The first axis of indirect (CA) ordination (Table 1, Fig. 2A) was highly fitted to sapling or larger tree coniferous cover; this axis clearly defined a coniferous cover gradient. The second axis added negligible fit for coniferous cover. In the language of this paper, we refer to coniferous cover as a first axis variable. The first and second axes together accounted for a cumulative 74% of the variance of the life-form data. The second axis was highly fitted to vascular plant herbaceous cover, whose weighted aver-

age centered at one end of the axis, and to cryptogam cover, centered at the other end. We interpret the second axis as a vascular to nonvascular plant gradient. Seedling density was a weak second axis variable centered in the cryptogam region.

The first axis of direct (CCA) ordination (Fig. 2B) was positively most associated with coniferous cover (fitting 79% of its variance) and negatively most associated with cover of *Danthonia intermedia* (52% fitted) and *Acomastylis rossii* (30% fitted). The second ordination axis was a vascular to nonvascular plant gradient, i.e., from high graminoid cover at negative gradient values to high lichen-moss cover at positive gradient values. This axis was also a snow gradient, with snow days increasing in the positive (up) direction. Other second axis vascular plants whose cumulative fit (from both axes) exceeded 12% of their variance were *Erigeron peregrinus*, *Oreobroma pygmaea*, and *Antennaria umbrinella*. These species usually achieved high canopy coverage where graminoid turfs were absent. Some forbs were mostly found on or near soil exposed by pocket gophers, soil erosion, or freeze-thaw cycles, suggesting a seral status for these species. However, vegetation structure in these dimensions did not explain variations in seedling density. Instead, seedling density was a third axis variable (inset of Fig. 2B) whose cumulative fitted variance (cfv) was 17%. Other third axis species (cfv >12%) were *Erigeron simplex*, *Erigeron melanocephalus* (combined as mat-forming rosette plants), *Vaccinium* spp., and *Sibbaldia procumbens*. The weighted average of seedling density centered in the positive sector of the moss-lichen gradient (inset Fig. 2B), while the weighted average of *Vaccinium* centered in the negative sector. Although the third axis was minor relative to the others, it did reveal the tendency of seedlings to rarely occur under *Vaccinium* (but see Stahelin, 1943 for the opposite tendency in burned forest openings at mostly lower elevations) and to more commonly occur where cryptogams had high cover.

In summary, macroplot TL1 is weakly structured in terms of vegetation architecture and seedling density. The architecture is transitional from a meadow to a forest. The coniferous influence of tall trees and numerous saplings pervades the 25 × 25 m macroplot, and meadow communities are breaking up as trees become dominant. Tree seedlings respond to a complex of variables of forest affinity (such as *Vaccinium* cover), weakening meadow influences (discussed in the other macroplots), and microenvironments affected by proximity to tree canopies, including layered branches.

TL2

This macroplot revealed the strongest relationships between seedlings and other microsite variables. CA ordination (Table 1, Fig. 3A) presented two contrasting gradients. The first axis was best fitted to cryptogam cover, accounting for 94% of cryptogam variance in the life-form data set. This cryptogam axis also accounted for moderate variance in snow duration (42% fitted) and seedling density (34% fitted). Life-form variables best fitted on the second axis were herbaceous cover, graminoids, and snow. Very high variance of mineral soil (gravel plus soil) was also associated with these axes (especially the second axis). On this site seedling establishment was favored at cryptogamic microsites and suppressed where mineral soil or vascular plants dominated. Seedling establishment was also favored on sites with least snow duration and with little recent soil disturbance.

The first axis of the CCA ordination is clearly a graminoid to snow gradient (Fig. 3B) with correspondence to graminoids and snow, respectively, −0.75 and 0.54. However, the first axis accounted for virtually none of the variation in seedling densi-

TABLE 1

Ordination of vegetation and environmental variables, Snowy Range, Wyoming, U.S.A.

