15. Landforms, Disturbance, and Ecotones

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Introduction

Ecotones are transition zones between adjacent vegetation communities (patches) that differ in composition and/or structure. Factors creating patterns in species distribution or vegetation structure within landscapes necessarily create ecotones. Forman and Godron (1986) distinguish environmental resource and disturbance patches, and we apply this concept to ecotones by distinguishing ecotones resulting from spatial variation in availability of resources from ecotones created by disturbance. In this chapter, *disturbance* refers to an ecotone-forming event of sufficient intensity and severity to create a patch (minimum area ca. 0.1 ha) that differs from preexisting and neighboring vegetation in structure and/or composition.

Our objective is to illustrate the ways in which landforms may control the spatial patterns of resource availability and the extent and location of disturbances, thus controlling the pattern of vegetation patches within the landscape. Our perceptions draw heavily from earlier work on ecotones by di Castri et al. (1988) and by Hansen et al. (1988). However, we depart from their work by emphasizing geomorphic aspects of landscapes and considering how classes of geomorphic influences on ecosystems outlined by Swanson et al. (1988) are expressed in the structure of ecotones. We use examples from the temperate coniferous forest of the H.J. Andrews Experimental Forest, Oregon (Andrews) and from the desert grasslands of

Figure 15.1. Locations of the two long-term ecological research (LTER) sites examined in this study.

the Jornada Experimental Range, New Mexico (Jornada) (Fig. 15.1)to examine the correspondence between the types and magnitudes of processes creating ecotones and the topology, orientation, and spatial distribution of those ecotones.

The diversity of patch-forming processes operating on landscapes is apparent in examples of processes common to the Andrews and the Jornada areas (Fig. 15.2). We distinguish geomorphic from nongeomorphic classes of disturbances, in that geomorphic events involve movement of soil, sediment, or bedrock. Energetic geomorphic processes, such as landslides or lateral shifts in river-channel position, create distinctive vegetation patches and ecotones. The location, intensity, and frequency of these geomorphic disturbance events are strongly controlled by landforms. On the other hand, geomorphic processes of low intensity, such as chronic, pervasive sheet erosion, may redistribute critical soil resources, thereby influencing the spatial pattern of resource-availability patches and their ecotones, without creating ecotones that we would class as having disturbance origin.

The interaction of landforms with nongeomorphic processes also contributes to formation of mosaics of vegetation patches with associated ecotones within these landscapes. The topographic setting of a particular site, such as its slope position, steepness, aspect, and elevation, influence the microclimate and availability of resources. Microclimatic conditions also influence the spatial patterns of some types of nongeomorphic disturbance (Swanson et al. 1988). For example, dry south-facing slopes may have

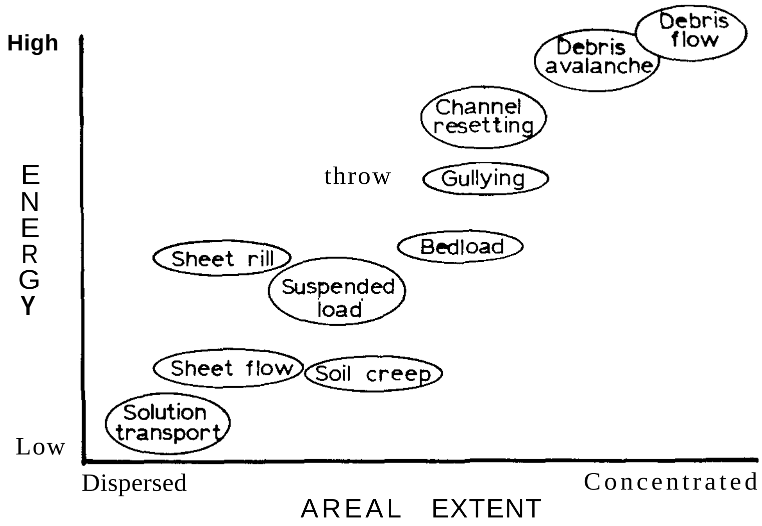

Figure 15.2. Relation of energy expenditure to areal extent of geomorphic processes at the Andrews and Jornada sites.

greater frequency and severity of wildfire, while sites exposed to strong winds may suffer extensive blow-down of trees during storms. Thus, the spatial pattern of vegetation patches resulting from underlying patterns of resource availability and nongeomorphic disturbances may also be influenced by landforms.

We approach this analysis by considering how landform influences may be manifest in ecotone pattern. For example, many disturbance processes follow gravitationally controlled flow paths; and we predict that ecotones in landscapes structured by these processes should be preferentially oriented parallel to the flow paths of materials (perpendicular to contour lines on topographic maps). In landscapes of simple topography where resource distribution is structured by topographic effects on microclimate and downslope redistribution of resources, we expect ecotones to parallel contour lines. In landscapes with complex topography and/or complex landform effects on ecotone-forming processes, we predict that ecotones will have quite varied orientation, with respect to downslope flowpaths.

Site Descriptions

H.J. Andrews Experimental Forest

The Andrews Forest is located in steep terrain of the western Cascade Range of Oregon (Fig. 15.1). Elevation ranges from 400 to over 1600 m. Average annual precipitation is approximately 2500 mm, falling mainly between November and March as snow at higher elevations and as rain in lower areas. Except for narrow openings in the forest canopy along streams, at rock outcrops, and in high elevation meadows, the area is generally forested with Douglas fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, true firs *(Abies* spp.), and other conifers.

