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Positive Feedback Between Tree Establishment and Patterns of Subalpine Forest Advancement, Glacier National Park, Montana, U.S.A.

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Abstract

The development and maintenance of several types of visually striking vegetation patterns are controlled by positive feedback between pattern and process. These patterns are particularly common at ecotones, where the influence of positive feedback may affect the position and dynamics of the boundary between the adjacent biotic communities. In this study, I use dendrochronology to examine the role of feedback between existing trees and the establishment and survival of seedlings in the advancement of linear, finger-like strips of subalpine forest in Glacier National Park, Montana. A general upslope, windward to leeward pattern of older trees followed by progressively younger trees was evident in all sample transects, although in some cases this pattern repeated several times along the length of a transect, with each repetition originating leeward of boulders. Overall advancement rates varied from 0.28 to 0.62 m yr⁻¹. The oldest trees established in the early to mid-1700s, but establishment and advancement increased rapidly after 1850, and peaked in the early 1900s. In addition, almost all seedlings established within 5 m downwind of existing trees between 1700 and 1850, while establishment beyond this distance was common after 1850. These patterns suggest that existing trees facilitate leeward seedling establishment and survival, by depositing wind-blown snow. These seedlings in turn modify their leeward environment, thus allowing forest advancement in a linear pattern. Feedback was critical for the survival of seedlings before 1800, and strongly controlled advancement between about 1800 and 1850, but appears to have had little effect on establishment patterns since that time. The importance of feedback between pattern and process may change over time and space as a result of changes in climatic conditions or biotic surroundings.

Introduction

Studies of the feedback loop between ecological pattern and process, a central theme of landscape ecology, can benefit from the study of visually striking vegetation patterns. For example, the phenomena of “fir waves” (e.g., Oshima et al., 1958; Sprugel, 1976; Reiners and Lang, 1979), and “ribbon forest” (e.g., Billings, 1969; Holtmeier, 1982; Butler et al., 2003) in subalpine environments, and “tiger bush” (e.g., White, 1969, 1970; Tongway et al., 2001) in arid and semiarid environments illustrate the importance of interactions between vegetation patterns and various climatic, hydrologic, and geomorphic processes. Ecotones, transition areas between adjacent ecological systems, provide another focus for the study of pattern-process interactions, as the systems and the abiotic and biotic factors influencing them interact at multiple scales to form unique characteristics over space and time (Wiens et al., 1985; Holland, 1988; Gosz and Sharpe, 1989; Gosz, 1991). In this study, I examine the effects of positive feedback between ecotone pattern and tree establishment by reconstructing the advancement of a portion of the alpine treeline ecotone on Lee Ridge in Glacier National Park, Montana.

BACKGROUND

At alpine treeline ecotones in the Rocky Mountains, closed forest dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), often break up into patches before giving way to tundra vegetation (Allen and Walsh, 1996; Baker et al., 1995), a pattern that is common for ecotones generally (Gosz, 1993). In windswept

locations, these patches may consist of elongated islands of krummholz, oriented parallel to the prevailing wind. Larger linear strips composed of both krummholz and dwarfed upright trees have been described as hedges (Holtmeier, 1982). Although many different terms have been used to classify alpine treeline ecotones, “timberline” usually refers to the upper limit of continuous, closed forest, “treeline” or “tree limit” are used to indicate the highest elevation of patches in which trees still maintain an upright, tree-like growth form, and “species limit” refers to the upper limit of krummholz growth forms (Wardle, 1974; Hustich, 1979; Hansen-Bristow and Ives, 1985; Slatyer and Noble, 1992; Kullman, 2002).

The ecotone on Lee Ridge contains linear patches of forest that differ from typical krummholz islands and hedges in several respects. First, they are dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) rather than subalpine fir or Engelmann spruce. Second, many of the patches actually extend like “fingers” from closed forest into tundra. Finally, while some of the fingers contain krummholz and dwarfed trees, they primarily consist of separate individuals that have established from seed rather than by layering, and that are near the same height as those in the closed forest below.

The fingers are most clearly defined in the upper portion of the tree limit zone of Lee Ridge, but they are also visible at lower elevations, where the tree limit grades into the timberline zone (Fig. 1). These lower fingers extend to the top of the ridge and contain trees that are generally taller and more upright than in the upper fingers. Interestingly, however, several of the largest individuals have a pronounced upslope basal sweep, some growing along the ground in the direction of the prevailing wind for as much as a few meters

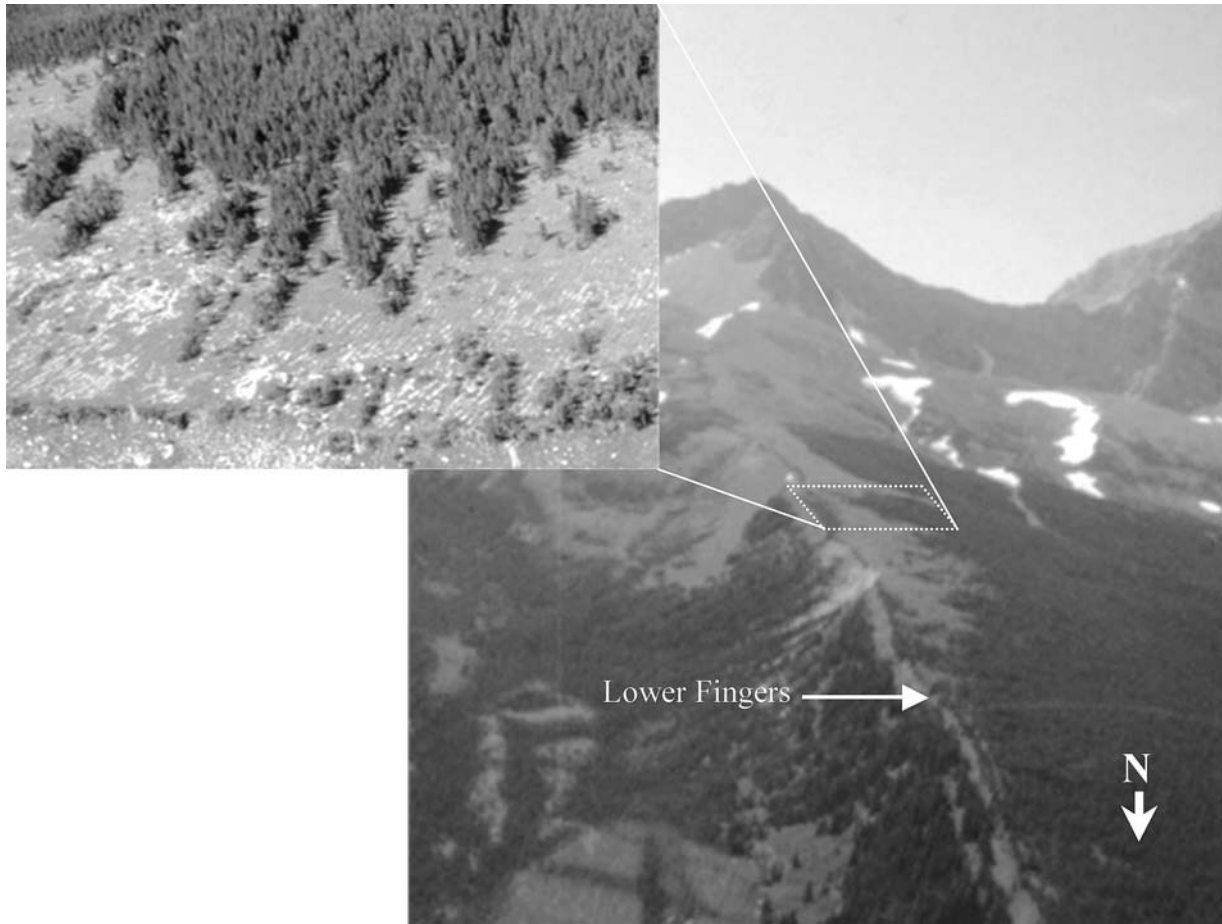


FIGURE 1. Aerial view of Lee Ridge, Glacier National Park, Montana, including locations of fingers in the upper (inset) and lower portions of the ridge. The fingers extend upslope from closed forest, in the direction of the prevailing westerly winds. Photo by D. Cairns, inset by G. Malanson.

before turning upright. Many of the trees exhibiting basal sweep also have a krummholz base (cf. Earle, 1993) characterized by a dense array of dead lower branches. These observations suggest that forests at this site formerly contained a mix of krummholz and dwarfed trees that have been able to change their growth form over time. Moreover, it suggests that the lower fingers were formerly similar in appearance to the upper fingers, and thus may provide insight into how the upper portion of the ecotone on Lee Ridge may change in the future.