	TL1			TL2		GL	
MACROPLOT:	101			99		100	
NUMBER OF square-meter PLOTS:							
ORDINATION axis:	AX1	AX2	AX3	AX1	AX2	AX1	AX2
INDIRECT ORDINATION (CA)							
Inertia	0.549			0.472		0.482	
Eigenvalue	0.284	0.124		0.238	0.112	0.191	0.103
Cum variance of life-form data (%)	52	74		51	74	40	61
CUM FIT AS PERCENT OF VARIANCE							
Name (acronym)							
Coniferous cover (conif)	99						
Total herbs (herbs)		98		40	96	70	91
Total forbs (forbs)		43		34		49	74
Total graminoids (gram)	14	57			75	53	61
Total lichens (lich)		81		68	77	65	70
Total mosses (moss)	17	69		79		58	61
Total cryptogams (cryp)	20	98		94		98	
Snow days (snow)				42	70	20	
Gravel and soil (grso)				35	98	17	94
Tree seedlings (sdlg)		12		34		14	27
DIRECT ORDINATION (CCA)							
Inertia	1.22			1.85		1.12	
Eigenvalue	0.302	0.143	0.085	0.346	0.210	0.190	0.074
WEIGHTED CORR WITH SPECIES AXES							
Life-form AX1	0.94	0.00	0.00	0.87	0.00	0.72	0.00
Life-form AX2	0.00	0.81	0.00	0.00	0.86	0.00	0.78
Coniferous cover (conif)	0.85						
Total herbs (herbs)							−0.44
Total graminoids (gram)	−0.64	−0.50		−0.75			
Total lichens (lich)					0.60		0.54
Total cryptogams (cryp)					0.63	0.45	
Snow days (snow)		0.61		0.54	−0.61	−0.60	
Gravel and soil (grso)				0.52			
Tree seedlings (sdlg)			0.27		0.74	0.26	0.44
CUM FIT AS PERCENT OF VARIANCE							
Life-form data	25	36	43	19	30	17	24
Species-Life-form relation	51	75	89	49	78	48	67
Tree seedlings (SDLG)			28		80	10	47
Coniferous cover (CONIF)	79					41	
Acomastylis rossii (ACRO)	30						
Antennaria umbrinella (ANUM)		23	37				
Chlorocrepis tristis (CHTR)						15	
Danthonia intermedia (DAIN)	52	77		55			
Deschampsia cespitosa (DECE)				13	16		
Erigeron peregrinus (ERPE)		28	34	12	16		18
Erigeron spp. (ERIG)			17	16	48		
Mixed Grass-Sedges (GRAM)							25
Juncus drummondii (JUDR)						20	26
Oreobroma pygmaea (ORPY)		26					
Potentilla diversifolia (PODI)					16		
Sibbaldia procumbens (SIPR)			16	33	52		
Trifolium dasyphyllum (TRDA)				17			
Vaccinium spp. (VACC)		13	32				

ties. Cryptogam cover corresponded well (0.63) with the second species axis. We interpret the second axis to be a vascular to nonvascular plant gradient strongly influenced by snow duration. Species whose scores centered along the second axis were *Danthonia intermedia* and *Trifolium dasyphyllum*, mostly dry meadow plants. Snow duration correlated (−0.61) with the second species axis and is a major environmental variable. Species clearly favoring exposed soil and longer snow duration were

Deschampsia cespitosa, *Sibbaldia procumbens*, and *Erigeron peregrinus*. Tree seedlings were centered at the opposite side of the soil and snow axes. They favored areas of reduced grass cover and were least probable in dry meadows or where snow lingered into the growing season. We note that this axis has a physical reality as a perpendicular gradient across the macroplot from the border of tall trees outside the south edge of the plot.

