Effects of feedbacks and seed rain on ecotone patterns

George P. Malanson
Center for Global and Regional Environmental Research & Department of Geography, University of Iowa, Iowa City, IA 52246, U.S.A. *

Abstract

Ecotones can be abrupt changes in vegetation on gradual abiotic gradients, such as some treelines, and so have been considered as potential indicators of response to climatic change and regulators of fluxes across landscapes. Factors of positive feedback for growth and establishment and seed rain from source areas have been suggested as playing a role in such patterns and dynamics. The effects of variation in feedback strength and seed rain on the abrupt pattern have not, however, been assessed. A spatially explicit computer simulation is used to represent an ecotone as might occur at a mountain treeline. The steepness of the abiotic gradient determines the general location of the treeline, while the strength of feedback determines how abrupt it is. Increased seed rain and seedling survival modify the dominant patterns by creating patches of krummholz or small seedings. The feedbacks are spatially autocorrelated and so create waves of mortality and regeneration on the simulated slopes comparable to dynamics observed on some mountains. These dynamics may mean that the pattern at the ecotone at any point in time is ephemeral and may respond differently to environmental change.

Introduction

Central to interest in landscapes are ecotones (Risser 1995), and they are areas of productive current research (*e.g.*, Kupfer and Malanson 1993, Milne *et al.* 1996) linking landscape ecology with a long tradition in plant community ecology (Clements 1905). Four characteristics of ecotones give them value for ecological research: as indicators of response of plant species to environmental gradients; as a locus for species diversity dependent on immigration (*i.e.*, sinks); as indicators of climatic change; and as regulators of the spatial flux of species, matter and energy. This research will address aspects of the first two of these characteristics, but with implications for the latter two. The purpose of this work is to use a spatially explicit simulation to investigate factors leading to abrupt ecotones and the role of spatial population processes at these ecotones. The focus will be on treelines, and alpine treelines provide a background for this study (*e.g.*, Slatyer and Noble 1992, Brown 1994).

Abrupt ecotones

As abrupt transitions, ecotones seemingly refute the paradigm of a continuum of vegetation change along an environmental gradient (*cf.* Austin and Smith 1989). Sharp boundaries would not necessarily refute the concept where there is a discontinuity in the environmental gradient itself, such as where disturbance creates a boundary, but in some case gradual abiotic environmental gradients have abrupt vegetational boundaries (van der Maarel 1990). The interpretation of such a pattern depends on the scale of examination (Gosz and Sharpe 1989). The local scale, where reproduction, growth and death of individual plants makes a difference in the pattern, is the focus of this work.

Treeline is often a case of a locally abrupt ecotone. Abrupt treelines at a local scale have been observed where trees border wetlands, grasslands, and tundra. Stevens and Fox (1991) concluded that treeline was largely a phenomenon expressing the carbon balance of trees, so that trees ended where

*Tel.: +1 319-335-0158; fax: 319-335-2725; mallanson@cgrer.uiowa.edu

their carbon balance was zero. This balance alone would not, however, explain an abrupt treeline on a gradual abiotic gradient. Wilson and Agnew (1992) detailed the possibility that positive feedback in the biological processes within one or both plant communities could account for an abrupt ecotone. In these cases the plants modify the environment that they experience so that a continuous abiotic gradient becomes discontinuous in terms of the potential carbon balance. The processes that might lead to a positive feedback include microclimate, *e.g.*, albedo and temperature in canopy and soil (*e.g.*, Bonan 1992, Chalita and Le Treut 1994) or effects on wind and thus on snow (Cairns 1994) or physical effects such as resistance to erosion (*e.g.*, Zonneveld 1995). These feedbacks compound the effects of competition and other processes affecting treeline position and pattern (Armand 1992, Malanson and Butler 1994). In addition to abrupt ecotones, positive feedback may be responsible for other spatial dependencies, such as ribbon forests or migration of krummholz patches (*cf.* Billings 1969, Benedict 1984).

The abrupt ecotone may also depend on establishment and a difference between seedling and adult survivorship; it is generally thought that trees are competitively superior on a resource gradient, but this assumption may oversimplify the relative competitive ability of the nonarboreal species, especially versus tree seedlings (Malanson and Butler 1994). Rare seedling survival can then produce the positive feedback. Although the possibility of a positive feedback for regeneration and growth is obvious, the pattern that might be produced for a feedback of a given strength has not been investigated.

Yamamura (1976) modeled abrupt boundaries for species based on the Volterra equations, but only for a single dimension. Noble (1993) modeled the response of a treeline to climatic change, where the climatic change is hypothesized to act as response to disturbance. In his model trees have a tendency to invade a grassland along a gradual abiotic gradient until their physiological limit is reached, but fires further restrict the treeline. In the primary model the advance is only by contagion. A positive feedback is included at a landscape scale by incorporating the observations of Hardt and Forman (1989) that concave boundaries advance faster than do convex ones. The treeline becomes smoother when this feedback is strengthened. Feedback from ecotone shape reduces the variability of response to simulated climatic change. Noble (1993) concluded that similar treelines affected by disturbance could be useful for monitoring climatic change only if the potential rate of advance was on the order of a canopy width every 5 yr.

Landscape sinks

Ecotones, because they may contain elements of different types of vegetation in the same area, can have greater diversity in their local area. Stevens (1992) suggested that on altitudinal as well as latitudinal gradients ecotones are likely to be species rich. He additionally noted that these areas may depend on the immigration of propagules to maintain populations because they are, by definition, at the margin of species ranges. If ecotones are dependent on immigration from populations closer to the median position of the species on the environmental gradient, then they represent sinks on the landscape (*cf.* Pulliam 1988).