The presence of such unusual patterns on Lee Ridge raises questions regarding their origin, as well as their potential effects on environmental processes. The concept of positive feedback switches (Wilson and Agnew, 1992) illustrates the potential for pattern to affect processes at ecotones. Positive feedbacks involve the modification of the environment by a community (used here to denote a general vegetation state that may include only one species), which makes the environment more suitable for that community. The term “switch” is used for these processes because they can switch the development of vegetation from one pathway to another, thus producing alternative stable states (e.g., Zimov et al., 1995).

It is important to note that “positive feedback” does not necessarily imply a “positive interaction” between communities (e.g., Bertness and Callaway, 1994). A community may have a beneficial or detrimental impact on itself or an adjacent community, depending on the type of feedback involved. Four types of switches have been identified, resulting from different combinations of one or both communities modifying an environmental factor in patches where they are or are not present. Each of these switches may produce one or more of the following vegetation conditions: (1) a stable vegetation

mosaic, where the two communities persist in different patches over time; (2) a sharpening of the boundary between communities across a gradual environmental gradient; (3) delayed vegetation change; or (4) accelerated vegetation change (Wilson and Agnew, 1992).

The consistent windward to leeward alignment of linear forest patches suggests the importance of directional, wind-mediated switches in producing the pattern. Moreover, Alftine and Malanson (2004) found that spatial patterns of the treeline in the upper portion of Lee Ridge could be approximated in a cellular automaton if such directional positive feedback was included. Although wind is involved in several processes affecting tree growth, the deposition of wind-blown snow as a result of trees reducing wind speeds has been shown to play a particularly important role in treeline patterns and dynamics. Walsh et al. (1994) found that an intermediate amount of snow is required to allow tree growth to occur at treeline locations in Glacier National Park. Too much snow can cause direct, mechanical damage (e.g., Kullman, 1989; Homma, 1997), or indirect effects such as a reduced growing season or desiccation due to frozen soil (Billings, 1969; Hansen and Klikoff, 1972; DeLucia, 1986). Conversely, snow has been shown to be important in protecting plants from damaging or desiccating winds, along with blowing snow and ice (Tranquillini, 1979; Frey, 1983; Hadley and Smith, 1983, 1986), and snowdrifts provide additional moisture to plants after peak stream flow in the spring and summer (Berg, 1987). Finally, snowdrifts increase the input (Bowman, 1992) and availability (Williams et al., 1998) of nutrients through atmospheric deposition and increased soil temperatures, respectively. Thus, in arid treeline sites with a moderate level of snow deposition, the leeward environment of existing patches may be enhanced for seedling

establishment and survival. Moreover, if the feedback is sufficiently strong, the switch may produce an acceleration of vegetation change.

The potential for feedback to accelerate vegetation change has important implications for the sensitivity of ecotones to climate change. Because ecotones often represent the distributional limits of the communities they divide, it has been suggested that changes in their positions may be useful in detecting climate change (e.g., Turner et al., 1988; Neilson, 1993; Risser, 1995), but others have argued that the movement of most ecotones is too slow to make them useful as climate change indicators (e.g., Noble, 1993; Kupfer and Cairns, 1996; Cairns and Malanson, 1997). However, ecotones that are controlled by positive feedback may respond more rapidly to changes in climate.

In this paper, I evaluate the effects of directional positive feedback on the pattern and dynamics of the ecotone on Lee Ridge by reconstructing the development of the lower elevation fingers. I use dendrochronology to reconstruct and map spatio-temporal patterns of forest advancement, in order to determine whether positive feedback between forest pattern and tree establishment can explain the observed patterns, and can produce an acceleration of vegetation change. I also evaluate the relative importance of feedback and climatic controls on the ecotone.

Study Area

Lee Ridge is located in the northeast corner of Glacier National Park, a 4×10^5 ha international biosphere reserve in northwestern Montana, adjacent to the Canadian border (Fig. 2). The park is bisected by the continental divide, which follows the northwest-southeast-trending Livingston and Lewis Ranges. The mountains consist primarily of Precambrian rocks overlying Cretaceous sedimentary layers, as a result of the extensive Lewis overthrust fault (Alt and Hyndman, 1986). Lee Ridge is a north-south-trending spur that slopes gradually downward to the west and north from the base of Gable Mountain, thus creating a bidirectional elevation gradient (see Fig. 1). Lee Ridge remained free of glacial ice through the Pleistocene, but does exhibit relict solifluction terraces (Walsh et al., 2003).

The continental divide splits the park into two contrasting environments. The climate west of the divide is dominated by warm, moist air masses originating over the Pacific Ocean. In contrast, the east side of the park, where Lee Ridge is located, is drier and more variable due to a combination of rainshadow effects, warm Chinook winds, and the influence of arctic air masses (Finklin, 1986). Data from a weather station established by the U.S. Geological Survey (USGS)–Biological Resources Division on Lee Ridge indicate that the ridge is dominated by strong westerly winds year round and is located in one of the driest areas in the park.

Methods

To reconstruct the spatio-temporal patterns of forest advancement, I collected field data in five transects with dimensions defined by the fingers themselves. The bases of the fingers were usually clearly distinguished from the lower-elevation closed forest by a group of trees, often dead or dying, which exhibited basal sweep and/or krummholz bases. Thus, I started each transect at this point and extended it upslope, stopping short of the top of the ridge to avoid a hiking trail. The width of each finger varied along its length, so I set each transect width equal to the width of the finger where it was most clearly defined, to the nearest meter.

In each transect, I recorded the species and diameter at breast height (dbh) of all live and dead standing trees (≥ 4 cm dbh), and the numbers of seedlings (stems 30 cm to 1.4 m tall) and saplings (stems > 1.4 m tall; < 4 cm dbh) by species in 5-m increments. I mapped the relative location of all live and dead standing trees, as well as boulders

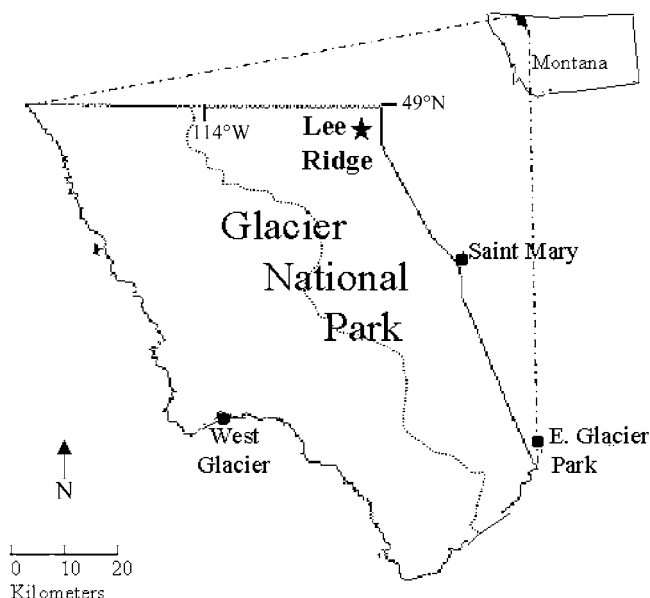


FIGURE 2. Study area, Lee Ridge. The dotted line running through the middle of the park represents the continental divide.

that could provide a shelter for seedling establishment, and determined the absolute locations of the transects using a GPS receiver. I cored at least 50% of all live trees in 10-cm diameter classes with an increment borer 20 cm from the ground. Finally, I cored 40 randomly selected trees in a cove between two of the transects in order to compare tree establishment in the fingers relative to the coves.