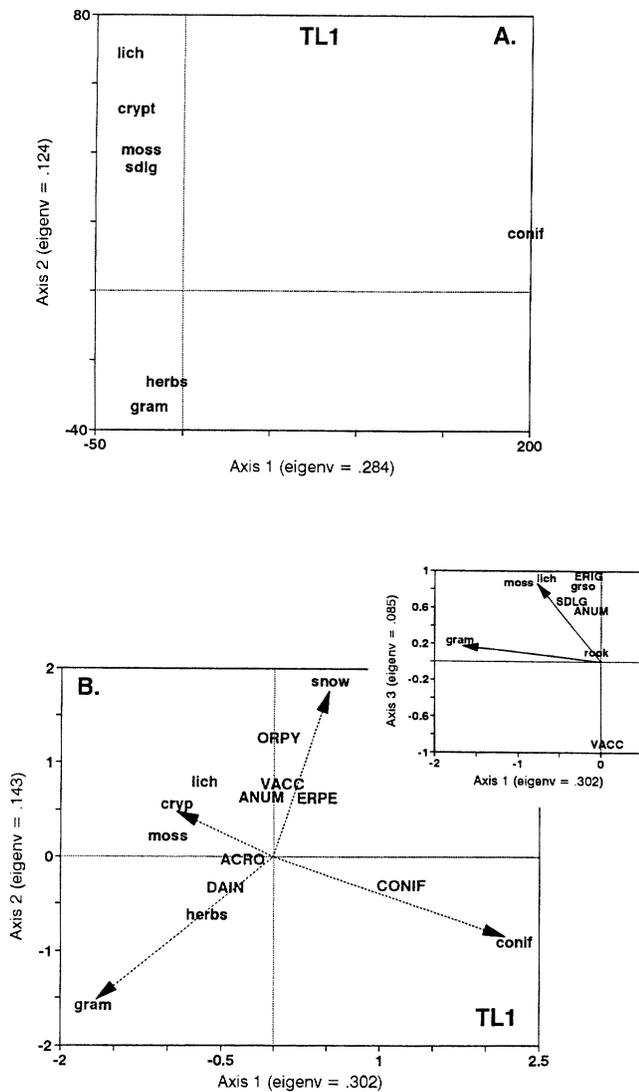Both ordinations revealed strong relationships between tree

FIGURE 2. Indirect (CA) ordination scores (A) and direct (CCA) ordination biplot (B) of tree seedling, life-form, and plant species variables in macroplot TL1. Names indicated by acronyms are given in Table 1.
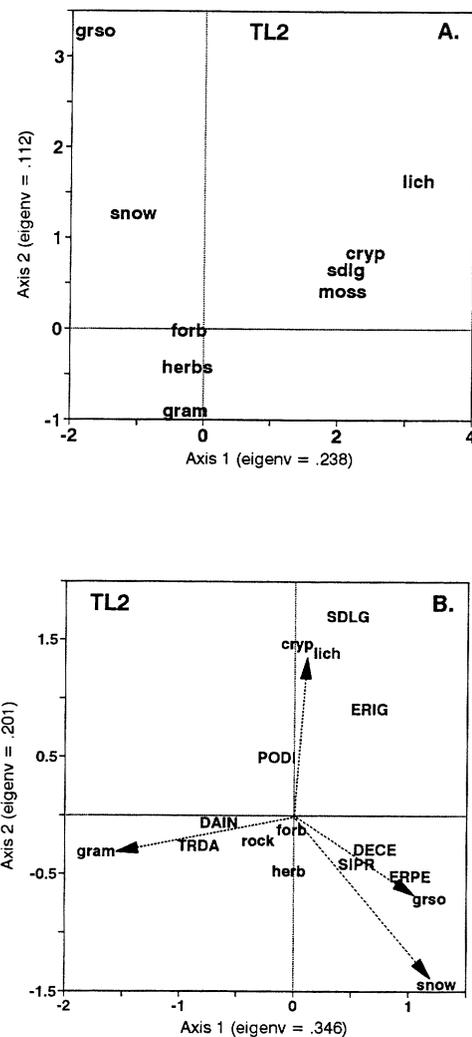

FIGURE 3. Indirect (CA) ordination scores (A) and direct (CCA) ordination biplot (B) of tree seedling, life-form, and plant species variables in macroplot TL2. Names indicated by acronyms are given in Table 1.

seedlings and plant community structure in this macroplot. Tree seedlings were limited in vascular plant communities much more than in cryptogam communities, a condition supported by field observations. Seedlings and associated cryptogams also favored microsites with early snow melt. Only *Erigeron melanocephalus* had positive association with seedlings, reflecting similar environmental requirements. *Erigeron melanocephalus* is an early seral opportunist, spreading vegetatively from areas of past soil disturbance or sheep grazing. There were few or no seedlings at microsites dominated by *Danthonia intermedia*. Otherwise there was little correspondence between seedling densities and other vascular plant species.

