Ecology, 78(2), 1997, pp. 632–641
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LODGEPOLE PINE (*PINUS CONTORTA*) ECOTONES IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO, USA

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Abstract. Because ecotones often represent the physiological or competitive limit-of-distribution of species, they serve to define a species' local distribution. We take a relatively new approach to gradient analysis to quantify the changes in forest dominance (basal area of dominant tree species) and environmental factors (elevation, slope, aspect, intercepted photosynthetically active radiation [PAR], summer soil moisture, and soil depth and texture) across current lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. Based on canonical correspondence analysis on data from eight 20 m wide, 140–480 m long vegetation transects, we found that lodgepole pine distribution, is described generally by elevation and moisture gradients, and to a lesser degree by soil characteristics. The first two ordination axes explained 72% of the variance in forest patterns. Environmental factors significantly correlated to the first ordination axis included: elevation, summer soil moisture, and percentage sand in the soil. Environmental factors significantly correlated to the second ordination axis included: growing-season soil moisture, surface rockiness, percentage silt, and percentage clay. However, superimposed on these general environmental gradients are ecotone-specific gradients that cannot be detected by typical gradient analysis approaches using only homogeneous plots. The basal area of lodgepole pine decreased nonlinearly and more sharply toward the ecotones than did the basal area of the neighboring tree species. Stepwise multiple linear regression and path coefficient analysis models showed that the basal area gradients of lodgepole pine into spruce/fir (*Picea engelmannii, Abies lasiocarpa*) forests correlated with summer soil moisture; lodgepole pine gradients into lower elevation ponderosa pine (*Pinus ponderosa*) forests correlated strongly with intercepted PAR, slope, percentage silt, soil depth, and percentage clay; and lodgepole pine gradients into limber pine (*Pinus flexilis*) forests correlated largely with elevation, intercepted PAR, percentage sand, and percentage clay. Furthermore, the factors controlling tree species distributions at ecotones are not symmetrical. For example, at the lodgepole pine to limber pine ecotone, different factors or different magnitudes of the same factors determined the upper limit of lodgepole pine and the lower limit of limber pine. We conclude that: (1) different factors control a species' upper and lower elevation limits; (2) unequal competition for resources occurs between tree species where their ranges overlap; and (3) generally, soil differences may not substantially restrain the movement of some forest types into neighboring types.

Key words: forest distributions; gradient analysis; lodgepole pine; Pinus contorta; *species–environment relationships; vegetation ecotones.*

INTRODUCTION

A landscape-scale approach that examines forest ecotones and environmental gradients may lead to an understanding of forest change by determining the current limits of establishment, growth, and persistence of a tree species under competition with other tree species. Canonical correspondence analysis (CCA; ter Braak 1986, 1987*a*, *b*, 1991) is the most commonly used gradient analysis technique in ecology and has proved to be a robust statistical technique (Palmer 1993*a*) in assisting to understand forest distributions relative to elevation and moisture gradients (Whittaker 1967, Peet 1981, Allen et al. 1991, Reed et al. 1993).

However, previous approaches to gradient analysis in the Colorado Rockies may be somewhat misleading. First, gradient analysis results may be influenced greatly by the locations of the sampling units, particularly if only "homogeneous" areas are selected for study (e.g., Peet 1981, Allen et al. 1991). Confining measurements of forest characteristics and environmental factors to homogeneous units may not represent species–environment relationships that dominate complex landscapes, exaggerating the distances between clusters in an ordination diagram (Fig. 1, Top). Furthermore, if sampling is confined to homogeneous sampling units, perhaps the more stable environments for

Manuscript received 17 January 1996; revised 21 May 1996; accepted 30 May 1996.

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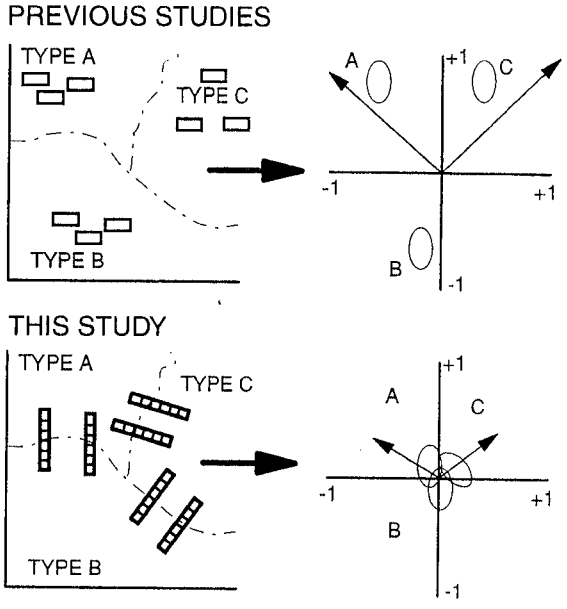

FIG. 1. (Top) Conceptual design of previous gradient analysis studies with sampling confined to homogeneous areas (vegetation types A, B, and C). Ordination clusters may be more pronounced with exaggerated species–environment relationship differences between clusters. (Bottom) Conceptual design of a study that includes homogeneous areas (terminal plots on transects) and heterogeneous areas in between. The latter design may help determine the physiological limits of vegetation types and the steepness of environmental gradients, and thus may contribute to an understanding of species–environment relationships in areas sensitive to vegetation change.

particular vegetation types, then ecologists would tend to learn more about "where stable communities reside" and less about "how species distributions may change." Peripheral areas of a population may have different patterns of establishment, growth, and survival than core (or central) areas of a population (Stohlgren 1992). Widely dispersed sample plots might imply that two forest types gradually fade into each other where, in fact, steep thresholds may exist (Risser 1995).