FOREST ADVANCEMENT PATTERNS AND RATES

I determined tree ages by preparing and cross-dating the tree cores using standard dendrochronological techniques, including ring width (Stokes and Smiley, 1968), latewood width and density (Filion et al., 1986), and frost rings (LaMarche, 1970). I used geometric approximation to correct samples that did not include the pith. I then determined tree ages, and mapped tree locations and establishment dates in 10-yr age classes.

To determine whether the fingers represent advancement of the forest limit on Lee Ridge, I examined the relationship between the distance from the base of a transect and tree age. Advancement should be identifiable as a negative relationship between these variables. However, infilling at the base of a finger would weaken the relationship without representing a reduction in advancement. A scatter plot of age and distance in this case would appear as a lopsided cloud of points, with a negatively sloped edge. Ecological phenomena frequently show such “factor-ceiling” distributions, because a given ecological factor may act as a constraint on the upper bounds of organism responses, but other (often unmeasured) factors may control the lower bounds (Thomson et al., 1996). Changes near the center of these distributions may be statistically indistinguishable from zero, while changes near the extremes of distributions are nonzero. In such situations, traditional correlation analyses are unable to convey the ecologically meaningful information contained in the edge of the distribution.

Quantile regression has been used for several applications in ecology (see Cade and Noon, 2003, for a review) to estimate rates of change along or near the upper boundary of response distributions. In this technique, regression lines are fit to different quantiles of the cumulative distribution function so that a certain proportion, τ , of the sample observations are less than or equal to the estimate. For example, the 50th (percentage) quantile represents the median of the distribution,

TABLE 1

Characteristics, composition, and structure of the five sample transects, and the entire study site.

Transect	1	2	3	4	5	Study site
Area (ha)	0.06	0.036	0.084	0.078	0.03	0.288
Length (m)	100	60	120	130	60	
Width (m)	6	6	7	6	5	
Azimuth (°)	58	63	60	56	62	
Base elevation (m)	1984	1976	1967	1964	1993	
Top elevation (m)	1996	1983	1981	1980	2000	
Trees (no.)						
Lodgepole pine	87	109	199	189	53	637
Subalpine fir	109	16	27	19	3	174
Engelmann spruce	20	3	4	6	12	45
Limber pine	0	2	1	3	4	10
Total	216	130	231	217	72	866
Basal area (m ² ha ⁻¹)						
Lodgepole pine	30.7	48.8	31.8	35.0	30.2	34.4
Subalpine fir	9.7	2.4	1.7	1.9	0.6	2.9
Engelmann spruce	8.2	0.6	0.6	0.8	6.6	3.4
Limber pine	0.0	0.1	0.1	0.4	6.5	0.9
Total	48.6	51.9	34.2	38.1	43.9	41.7
Density (ha ⁻¹)						
Lodgepole pine	1450.0	3027.8	2369.0	2435.9	1733.3	2211.8
Subalpine fir	1816.7	444.4	321.4	243.6	100.0	604.2
Engelmann spruce	333.3	83.3	47.6	64.1	400.0	156.3
Limber pine	0.0	55.6	11.9	38.5	133.3	34.7
Total	3600.0	3611.1	2750.0	2782.1	2366.6	3006.9

such that 50% of the observations are less and 50% greater than the estimate; for a 60th quantile estimate, 60% of the observations are less and 40% greater, and so forth. Although quantiles at or near the upper boundary of factor-ceiling distributions will best represent a limiting relation, Cade et al. (1999) suggest testing a range of quantiles in order to maximize the trade-off between increasing response and loss of precision in the estimate associated with wider confidence intervals at extreme quantiles. I used the 20th, 40th, 60th, and 80th quantiles to determine whether the slope of the relationship between distance from the base of a transect and tree age was significantly different from zero, and whether this relationship changed at different levels of the response distribution.

To determine whether an acceleration of vegetation change has occurred at the study site, I calculated advancement rates at two scales. At the transect scale, I determined the distance from the base to the top of each transect, and divided this value by the number of years between the establishment of the first tree and the furthest upslope tree in the transect. In addition, because the purpose of this study was to examine the finer-scale feedback between existing trees and subsequent tree establishment, I also calculated advancement based on the establishment of new trees within 5 m upslope of existing trees. Any tree that established upslope of the 5-m limit of an existing tree was considered to provide a separate base for calculating advancement in subsequent years. Trees that established downslope of an existing tree were considered to represent infilling, and were not used to calculate advancement.

Results

I took core samples from 494 trees (57% of all live trees in the transects), and 96% of these were successfully cross dated. The mean number of years added to samples that did not include the pith was 4.8 yr (range 0–30 yr). In addition, due to either heart rot or low

TABLE 2

Quantile regression statistics for the five sample transects, including selected regression quantiles (τ), estimates of β_0 and β_1 , 95% confidence intervals for β_1 , and P for $H_0: \beta_1 = 0$ for the model $y = \beta_1 x + \beta_0$, where $y =$ tree age and $x =$ distance from the base of a transect.

τ	b_1	b_0	95% CI for β_1	P
Transect 1				
20th	-0.32	95.84	-0.51 to -0.14	<0.01
40th	-0.30	113.24	-0.67 to 0.07	0.111
60th	-0.29	133.04	-0.85 to 0.27	0.306
80th	-0.68	183.98	-1.22 to -0.14	<0.05
Transect 2				
20th	-1.04	81.15	-1.59 to -0.49	<0.001
40th	-1.90	129.18	-2.47 to -1.33	<0.001
60th	-2.32	155.56	-3.15 to -1.49	<0.001
80th	-3.06	203.25	-3.65 to -2.47	<0.001
Transect 3				
20th	-0.30	57.52	-0.56 to -0.05	<0.05
40th	-0.36	70.36	-0.57 to -0.15	<0.01
60th	-0.52	95.09	-0.73 to -0.32	<0.001
80th	-0.47	126.91	-0.84 to -0.10	<0.05
Transect 4				
20th	-0.32	62.37	-0.64 to 0.01	0.057
40th	-0.24	73.86	-0.40 to -0.09	<0.01
60th	-0.38	100.83	-0.53 to -0.23	<0.001
80th	-0.42	120.15	-0.53 to -0.30	<0.001
Transect 5				
20th	-0.36	69.49	-0.81 to 0.10	0.126
40th	-0.59	92.02	-1.35 to 0.18	0.132
60th	-0.33	104.00	-1.82 to 0.15	0.653
80th	-0.95	152.91	-3.10 to 0.19	0.375

branches, 8 samples (1.6% of total) could not be cored at 20 cm. The mean coring height for these samples was 47.5 cm (range 25–120 cm). The total number of samples with potential dating problems (including cross dating, pith correction values greater than 10 yr, and coring heights greater than 20 cm) represented less than 14% of the total data set.

The five sample transects had generally similar structural and compositional characteristics (Table 1). They varied considerably in length, but most were about 6 m wide, and all were oriented from west-southwest to east-northeast. Lodgepole pine was dominant in all of the transects in terms of basal area and in four in terms of density. Basal area for subalpine fir and Engelmann spruce was similar across the transects, but fir occurred in considerably higher densities than spruce. Limber pine (*P. flexilis*) (1% of all live trees) was either a minor component or was absent in all transects.

ADVANCEMENT PATTERNS

The quantile regression analyses showed negative slopes for all quantiles in all transects (Table 2, Fig. 3), and slopes were steepest for the 80th quantile estimate in four of the five transects (1, 2, 4, and 5; 60th quantile for transect 3). Slopes were significantly ($P < 0.05$ or less) different from zero in transects 1, 2, 3, and 4, and the significantly different slopes occurred most frequently in the 80th quantile.

Several similarities in spatial patterns of advancement may be identified among the transects. For example, most of the oldest trees established at or near the base of the fingers. Although a general trend of decreasing tree age leeward of the oldest trees is evident, some of the transects (particularly 3 and 4) show a repeating windward to leeward

pattern of old trees followed by successively younger trees. In most cases, each repetition began leeward of boulders, and the locations of the oldest trees coincided generally with groups of dead trees.