At Arctic and alpine treelines few if any trees produce seeds (Tranquillini 1979). Reproduction at these sites must depend on the seed rain from trees in more amenable environments; even so, seedling mortality may be exceptionally high, and tree seedling establishment in tundra is rare (Weisberg and Baker 1995). In a modification of his model, Noble (1993) included the possibility that individual trees could establish by dispersal rather than direct contagion with extant trees. Dispersal increased the rate of advancement, but also increased the variability of the treeline so that again the noise was greater than the potential signal of response to climatic change. Increased seed rain from a larger, nearby source relative to a smaller or more distant source, could influence the pattern as well as the diversity of treeline. Seed rain from a nearby sources is essentially another form of positive feedback (Green 1990).

Rationale

A variety of patterns have been observed at treeline ecotones. Walsh *et al.* (1992) noted that forms at treeline in Glacier National Park, Montana, are spa-
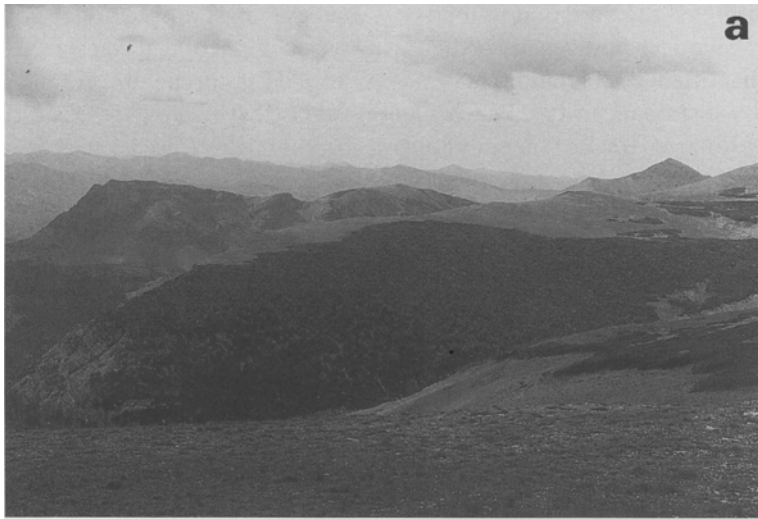
Fig. 1. Treeline pattern takes several forms, common among them are: a, straight lines; b, interdigitation with tundra; and c, scattered patches; in Glacier National Park, Montana.

tially variable, and attributed the variation to topo-graphically controlled abiotic heterogeneity; Allen and Walsh (1996) quantified this relation. Other than sites controlled by disturbance (*e.g.*, Walsh *et al.* 1994) the main forms of treeline are abrupt straight lines, interdigitating upslope extensions, and isolated patches (Fig. 1a,b,c). A question that arises is: How much pattern can be due to auto-genic processes versus abiotic spatial heterogene-ity? Two-dimensional pattern may develop even on a homogeneous plane or a plane with a one-dimen-sional gradient due to autogenic processes (*e.g.*, Wilson and Nisbet 1995).

In this research, the positive feedback hypothe-sis, seed rain, and the steepness of the environmen-tal gradient are examined as potential controls on the pattern of treeline, and the pattern of abundance along the environmental gradient is the focus. Hus-ton (1992) argued that individual-based simula-tions, specifically the JABOWA-FORET model, are well suited to examining plant competition the-ory as well as applied ecological questions. Shugart *et al.* (1988), Huston and Smith (1987), and Smith and Huston (1989) have similarly used a simulation model to examine the responses of species along environmental gradients. B. Milne (on World Wide Web, 9 November 1995: http://algodones.unm.edu/~bmilne/homepage.html) is currently using such a model to examine a pinyon-juniper/grassland eco-tone.

Methods

A spatially explicit version of the JABOWA-FORET model (Botkin *et al.* 1972, Shugart and West 1977; *cf.* Hanson *et al.* 1990, Malanson *et al.* 1996), which has been used by researchers to examine the dynamics of forest stands in many contexts (Botkin 1993), allows the desired tests. I used an extreme simplification of the simulation as the principle vehicle for conducting simulation runs. The model includes the competition and pop-ulation dynamics found in many forests; the funda-mental growth equation is:

$$D = \{G_iD[1-(DH/D_{max}H_{max})]\} *$$

$$(274+3b_2D-4b_3D^2)^{-1} * f(environment),$$

where Gi is an empirical constant that determines when a tree of a species grows most; D is the diam-eter, H is the height, b_2 and b_3 are empirical con-stants that relate height and diameter for a species. In this work I used values to represent a single tree species, *Abies lasiocarpa*: shade tolerant, G = 160, D_{ma} = 80, H_{max} = 1600, b_2 = 52, b_3 = .45, but the emphasis is on generality, not this species or its ecotonal responses. D is reduced by shading, so that:

$$I = D * 1.32 * (1-e^{-2.51 * AL-.07}),$$

where I is the increment in dbh and AL is available light after the shading of taller trees is accounted (using the equation for intermediate shade toler-ance from Bonan 1992). Instead of the *f*(environ-ment) being a site quality based on multiplicative relations between variables such as temperature, available moisture, soil depth, and/or soil nitrogen, I set specific gradients of site quality on the grid as initial conditions and compared the results for dif-ferent gradients, among other factors. The original model represented a single 10 × 10 m stand of trees. I used a 50 × 80 grid of cells representing 500 × 800 m continuous plane of potential forest. I considered using a wider grid or a wrap-around cylinder to eliminate edge effects (Haefner *et al.* 1991), but a limited grid actually represents a mountain slope. The rows are homogeneous in order to simulate a single gradient. I simulated dis-persal across the grid while varying four major parameters: the length and shape of the gradient of site quality; dispersal probability, which determines the seed rain; seedling mortality; and the strength of the positive feedback that tree occupancy of a site has on site quality.