To define, measure, and predict changes in the distribution and dominance of tree species, ecotones are a reasonable place to start. Ecotones may respond quickly to changes in environmental conditions (Holland et al. 1991, Cornelius and Reynolds 1991, Hansen and di Castri 1992, Gosz 1993, Risser 1993, Rusek 1993, Weisberg and Baker 1995). Risser (1995) argued that we must understand the steepness of environmental gradients between homogeneous vegetation associations before we can understand the dynamic nature of landscapes. Gradient analysis based on replicated, randomly selected transects (i.e., contiguous plots; Wesser and Armbruster 1991) that cross ecotones may provide information on: (1) the steepness of environmental gradients and the response of different species to those gradients; and (2) the magnitude of environmental change needed to shift the competitive advantages of species where they coexist (Fig. 1, Bottom).

We investigated species–environment relationships focusing on forest ecotones in the middle elevations (2530–3080 m) of Rocky Mountain National Park. Peet's (1981) elevation–moisture gradient analysis served as a working hypothesis to be tested with additional field studies, focusing on ecotonal portions of the landscape. Our primary objectives were to: (1) quantify the relationships of tree species composition and basal area to environmental factors across current lodgepole pine ecotones; and (2) develop empirical models describing the environmental limits of lodgepole pine and neighboring forest tree species. A secondary objective was to establish a series of unbiased, long-term study transects to monitor vegetation change and validate models in the future.

Study Area and Methods

Study area

The Colorado Front Range is a major range of the southern Rocky Mountains. Spanning 300 km from Wyoming on the north to the Arkansas River on the south, Front Range elevations rise from the plains at 1600 m to >4300 m. This mountain region embraces a wide array of vegetation, including shortgrass steppe, shrub-steppe, montane pine and fir forests, subalpine forests, and alpine tundra. Latitudinal and elevation arrangements of species distributions have been attributed to temperature and precipitation, as typically influenced by elevation and topographic position (Peet 1981, Allen et al. 1991). Common tree species (generally from low to high elevations) are: ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), blue spruce (*Picea pungens*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and limber pine (*Pinus flexilis*). Paleoecological evidence suggests that since the distributions of tree species probably changed faster than soil depth and texture in many areas (Madole 1976, Stohlgren 1996), forest ecotones in the Rocky Mountains of Colorado may be sensitive indicators of climate change.

Vegetation sampling and environmental measurements

Eight transects (140–480 m long, 20 m wide) consisting of 98 20 × 20 m plots were established between 1992 and 1994 in Rocky Mountain National Park, Colorado, USA (Table 1). Six of the eight transects were located in an unbiased manner using a stratified random sampling design based on the vegetation cover type map of the Park and a geographic information system (GIS). The vegetation map was created from 1:15 840 scale, 1987 natural-color aerial photography and depicts dominant species and secondary species (where present). We then used GIS commands to classify seven

TABLE 1. Ecotone transects in Rocky Mountain National Park, Colorado, USA. LP = lodgepole pine; SF = spruce/fir; LB = limber pine; PP = ponderosa pine.

Transect name	Ecotone type	No. of plots	UTM E UTM N (m)†	Elevation (m)	Slope (%)	Aspect (°)	Est. age (yr)
Aspenglen	PP-LP	24	449475 4471602	2530–2610	4.0–9.0	135	180
Deer Ridge	PP-LP	14	447399 4470812	2740–2800	5.0–8.0	270	130
Upr. Beaver	PP-LP	9	449361 4468475	2530–2550	6.0–7.0	180	130
Bear Lake	LP-SF	11	445000 4462297	2870	9.0–14.0	0–22	90
Hitchens's	LP-SF	7	426802 4475867	2960–2990	7.0–14.0	270	110
Lawn Lake	LP-LB	10	446227 4475343	3020–3080	5.0–7.0	90	130
Meeker Dr.	LP-LB	10	451653 4455112	3000–3050	5.0–7.0	270	100
Wild Basin	LP-LB	13	452459 4451880	2980–3080	4.0–7.0	0	120

† UTM E/N = Universal Transverse Mercator grid system East/North.

forest types: lodgepole pine, aspen, Douglas-fir, limber pine, ponderosa pine, blue spruce, and spruce/fir mix. The vegetation map was combined with an aspect map that was derived from 1:24 000 scale U.S. Geological Survey Digital Elevation Models using a 30-m cell size. We then created a 200-m strip along all the areas where, for example, lodgepole pine was adjacent to another forest type. Thus, we had a layer in the database for the major lodgepole pine ecotones types (Table 1). We then set the GIS working mask to each aspect class (N, S, E, W), and used a random function to select sites from each ecotone type and aspect. The potential starting locations for transects were selected random points that were in relatively homogeneous vegetation types (i.e., surrounded by nine 30 × 30 m cells of similar vegetation), but within 100–200 m of another vegetation type.