The natural disturbance regime of this landscape included wildfire of low to high severity with return periods of 100 years or more (Teensma 1987), landslides and associated debris flows (Swanson and Dyrness 1975), lateral river channel changes, root rots, and wind throw. Forest management since 1950 has created a network of roads and a mosaic of clearcuts (average area approximately 20 ha, with a range of 0.5 to 100 ha), covering about 30% of the Andrews area.

Landforms of the Andrews Forest vary markedly in the down-valley direction. The upper basin bears the imprint of glaciation—a steep-walled, U-shaped valley. The lower part of the basin has not been significantly glaciated, so it is a V-shaped valley, with deeply incised tributary streams. The dendritic drainage network collects water from tributaries, forming a single main channel, which flows along a valley floor of varying width. Stream discharge increases in the down-valley direction.

Jornada Experimental Range

The Jornada Site is located on the flanks of Mount Summerford in southern New Mexico, 40 km northeast of Las Cruces (Fig. 15.1). The landscape is dominated by a broad, gently sloping piedmont, with gradients ranging from <1 to 10%, and with elevations ranging from 1300 to 1500 m. This piedmont extends 2.7 km from the base of the steep, rocky slopes of Mount Summerford to the center of a playa lake. Annual precipitation averages 234 mm, 70% occurring in intense convective storms during the growing season (Malm and Houghton 1977). Landforms do not concentrate the runoff from these storms into a single channel. Instead, runoff flows through a network of small gullies lacing the surface, and total flow usually decreases downslope across the piedmont surface as water infiltrates gully floors and intergully areas. This semidesert grassland (Brown 1982) is best described as a mosaic of shrub communities interspersed with grasslands (Stein and Ludwig 1979).

The disturbance regime within this landscape contrasts sharply to that of the Andrews Forest. Disturbances such as drought and grazing of domestic livestock are extensive, affecting the entire landscape. Decades of overgrazing were followed by increases in the range of shrubs and concurrent loss of much of the former grasslands. These pervasive disturbances affect most of the landscape more or less evenly, without creating the mosaics of disturbance patches characteristic of the Andrews Forest. Patch formation by processes such as ant and gopher activity is common within the Jornada landscape (Whitford et al. 1987), but these processes are not effective in creating patches and ecotones of the scale considered here.

Study Sites and Data Sources

Two study sites in the Andrews Forest and one at the Jornada were identified and delimited by topographic divides, so as to enclose drainage basins. The upper Andrews site consists of 9.2 km^2, encompassing the headwater basin of Lookout Creek. The lower Andrews site extends across the lower valley of Lookout Creek and covers 10.7 km^2. The Jornada site entirely encompasses a small, internally drained basin with a drainage area of 8.3 km^2.

Plant associations of the Andrews were defined on the basis of expected climax vegetation (Zobel et al. 1976). Successional seres, if they exist, are not known for the Jornada, which makes it impossible to determine expected climax vegetation. However, Stein and Ludwig (1979) believe that the vegetation pattern of the Jornada area closely resembles the primeval pattern, so we examine current vegetation patterns for the Jornada. These associations were delineated and mapped, using field and aerial photographic techniques.

Analysis of the orientation of disturbance ecotones is restricted to the lower Andrews site, where the history of disturbances has been mapped. Wildfire ecotones were examined on maps of stands in which at least 75% of the preexisting old-growth forest was killed (based on interpretation of aerial photographs) by fires in the 1800–1900 period. Dates of wildfires included in this analysis are derived from counts of tree rings, to determine total tree ages and ages of fire scars (Teensma 1987). The history of clearcutting is readily determined from aerial photographs, maps, and written records. Debris flows, the rapid movement of 100–10,000 m^3 of soil, alluvium, and woody debris down stream channels, were mapped in the field and from aerial photographs (Swanson and Dyrness 1975).

We sampled fluvial disturbance patches in two streamside sites. A 0.9 km-long unconstrained stream reach was located where the valley floor (floodplain and terrace surfaces ≤ 3 m above low water level) is 6.9 times wider than the width of the stream channel. Due to the wide valley floor and low floodplain heights, the stream in this reach is not constrained and may cut new channels during flood events. The second site was located along a 1.4 km-long constrained stream reach where the valley floor is only 1.3 times wider than the channel width. Here, adjoining hillslopes and exposed bedrock prevent lateral channel migration during flood events. Geomorphic surfaces and associated vegetation created by disturbances in riparian zones of the Andrews forest were mapped in the field at a scale of 1:480.

Methods

To evaluate effects of landforms on ecotone structure, we analyze maps of vegetation patches defined in terms of plant associations and disturbance origin. Our analysis in both the Andrews and Jornada landscapes focused

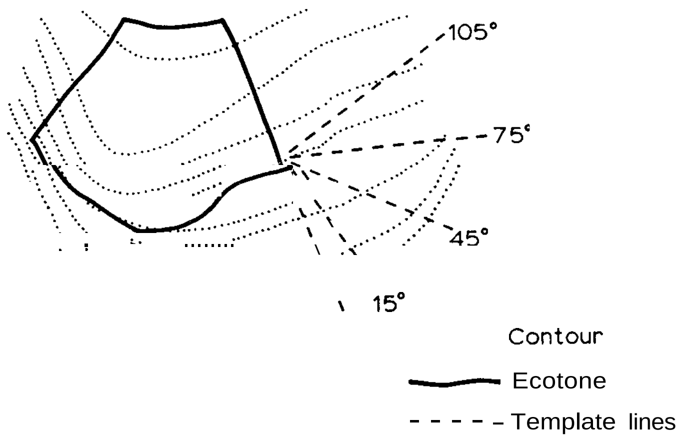

Figure 15.3. Method for determining classes of angles between ecotones and reference lines, which are either contour lines or flow paths. In this case, the 0" orientation parallels a gravitationally determined flow path perpendicular to the contour line.