Environmental gradient

The environmental gradient of site quality [*f*(envi-ronment)] varies from 0.0 to 1.0. I set the gradients as abrupt, short, and long (Fig. 2). The abrupt gra-dient linearly crosses the range from 0.0 to 1.0 in 10 rows of the grid. Two longer gradients span up to 75 rows and are set so that the site quality is 0 in rows 1 to 5 and then increases according to the function
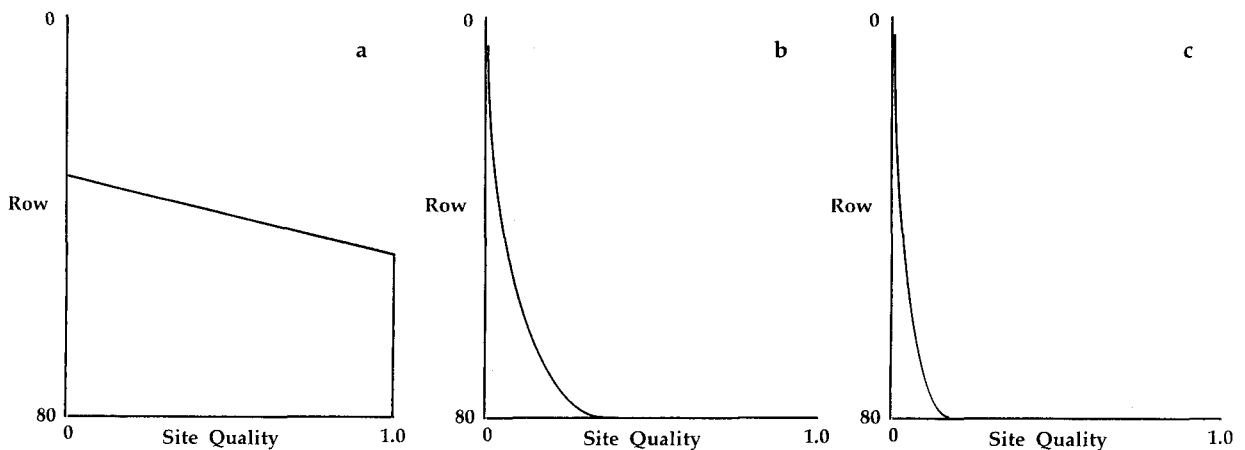
$$SQ = (.0071*row)^a,$$

Fig. 2. Gradients of Site Quality used as initial conditions: a) abrupt; b) moderate; c) gradual.

where a is either 2 or 3, but with the site quality of row 80 always set at 1.0. Variability is added: in any given year a row has a 1/3 chance of having the site quality of plus or minus one row. By using a simple gradient, the effects of autogenic processes on spatial pattern can be assessed.

Seed rain

Dispersal is modeled not for individual seeds but for the probability of dispersal for the species from one cell to another. An annual seed source on each cell depends on a seed crop probability of 1 in 3 years and site quality, which must be greater than a random number 0 to 1. Seed rain from occupied cells to other cells depends on a negative algebraic decay:

$$p = d^{-a},$$

where p is dispersal probability for distance d, in number of 10 m cells. I set a lower limit for probability of .001 (*cf.* Malanson and Armstrong 1996). Portnoy and Willson (1993) found that the tail of this distribution more commonly matches the tail of seed dispersal by plants. Thus the seed rain depends on the distance to and number of cells that are potential sources; cells at treeline, where the site quality is at .0025, will produce seeds 1 in 1,200 years. While any cell is within the possible range of any other, most seed rain is from nearby cells and so is another spatially dependent positive

feedback. I ran simulations with –a set from among –.95, –1.1 and –1.5; these values produce annual migration rates of c. 500, 200, and 100 m yr^{-1}, which compare well with ranges of Holocene migration represented by isopols (Malanson and Cairns 1996). No restriction for light or shade is used for establishment. While seed rain does not depend on the abundance of trees at a source site, only on presence or absence, the value would be highly correlated because abundance is a function of site quality.

Seedling survival

Mortality is modeled in two ways: inherent risk of death and competition-induced death (Botkin 1993). Competition-induced mortality is a function of slow growth; if a tree diameter grows more slowly than .1 cm per year, then it has the relatively high annual probability of death of 0.368 (Botkin 1993, p. 93). While this minimum level of growth is a simplification, it does incorporate effects of both competition and site conditions. Although this procedure is based on limited studies and may not apply precisely to a specific species at treeline, it is the differences simulated that should be revealing. In addition to this means of mortality I added a function in which every seedling less than 5 years of age has an annual probability of death of .368; thus the probability of survival to age 5 is .368^5.
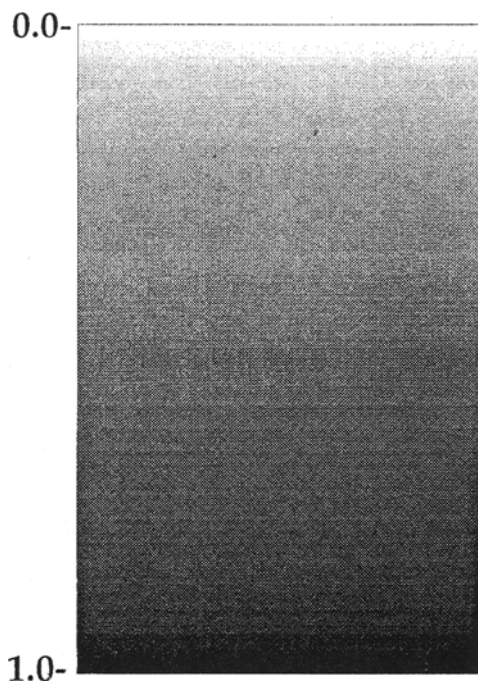
0.0-

1.0-

Fig. 3. Gray scale for the following figures showing relative abundance calculated from basal area.

Positive feedback

The site quality of a given cell is increased if a neighboring cell is occupied. I increased site quality as a function of neighbor basal area:

$$Q = d*S*B/5000,$$

where S is feedback strength, B is basal area in cm^2, and d is 1 for cells sharing a side or .707 (difference in center to center distance) for cells sharing only a corner. I used feedback strength values of 0, 0.1 and 0.5. At 0.1 and .5 a surrounded cell could possibly have its site quality increased by .7 or up to the upper limit of 1.0 used for any cell, respectively.