Using U.S. Geological Survey 7.5′ quadrangle maps and a global positioning system, we located two replicate ecotone transects moving from lodgepole pine to spruce/fir, and three replicate transects each from lodgepole pine to limber pine and ponderosa pine. Two of the transect starting points (Bear Lake and Hitchen's Gulch) were selected subjectively, closer to roads and trails, to more easily test field sampling techniques (and because lodgepole to spruce/fir ecotones were difficult to identify from the vegetation map based on a minimum mapping unit size of 2 ha. In each case, no prior information was available on vegetation density or basal area, or on soil characteristics (i.e., depth, texture, moisture), so we are confident that selecting the starting locations for these transects did not strongly bias results. Three engraved, copper-topped stainless steel survey stakes, each with accurate spatial coordinates, permanently mark each transect.

At each study site, the transects were established across major environmental gradients (i.e., aspect or elevation; Table 1) such that the two terminal 20 × 20 m plots at each end of the transect were in homogeneous stands of their respective forest types. In all 20 × 20 m plots, we measured slope (clinometer; to the nearest degree), aspect (compass; to the nearest degree), and elevation (altimeter calibrated with a Trimball Pathfinder Professional global positioning system and differential corrections for the three survey stakes). Each tree (>2.54 cm at 1.4 m above the ground) was numbered and mapped relative to a georeferenced plot center. For each mapped tree, we recorded species, diameter at breast height (dbh; to the nearest 0.1 cm), and status (living or dead). We converted tree diameter to basal area (in square centimetres) and summed these values by species for each plot (in square metres per hectare). Tree cores were taken at dbh (and corrected for time to reach dbh) from three to five trees per plot to get crude estimates of stand age (±10 yr) and to assure that the ecotones do not represent disturbance boundaries rather than environmental gradients.

Within each 20 × 20 m plot, composite soil samples were collected from the top 15 cm of mineral soil at the plot center and subplot centers. These composite samples were sifted through a 2-mm mesh sieve prior to particle-size analysis of the remaining soil fraction (Gee and Bauder 1986). The >2 mm fraction was highly variable (mean 35%, range 9–61%) and was not used in the multivariate analysis described below to prevent multicollinearity of the sand, silt, and clay fractions. Soil depth was measured at 36 sites selected systematically in each 10 × 10 m subplot by pounding a steel rod as deep as possible (up to 40 cm). Soil depths were then averaged for each plot. Surface rockiness was the percentage of soil depth measurements that were impenetrable due to surface rock.

A Decagon Sunfleck Ceptometer (Model SF-80) was used to measure photosynthetically active radiation

(PAR; 400–700 nm, in micromoles per square meter per second) beneath the forest canopy between 1000 and 1400 on cloudfree days in late June or early July. The ceptometer was held horizontally 1 m above ground level, and five readings (80 sensors per reading) were taken at cardinal directions and subplot centers in each 10 × 10 m subplot, and then averaged for each plot. Measurements also were taken in canopy openings to calculate a PAR index (average plot reading divided by the maximum open-canopy reading for the day). The PAR index may be interpreted as an index of the stand's leaf area, or the relative potential of an area to produce additional leaf area and basal area in open stands (assuming all other environmental factors are equal).

We used a Trace System1 Time Domain Reflectometer (TDR; Model 6050X1) to measure growing-season soil moisture in the top 15 cm of soil. Soil moisture readings were taken at 2-m intervals along the center line of each 10 × 10 m subplot. Readings were taken between late June and early-August after 2 d without rain to be representative of mid-growing-season conditions for the various ecotone types.

Statistical procedures

All data variables were assessed for normality (SAS 1990) prior to the statistical analyses, and appropriate transformations were performed when necessary to improve normality according to Zar (1974). Basal area, slope, elevation, growing-season soil moisture, and soil depth data were not transformed. Log_{10} transformations were used on the PAR index, surface rockiness, and soil silt and clay fractions. An arcsine transformation was used on the soil sand fraction, because this transformation worked better on wide-ranging percentages (Zar 1974).

Basal area by species and all environmental variables in the terminal two plots and middle plots of each ecotone type (i.e., lodgepole to ponderosa pine; lodgepole to limber pine, and lodgepole to spruce/fir) of each transect were evaluated with standard analysis of variance tests (ANOVA; SAS 1990). Where the ANOVA revealed a significant difference (at $\alpha = 0.05$) among groups, Ryan-Einot-Gabriel-Welsch (REGWF test; SAS 1990) multiple range tests were used to detect significant differences ($\alpha = 0.05$) among means. The REGWF test controls the experimentwise error rate and is appropriate for this type of data (Day and Quinn 1989).