on the orientation of ecotones with respect to slope (i.e., relative to contour lines crossing the slope or flow paths oriented downslope). The maps of plant associations or disturbance patches were overlayed onto a topographic base map. Ecotone orientations were measured with reference to contour lines on maps with contour intervals of 15.3 m (50 feet) for Andrews and 3.1 m (10 feet) for Jornada. Ecotones surrounding fluvial and debris flow disturbance patches were a special case because valley floors were narrow and poorly represented by contour lines. For these disturbance patches, the down-valley direction was used as the reference line. This reference line followed the valley axis but did not follow individual meanders of the stream channel within straight, unconstrained reaches. We use the downslope (equivalent to down-valley) direction as a common reference orientation for presenting all data.

Using a transparent template marked with classes of angles (0-15°, 16-45°, 46–75', and 76–90"), ecotones were delineated into segments based on the angle between the ecotone and the reference lines (Fig. 15.3). The lengths of ecotone segments were measured and summed within each class. The map scale was then used to convert the measured lengths of ecotone into kilometers per angle class and then standardized by the number of degrees within each class, to give kilometers of ecotone per degree of angle between the ecotone and the downslope direction. Next, the values were converted into percentages, to show the relative orientations of ecotones within the landscape, without confounding results by the total length of each type of ecotone present. Both the area of each patch and the total landscape area were measured, to compute the edge density (km of edge per km2 of landscape) and the edge-to-area ratios for each patch/ecotone type. Additionally, we noted whether the undisturbed forest canopy was located upslope or downslope of the ecotone-bounding disturbance patches created by clearcut and wildfire.

The frequency distribution of ecotone lengths in each angle class was tested against the expected distribution with the chi-square statistic. The expected (or null) distribution, given totally random orientation of ecotones on the landscape, was that the total length of ecotone per degree should be equal for each angle class. A simple chi-square was used to test for differences in ecotone distribution within a single study site or disturbance type. Contingency tables were constructed and used to test for differences between sites or disturbance types.

Results

Resource Availability and Plant Association Ecotones

The Jornada and Andrews landscapes offer an interesting gradient of increasing topographic complexity over which to observe landform effects on resource availability ecotones. The Jornada is a flat plain of moderate slope. The upper Andrews landscape resembles a U-shaped plain folded around an axis parallel to the main stream. The most complex landscape, the lower Andrews area, resembles a folded plain, similar to the upper Andrews, but folded a second time about the minor axes parallel to tributary streams and at approximately right angles to the axis of the main fold.

The planar Jornada landscape exhibits a strong pattern of ecotones and vegetation zones crossing the slope, oriented perpendicular to gravitationally controlled flow paths (Fig. 15.4, Table 15.1). Almost 70% of the total length of ecotone between patches delineated on the basis of vegetation type plant associations crosses the slope within 75" to 105" of the downslope flow path. Ecotones with other orientations are scarce, indicating that disturbances and landform effects on microclimate are minor in this landscape, with a topographically simple land surface and uniform aspect.

In this arid environment, surface water movement appears to control patterns of vegetation (Wondzell et al. 1987). Because the flow paths of water in channels and on interchannel areas are all parallel, water tends to move across the landscape in a broad front, parallel to contour lines, much like a diffusion front through a permeable medium. Soils of contrasting hydrological properties form bands crossing the slope. The soil patterns reflect episodes of erosion and deposition since the mid-Pleistocene. Some soil units experience net runon and support perennial grasslands; other units, which have net runoff, support drought-tolerant shrubs. The overall

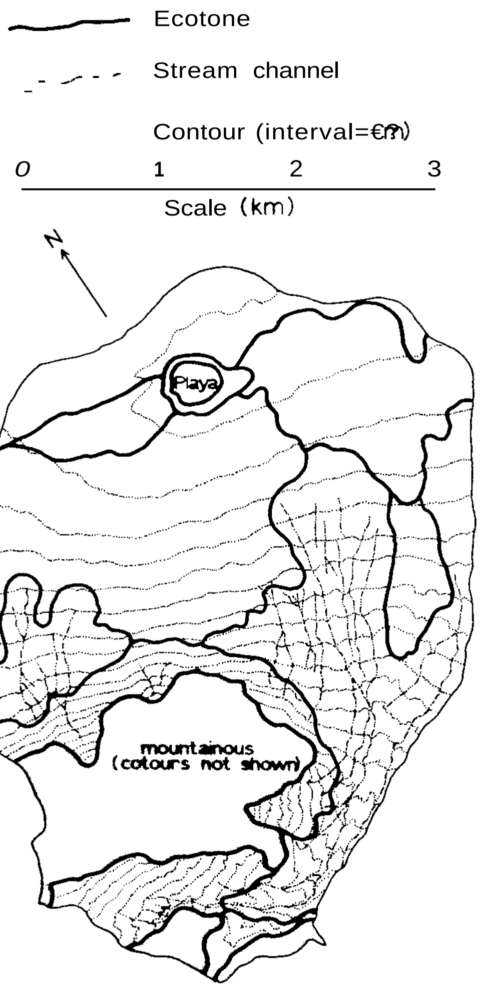

Figure 15.4. Plant association map for Jornada. The Jornada plain extends downward to the northeast, toward the playa.

effect is that the Jornada landscape we examine is composed predominantly of a series of units of distinctive soil and vegetation properties oriented across the planar landscape perpendicular to flow paths.