Temporal patterns of establishment also varied among the transects (Fig. 4). Mean tree ages between transects were significantly different (t -tests, $P < 0.05$) for all pairs except transects 2 and 5, and transects 3 and 4. Several trees established during the 1700s in transect 1, while none to a few established in the other transects. In addition, peaks of establishment occurred during the 1940s or 1950s in transects 2, 3, and 4, while the peaks for transects 1 (1880s) and 5 (1900s) occurred earlier. Similarities among the transects include higher overall establishment during the 1900s compared to the previous two centuries, and low establishment during the 1910s. Trees in all transects were significantly older (t -tests, $P < 0.001$) than those in the cove.

ADVANCEMENT RATES

Patch-scale advancement rates were similar among the transects, while transect-scale rates were more variable (Table 3). Transects 3 and 1 had the highest overall rates, each greater than 0.5 m/yr. Transect 4 followed closely at 0.48 m/yr, and transects 5 and 2 had the lowest rates at 0.32 and 0.28 m/yr, respectively. Rates at the patch scale fell in the same order by transect, but they were 2–4 times smaller than those at the transect scale.

Discussion

TRANSECT CHARACTERISTICS

The similarities in the dimensions of the transects suggest that similar processes were responsible for the development of the fingers. For example, the fact that all of the transects were oriented generally west to east suggests the importance of the dominant westerly winds in controlling the ecotone patterns. The similarity in width among the transects, combined with the fact that tree ages were consistently older in the transects compared to the sampled cove, suggests that these winds may be funneled around existing trees at high speeds, thus preventing expansion in the intervening areas, as suggested by Wilson and Agnew's (1992) reaction switch, and as observed in other treeline environments (Scott et al., 1993).

The structural and compositional characteristics of the transects also exhibit some important similarities and differences. For example, lodgepole pine had the highest basal area in all of the transects, and the highest density in all but one. This is unusual for treeline locations in Glacier National Park, which are usually dominated by subalpine fir (Cairns, 2001). Carter and Smith (1988) found that lodgepole pine had greater water-use efficiency than either subalpine fir or Engelmann spruce on open, dry sites at low elevations. The windy, low-elevation (75 m below the park average) treeline conditions on Lee Ridge may therefore give lodgepole pine a competitive advantage. Alternatively, although there was no direct evidence of recent fires near my study site, extensive crown fires may have occurred in the past, killing most trees and increasing the abundance of lodgepole pine seeds relative to other species.

FEEDBACK AND SPATIAL PATTERN

The fact that the slopes of the regression lines for all transects were negative illustrates that advancement has taken place within the study site, and the general increase in slope steepness toward the tops of the response distributions indicates that infilling has also occurred. Moreover, the regression analyses suggest the importance of feedback in the advancement process. In particular, the windward to leeward pattern of successively younger trees suggests that established trees

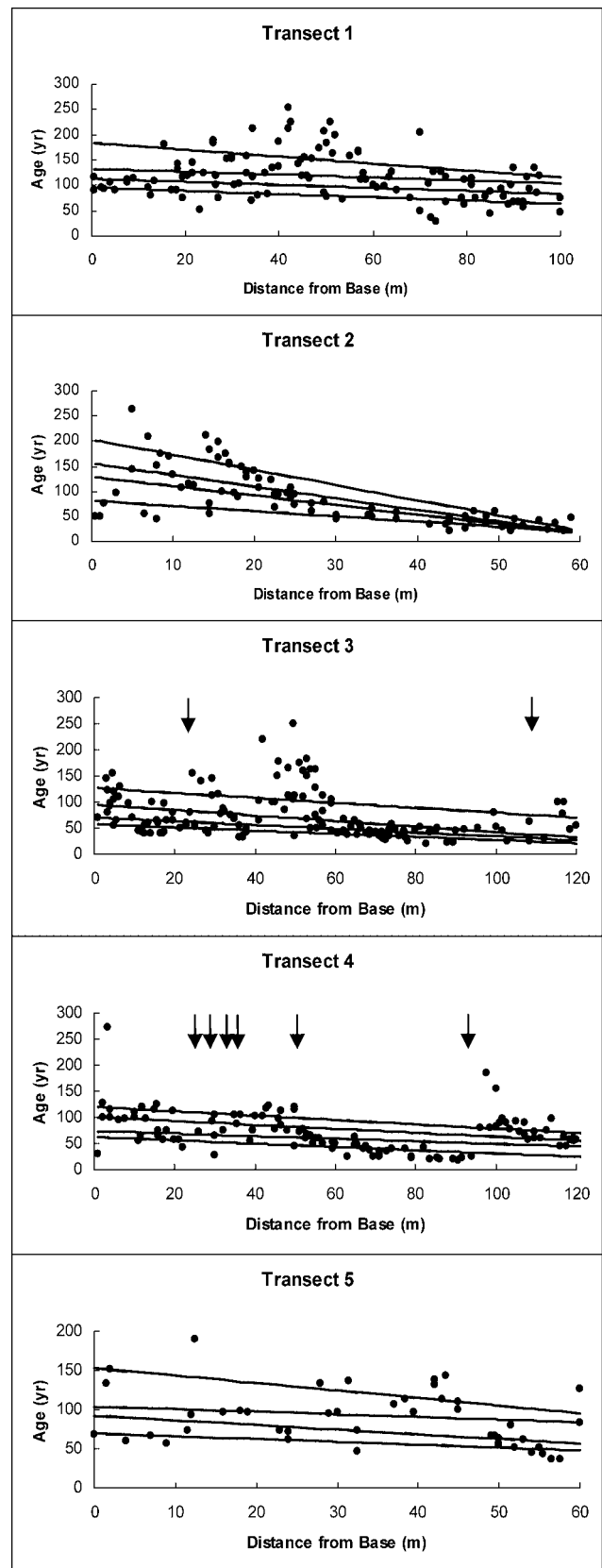


FIGURE 3. Quantile Regression graphs illustrating forest advancement in the five sample transects. Arrows indicate the locations of boulders.