Unlike TL1, macroplot TL2 is not in structural transition between forest and meadow. Vegetation patterns are relatively fixed, suggested by the sharp ecotones. The macroplot, to be sure, is influenced by the neighboring ribbon forest, but this influence is little affected by yearly tree growth. The ribbon forest doubtless influences the pattern of meadow communities in this macroplot. This pattern is obvious, in contrast to macroplot TL1. Patch dynamics caused by pocket gophers and other disturbances occur in TL2, but this is intrinsic to the patterns oth-

erwise caused by trees, variations in glacial deposits, and soils—all of which are fixed from a seedling perspective. The relative constancy of pattern in TL2 may partly explain the stronger seedling relationships to plant community architecture and snow gradients.

GL

CA ordination (Table 1, Fig. 4A) produced a first axis herbaceous-to-cryptogam cover gradient. Cryptogams were centered positively, and cover by graminoids and forbs were centered negatively. However, vegetation structure had only minor relationship to seedlings, since only 14% of seedling variance was fitted by this axis. The second axis is a gradient from exposed soil with sparse or no vascular plant vegetation to dense herbaceous cover (forbs plus graminoids). The significance of this ordination is the identification of seedlings with cryptogams on the first axis and with mineral soil on the second axis. In the latter instance, several square-meter plots with seedlings were located in the small drainages where soil was deposited by snow-melt runoff.

CCA ordination resulted in four major gradients (Fig. 4B): lichens, total cryptogams, total herbaceous cover, and snow du-
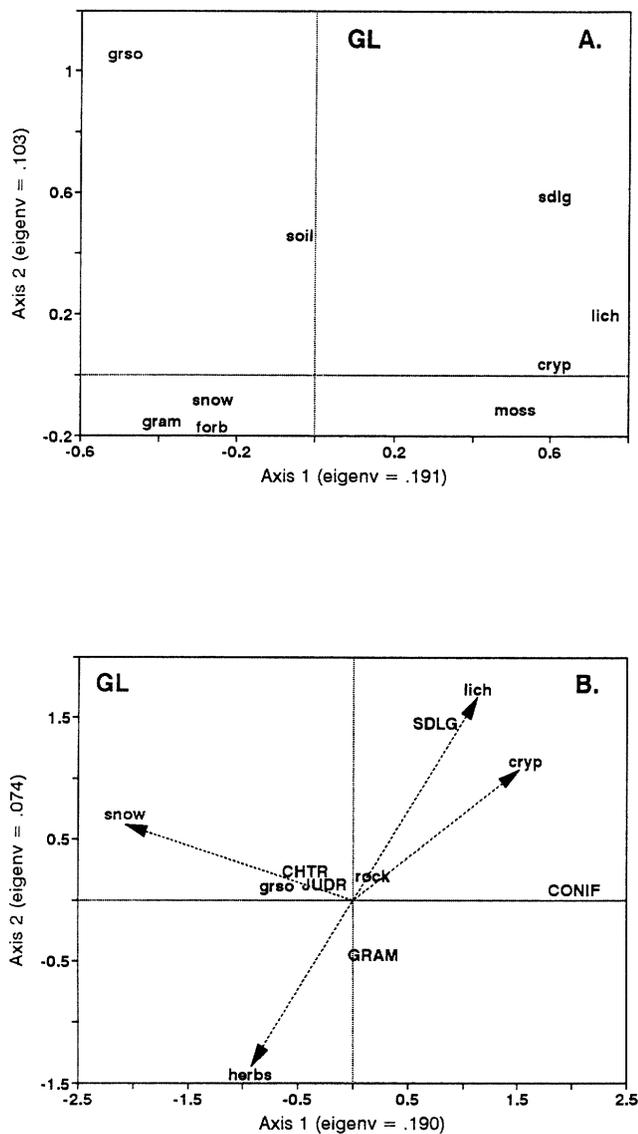
FIGURE 4. Indirect (CA) ordination scores (A) and direct (CCA) ordination biplot (B) of tree seedling, life-form, and plant species variables in macroplot GL. Names indicated by acronyms are given in Table 1.

ration. First axis variables were snow duration and cryptogam cover. Axis 1, therefore, can be described as a snow-to-cryptogam gradient (high snow days/low cryptogam to low snow days/high cryptogam cover). Other first axis variables were tree and sapling coniferous cover and, rather minor, *Juncus drummondii*, and *Chlorocrepis tristis*. Lichens and herbaceous cover were most correlated to the second axis, which we interpret as a vascular to nonvascular plant gradient (high vascular plant/low cryptogam cover to high cryptogam/low herbaceous cover). Tree seedlings are a second axis variable associated with lichen-dominated plots, reduced herbaceous cover, and short duration of snow.