An exception to the cross-slope pattern of ecotones between vegetation types occurs where the topography of the mountain front and upper piedmont concentrates runoff into relatively dense networks of gullies on an alluvial fan surface. These areas experience local episodic flow peaks, but not of sufficient magnitude to create disturbance patches at the scale considered here. Rather, this network of gullies, developed over the Quater-

Table 15.1. Orientation of Plant-Association Ecotones Relative to Downslope Direction[a]

Angle Between Ecotone and Downslope Direction	Ecotone Length (%)		
	Jornada	Upper Andrews	Lower Andrews
-15-+15°	16	14	24
16- 45°	8	16	22
46- 75°	8	14	14
76-105°	68	56	40

[a]Frequency distributions of ecotone were significantly different ($p < 0.01$) between each study site and from the expected distribution of ecotone within each study site.

nary, efficiently removes soil, water, and organic matter from the entire fan surface. Consequently, the fan surface has limited water and, possibly, nutrient resources (Wondzell et al. 1987) and is dominated by the drought-tolerant evergreen shrub, *Larrea tridentata.* This vegetation zone extends downslope, forming some segments of ecotones that cross contour lines at high angles (Table 15.1). In this resource-limited system, these flow paths represent concentrated zones of resource removal, with the net effect of creating resource availability ecotones that resemble disturbance-generated ecotones.

The upper Andrews area is characterized by steep, paired valley walls of high relief, where orographic effects on microclimate are strong. In this landscape, a high proportion of the total length of ecotone between plant associations crosses slopes roughly parallel to contour lines and to the axis of the main valley (Figure 15.5, Table 15.1), perpendicular to the flow paths of materials moving down valley walls. We believe that orographic effects on microclimate in the upper Andrews exert a greater control on the distribution of the plant associations than does downslope movement of material. Relevant factors include the high relief and midlatitude (45°N) location of the Andrews, which together create significant topographic shading effects. Surface flow of water is uncommon in the Andrews landscape because the infiltration capacity of soil greatly exceeds precipitation intensities, except in sites disturbed by heavy equipment. Unlike the Jornada, aspect is not uniform in the upper Andrews landscape, and this is reflected in the cross-valley asymmetry of plant associations.

The dissected lower Andrews landscape (Fig. 15.6) is characterized by high relief and complex topography, resulting from numerous tributary valleys separated by steep ridges. Here, the orientations of ecotones between plant associations tend to run at all angles to the downslope direction (Table 15.1). Topographic complexity apparently results in a diversity of site characteristics (e.g., elevation, relative hillslope position, aspect,

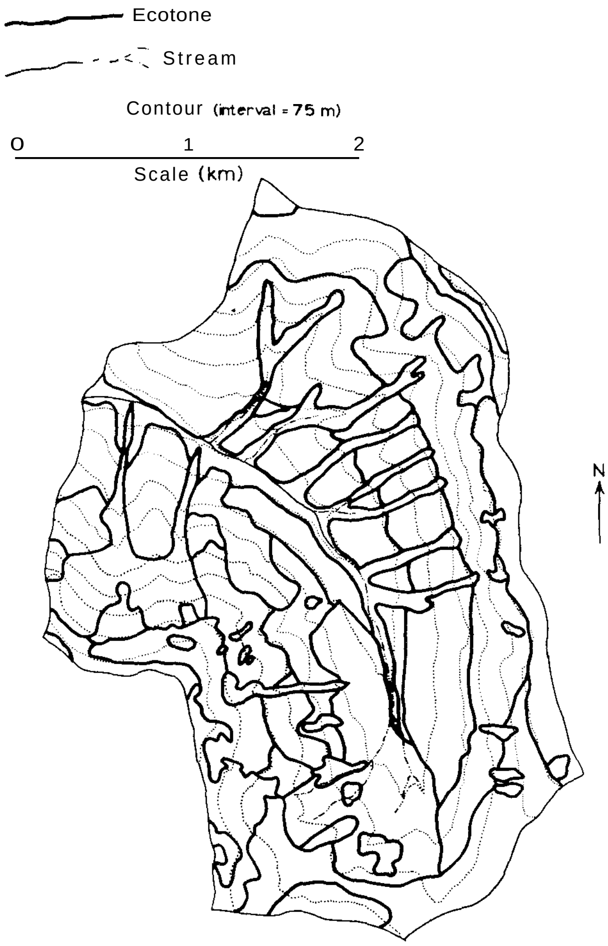

Figure 15.5. Plant association map for upper Andrews.

steepness), which combine with other factors, such as wind stress (e.g., dessication) and cold air drainage down steep tributary valleys, to produce a complex pattern of resource availability. Thus, ecotones bounding vegetation patches defined by plant associations in this topographically complex landscape seem to have a less predictable orientation relative to landforms and flow paths than in topographically simpler terrain.