Analyses

Information from the simulations is analyzed visually on plots of relative basal area on the 50×80 grid (Fig. 3). Basal area is the variable of choice because the model computes diameters of individual trees and all other possible variables, such as biomass, would be direct functions of basal area. It

is to be expected that seed rain provides the opportunity for feedback to operate, increasing survivorship and growth, and thus affecting the pattern observed. The individual effects are revealed by comparing the simulations to that with the most gradual nonlinear gradient, moderate dispersal probability (a=1.1), no extra seedling mortality, and moderate positive feedback strength (s=.1) as a standard.

Results

Gradient length, seed rain, seedling mortality, and feedback strength can all have an influence on an ecotone; some more strongly influence pattern while others affect absolute position relative to site quality.

Gradient length

For an abrupt linear gradient there is an abrupt switch from high basal area forest to two rows of low basal area ecotonal trees to no trees (Fig. 4a). The pattern becomes more interesting when the longer, nonlinear gradients are examined (Fig. 4b,c). The effects of the difference in nonlinearity are slight, but affect just where on the slope the ecotone is found. In general the actual extreme position of the ecotone on the slope (in the simulations the top row occupied in even one cell) is where the site quality reaches .0025. In both cases the gradient is less abrupt, but the patterns seen are generally to have scattered patches of small seedlings and krummholz and then a fairly abrupt transition to trees (greater basal area). The nature of the transition varies with seed rain and feedback strength.

Seed rain

With differences in seed rain the abruptness of the ecotone is generally similar, but the position of the treeline on the slope changes (Fig. 5). With highest seed rain small seedlings extend slightly farther upslope (one row in the simulation; Fig. 5c) than with moderate seed rain (Fig. 5b), which in turn has small seedlings and krummholz moderately
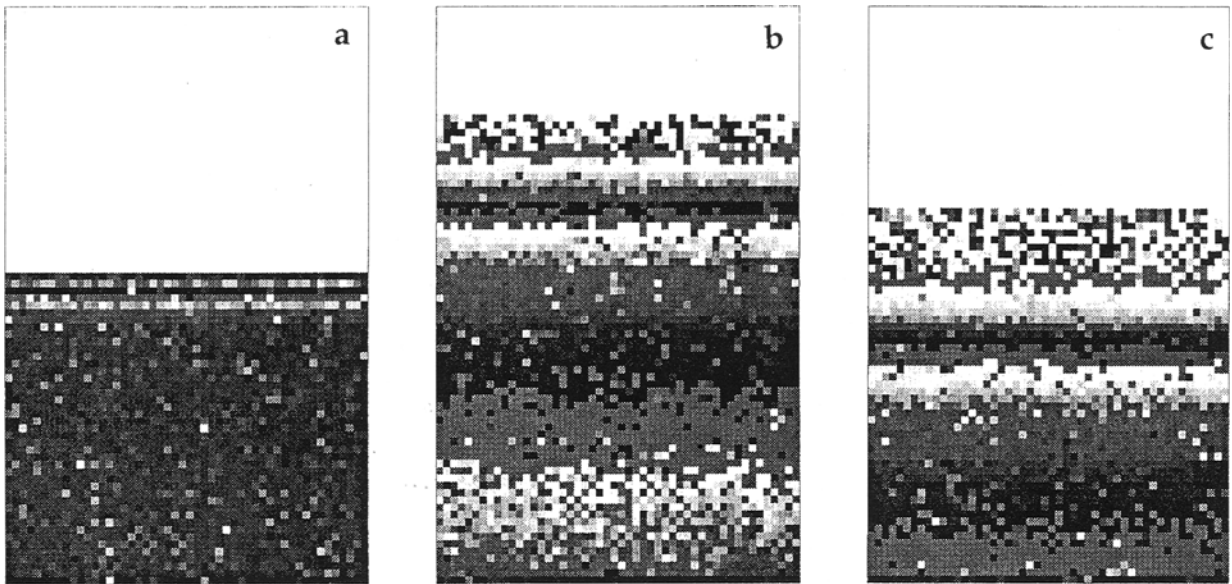
Fig. 4. Pattern of abundance along the gradients for the a) abrupt; b) moderate; c) gradual gradients; seed rain and feedback are moderate, seedling mortality low.
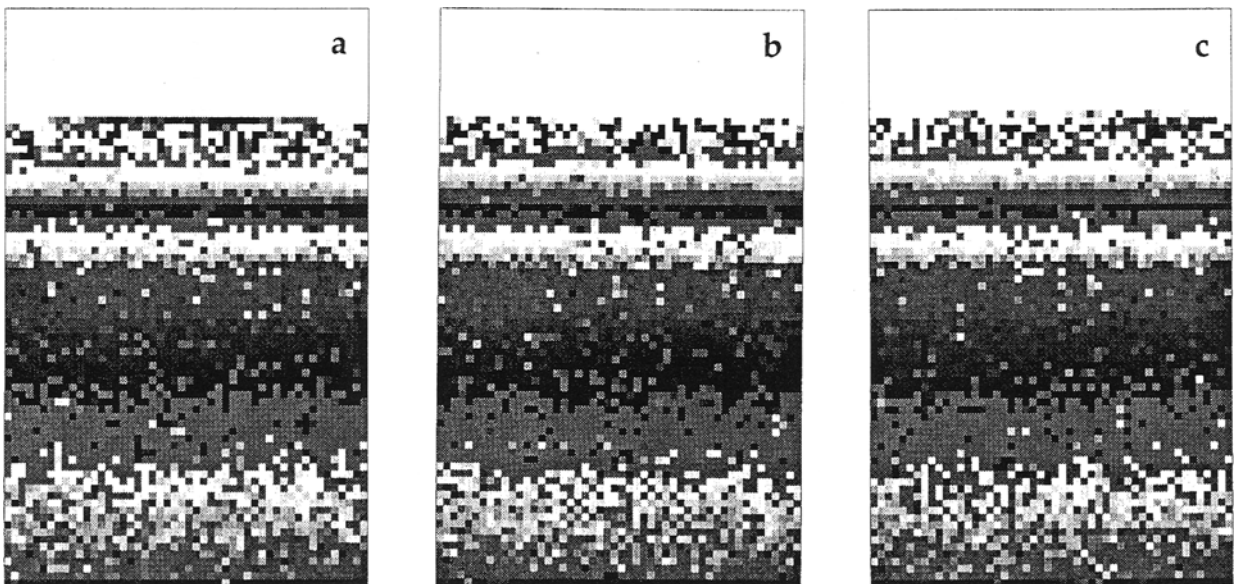