We used canonical correspondence analysis (CCA; CANOCO software version 3.12; ter Braak 1987*b*, 1991) to characterize the relationship between forest dominance (basal area by species) and environmental measures (elevation, slope, and aspect, PAR index, soil depth, surface rockiness, growing-season soil moisture, and soil sand, silt, and clay fractions). CCA is a direct gradient analysis technique that constrains the extracted pattern of vegetation to a linear combination of the measured environmental variables (ter Braak 1986, 1987*a*), and it is a proven, robust method for describing species–environment relationships (see Palmer 1993*a* for a complete review; Reed et al. 1993). All the default options were selected in the CCA (i.e., no special weighting of species or environmental factors, no samples were excluded from the analysis). We assessed all environmental variables for multicollinearity problems and none were found. Monte Carlo permutation tests (99 random permutations) were performed to test the significance of the first canonical axis (ter Braak 1991).

Finally, stepwise linear regression (SAS 1990) and path coefficient analysis (Dewey and Lu 1959, Wesser and Armbruster 1991) were used to evaluate the direct and indirect relationships of the environmental factors to tree species basal area. The forward linear regression models included only variables meeting the default $P < 0.15$ criterion. We rely on forward stepwise regression, the most widely used multiple regression model (Neter et al. 1990), to compare the different ecotone types in a consistent manner. This regression model may not always result in the "best" regression model for all ecotone types (see Neter et al. 1990: 452–453), but the reported relationships agreed with CCA results and field observations. Path coefficient analysis simply displays the standardized partial-regression coefficient (direct influence) of an environmental factor on species basal area, with significant ($P < 0.05$) simple correlation coefficients (indirect influences) shown among environmental variables, and the residual factors ($R_X = \sqrt{(1 - R^2)}$) from the stepwise linear regressions (Dewey and Lu 1959).

Results

Canonical correspondence analysis of ecotones

Results of the canonical correspondence analysis (CCA; Fig. 2) reveal species–environment relationships from lodgepole pine (near the center of the diagram) across ecotones to other forest types. The first two canonical axes explained 72% of the cumulative variance. Environmental factors that correlated significantly ($P < 0.001$) with canonical axis 1 included: elevation ($r = -0.76$), growing season soil moisture ($r = -0.68$), and percentage sand ($r = 0.63$). Environmental factors that correlated significantly with canonical axis 2 included: growing-season soil moisture ($r = 0.69$), surface rockiness ($r = -0.68$), percentage silt ($r = 0.63$), and percentage clay ($r = 0.51$). The correlation matrix showed that soil depth was significantly and negatively correlated to surface rockiness ($r = -0.82$), and that soil moisture was positively correlated with percentage silt ($r = 0.62$) and percentage clay ($r = 0.45$). Monte Carlo permutation tests showed that the first canonical axis was highly significant (eigenvalue = 0.67, F ratio = 30.07, df = 98, $P < 0.01$).

The ecotone from lodgepole pine to ponderosa pine

ANOVA results of the lodgepole to ponderosa pine ecotone also showed a rapid decrease in lodgepole pine

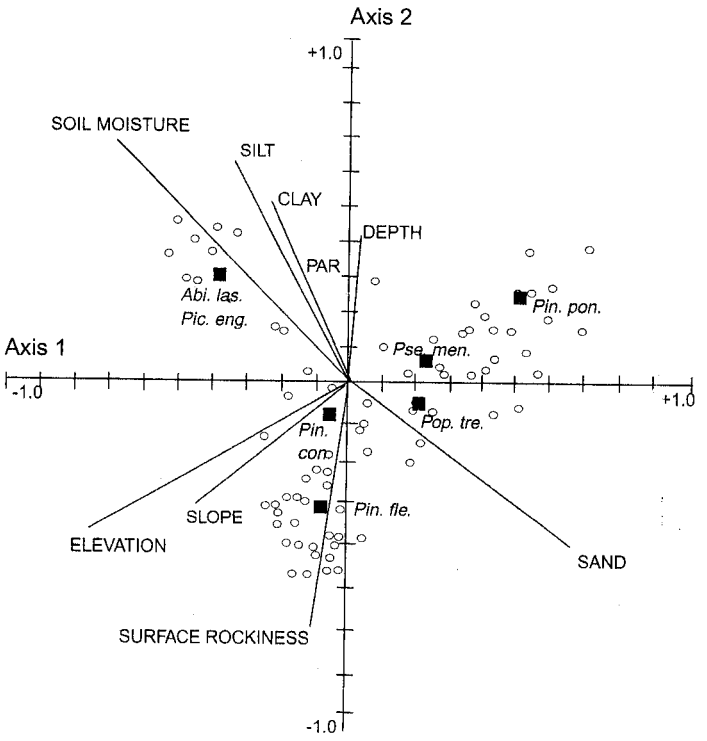

FIG. 2. Canonical correspondence analysis ordination. Open circles represent 20 × 20 m plots. *Abi. las.* = *Abies lasiocarpa*; *Pic. eng.* = *Picea engelmannii*; *Pin. fle.* = *Pinus flexilis*; *Pin. con.* = *Pinus contorta*; *Pop. tre.* = *Populus tremuloides*; *Pse. men.* = *Pseudotsuga menziesii*.

basal area along the gradient (down 80% in the ecotone plots; Table 2). Conversely, ponderosa pine basal area decreased less than half, moving into lodgepole pine stands. None of the environmental factors differed statistically at $\alpha = 0.05$, however, ponderosa pine sites were slightly lower in elevation, growing-season soil moisture, and surface rockiness, and had less steep slopes.