Even within such a complex landscape, a large component of ecotone length crosses slopes within 76° to 105° of the downslope flow path (Table 15.1). The tributary valleys of lower Andrews are sufficiently well developed that plant associations of the main valley extend laterally into tributary basins, creating ecotones that parallel the contours along toe slopes

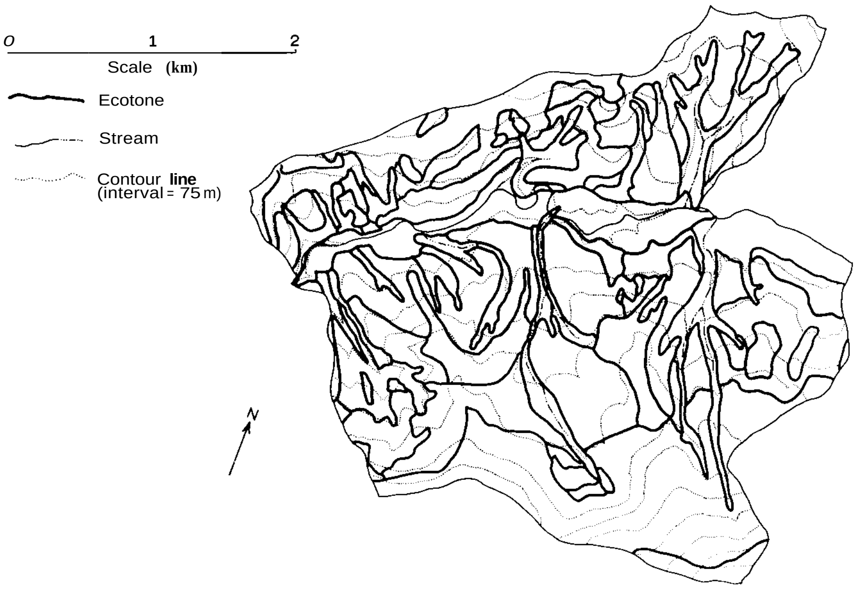

Figure 15.6. Plant association map for lower Andrews.

and streamside benches. Also, the ridgelines and extreme upper slopes of valley walls bounding the main basin are little dissected, so orographic influences on microclimate tend to create ecotones crossing slopes, as in the upper Andrews.

Disturbance Ecotones

Ecotone Orientation

Wildfire. Before fire suppression became effective in the Andrews area early this century, wildfire was an important disturbance process (Teensma 1987). We examined wildfire ecotones by considering the pattern of burning during the period from 1800 to 1900 in the lower Andrews (Fig. 15.7), which can be observed in aerial photographs as patches of young to mature forest stands within a matrix of old-growth (400–500 years in age) forests. The spotty fire pattern and evidence of underburning in intervening areas suggest that much of this burning was of low to moderate intensity and did not involve rapid spread driven by strong winds.

Ecotones surrounding wildfire disturbance patches are preferentially oriented across slope (Fig. 15.7, Table 15.2). This ecotone pattern may have resulted, in part, from effects of ridges and valley floors impeding fire spread. Also, some wildfires may have backed downslope and stopped at changes in fuel abundance or moisture conditions—resource availability factors—which would account for some of the similarities of ecotone

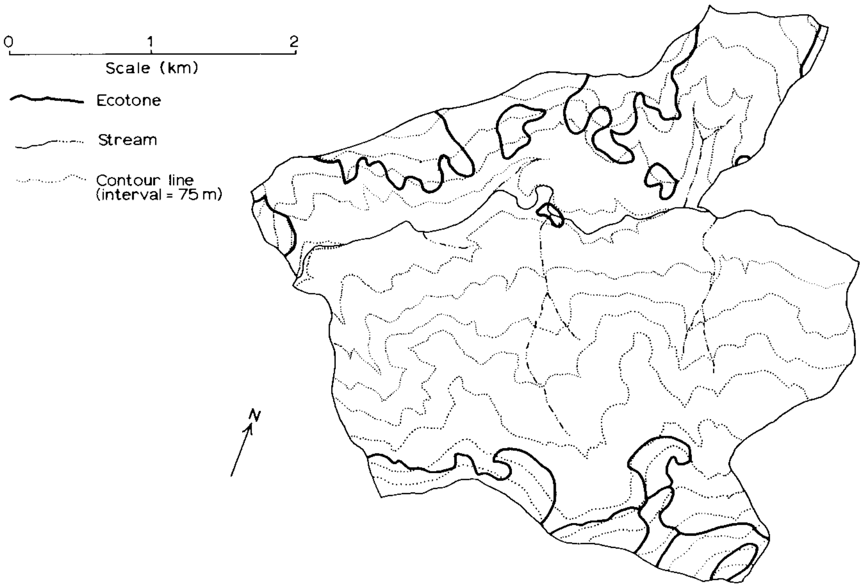

Figure 15.7. Map of areas of crown fire in 1800s in lower Andrews landscape

Table 15.2. Orientation of Disturbance Ecotones Relative to Downslope Direction at the H.J. Andrews Experimental Forest[a]

Angle Between Ecotone and Downslope Direction	Ecotone Length (%)				
	Nongeomorphic Disturbance		Geomorphic Disturbance		
			Fluvial		Debris Flow
	Wildfire	Clearcuts	Unconstrained	Constrained	
−15–+15°	23	33	66	81	92
16– 45°	23	21	28	14	<1
46– 75°	11	11	4	3	0
76– 105°	42	35	2	2	8

[a]Frequency distributions of ecotone were significantly different ($p < 0.01$) between each study site and different from the expected distribution of ecotone within each study site.

orientation between wildfire and plant associations in the study area (Tables 15.1 and 15.2). The tendency of fire to burn upslope, driven somewhat by its own convective winds and preheating effects on the upslope side of the fire front, is reflected in the nearly 3:1 difference in occurrence of the disturbance on upslope areas, with undisturbed forest below (Table 15.3).

Table 15.3. Orientation of Wildfire and Clearcut Ecotones in the H.J. Andrews Expermental Forest Relative to Downslope Direction, Noting Presence of Forest (Undisturbed Area) Above or Below the Disturbed Area[a]

Angle Between Ecotone and Downslope Direction	Ecotone Length (%)		
	Forest (Above)		Forest (Below)
Wildfire			
±15"		14	
16- 45°	8		38
46- 75°	4		8
76-105°	10		18
Clearcut			
±15°		20	
16- 45°	16		21
46- 75°	7		5
76-105°	21		9

aFor the ±15° class, the location of forest is not distinguished. Frequency distributions of ecotone were significantly different ($p < 0.01$) between each study site and different from the expected distribution of ecotone within each study site.