Fig. 5. Pattern of abundance for the three levels of seed rain: a) low, b) moderate, c) high; gradient and feedback are moderate, seedling mortality is low.

farther upslope (three rows in the simulation) than with low seed rain (Fig. 5a). Higher seed rain in both instances extends occupancy from the row with site quality of .0025 to the row with site quality of .0018, while lower seed rain reduces occupancy to rows with site quality of .0062 or greater – all prior to feedback. With more detail at the ecotone itself, it appears that a higher seed rain contributes to greater variability in the abundance at each occupied site as well as more occupied sites.
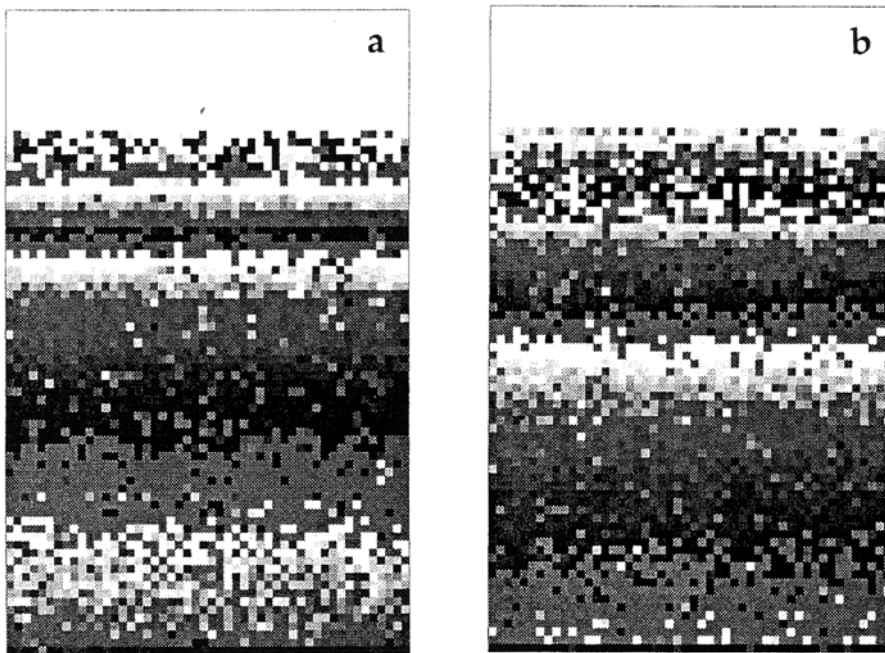
Fig. 6. Pattern of abundance for the two levels of seedling mortality: a) low, b) high; gradient, seed rain, and feedback are moderate.
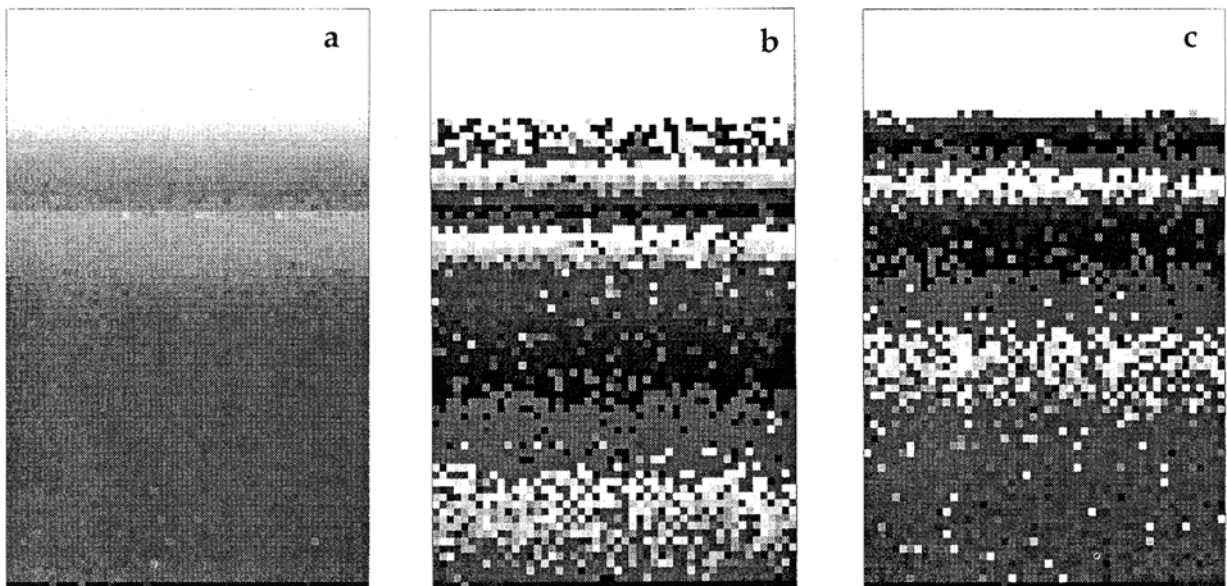

Fig. 7. Pattern of abundance for the three levels of positive feedback: a) low, b) moderate, c) high; gradient and seed rain are moderate, seedling mortality is low.