Path coefficient analysis showed that different environmental factors may control the lower limit of lodgepole pine and the upper limit of ponderosa pine (Fig. 3). Five environmental factors were significant and accounted for 78% of the variance in lodgepole pine basal area along the transects (adjusted $R^2 = 0.73$). The strongest direct influences, based on the standardized partial regression coefficients (β_s), included: PAR ($\beta_s = -0.59$), slope ($\beta_s = 0.45$), and silt ($\beta_s = -0.42$). This suggests that an increasing slope and decrease in percentage silt are correlated with an increase in lodgepole pine basal area. The PAR index readings were higher in ponderosa pine stands and may be interpreted as the potential to produce additional leaf area index and basal area (but this potential may be limited by soil characteristics and water/nutrient availability). Lodgepole pine basal area increased as slope increased and where more water may have been available for primary production.

TABLE 2. Mean basal area of tree species measured at two terminal 20 × 20 m plots and two ecotone plots per transect from lodgepole pine (LP) to ponderosa pine (PP), spruce/fir (SF), or limber pine (LB). Means with the same trailing letters are not significantly different (at $\alpha = 0.05$).

Characteristic	Lodgepole forest	Ecotone	Other forest type	ANOVA	
				F	*P*
Lodgepole pine to ponderosa pine (n = 6 plots each, df = 2, 15)					
LP basal area (m^2/ha)	22.8 a	4.2 b	1.0 b	57.8	0.0001
PP basal area (m^2/ha)	9.0 a	7.8 a	16.2 a	1.2	0.3200
Lodgepole pine to spruce/fir (n = 4 plots each, df = 2, 11)					
LP basal area (m^2/ha)	23.2 a	10.0 b	2.5 b	6.8	0.0161
SF basal area (m^2/ha)	21.8 a	23.0 a	38.0 a	3.1	0.0960
Lodgepole pine to limber pine (n = 6 plots, df = 2, 15)					
LP basal area (m^2/ha)	30.5 a	7.5 b	3.0 b	45.1	0.0001
LB basal area (m^2/ha)	0.8 a	6.5 b	10.2 b	6.7	0.0085

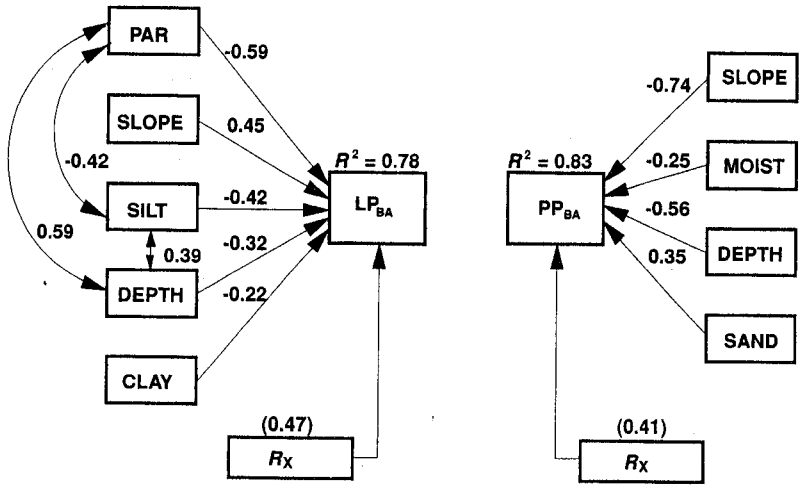

FIG. 3. Path coefficient diagram of environmental factors influencing lodgepole pine basal area (LP_{BA}) and ponderosa pine basal area (PP_{BA}). Direct arrows to LP_{BA} or PP_{BA} include standardized partial regression coefficient values, while arrows between environmental variables are simple correlation coefficients. R^2 is the coefficient of multiple determination.

The factors correlated with increased ponderosa pine basal area along the ecotone transects were slightly different (and the relative strengths of the coefficients were different) than the factors correlated with increased lodgepole pine basal area (Fig. 3). Ponderosa pine basal area was negatively correlated with slope, soil depth, and growing-season soil moisture, and positively correlated with percentage sand (R^2 = 0.83; adjusted R^2 = 0.78).

The ecotone from lodgepole pine to spruce/fir

Lodgepole pine basal area decreased sharply between the lodgepole pine and spruce/fir forests (Table 2), coinciding with increased growing-season soil moisture from 9.0 to 12.1% ($P < 0.05$). Spruce/fir basal area only decreased by less than half as the forest type graded into lodgepole pine stands. Soils under the spruce/fir type were highly variable but tended to be slightly deeper and less rocky than soils under lodgepole-pine-dominated plots. Soil texture differences along the transects also were inconclusive, although there was generally more silt and clay in the spruce/fir and ecotone areas than in the homogeneous lodgepole pine plots.