In summary, the combined ordinations indicate that seedlings in plot GL were most associated with high cryptogam cover and were unlikely to be found where mixed grasses and sedges or high total herbaceous cover existed. Seedlings were favored in square-meter plots with shorter snow duration. There were no vascular plant species strongly associated with microsites of tree seedling establishment or survival.

Discussion

COMPARISON BETWEEN MACROPLOTS

In this section we argue that the three contrasting macroplots all shared common features at microsites having *Picea* and *Abies* seedlings. Numerous researchers have remarked about the ability of CANOCO to discern actual (real) relationships (as correlation or correspondence) in noisy data (Palmer, 1993; ter Braak, 1988: 43). As we discuss later, there is also ecological reason to suggest correspondence between cryptogamic sites and seedlings. These microsites had better than average cover of cryptogams (lichens and mosses), poorer than average cover by vascular herbs (especially grasses and sedges), and early dates of snowmelt averaged over two years. In comparing the macroplots we also conclude that there is no best vascular plant species as a predictor of seedling density in the study area. Instead, vegetation life form (plant community structure) is a better indicator of microsites favoring seedling establishment.

Macroplot TL1 had the weakest relationship of seedling density to cryptogam dominance in square-meter plots. At this site tree seedling/meadow community structure relationships were lessened by the strong presence and environmental effects of conifer saplings and large trees. The ordinations suggest that meadow influences upon seedling establishment are waning as succession proceeds toward forest. *Picea* and *Abies* have been invading this meadow for over 50 yr, and some saplings had reached heights of 2 to 3 m and had enough biomass to exert their own environmental changes in nearby square-meter plots. These tree effects include, among many others, shading and redistribution of snow, either of which can affect trees seedlings near their tolerance threshold of seasonal carbohydrate production. The expression of meadow vegetation structure was weakened by developing forest characteristics, including local dominance by *Vaccinium scoparium*, a common forest shrub. Having said this, we note that residual meadow plants such as *Danthonia intermedia* (a grass) and *Acomastylis rossii* (a forb) are negatively correlated with seedling density. The chance of seedling establishment is low where these herbs have higher than average cover.

In macroplot TL2, the earliest of the three macroplots to emerge from snowpack, we found the greatest seedling numbers and strong relationships among seedlings and aboveground vegetation architecture. The high seedling numbers may simply reflect that more seeds occurred here. Nevertheless, at this macroplot seedlings displayed a clear pattern that was strongly correlated with vegetation structure and snow persistence, but weakly conformed to plant communities. The major environmental axes of cryptogam cover, graminoid cover, and snow days provided contrasting gradients along which seedling densities differentiated. Seedling densities and cryptogam cover were positively correlated, and seedling densities were negatively correlated to both graminoid cover and snow days. Dry meadow turf communities, dominated by *Danthonia intermedia*, contained few seedlings; square-meter plots having high total herb cover also had few seedlings. Thus gradient analysis provided results consistent with those from TL1 but without the complication of coniferous cover within the macroplot.

Macroplot GL had the shortest growing season and fewest seedlings. Seedling variance associated with ordination axes (in both indirect and direct ordinations) was intermediate between TL2 and TL1. Compared to the other macroplots, seedling numbers in GL could reflect smaller seed influx, more severe environmental conditions, or both. The species-life-form correlation was the lowest, accounting for 67% of the cumulative variance

of the ordination axes, in contrast to 78% and 75% of the ordination axes of TL2 and TL1, respectively. The plant community in much of GL was *Sibbaldia procumbens–Oreobroma pygmaea* Komárková (1979)—clearly different from plant communities in the other macroplots and with more tundra vegetation features (Komárková, 1979). These features notwithstanding, gradient analysis in GL produced the same results. Seedling occurrences were mostly higher in cryptogamic (lichen) microsites, in sites of least snow persistence, and where least dominated by vascular herbaceous plants.