Seedling mortality

Increased seedling mortality has little or no effect on the ecotone pattern when seed rain and feedback strength are at moderate levels (Fig. 6). The likely explanation is that seedling establishment is so rare in any case at treeline that additional mortality is not expressed in the pattern.
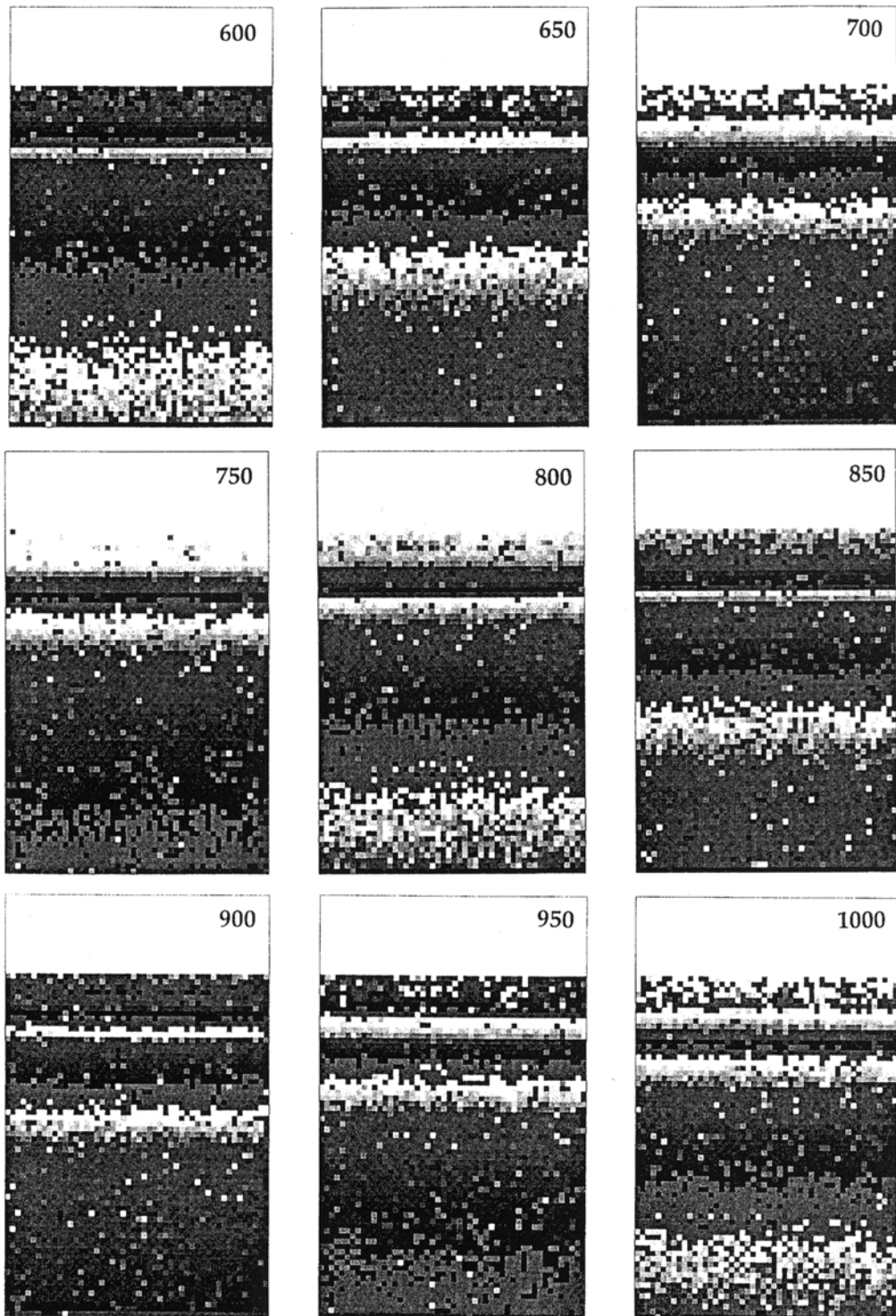
Fig. 8. Pattern of abundance at 50 yr intervals from year 600 to 1000; gradient, seed rain, and feedback are moderate, seedling mortality is low.

Feedback strength

A slight difference between high and low levels of feedback is evident, but both of these cases contrast strongly with the case of no feedback (Fig. 7). Weak feedback produces a pattern with a scattering of seedlings and krummholz (a gradual increase in basal area) across several rows before an abrupt transition (Fig. 7b). With a strong feedback, the transition is more abrupt and the area of larger trees is slightly higher on the slope (Fig. 7c). With no feedback, however, the transition is very gradual (Fig. 7a).

Dynamics

In some of the cases referred to above, a secondary area of low basal area occurs somewhere on the slope below the ecotone (*e.g.*, Figs. 4–7). The reason for such a result is only seen when one examines the pattern through time. When the results are displayed at a 50 yr interval, this low is seen as a wave that moves up the slope and crashes on the shoals of the ecotone; *i.e.*, the low values can be traced through time as moving from the base of the slope toward the ecotone (Fig. 8). An effect at the ecotone is rare, but may be significant (*e.g.*, Fig. 8, year 750).

Discussion

Recent research in ecology has shown that autogenic processes can create spatially heterogeneous patterns on a homogeneous plane or a simple cline (Wilson and Nisbet 1995). Here, the ecotone is often abrupt even when the underlying environmental gradient is not. The positive feedback switch (sensu Wilson and Agnew 1992) is a major factor determining this abrupt change. Seed rain, another positive feedback, also affects the pattern at the ecotone, but only by modifying the occupancy of the marginal sites, not in altering the shape of the abrupt change. At least two treeline patterns can develop due to autogenic processes versus abiotic spatial heterogeneity: a straight abrupt treeline and isolated patches. Upslope interdigitation of trees and tundra (Fig. 1b) probably has some degree of control by slope shape. The relations between process and pattern seen here can be examined in more

detail by simulating for more specific slope conditions and comparing the results to pattern observed through remote sensing (*e.g.*, Walsh *et al.* 1992, Allen and Walsh 1996).