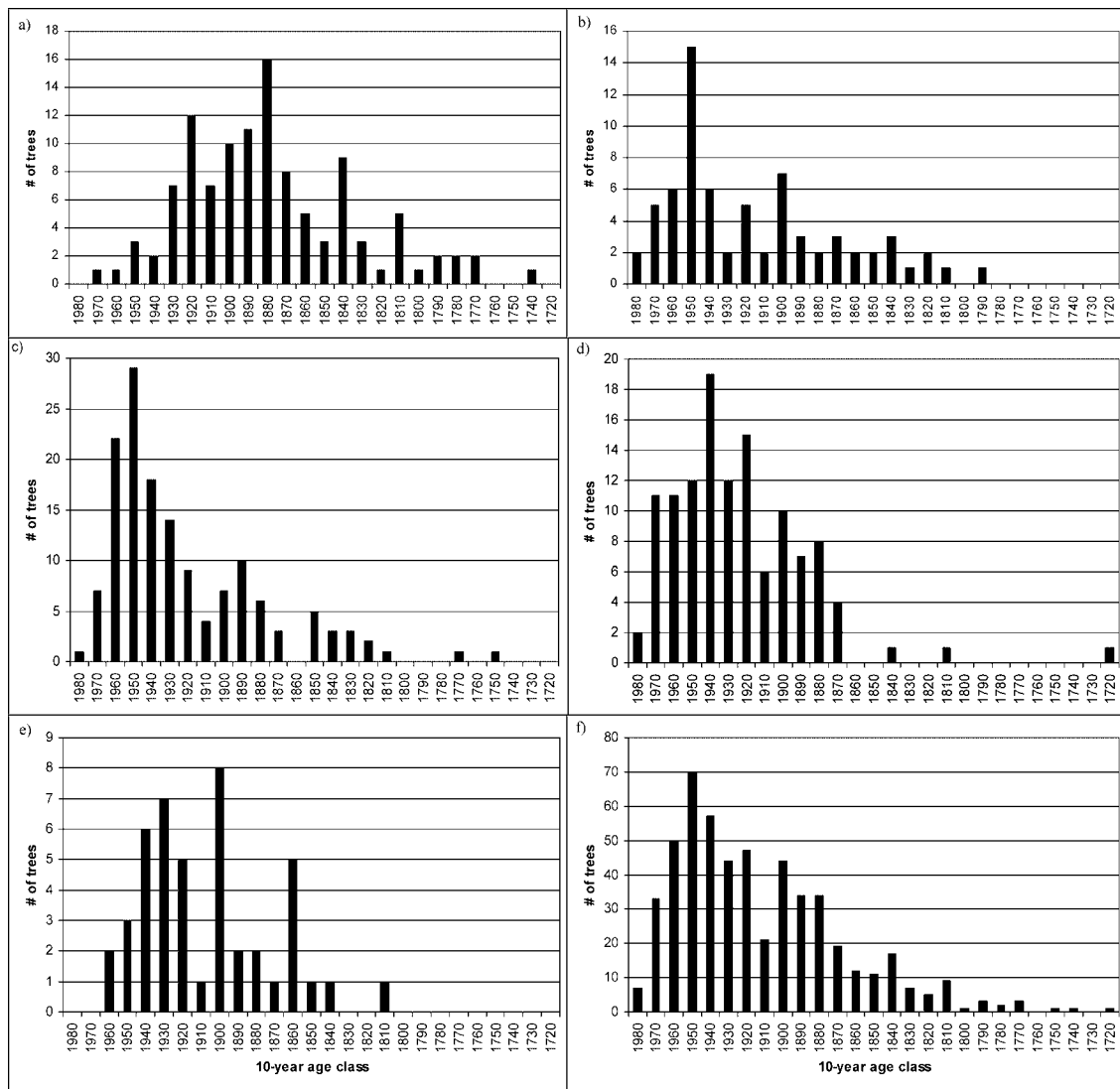


FIGURE 4. Histograms showing establishment of trees in 10-yr age classes for (a) transect 1, (b) transect 2, (c) transect 3, (d) transect 4, (e) transect 5, and (f) all transects.

improve the microenvironment for new seedlings. Variations in this expected pattern are not surprising, given the fact that the movement of ecotones is typically heterogeneous over both time and space (e.g., Payette and Filion, 1985; Kullman, 1986; Malanson, 1993; Lloyd and

TABLE 3

Forest advancement rates by transect within 5 m of existing trees (patch scale) and for each transect (transect scale).

Transect	Advancement rate (m yr ⁻¹)
	Patch-scale
1	0.14
2	0.12
3	0.15
4	0.12
5	0.08
	Transect-scale
1	0.57
2	0.28
3	0.62
4	0.48
5	0.32

Graumlich, 1997; Payette et al., 2001). Nevertheless, many of the differences among the transects may be explained by the fact that the feedback-induced pattern is superimposed on other, spatially variable factors.

The influence of boulders, for example, is evident in transects 3 and 4, where trees were able to establish tens of meters upslope from the closed forest or from existing patches. Although trees were occasionally able to establish well in advance of existing trees in the other transects, which did not contain boulders, such jumps were generally not as common or as large. The boulders thus appear to have provided safe sites for advanced seedling establishment, as has been suggested in the development of krummholz islands and hedges (Klikoff, 1965; Marr, 1977; Holtmeier, 1982). Therefore, when several boulders are present within a finger, the resulting pattern is a repeating sequence of old trees followed by successively younger trees leeward.

In addition to boulders, differences in microtopography also explain some of the differences in the spatial pattern of advancement among the fingers. Although I did not measure microtopographic variations, relict solifluction terraces cover most of Lee Ridge upslope from my study site (Walsh et al., 2003). The terraces are oriented at acute angles (roughly 20°; see Fig. 1 inset) relative to fingers on this upper slope. In some areas, the terraces appear to be providing shelter

from wind, just like the boulders, in which seedlings can successfully establish, and then produce hedges or krummholz islands. The edges of these terraces may also produce turf exfoliation sites (Butler et al., 2004), which are more penetrable and thus more favorable microsites for seedling establishment. Although these terraces are not as evident in my study site, they are visible in a few areas, particularly in the higher elevation transects (1 and 5). This may explain why some of the first trees to establish in these fingers are located near the middle or top of these transects, despite the fact that climatic conditions were presumably harsher compared to the other fingers, and that no boulders were present.

A final factor that could explain variations in spatial patterns among the transects is caching of limber pine seeds by Clark's nutcracker (*Nucifraga columbiana*). Although limber pine was rare, clusters of saplings were present in the study site, indicating regeneration from seed caches (Casey and Tomback, 1994). Moreover, most of the dead trees identified in the transects were limber pine, which also grew in clusters. It is possible that past establishment of these clusters also allowed the development or extension of fingers.

FEEDBACK MECHANISMS

Direct observations, and snow surveys conducted by the USGS–Biological Resources Division on Lee Ridge, show that snow deposition is enhanced leeward of existing trees. Thus, it is likely that wind-snow feedback plays an important role in the observed patterns. Given the fact that trees within the fingers maintain canopies well above the snowpack level and show little evidence of wind-damaged foliage, it seems most likely that increased spring and summer moisture, rather than protection from winter winds, is the primary feedback mechanism. The importance of soil moisture in moderating the influence of temperature over the position of treeline ecotones has been suggested by other studies (e.g., Weisberg and Baker, 1995; Hessel and Baker, 1997; Lloyd and Graumlich, 1997; Cairns and Malanson, 1998).

The leeward environment of existing trees may also be improved through the increased input and availability of soil nutrients, again tied to snow deposition. Sediment traps placed within and leeward of krummholz patches on Lee Ridge show little deposition (D. R. Butler, personal commun.), but krummholz soils throughout Glacier National Park are generally deeper and more nutrient-rich compared with tundra soils (Malanson and Butler, 1994; Cairns, 1999). At other treeline sites in the Rocky Mountains, migrating krummholz islands have been shown to reduce soil carbon in areas unaffected by enhanced snowpack (Pauker and Seastedt, 1996), but moderate to heavy snowdrifts increased the deposition and cycling of nutrients, particularly carbon and nitrogen (Bowman, 1992; Holtmeier and Broll, 1992; Williams et al., 1998).

Recent studies in the Medicine Bow Mountains in Wyoming have suggested that existing trees may also improve conditions for seedling establishment and survival during the summer by reducing temperatures and intense UV radiation during the day, and increasing soil temperatures at night (Smith et al., 2003; Johnson et al., 2004). However, the intensity of UV radiation is probably less important on Lee Ridge, which is 1000 m lower in elevation than the Medicine Bow sites. Moreover, the increase in night-time soil temperatures around existing trees in the summer should be isotropic, and thus cannot explain the directional advancement of the fingers.

ACCELERATION OF VEGETATION CHANGE

The overall pattern of advancing fingers with intervening coves implies the presence of an acceleration of vegetation change. Where existing trees, boulders, microtopographical variation, or other

conditions made initial seedling establishment possible, trees have been able to replace tundra vegetation via positive feedback. In contrast, the coves, where either no feedback is operating, or a reaction switch may actually be delaying the change from tundra to trees, appear to be undergoing a more gradual and more recent invasion by trees. Such a reaction switch would explain why advancement in the coves is taking place more slowly than in the fingers, the opposite pattern than is expected from research on the shape and dynamics of landscape boundaries (e.g., Hardt and Forman, 1989).

The possibility of an acceleration of vegetation change could also be assessed through comparison of advancement rates with other studies of changes in alpine treeline ecotones. Such comparison is difficult, however, because other studies either do not report advancement rates, or base advancement on a different component of the ecotone, such as the establishment of new seedlings and saplings rather than mature trees, or expansion resulting from krummholz stems changing to upright trees. Nevertheless, Kullman (1986) did calculate advancement rates based on newly established tree-size individuals in the Swedish Scandes that are similar to those calculated for the fingers (mean 0.52 m/yr). The overall rates for the fingers are sufficiently high that changes could be detected in the field, or through high-resolution aerial photography or remote sensing.