Path coefficient analysis of the lodgepole pine to spruce/fir ecotone reinforced the ANOVA results (Fig. 4). The stepwise regression found that growing season soil moisture was correlated negatively to lodgepole pine basal area, however, only 39% of the variance was explained (adjusted R^2 = 0.36). Growing-season soil moisture was positively correlated to percentage silt (r = 0.71). Spruce/fir basal area was influenced largely by soil depth and elevation (R^2 = 0.58). Spruce/fir basal area did not decrease rapidly with elevation partly because of the site selection of the transects. The Bear Lake transect was at a constant elevation, contouring around the side of a mountain. The Hitchen's Gulch transect increased only 30 m in elevation from lodgepole pine to spruce/fir stands. However, elevation was correlated strongly with soil depth (r = 0.94) and soil depth was negatively correlated with surface rockiness (r = −0.91). Along these transects, spruce/fir basal area was strongly associated with growing-season soil moisture (r = 0.55) and percentage clay (r = 0.52).

The ecotone from lodgepole pine to limber pine

Lodgepole pine basal area decreased sharply along the lodgepole pine to limber pine ecotone (Table 2). Conversely, limber pine basal area only dropped by half from the homogeneous limber pine stands to the

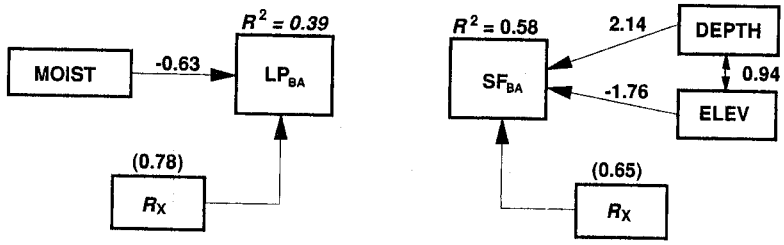

FIG. 4. Path coefficient diagram of environmental factors influencing lodgepole pine basal area (LP_{BA}) and spruce/fir basal area (SF_{BA}). Arrows are analogous to those in Fig. 3.

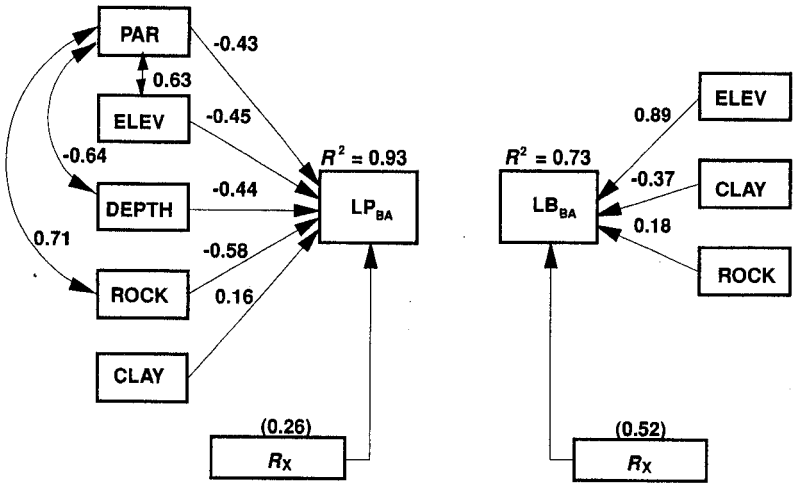

FIG. 5. Path coefficient diagram of environmental factors influencing lodgepole pine basal area (LP_{BA}) and limber pine basal area (LB_{BA}). Arrows are analogous to those in Fig. 3.

ecotone. Elevation and surface rockiness were significantly lower in the homogeneous lodgepole pine plots compared to the ecotone and limber pine plots. There were no obvious differences in soil depth and percentages of sand, silt, or clay along the lodgepole pine to limber pine transect.

Path coefficient analysis showed that different environmental factors may control the upper limit of lodgepole pine and the lower limit of limber pine (Fig. 5). Five environmental factors explained 93% of the variance in lodgepole pine basal area along the transects (adjusted $R^2 = 0.91$). The strongest direct influence, based on the standardized partial regression coefficients, was surface rockiness ($\beta_s = -0.58$), but this was followed closely by the PAR index ($\beta_s = -0.43$), elevation ($\beta_s = -0.45$), and soil depth ($\beta_s = -0.44$). Increasing percentage clay was a minor, but significant parameter associated with increased lodgepole pine basal area. The indirect influences on lodgepole pine basal area showed that higher elevation sites had shallower, rocky soils prohibiting high lodgepole pine basal area, thus the PAR index readings were higher in the limber pine stands (Fig. 5).

Only three factors directly influenced limber pine basal area along the ecotone transects ($R^2 = 0.73$; adjusted $R^2 = 0.70$), with the strongest being elevation ($\beta_s = 0.89$). Surface rockiness ($\beta_s = 0.18$) appeared less important in influencing limber pine basal area than it was influencing lodgepole pine basal area in the other direction (Fig. 5).

DISCUSSION

Comparison to previous research

Direct comparisons to past gradient analysis studies in the Rocky Mountains are difficult because of the study design differences (Fig. 1). Another major difference between our research and previous research is scale. Peet (1981) established over 300 0.1-ha plots in a 1000-km^2 study area. Allen et al. (1991) combined information (including Peet's data) from Taos, New Mexico to the Medicine Bow Mountains in Wyoming. The scale of our research ranges from plots (20 × 20 m) to transects hundreds of meters along individual ecotone transects to between transects (across tens of kilometers) to define the species–environment relationships influencing the distribution of lodgepole pine relative to potential competitors. Despite the differences in scale, study design, sample size, and the way in which moisture gradients were quantified, the three gradient analysis studies identified elevation and soil moisture index to be the most important correlates of tree species (Peet 1981, 1988, Allen et al. 1991, this study). However, the previous studies tell us little about the thresholds of any of the forest types.