Clearcutting. The orientation of ecotones at the edges of clearcut units in the Andrews (Fig. 15.8) differs somewhat from that of wildfire. Ecotones bounding clearcuts are preferentially oriented across and upslope–downslope as a result of logging and silvicultural systems used in the area (Table 15.2). Segments of ridges, valley floor margins, and roads are commonly used as upper and lower boundaries of cutting units, and each of these features is commonly nearly horizontal. Upslope–downslope lateral edges of cutting units are created in part to facilitate slash burning, because burning upslope toward a stand edge oriented 46–75' to the downslope direction with forest above would be difficult to contain unless that ecotone coincided with a ridge.

To some extent, clearcut ecotones also reflect the flow of material across the land surface. Uphill transport of cut logs, using cables, results in development of radial logging patterns with an apex at the uphill end, indicated by the 16–45" ecotone:flow-path direction angles, with undisturbed forest above the ecotone (Table 15.3).

Debris Flow. Debris flows originating in forested, clearcut, and roaded areas are common events in the lower Andrews landscape. Debris flows involve the rapid (5–10 m sec-l) movement of organic and inorganic material down small stream channels, with resulting disturbance of the valley floor adjacent to first- through third-order channels. Debris flows are usually constrained by valley walls and other landforms, so the resulting disturbance patches are elongate in the up–down valley direction. Consequently, ecotones and flow direction are strongly parallel (Table 15.2).

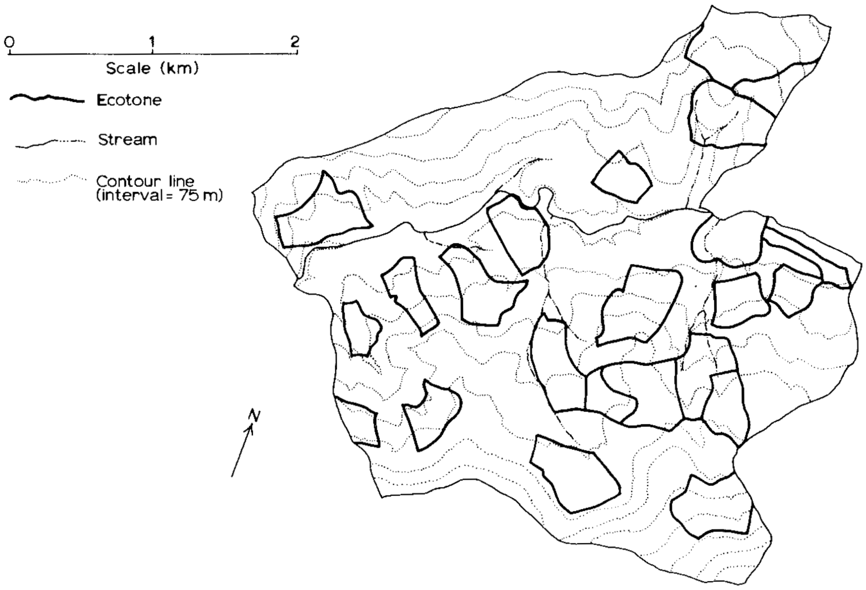

Figure 15.8. Map of clearcut areas in lower Andrews.

Fluvial Disturbance. Lateral channel changes over the past century, particularly in the major flood of December 1964, have created a series of fluvial disturbance patches along lower Lookout Creek in the Andrews. The ecotones of fluvial disturbance patches that originated during the 1964 flood are preferentially oriented parallel to the downstream flow path (Table 15.2). Ecotones in the constrained reach have greater tendency to parallel the flow-path direction than those in the unconstrained reach because fluvial disturbance patches are more elongate in the narrow confines of the constrained valley floor.

Hydrologic Energetics of Landscapes—A Basis for Comparison

A context for interpreting the lateral extent and downstream patterns of fluvial disturbance ecotones is provided by examining both the spatial variation in fluvial energy down the flow path and the resistance of streamside landforms and ecosystems to disturbance. Fluvial energy available for landscape alteration can be expressed as stream power (a):

$$\Omega = \gamma Q s \qquad (1)$$

involving the specific weight of water (γ), channel slope (s), and discharge (Q), which we have estimated for events with a 5-year return interval. Long-term records from gauging stations and measurements of channel slope for the Andrews were used to calculate stream power as a function of