ESTABLISHMENT PATTERNS AND CLIMATIC CONTEXT

The oldest trees identified in four of the five sample transects established between 1720 and 1750. However, the presence of dead trees, which were also sampled but could not be cross dated, raises questions regarding the timing of tree establishment. It is possible that these dead trees established before the oldest live trees, especially considering that most of the dead trees were limber pine, a common pioneer species (Burns and Honkala, 1990; Rebertus et al., 1991). Nevertheless, the oldest live trees were lodgepole pine rather than limber pine, and some regeneration of limber pine is occurring at the study site. The locations of dead trees, especially if combined with unsampled trees, may, however, explain why some live trees were apparently able to establish more than 5 m upslope of sampled trees. If all trees were dated, it is possible that a more clear sequence of progressively younger trees from west to east would be evident.

Regardless of whether the oldest live trees were the first to establish, the commencement of forest advancement in the study site pre-dates the approximate end of the Little Ice Age in Glacier National Park, in the mid-nineteenth century (Carrara and McGimsey, 1981; Carrara, 1989; Hall and Fagre, 2003). Nevertheless, advancement and increases in numbers of trees were very gradual through the end of the eighteenth century, suggesting that climatic conditions were indeed still very harsh during this time.

It is also interesting to note that more than half of the trees that established during the eighteenth century exhibited basal sweep and/or a krummholz base. In a study of the arctic treeline, Payette et al. (1989) suggested that “creeping spruces” (krummholz) were unable to enhance snow drifting at exposed sites, thus preventing seedling establishment at these sites. However, if krummholz individuals were able to change their growth form, as is suggested by the upright trees with basal sweep at my study site, then they would be able to reduce wind speed sufficiently to deposit snow immediately around and leeward of their stem (e.g., Earle, 1993). Thus, when the first trees in the transects established, feedback effects may have been very small. But as they began to change to a more vertical orientation under improving climatic conditions, feedback, and thus tree establishment and advancement rates, would have been enhanced.

The increase in advancement and numbers of trees during the early to mid-1800s suggests that climatic conditions were becoming more favorable during this period. Nevertheless, almost all establish-

ment and advancement during this period occurred either adjacent to or within 5-m upslope of trees or boulders, suggesting that feedback was necessary for the survival of new trees.

Between 1850 and 1880, in contrast, trees in transects 1, 4, and 5 established more than 5 m upslope of existing trees or boulders. These patterns combined with the doubling or tripling of establishment rates between 1880 and 1900 in transects 1, 3, and 4 suggest that climatic conditions in the latter half of the nineteenth century were becoming sufficiently favorable to reduce the importance of feedback.

Patterns and rates of establishment among the transects were more variable in the first half of the twentieth century. However, rates dropped considerably for all transects between 1910 and 1920, raising questions regarding extreme or anomalous climatic events that may have restricted establishment during this time period. Many samples at my study site recorded a frost ring early in the growing season of 1910. An extreme late frost event may have caused reduced reproduction in subsequent years. Many of the newly established trees during this time represented increases in density rather than advancement, but in several cases they continued to establish beyond 5 m upslope of existing trees. Over the next 20 yr the distances between existing and newly established trees increased even more, and establishment rates either increased or remained the same in all transects.

Establishment generally continued to increase toward the middle of the twentieth century, reaching an overall peak between 1950 and 1960. Most new trees were scattered evenly, indicating that most of this establishment represented infilling. However, trees were concentrated near the top of transect 1, indicating that conditions had improved sufficiently to allow establishment at the highest elevations of the study site.

The decline in establishment rates in most of the transects over the last 30 yr, especially between 1980 and 1990, and the concentration of most new trees near the tops of the transects seem to represent another abrupt change. This may be explained by the fact that seedlings and saplings, which were present in all transects, were not sampled. However, data from seedlings sampled higher on the ridge also indicate an abrupt drop in establishment beginning in 1980, possibly in response to a switch to a positive phase of the Pacific Decadal Oscillation cycle (Alfline et al., 2003).

EFFECTS OF CLIMATE VS. FEEDBACK

The lack of synchronicity in the timing of advancement among the transects, particularly prior to the twentieth century, suggest that local-scale processes, including biotic and abiotic feedback effects, were more important than regional-scale climate in determining pattern and process. However, spatio-temporal patterns of advancement within each transect suggest that thresholds may exist, in which the relative importance of climate and feedback in controlling establishment and advancement rates switches over time, causing differences in the rates. For example, conditions between the eighteenth and early nineteenth centuries were apparently too harsh for much establishment and advancement to occur. Feedback then appears to have played an important role in increases in establishment and advancement during the early to mid-nineteenth century. The dramatic increase in establishment toward the end of the nineteenth century seems to represent another threshold, since advancement occurred over a broader scale, suggesting that continually improving climatic conditions had reduced the importance of feedback. Variation in the strength of feedback in response to climate variability has been identified previously in the facilitation of tree establishment by nurse shrubs in Argentina (Kitzberger et al., 2000), and threshold effects of temperature on tree growth rates have been identified at the treeline in the Alps (Paulsen et al., 1999). These results are also consistent with the prediction that positive interactions between plants will be most common in areas of

high physiological stress (e.g., Bertness and Callaway, 1994; Hacker and Gaines, 1997), in that the importance of these interactions seems to have diminished over time as physiological stress decreased.

KRUMMHOLZ ISLANDS, HEDGES, AND FINGERS

The importance of feedback in producing and maintaining krummholz islands and hedges (Marr, 1977; Holtmeier, 1982; Benedict, 1984; Alfline and Malanson, 2004), and the influence of krummholz islands on seedling establishment (Camarero and Gutiérrez, 1999, 2002) have been identified previously. However, only one other study (Minnich, 1984) suggests that feedback may play a role in producing linear patterns of upright forest near treeline. This study mentioned the existence of trees in “row configuration” on Mount San Gorgonio in the San Bernardino Mountains of California, and although the specific cause of this pattern was not investigated, the rows occurred near ridgetops in the most wind-exposed areas. In addition, the orientation of these rows changed according to spatial differences in local storm winds, suggesting that established trees improved conditions for downwind individuals. Interestingly, the dominant tree species in these rows was also lodgepole pine (although var. *murrayana*). It may be that as a generalist species, lodgepole pine is more tolerant of the dry conditions produced by strong winds and is able to respond well to slight improvements in microclimate. In addition, lodgepole pine does not reproduce vegetatively through layering, as subalpine fir and Engelmann spruce do. This helps to explain why the fingers on Lee Ridge and the rows on Mount San Gorgonio differ from the hedges described by Holtmeier (1982).

Conclusions

Positive feedback between existing trees and seedling establishment and survival plays an important role in the finger-like pattern of the boundary between upright forest and tundra vegetation on Lee Ridge. The fingers represent the advancement of subalpine forest as a result of existing trees depositing wind-blown snow. The importance of feedback appears to have varied over time according to the following sequence: (1) between 1730 and about 1800, feedback was critical for the slow advancement, and possibly even the survival, of trees; (2) between about 1800 and 1850 feedback allowed advancement to occur much more rapidly; (3) after 1850, the importance of feedback began to be reduced under continually improving climatic conditions at the end of the Little Ice Age.

Alpine treeline ecotones have received much attention recently due their potential as indicators of climate change. However, the sensitivity of ecotones to climate can vary spatially and temporally (e.g., Luckman and Kavanagh, 2000; Kullman, 2002). Previous studies of treeline ecotones in Glacier National Park indicated little to no change in the location of the ecotone (Butler et al., 1994; Klasner and Fagre, 2002). Yet, the ecotone on Lee Ridge has shown sensitivity to climate (Alfline et al., 2003), modified by positive feedback. Nevertheless, the importance of feedback appears to have changed over time and space even within the ecotone on Lee Ridge. While feedback may no longer play an important role in the maintenance of the lower elevation fingers, it may still be controlling the patterns and dynamics of the upper fingers, where climatic conditions are still quite harsh. Thus, continued advancement of this upper portion of the ecotone may be expected. The importance of feedback in this area may, however, also be diminished in the future under continually improving climatic conditions. Identifying climatic thresholds at which feedback increases or decreases in importance could further indicate whether this site or other ecotones would be useful in monitoring future climatic changes.