CRYTOMGAMIC SEEDBEDS AND PLANT COMPETITION

Given that the length of growing season is adequate for seedling survival and other conditions notwithstanding, the life-form architecture of plant communities affects seedling success. In grass-sedge turfs or where total vascular plant dominance is high, seedlings may fail to germinate or survive on microspaces already occupied by vascular plants. The effect of prior occupancy has been described or inferred in competition studies in other alpine/subalpine meadow ecosystems (Noble and Alexander, 1977; del Moral, 1983; Egerton and Wilson, 1993; Woodward et al., 1995). At mostly lower elevations in fire-created openings within the subalpine forest, Stahelin's study (1943) also highlighted closed grass-sedge turfs as especially inimical to seedling establishment. The competition may be for soil moisture, light, and/or nutrients (Sims and Mueller-Dumbois, 1968; Alexander et al., 1985; Cui and Smith, 1991).

Although lichens and mosses apparently impose less competition for these resources, they indicate other environmental conditions that also may limit tree seedling establishment. For example, we observed lichen-dominated microsites saturated with snowmelt runoff, which might induce soil oxygen deficits and freeze-thaw activity in the early season, but the same sites were hot, dry, and cracked in late summer. On the other hand these cracks open up mineral soil and may provide a seed planting mechanism. We also observed seedlings and saplings along rock edges, which may provide seed planting mechanisms (as soil dries, cracks develop at the rock margins) and increased water availability in late season from rain running off rocks. For tree seedlings there is at best a fine distinction between the ills of vascular plant competition and extremes of microclimates displayed where cryptogams dominate. This narrow window for seedling establishment helps explain the lower correlations between seedlings and other site variables in plots TL1 and GL, as discussed above.

CLIMATE FORCING

Do microsite features at seedling locations yield clues to future change? As pointed out by others (Grant and French, 1990; Moir and Huckaby, 1991; Earle, 1993; Payette and Lavoie, 1994; Hessl and Baker, 1997), vegetation dynamics at the forest/tundra ecotone, and especially in patch forest and patch krummholz environments with infrequent natural disturbances, are sensitive to climatic change. Where numerous interactive factors are at play, we are unsure exactly how this translates to microsite dynamics, but our study suggests some possibilities. Clearly, snow is an important agent (Walker et al., 1993). The length of season affected by snow amount and persistence had weighted correlation >absolute 0.5 (Table 1) to community life-form variables in each macroplot. Our study also indicated that tree seedlings favored meadow microsites that have a strong cryptogamic presence.

To link this study with effects of climate change scenarios upon tree expansion into openings, we propose a three step process beginning with microsuccession. We envision a generalized successional sequence: exposed soil (including less persistent snowbanks) → lichen or lichen-moss dominance → tree seedling/cryptogams/seral herbs (such as *Erigeron melanocephalus, Antennaria umbrinella,* and certain *Carex* spp.) → forbs/graminoids/established tree seedlings → trees emergent in meadows (Moir and Lee, 1990) → tree copses or krummholz or symmetric-crowned sapling stands (Wooldridge et al., 1996; Regan et al., 1998). This microsuccession is especially possible in patch forest and patch krummholz environments (Weisberg and Baker, 1995a, 1995b). Microsites most receptive to tree seedlings are in the third stage of the proposed sere. The next step to climate linkage is to recognize that the collective openings in the patch forest and patch krummholz environments usually contain a fine-grained pattern of plant communities (*sensu* Komárková, 1979) across wet to dry microsites and a short to long snowpack duration gradient. Some microsites are more sensitive to climate change than others. For example, under drier climates wet meadows retreat. In the Snowy Range few microsites at present admit the above sere; there is little or no sign of tree invasion, particularly at dry- or wet-meadow extremes. The third step is to relate any of the four climate change patterns (Fig. 1) to changes in the microenvironmental mosaics of these openings. Patch ecotones, and the vegetation on either side, expand or constrict, depending upon climate change scenarios, and local disturbances create the possibilities of the above generalized sere. The intensity of tree invasion would vary because of the many interactive factors from microsite to microsite, but disturbances such as livestock grazing or pocket gopher activity, that break vascular plant dominance, would initiate the sere. Colder or cold-wet climates would preclude the tree establishment stage of the sere where wet meadows expand or snowpack lingers. We suggest that tree seedlings would not establish even at cryptogamic sites if the growing season becomes too short. A warming climate (especially a warm, summer-wet climate that reduces drought stress, Fig. 1), accompanied by release of vascular plant dominance in present-day dry meadows, would create a greater opportunity for tree seedling establishment than we have observed in the Snowy Range.

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