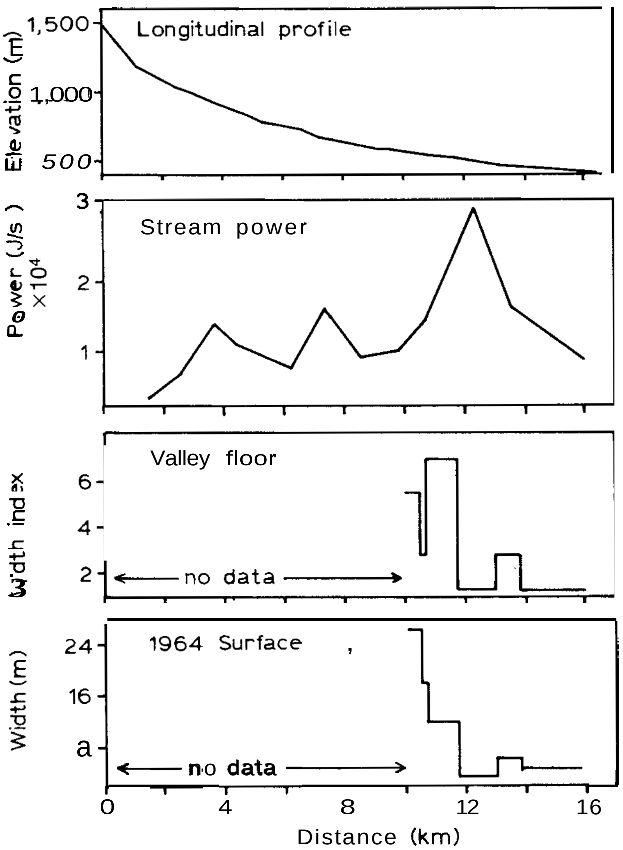

Figure 15.9. Downstream–down-flow-path variation in streambed elevation, stream power, valley floor width index (width of valley floor ≤ 3 m above low flow water surface/width of active channel), width of geomorphic surface originating in the 1964 flood. The ordinate axis shows distance downstream from the drainage divide in the upper Andrews and extending through the lower Andrews study area.

distance from drainage divide (Fig. 15.9). The general pattern is a downstream increase in stream power, as a result of increasing discharge, although local peaks in stream power occur where the channel slope increases.

Stream reaches with higher stream power do not neatly correspond with zones of high incidence of fluvial disturbance patches. Instead, fluvial disturbance patches display a complex relationship with stream power. Streamside disturbance patches exceeding 10 m width are first developed at a distance of nearly 7 km from the drainage divide, where stream power exceeds 10^4 $J \cdot s^{-1}$ (Fig. 15.9). Upstream of this point, streams do not have sufficient energy or sediment supply to create valley-floor geomorphic surfaces of fluvial origin on the time and space scales considered here. Furthermore, the narrow valley floor and extensive bedrock control of headwater valleys limit opportunity for fluvial reworking of valley bottom sediments and creation of disturbance patches. In the 7 to 12 km and the 13 to 14 km reaches, both stream power and sediment supply are sufficient for fluvial disturbance and development of valley-floor geomorphic surfaces. Highest values of stream power occur in the 12 to 13 km reach, where channel constraint by a large landslide and bedrock outcrops steepens and narrows the channel. However, these geomorphic features and the resulting narrow valley floor limit the ability of the stream to create disturbance patches in the riparian forest.

This example points up the importance of landform constraints on the expression of disturbance patches and ecotones within the Andrews fluvial system. Relations between stream power and disturbance may differ greatly among systems. In basins with much higher sediment loads, for example, stream reaches with low gradient and stream power may be prone to disturbance by sediment deposition. We believe that fluvial disturbances in the Andrews are dominated by erosion processes, mediated, in some cases, by movement of large woody debris.

Appropriate hydrological data for calculating stream power along flow paths are not available for the Jornada. However, we expect a very different longitudinal pattern of stream power in the Jornada landscape, where discharge can decrease in the downstream direction, as a result of infiltration and development of distributary channels, which spread the flow laterally. Stream power should correspondingly decrease downstream, as well, and may remain below the threshold stream power necessary to form disturbance patches.

The potential energy of the Andrews and Jornada landscapes can be compared in more general terms that help explain contrasts in the relative importance of disturbance ecotones. The annual potential hydrological energy of a landscape can be quantified by integrating the potential energy available from precipitation over the entire drainage basin. The resulting measure of potential hydrological power at the basin scale can be expressed as

$$\Omega_B = \sum_j \gamma P_j A_j z_j \qquad (2)$$

where P is average annual precipitation falling in elevation band j, which has area, A, and mean elevation, z, above the mouth of the drainage basin. By this approach, the Andrews has $1.8 \cdot 10^{13}\ \mathrm{J \cdot km^{-2} \cdot yr^{-1}}$ of hydrological potential energy, and the Jornada landscape has $2.0 \cdot 10^{11}\ \mathrm{J \cdot km^{-2} \cdot yr^{-1}}$ of potential energy, roughly a 100-fold difference. The contrast would be even greater if we considered actual runoff, which is about 65% of precipitation at the Andrews, but much less at Jornada (no available data). In light of the differences in potential hydrological energy between these landscapes, it seems reasonable that geomorphic processes have not created a landscape-scale mosaic of disturbance patches within the Jornada. The Andrews Forest, in contrast, is an energy-rich landscape, in which steep slopes and dendritic drainage patterns concentrate abundant surface water flow so that shear stresses locally exceed the biotic and geomorphic resistance of streamside areas and create disturbance patches at some points along the fluvial system.

Ecotone Density

The complex landforms and high level of energy available to create disturbance patches results in a relatively high density of ecotones in the Andrews landscape (Table 15.4). The lower Andrews has over twice the density of plant association ecotones as Jornada and a density of disturbance ecotones that exceeds the ecotone density of plant association patches at the Jornada.

The relative ecotone density for different patch-forming agents does not reflect the areal extent of patches because of large differences in patch shapes. Debris flow patches, for example, are long and narrow, so edge:area ratio is much higher than is the case for more equidimensional patches, such as those created by clearcutting or wildfire.