The nonlinear decrease in lodgepole pine basal area from homogeneous to mixed stands was unknown. Peet (1981) reported lodgepole pine basal area averaged ≈32 m^2/ha in homogeneous stands, while we averaged ≈26 m^2/ha in homogeneous stands (terminal transect plots; Table 2). We know from Peet (1981) that lodgepole pine basal area was reduced in mixed-species stands, but because the sample sites were not contiguous, there was no way of knowing if the decline in basal area was precipitous or gradual, and isolating the key environmental factors associated with the decline was not possible.

The precipitous declines in lodgepole basal area do not appear strongly associated with suface soil texture, rockiness, or soil depth (to 40 cm). This suggests that temperature and moisture gradients, which are important factors at large scales (Peet 1981, Allen et al. 1991) and finer scales (Fig. 2), interact strongly with interspecific competition (more important at finer scales; Table 2), to define a tree species' local distribution.

Defining a species' local distribution: a lodgepole pine example

CCA results suggest that slight increases in growing-season soil moisture may favor spruce and fir over lodgepole pine (Fig. 2). Limber pine obtains dominance at high-elevation sites with increased surface rockiness and decreased soil depth. Ponderosa pine and Douglas-fir are found at lower elevation sites with less steep slopes, respectively. Symmetrical competition for resources between two tree species might result in: (1) linear, gradual declines in basal area of both species along the transect, coinciding with gradual changes in environmental factors; and (2) the same factors and magnitude of factors associated with basal area declines. However, we found nonlinear responses in tree basal area with only gradual changes (i.e., few significant differences) in most environmental factors (Table 2, Figs. 3–5). We found also that the lower and upper limits of lodgepole pine distribution likely are controlled by different groups of environmental factors, and by different magnitudes of influence (i.e., standardized partial regression coefficients) from the same environmental factors (Figs. 3–5).

The lower limit of lodgepole pine and the upper limit of ponderosa pine, for example, appear to be influenced by somewhat different factors (Fig. 3). Above the lodgepole to ponderosa pine ecotone, lodgepole pine dominates on the steeper slopes and on slightly more rocky soils. At, and below the lodgepole pine to ponderosa pine ecotone, ponderosa pine can dominate basal area. Reduced total basal area, along with an increased proportion of fine fuels from ponderosa pine litter, may increase the frequency of surface fires. A decrease in fire return interval from ≈100–200 yr for many lodgepole pine stands to <40 yr for many ponderosa pine stands, would likely favor the spread of ponderosa pine. There may also be physiological factors that help define the ponderosa pine to lodgepole pine ecotone. Ponderosa pine seedlings are more sensitive to cold than lodgepole pine (Cochran and Berntsen 1973). This may partly explain the inverse pattern of lodgepole pine below ponderosa pine stands in cold air drainages (Knight 1994).

Near the lodgepole to spruce/fir ecotone, lodgepole pine basal area decreased gradually as the vegetation type grades into spruce/fir areas (Table 2). However, spruce/fir basal area was substantial in many lodgepole pine-dominated stands. The low amount of variation explained (R^2 = 0.39–0.58; Fig. 4) by the multiple regression analysis (relative to the other ecotone types; R^2 = 0.73–0.93; Figs. 3 and 5) is one indication of environmental similarity along the lodgepole pine to spruce/fir ecotone. The understory trees along the entire lengths of the transects were dominated by the shade-tolerant fir. In the absence of fire, spruce and fir will invade and dominate in many upper elevation lodgepole forests (Peet 1981). However, after an inevitable stand-replacing fire, lodgepole pine can regain many drier, rockier sites temporarily, and retain dominance in some of those sites. The entire Bear Lake transect location burned around 1900, thus all the tree species are in the same successional stage. The wetter, more northerly plots regenerated as spruce/fir forests, while the slightly rockier sites with less silt and clay regenerated into lodgepole pine—with a gradation of the forest types at the ecotone. At lodgepole pine to spruce/fir ecotones, drier conditions following a fire likely would favor lodgepole pine over broader areas of previously spruce/fir forests (Peet 1981, 1988).

The upper limit of lodgepole pine at the ecotone with limber pine appears correlated largely with increased surface rockiness and elevation, and shallower soils (Fig. 5). But, there was also the greatest difference in the variation explained between the factors influencing lodgepole pine basal area (R^2 = 0.93; adjusted R^2 = 0.91) and the factors influencing limber pine basal area (R^2 = 0.73; adjusted R^2 = 0.70). That is, the upper limit of lodgepole pine is more predictable than the lower limit of limber pine. In the ecotone plots, limber pine basal area was >46% of the total stand basal area. But in the limber-pine-dominated stands, lodgepole pine maintained 23% of the total basal area, whereas in the lodgepole-pine-dominated stands, limber pine maintained only 2.7% of the total basal area. Although the ecotone had significantly more surface rock (and probably much more subsurface rock) than the lodgepole pine end of the transects, the soil textures were nearly identical. For some reason, perhaps due to climate change or a shifting competitive advantage, lodgepole pine may be successfully extending into the limber pine type on these transects.