Only in the case of no positive feedback do the simulations show evidence for the sigmoid wave pattern observed by Timoney *et al.* (1993) at Arctic treeline. At Arctic treeline the environmental gradient may be much more gradual than that represented here; the seed rain may be much lower, and there is certainly environmental variability at any latitude, whereas the rows are homogeneous in the simulations. As such, the simulations may more closely resemble a small section of alpine treeline on a mountain slope. Transverse pattern still is evident at the ecotone, but there is not a clear sigmoid wave because the transition from area with scattered patches of seedlings or small krummholz to a continuous cover of krummholz and trees is so sudden. The beginning of a miniature sigmoid wave may be evident in those scattered patches, however. The nature of the boundary may also be affected by competition (Malanson and Butler 1994), not addressed in this single-species model.

The simulation reveals that dispersal can be a critical part of the occupancy of potential habitats. Greater seed rain expands the habitat upslope and it increases the density and biomass in the seedling and krummholz patches uppermost on the slope. Additionally, the simulation reveals that patches at the edge of habitability are in fact sinks dependent on immigration. In these rows, where tree and non-tree vegetation are mixed, are areas of higher diversity, that are not self sustaining: without a seed rain, the area would be devoid of trees, not an area of higher diversity.

The dynamics represented in the model pose problems of interpretation. The possibility of the phenomenon is real: a number of studies in Japan have addressed a similar pattern in forests dominated by *Abies* spp. (*e.g.*, Gomi *et al.* 1956, cited by Sato and Iwasa 1993; *cf.* Foster 1988, for New Hampshire, USA). Usually this is seen as spatially autocorrelated disturbance, where death of trees leads to susceptibility of neighbors to wind and ice damage. In this study, disturbance are not spatially autocorrelated, so the first part of the explanation lies in the way that mortality is simulated. Individual trees die as a function of their age, size, and current growth. Self-thinning occurs stochastically

through the possible lifespan of trees, but mature trees in any one row are then likely to reach a similar size at a similar age with the same site quality determining current growth, and so tend to die at the same time; trees in nearby rows will be similarly affected, but those in rows with higher site quality will not die as regularly because they grow better while those in rows of lower site quality will not die as regularly because they are smaller. This mortality is revealed in the simulations with no feedback, when the drop in abundance appears in one location, and the phenomenon of a traveling wave of mortality is not seen. The wave is a product of the spatial dependence of site quality of a cell on its neighbors. As mortality occurs on a row, the neighboring cells suffer a decrease in site quality because the positive feedbacks of shading and reduced wind are less. The wave tends to move upslope (from rows of higher initial site quality to rows with less) because the effect is greater where the positive feedback is a greater proportion of the total site quality. Where other models have produced this wave phenomenon by including specific disturbances (e.g., Sato and Iwasa 1993), this simulation produces the same result by including the inverse, a positive feedback in reproduction and growth.

These simulated treeline dynamics are thus dependent to a degree on a relatively even age structure at any given elevation. In simulations extended to 2000 years, the even age structure is maintained with feedback in the waves of mortality, but without feedback it is lost and a more gradual gradient wihthout concentrations of mortality is maintained. A consequence for the dynamics and functions at treeline is that interpreting the pattern at any one place and time for an actual treeline (e.g., the 20th century stability reported by Butler et al. 1994) may be too short a view to understand where in the wave the dynamics actually are. Extensive areas of recently (<100 yr) dead trees and krummholz may be observed in some treeline locations, but this mortality cannot be definitively attributed to autogenic processes. Thus the potential for ecotones to act as indicators of climatic change may be compromised by spatially autocorrelated population dynamics as well as the problems indicated by Neilson (1993), Noble (1993), and Woodward (1993). The potential for the positive feedback to create sudden phase changes with

climatic change (suggested by B. Milne, pers. comm.; cf. Milne et al. 1996) may not be dramatic, but it may also depend on the existing spatial dynamics. Also, seedling mortality could possibly play a larger role in a changing climate because seedling establishment is necessary for upslope movement. How ecotones affect the flux of energy, matter, or species across the landscape may also be affected, because these fluxes depend on ecotone structure. Defining a specific temporal scale may be as important as spatial scale in ecotone research.

Acknowledgements

References

Allen, T.R. and Walsh, S.J. 1996. Spatial and compositional pattern of alpine treeline, Glacier National Park, Montana, USA. ms. in review.

Armand, A.D. 1992. Sharp and gradual mountain timberlines as a result of species interaction. In Landscape boundaries. pp. 360–378. Edited by A.J. Hansen and F. di Castri. Springer-Verlag, New York.

Austin, M.P. and Smith, T.M. 1989. A new model for the continuum concept. Vegetatio 83: 35–47.

Benedict, J.B. 1984. Rates of tree-island migration, Colorado Rocky Mountains, USA. Ecology 65: 820–823.

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

Bonan, G.B. 1992. A simulation analysis of environmental factors and ecological processes in North American boreal forests. In A Systems analysis of the global boreal forest. pp. 404–427. Edited by H.H. Shugart, R. Leemans and G.B. Bonan. Cambridge University Press, Cambridge.

Botkin, D.B. 1993. Forest dynamics. Oxford University Press, Oxford.

Botkin, D.B., Janak, J.F. and Wallis, J.R. 1972. Rationale, limitations, and assumptions of a northeastern forest growth simulator. IBM J. Res. and Dev. 16: 101–116.

Brown, D.G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance. J. Veg. Sci. 5: 641–656.

Butler, D.R., Malanson, G.P. and Cairns, D.M. 1994. Stability of alpine treeline in northern Montana, USA. Phytocoenologia 22: 485–500.

Cairns, D.M. 1994. Development of a physiologically mecha-

nistic model for use at the alpine treeline ecotone. Phys. Geogr. 15: 104–124.

Chalita, S. and Le Treut, H. 1994. The albedo of temperate and boreal forest and the Northern Hemisphere climate: a sensitivity experiment using the LMD GCM. Clim. Dynam. 10: 231–240.