This study suggests that local treeline sites with unusual

vegetation patterns may be useful for monitoring climate change, if those patterns are controlled by a positive feedback mechanism that would produce an acceleration of vegetation change. The similarity of the patterns in this study to those of the contrasting environment of Mt. San Gorgonio indicates potential generality. If positive feedback can override climatic controls on alpine treeline ecotones, objections to their potential as indicators of climate change (e.g., Noble, 1993; Kupfer and Cairns, 1996; Cairns and Malanson, 1997) may not apply.

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References Cited

- Alftine, K. J., and Malanson, G. P., 2004: Directional positive feedback and pattern at an alpine treeline. *Journal of Vegetation Science*, 15: 3–12.
- Alftine, K. J., Malanson, G. P., and Fagre, D. B., 2003: Feedback-driven response to multidecadal climatic variability at an alpine treeline. *Physical Geography*, 24: 520–535.
- Allen, T. R., and Walsh, S. J., 1996: Spatial and compositional pattern of alpine treeline, Glacier National Park, Montana. *Photogrammetric Engineering and Remote Sensing*, 62: 1261–1268.
- Alt, D., and Hyndman, W., 1986: *Roadside Geology of Montana*. Missoula, MT, Mountain Press, 427 pp.
- Baker, W. L., Honaker, J. J., and Weisberg, P. J., 1995: Using aerial photography and GIS to map the forest-tundra ecotone in Rocky Mountain National Park, Colorado, for global change research. *Photogrammetric Engineering and Remote Sensing*, 61: 313–320.
- Benedict, J. B., 1984: Rates of tree-island migration, Colorado Rocky Mountains, USA. *Ecology*, 65: 820–823.
- Berg, N. H., 1987: Krummholz snowdrifts: hydrologic implications at a Colorado treeline site. In: Troendle, C. A., Kaufmann, M. R., Hamre, R. H., and Winokur, R. P. (tech. coords.), *Management of Subalpine Forests: Building on 50 years of Research*. USDA Forest Service General Technical Report GTR-RM-149, 141-1, 263 pp.
- Bertness, M. D., and Callaway, R., 1994: Positive interactions in communities. *Trends in Ecology and Evolution*, 9: 191–193.
- Billings, W. D., 1969: Vegetational pattern near timberline as affected by fire-snowdrift interactions. *Vegetatio*, 19: 192–207.
- Bowman, W. D., 1992: Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arctic and Alpine Research*, 24: 211–215.
- Burns, R. M., and Honkala, B. H. (tech. coords.), 1990: *Silvics of North America: I. Conifers*. USDA Forest Service, Agriculture Handbook 654, Washington, DC, 681 pp.
- Butler, D. R., Malanson, G. P., and Cairns, D. M., 1994: Stability of alpine treeline in Glacier National Park, Montana, USA. *Phytocoenologia*, 22: 485–500.
- Butler, D. R., Malanson, G. P., Bekker, M. F., and Resler, L. M., 2003: Lithologic, structural, and geomorphic controls on ribbon forest patterns in a glaciated mountain environment. *Geomorphology*, 55: 203–217.
- Butler, D. R., Malanson, G. P., and Resler, L. M., 2004. Turf-banked terrace treads and risers, turf exfoliation and possible relationships with advancing treeline. *Catena*, 58: 259–274.
- Cade, B. S., and Noon, B. R. 2003: A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 8: 412–420.
- Cade, B. S., Terrell, J. W., and Schroeder, R. L., 1999: Estimating effects of limiting factors with regression quantiles. *Ecology*, 80: 311–323.
- Cairns, D. M., 1999: Multi-scale analysis of soil nutrients at alpine treeline in Glacier National Park, Montana. *Physical Geography*, 20: 256–271.
- Cairns, D. M., 2001: Patterns of winter desiccation in krummholz forms of *Abies lasiocarpa* at treeline sites in Glacier National Park, Montana. *Geografiska Annaler*, 83A: 157–168.
- Cairns, D. M., and Malanson, G. P., 1997: Examination of the carbon balance hypothesis of alpine treeline location in Glacier National Park, Montana. *Physical Geography*, 18: 125–145.
- Cairns, D. M., and Malanson, G. P., 1998: Environmental variables influencing carbon balance at the alpine treeline ecotone: a modeling approach. *Journal of Vegetation Science*, 9: 679–192.
- Camarero, J. J., and Gutiérrez, E., 1999: Structure and recent recruitment at alpine forest-pasture ecotones in the Spanish central Pyrenees. *Ecoscience*, 6: 451–464.
- Camarero, J. J., and Gutiérrez, E. 2002: Plant species distribution across two contrasting treeline ecotones in the Spanish Pyrenees. *Plant Ecology*, 162: 247–257.
- Carrara, P. E., 1989: Late Quaternary glacial and vegetative history of the Glacier National Park region, Montana. U.S. Geological Survey Bulletin 1902, 64 pp.
- Carrara, P. E., and McGimsey, R. G., 1981: The late-neoglacial histories of the Agassiz and Jackson Glaciers, Glacier National Park, Montana. *Arctic and Alpine Research*, 13: 183–196.
- Carter, G. A., and Smith, W. K., 1988: Microhabitat comparisons of transpiration and photosynthesis in three subalpine conifers. *Canadian Journal of Botany*, 66: 963–969.
- Casey, K. S., and Tomback, D. F., 1994: Growth form distribution and genetic relationships in tree clusters of *Pinus flexilis*, a bird-dispersed pine. *Oecologia*, 98: 402–411.
- DeLucia, E. H., 1986: Effect of low root temperature on net photosynthesis, stomatal conductance, and carbohydrate concentration in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. *Tree Physiology*, 2: 143–154.
- Earle, C. J., 1993: *Forest Dynamics in a Forest-Tundra Ecotone, Medicine Bow Mountains, Wyoming*. Ph.D. Thesis. Seattle, University of Washington, 141 pp.
- Filion, L., Payette, S., Gauthier, L., and Boutin, Y., 1986: Light rings in subarctic conifers as a dendrochronological tool. *Quaternary Research*, 26: 272–279.
- Finklin, A. I., 1986: *A climatic handbook for Glacier National Park, with data for Waterton Lakes National Park*. USDA Forest Service General Technical Report GTR-INT-204, 124 pp.
- Frey, W., 1983: The influence of snow on growth and survival of planted trees. *Arctic and Alpine Research*, 15: 241–251.
- Gosz, J. R., 1991: Fundamental ecological characteristics of landscape boundaries. In: Holland, M. M., Risser, P. G., and Naiman, R. J. (eds.), *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*. New York, Chapman and Hall, 8–30.
- Gosz, J. R., 1993: Ecotone hierarchies. *Ecological Applications*, 3: 369–376.
- Gosz, J. R., and Sharpe, P. J. H., 1989: Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. *Landscape Ecology*, 3: 229–243.
- Hacker, S. D., and Gaines, S. D., 1997: Some implications of direct positive interactions for community species diversity. *Ecology*, 78: 1990–2003.
- Hadley, J. L., and Smith, W. K., 1983: Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, USA. *Arctic and Alpine Research*, 15: 127–135.
- Hadley, J. L., and Smith, W. K., 1986: Wind effects on needles of timberline conifers: seasonal influence on mortality. *Ecology*, 67: 12–19.
- Hall, M. H. P., and Fagre, D. B., 2003: Modeled climate-induced glacier change in Glacier National Park, 1850–2100. *Bioscience*, 53: 131–140.
- Hansen, D. H., and Klikoff, L. G., 1972: Water stress in