The ecotonal transects used here produced some unexpected results. Based on previous studies and vegetation–soils paradigms (e.g., Allen and Peet 1990, Franklin et al. 1993), we expected to find sharp discontinuities in soil characteristics along the ecotone transects associated with sharp declines (or increases) in the basal area of the dominant tree species. Instead we found: (1) generally continuous soils or slightly changing soil characteristics on most transects; and (2) considerably higher basal areas of competing species (ponderosa pine, spruce/fir, and limber pine) well into the lodgepole-pine-dominated stands (Table 2). Since soil textures change negligibly on the time scale of substantial climate changes, we see little evidence that soils will substantially restrain the movement of any of the forest types into neighboring types.

Environmental forcing of vegetation change

An important caveat to our present research is that individual trees and species actually respond to factors not directly measured in gradient analysis research. For example, elevation is measured often as a surrogate for annual mean temperature or growing-degree-days. There is ample evidence that average maximum daily

temperatures decrease with increasing elevation. This adiabatic lapse rate is ≈1°C per 100 m between 2704 and 3316 m during the growing season in the nearby Medicine Bow Mountains (DeLucia and Smith 1987). Thus, there could be differences of 0.5–1°C across the lodgepole to limber pine transects, 10–20% of the potential 5°C difference in maximum daily temperature across the elevation range of lodgepole pine in our study area (Table 1). Topographic position, aspect, and exposure are measured often as a surrogate for moisture availability. Ecologists realize that these surrogate measurements can explain much of the variation in describing vegetation patterns (Figs. 2, 3, and 5), though the direct link to ecological processes forcing the patterns remains somewhat obscure. Functional connections may be needed to infer changes in response to altered climate. However, mean annual temperature, growing-season water availability, total solar radiation, and growing-degree-days are difficult to measure at the scale of tens of meters, vary spatially and temporally in complex ways, and require long-term data for accuracy assessment. Likewise, inter-and intraspecific competition, herbivory, disease, and fire influence forest species distributions (e.g., Peet 1981, Stohlgren et al. 1993, Knight 1994, Villalba et al. 1994).

Risser (1995) suggests that ecotones best suited for study would be those that recover rapidly after both climate change and disturbance. This is certainly true of the forest ecotones in Rocky Mountains. Data from long vegetation transects across ecotones can be an efficient way to investigate the environmental forcing of vegetation change (Stohlgren 1994). Important environmental variables for detailed monitoring can be identified. For example, slight increases in growing-season soil moisture and decreases in growing-degree-days may give a competitive advantage to spruce and fir over lodgepole pine. In contrast, a warmer, drier climate may increase the range of lodgepole and limber pine areas, squeezing spruce and fir stands from currently marginal habitat. Monitoring temperature, soil moisture, and tree growth rates may allow for accurate predictions of the changes in lodgepole pine distributions at the ecotone transects.

Information on soils is far from complete. Preliminary data from soil pits (M. Peterson, Natural Resource Conservation Service, Greeley, Colorado, *unpublished data*) suggest that soils may be more different below the 15-cm layer than we reported here. Particle size is somewhat variable along most transects, as is soil depth and surface rockiness. Further research on the affinity of certain tree species to edaphic characteristics is warranted. At present, we cannot be certain whether the degree of soil gradient discontinuity correlates to vegetation stability. Changes in regeneration patterns following fire, insect outbreaks, and disease (Veblen et al. 1991*a*, *b*, Hadley and Veblen 1993) as influenced by immediate postdisturbance climate, competition, herbivory, and disease likely will override the minor soils differences we find here.

Evaluating species–environment relationships at ecotones may provide important insights to vegetation change (Prentice 1992, Risser 1995). Traditionally, ecologists have focussed attention on more-or-less homogeneous and, perhaps, the more stable communities (Palmer 1993*b*). Species-specific responses to climate change (Stohlgren et al. 1993), and anthropogenic nitrogen inputs to these ecosystems (Baron 1991), may further complicate predictions of vegetation change.

The value of long-term transects as "vegetation time capsules" cannot be understated (Stohlgren et al. 1995). Because the transects are accurately georeferenced, ecologists will be able to return to these same sites 50 and 100 yr from now. Our present studies help to generate hypotheses and develop simple mathematical models of vegetation change. The test of our hypotheses and validation of the models will come from the next generation of ecologists.

Acknowledgments

The authors thank the field technicians Greg Newman, April Owen, Yasuhiro Onami, Rob Muckenthaler, and Victoria Steele. Geneva Chong, Lisa Schell, and Paul Anliker assisted with the soil texture work. Ron Thomas and Nancy Thorwardson provided geographic information system support. The staff of Rocky Mountain National Park helped in logistical support. Lisa Schell provided graphics support. Dan Binkley and three anonymous reviewers provided many helpful suggestions on earlier versions of the manuscript. The National Park Service and the National Biological Service provided funding for this long-term project. To all we are grateful.

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