Clements, F.E. 1905. Research methods in ecology. University Publishing Company, Lincoln, Nebraska.

Foster, J.R. 1988. The potential role of rime ice defoliation in tree mortality of wave-regenerated balsam fir forests. J. Ecol. 76: 172–180.

Gomi, S., Katsuno, Y. and Imai, K. 1956. Notes on the phenomenon "Shimagare" in the Mts. Yatsugatake. Saishuu to Shiiku 18(3): 66–72. (in Japanese)

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.

Green, D.G. 1990. Landscapes, cataclysms and populations explosions. Math. Comp. and Mod. 13: 75–82.

Haefner, J.W., Poole, G.C., Dunn, P.V. and Decker, R.T. 1991. Edge effects in computer models of spatial competition. Ecol. Mod. 56: 221–244.

Hanson, J.S., Malanson, G.P. and Armstrong, M.P. 1990. Landscape fragmentation and dispersal in a model of riparian forest dynamics. Ecol. Mod. 49: 277–296.

Hardt, R.A. and Forman, R.T.T. 1989. Boundary form effects on woody colonization of reclaimed surface mines. Ecology 70: 1252–1260.

Huston, M. 1992. Individual-based forest succession models and the theory of plant competition. In Individual-based models and approaches in ecology. pp. 408–420. Edited by D.L. DeAngelis and L.J. Gross, L.J. Chapman and Hall, New York.

Huston, M. and Smith, T. 1987. Plant succession: life history and competition. Am. Natur. 130: 168–198.

Kupfer, J.A. and Malanson, G.P. 1993. Observed and modeled directional change in riparian forest composition at a cutbank edge. Landscape Ecology 8: 185–199.

Malanson, G.P. and Butler, D.R. 1994. Competitive hierarchies, soil fertility gradients, and the elevation of treeline in Glacier National Park, Montana. Phys. Geogr. 15: 166–180.

Malanson, G.P. and Armstrong, M.P. 1996. Dispersal probability and forest diversity in a fragmented landscape. Ecol. Mod. 87: 91–102.

Malanson, G.P. and Cairns, D.M. 1996. Effects of dispersal, population delays, and forest fragmentation on tree migration rates. unpublished ms.

Malanson, G.P., Armstrong, M.P. and Bennett, D.A. 1996. Fragmented forest response to climatic warming and disturbance. In GIS and environmental modeling. Edited by M.F. Goodchild, L.T. Steyaert, B.O. Parks, M.P. Crane, C.A. Johnston, D.R. Maidment and S.J. Glendinning. GIS World, Ft. Collins, CO, 243–247.

Milne, B.T., Johnson, A.R., Keitt, T.H., Hatfield, C.A., David, J. and Hraber, P. 1996. Detection of critical densities associated with pinon-juniper woodland ecotones. Ecology, in press.

Neilson, R.P. 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecol. Appl. 3: 385–395.

Noble, I.R. 1993. A model of the responses of ecotones to climate change. Ecol. Appl. 3: 396–403.

Portnoy, S. and Willson, M.F. 1993. Seed dispersal curves: behavior of the tail of the distribution. Evol. Ecol. 7: 25–44.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652–661.

Risser, P.G. 1995. The status of the science examining ecotones. BioScience 45: 318–325.

Sato, K. and Iwasa, Y. 1993. Modeling of wave regeneration in subalpine Abies forests: population dynamics with spatial structure. Ecology 74: 1538–1550.

Shugart, H.H. and West, D.C. 1977. Development of an Appalachian deciduous forest model and its application to assessment of the impact of the chestnut blight. J. Env. Man. 5: 161–179.

Shugart, H.H., Bonan, G.B. and Rastetter, E.B. 1988. Niche theory and community organization. Can. J. Bot. 66: 2634–2639.

Slatyer, R.O. and Noble, I.R. 1992. Dynamics of montane treelines. In Landscape boundaries. pp. 346–359. Edited by A.J. Hansen and F. di Castri. Springer-Verlag, New York.

Smith, T.M. and Huston, M. 1989. A functional classification of plant types: linking spatial and temporal pattern in plant communities. Vegetatio 83: 49–69.

Stevens, G.C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am. Nat. 140: 893–911.

Stevens, G.C. and J.F. Fox. 1991. The causes of treeline. Ann. Rev. Ecol. and Syst. 22: 177–191.

Timoney, K.P., La Roi, G.H. and Dale, M.R.T. 1993. Subarctic forest-tundra vegetation gradients: the sigmoid wave hypothesis. J. Veg. Sci. 4: 387–394.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Springer-Verlag, Berlin.

van der Maarel, E. 1990. Ecotones and ecoclines are different. J. Veg. Sci. 1: 135–138.

Walsh, S.J., Malanson, G.P. and Butler, D.R. 1992. Pattern of alpine treeline, Glacier National Park, Montana, USA. In Geographical Snapshots of North America. pp. 167–171. Edited by D.G. Janelle. Guilford Press, New York.

Walsh, S.J., Butler, D.R., Allen, T.R. and Malanson, G.P. 1994. Influence of snow patches and snow avalanches on the alpine treeline ecotone. J. Veg. Sci. 5: 657–672.

Weisberg, P.J. and Baker, W.L. 1995. Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. Can. J. For. Res. 25: 1326–1339.

Wilson, W.G. and Nisbet, R.M. 1995. Cooperation and competition along smooth environmental gradients. unpubl. ms.

Wilson, J.B. and Agnew, A.D.Q. 1992. Positive-feedback switches in plant communities. Adv. Ecol. Res. 23: 263–336.

Woodward, F.I. 1993. The lowland-to-upland transition – modelling plant responses to environmental change. Ecol. Appl. 3: 404–408.

Yamamura, N. 1976. A mathematical approach to spatial distribution and temporal succession in plant communities. Bull. Math. Biol. 38: 517–526.

Zonneveld, I.S. 1995. Vicinism and mass effect. J. Veg. Sci. 5: 441–444.