Discussion

These perspectives concerning landform effects on ecotones may be useful for evaluating ecotone stability in the past and future. Tworelated factors should be considered: (1) degree of resource-availability control and (2) degree of landform control on ecotone location and stability. We hypothesize that ecotones with greatest stability are those with strongest influence of landforms and most persistent resource availability control on ecotone location. For example, where pronounced landforms, such as ridges, determine patterns of resource availability, ecotones should be stable on a geological time scale, although disturbance or climate change may alter vegetation on either side of the ecotone. Ecotones controlled by slow-to-

Table 15.4. Density of Ecotones of Various Types and Areas Sampled in the Andrews and Jornada Landscapes

	Density of Ecotones (km/km2 of drainage basin area)		
Type of Ecotones	Jornada	Upper Andrews	Lower Andrews
Plant association	3.26	4.54	7.12
Wildfire	—	—	1.55
Clearcut	—	—	3.27
Debris flow	—	—	1.96

change, edaphic factors regulated by pedogenic and geomorphic processes operating over long periods of time, such as in the Jornada landscape, should also be stable over long periods. Shifts in distributions of some species resulting from major forcing events, such as climate change, may be inhibited where pronounced landforms or conservative soil properties impede vegetation change and sustain a long-term imprint on location of ecotones.

Ecotones controlled by geomorphic disturbances are more transient. Infrequent disturbances, such as landslides, may require time periods of more than a century in ecosystems that are typified by the Andrews Forest before successional processes merge the disturbance patch with the undisturbed forest matrix. Because soil is also disturbed by such processes, ecotones may be maintained over time scales required to redevelop the soil profile within the disturbance patch. On the other hand, sites of repeated disturbance, such as certain streamside areas, may have persistent ecotones that are actually maintained by disturbance.

The most transient ecotones tend to be those created by nongeomorphic disturbances, because they may be erased by subsequent disturbance or by secondary vegetation succession. In locations where disturbances are frequent, but disturbance pattern is not constrained by landforms, ecotones may be highly transient, as successive disturbances overprint ecotones created by earlier disturbances. Elimination of such ecotones occurs more rapidly than geomorphic disturbance ecotones, because soils are not disturbed, and the long-term process of soil formation is not involved in recovery of the disturbance patch.

In landscapes of low relief where soil patterns are not tightly constrained by landforms, chronic disturbances (such as overgrazing) may alter surface hydrology over periods of 10s to 100s of years. These changes can result in altered rates of erosion and deposition, leading to new patterns of resource availability, thus changing ecotones on the time scale of decades to centuries. The new ecotone pattern may be very persistent even after grazing is stopped because of loss of developed soil profiles and establishment of long-lived shrub species. This scenario has been played out in the Jornada landscape (Wondzell et al. 1987, Schlesinger et al. 1990).

Effects of climate change on disturbance-created ecotones will be a function of its effect on disturbance processes and on the resistance of landscapes to change. Because major landform features strongly influence ecosystem patterns in some landscapes and are relatively unchanging on the time scale of millennia and longer, climate change may have little effect on some aspects of the pattern of ecotones on a landscape. For example, climate change may induce change in the species composition and the disturbance regime of patches, but topographic features may fix the location of some ecotones bounding them. Climate change may also lead to changes in the hydrological potential energy of a landscape, which, over the long term, determines the magnitude, frequency, and spatial extent of certain types of geomorphic disturbances.

Conclusions

The Andrews and Jornada landscapes contrast strongly in form, dominant processes, and the energy available to drive landscape disturbance. Patches and their ecotones in landscapes of low topographic relief, complexity, and hydrologic energy, such as the Jornada, appear to be patterned by long-term redistribution of critical resources (see also Cornet et al, Chapter 16, this volume). Resulting ecotones are predominantly oriented across slope, perpendicular to paths of water flow. In areas of arid climate, where water is not concentrated by landforms, such as the Jornada, runoff events seldom produce sufficient fluvial power to create disturbance patches (Fig. 15.1).

Landform influences on microclimate and vegetation patterns are greatest in landscapes with highest topographic complexity and relief. If the landscape has simple form but great topographic relief, such as the upper Andrews, ecotones tend to parallel contours due to orographic effects, topographic shading, and other factors. Where topography is complex, such as the lower Andrews, the pattern of patches and ecotones is also complex. Thus, the available data on density of plant association (resource availability) ecotones follow a trend of increased ecotone density with increased topographic complexity (Table 15.4).

Because the potential energy of the Andrews landscape is high, many of the processes operating in the Andrews landscape fall within the disturbance field of high energy expenditure (Fig. 15.1). Patches and ecotones created by geomorphic disturbances are prominent features of vegetation patterns in the Andrews landscape (Table 15.3). These geomorphic disturbances create long narrow patches, with most of the ecotone paralleling flow paths. Further, the prominent landforms of the Andrews constrain the expression and location of these disturbances, as seen for fluvial disturbances along the stream network.

Patterns in the Andrews Forest also show a complex history of disturbance by wildfire, clearcutting, and other nongeomorphic processes. With respect to disturbance by wind-toppling of vegetation, the great stature of conifer forests at the Andrews (50 to 90 m tall) reflects much greater potential energy than the 1 to 2 m tall vegetation at the Jornada. Greater fuel concentration and continuity in the Andrews also results in much greater wildfire potential. The aggregate effect is a greater imprint of disturbance on the Andrews landscape (Table 15.4). Each type of nongeomorphic disturbance creates ecotones with characteristic orientation relative to downslope flow paths.

Although the Andrews and Jornada landscapes contrast in energy and density of ecotones, opportunities for direct comparison are limited by the difficulty of defining criteria for ecotone identification that are independent of the species and physiognomic characteristics of a particular ecosystem. Even so, comparative analysis yields insights into effects of landforms and flow paths of material and disturbances on broad aspects of the ecotonal structure of landscapes.

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