- krummholz, Wasatch Mountains, Utah. *Botanical Gazette*, 133: 392–394.
- Hansen-Bristow, K. J., and Ives, J. D., 1985: Composition, form, and distribution of the forest-alpine tundra ecotone, Indian Peaks, Colorado, USA. *Erdkunde*, 39: 286–295.
- Hardt, R. A., and Forman, R. T. T., 1989: Boundary form effects on woody colonization of reclaimed surface mines. *Ecology*, 70: 1252–1260.
- Hessl, A. E., and Baker, W. L., 1997: Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. *Arctic and Alpine Research*, 29: 173–183.
- Holland, M. M., 1988: SCOPE/MAB technical consultations on landscape boundaries. *Biology International*, 17(Special Issue): 47–104.
- Holtmeier, F.-K., 1982: “Ribbon-forest” and “hedges.” Strip-like distribution patterns of trees at the upper timberline in the Rocky Mountains. *Erdkunde*, 36: 142–153.
- Holtmeier, F.-K., and Broll, G., 1992: The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, U.S.A. *Arctic and Alpine Research*, 24: 216–228.
- Homma, K., 1997: Effects of snow pressure on growth form and life history of tree species in a Japanese beech forest. *Journal of Vegetation Science*, 8: 781–788.
- Hustich, I., 1979: Ecological concepts and biogeographical zonation in the North: the need for a generally accepted terminology. *Holarctic Ecology*, 2: 208–217.
- Johnson, D. M., Germino, M. J., and Smith, W. K., 2004: Abiotic factors limiting photosynthesis in *Abies lasiocarpa* and *Picea engelmannii* seedlings below and above the alpine timberline. *Tree Physiology*, 24: 377–386.
- Kitzberger, T., Steinaker, D. F., and Veblen, T. T., 2000: Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, 81: 1914–1924.
- Klasner, F. L., and Fagre, D. B., 2002: A half century of change in alpine treeline patterns at Glacier National Park, Montana, U.S.A. *Arctic, Antarctic and Alpine Research*, 34: 49–56.
- Klikoff, L. G., 1965: Microenvironmental influence of vegetational pattern near timberline in the central Sierra Nevada. *Ecological Monographs*, 35: 187–211.
- Kullman, L., 1986: Recent tree-limit history of *Picea abies* in the southern Swedish Scandes. *Canadian Journal of Forest Research*, 16: 761–771.
- Kullman, L., 1989: Recent retrogression of the forest-alpine tundra ecotone (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) in the Scandes Mountains, Sweden. *Journal of Biogeography*, 16: 83–90.
- Kullman, L., 2002: Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, 90: 68–77.
- Kupfer, J. A., and Cairns, D. M., 1996: The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography*, 20: 253–272.
- LaMarche, V. C., Jr., 1970: Frost-damage rings in subalpine conifers and their application to tree-ring dating problems. In: Smith, J. H. G., and Worrall, J. (eds.), *Tree-ring Analysis with Special Reference to Northwest America*. University of British Columbia Faculty of Forestry Bulletin No. 7, 99–100.
- Lloyd, A., and Graumlich, L., 1997: Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*, 78: 1199–1210.
- Luckman, B. H., and Kavanagh, T. A., 2000: Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio*, 29: 371–380.
- Malanson, G. P., 1993: Comment on modeling ecological response to climatic change. *Climatic Change*, 23: 95–109.
- Malanson, G. P., and Butler, D. R., 1994: Tree-tundra competitive hierarchies, soil fertility gradients, and treeline elevation in Glacier National Park, MT. *Physical Geography*, 15: 166–180.
- Marr, J. W., 1977: The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology*, 58: 1159–1164.
- Minnich, R. A., 1984: Snow drifting and timberline dynamics on Mount San Gorgonio, California, U.S.A. *Arctic and Alpine Research*, 16: 395–412.
- Neilson, R. P., 1993: Transient ecotone response to climatic change: Some conceptual and modelling approaches. *Ecological Applications*, 3: 385–395.
- Noble, I. R., 1993: A model of the responses of ecotones to climate change. *Ecological Applications*, 3: 396–403.
- Oshima, Y., Kimura, M., Iwake, H., and Kuroiwa, S., 1958: Ecological and physiological studies on the vegetation of Mt. Shimagare. I. Preliminary survey of the vegetation of Mt. Shimagare. *Botanical Magazine of Tokyo*, 71: 289–300.
- Pauker, S. J., and Seastedt, T. R., 1996: Effects of mobile tree islands on soil carbon storage in tundra ecosystems. *Ecology*, 77: 2563–2567.
- Paulsen, J., Weber, U. M., and Körner, C., 1999: Tree growth near treeline: Abrupt or gradual transition with altitude? *Arctic, Antarctic, and Alpine Research*, 32: 14–20.
- Payette, S., and Filion, L., 1985: White spruce expansion at the tree line and recent climate change. *Canadian Journal of Forest Research*, 15: 241–251.
- Payette, S., Filion, L., Delwaide, A., and Begin, C., 1989: Reconstruction of tree-line vegetation response to long-term climate change. *Nature*, 341: 429–432.
- Payette, S., Fortin, M.-J., and Gamache, I., 2001: The subarctic forest-tundra: The structure of a biome in a changing climate. *BioScience*, 51: 709–718.
- Rebertus, A. J., Burns, B. R., and Veblen, T. T., 1991: Stand dynamics of *Pinus flexilis*-dominated sub-alpine forest in the Colorado Front Range. *Journal of Vegetation Science*, 2: 445–458.
- Reiners, W. A., and Lang, G. E., 1979: Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. *Ecology*, 60: 403–417.
- Risser, P. G., 1995: The status of the science examining ecotones. *BioScience*, 45: 318–325.
- Scott, P. A., Hansell, R. I. C., and Erickson, W. R., 1993: Influences of wind and snow on northern tree-line environments at Churchill, Manitoba, Canada. *Arctic*, 46: 316–323.
- Slatyer, R. O., and Noble, I. R., 1992: Dynamics of montane treelines. In: Hansen, A. J., and diCasteri, F. (eds.), *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. New York, Springer-Verlag, 346–359.
- Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M., 2003: Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.
- Sprugel, D. G., 1976: Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. *Journal of Ecology*, 64: 889–911.
- Stokes, M. A., and Smiley, T. L., 1968: *An Introduction to Tree-Ring Dating*. Chicago, University of Chicago Press, 73 pp.
- Thomson, J. D., Weiblen, G., Thomson, B. A., Alfaro, S., and Legendre, P., 1996: Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology*, 77: 1698–1715.
- Tongway, D. J., Valentin, C., and Seghieri, J. (eds.), 2001: *Banded Vegetation Patterning in Arid and Semiarid Environments. Ecological Processes and Consequences for Management*. New York, Springer-Verlag, Ecological Studies 149, 251 pp.
- Tranquillini, W., 1979: *Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitudes with Special Reference to the European Alps*. Berlin, Springer-Verlag, 137 pp.
- Turner, M. G., Gardner, R. G., and O'Neill, R. V., 1988: Potential responses of landscape boundaries to global environmental change. In: Holland, M. M., Risser, P. G., and Naiman, R. J. (eds.), *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*. New York, Chapman and Hall, 52–75.
- Walsh, S. J., Butler, D. R., Allen, T. R., and Malanson, G. P., 1994: Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science*, 5: 657–672.
- Walsh, S. J., Bian, L., McKnight, S., Brown, D. G., and Hammer, E.

- S., 2003: Solifluction steps and risers, Lee Ridge, Glacier National Park, Montana, USA: a scale and pattern analysis. *Geomorphology*, 55: 381–398.
- Wardle, P., 1974: Alpine timberlines. In: Ives, J. G., and Barry, R. G. (eds.), *Arctic and Alpine Environments*. London, Methuen, 370–402.
- Weisberg, P. J., and Baker, W. L., 1995: Spatial variation in tree seedling and krummholz growth in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. *Arctic and Alpine Research*, 27: 116–129.
- White, L. P., 1969: Vegetation arcs in Jordan. *Journal of Ecology*, 57: 5461–5464.
- White, L. P., 1970: 'Brousse tigré' patterns in southern Niger. *Journal of Ecology*, 58: 549–553.
- Wiens, J. A., Crawford, C. S., and Gosz, J. R., 1985: Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos*, 45: 421–427.
- Williams, M. W., Brooks, P. D., and Seastedt, T. R., 1998: Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, U.S.A. *Arctic and Alpine Research*, 30: 26–30.
- Wilson, J. B., and Agnew, A. D. Q., 1992: Positive-feedback switches in plant communities. *Advances in Ecological Research*, 23: 263–336.
- Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., Reynolds, J. F., and Chapin, M. C., 1995: Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist*, 146: 765–794.

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