gie 19:140-169.
Turnbull, W.J., E.S. Krinitzky, and L.J. Johnson. 1950. Sedimentary geology of the alluvial valley of the Mississippi River and its bearing on foundation problems. Pages 210-226 *in* P.D. Trask, editor. Applied sedimentation. John Wiley, New York, New York, USA.
Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology. BioScience 37:119-127.
Walker, L.R., J.C. Zasada, and F.S. Chapin III. 1986. The role of life history processes in primary successions on an Alaskan floodplain. Ecology 67:1243-1253.
Ware, G.H., and W.T. Penfound. 1949. The vegetation of the lower levels of the floodplain of the South Canadian River in central Oklahoma. Ecology 30:478-484.
West, D.C., H.H. Shugart, and D.B. Botkin (editors). 1981. Forest succession: concepts and application. Springer-Verlag, New York, USA.
Westoby, M. 1987. Soil erosion, as a landscape ecology phenomenon. Trends in Ecology and Evolution 2:321-322.
Whitmore, T.C., and G.T. Prance (editors). 1987. Biogeography and Quaternary history in tropical America. Clarendon Press, Oxford, England.
Wiens, J.A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81-120.
Wiens, J.A., J.F. Addicott, T.J. Case, and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. Pages 145-153 *in* J. Diamond and T.J. Case, editors. Community ecology. Harper and Row, New York, USA.
Winkley, B.R. 1977. Manmade cutoffs on the lower Mississippi River: conception, construction and river response. United States Corps of Engineers, Vicksburg, Mississippi, USA.
Wolman, M.G., and L.B. Leopold. 1957. River flood plains: some observations on their formation. United States Geological Survey Professional Paper 282-C.

Key words: Amazon River, ecotone, landscape ecology, patch dynamics.

CHAPTER 5

LANDSCAPE DISTURBANCES AND LOTIC ECOTONES

Robert C. Wissmar and Frederick J. Swanson

ABSTRACT

This chapter discusses lotic ecotones of uplands and the importance of landscape disturbances in controlling ecotone function and stability. Lotic ecotones are described as zones of transition between adjacent ecological systems having characteristics uniquely defined by space and time scales and by the strength of interactions between systems. They are considered to be sensitive to gradients of limiting factors and landscape changes caused by physical and biological disturbances. In uplands or headwaters of mountain stream systems, physical disturbances, and interactions with landform conditions and hydrologic regimes, are of major importance in determining the structure and dynamics of ecotones. Lotic ecotones of high relief landscapes are viewed as being less stable than those of lowlands because they are subject to more frequent and diverse disturbances and complex topographic effects. Landform slopes, topographic aspects, edaphic gradients, and other geomorphic factors influence gravity-driven flow paths of materials and the availability of water and energy to transport materials. Disturbances such as landslides and floods, in narrow upland valleys, combine to exert lateral control on upland lotic ecotones. These controls on ecotone function and stability can be most evident in ecotones near lotic systems having steep channel slopes where fluvial and geomorphic processes strongly influence the development of riparian vegetation.

Field and modelling studies suggest several approaches for evaluating temporal and spatial effects of disturbance regimes and topographic factors on ecotonal riparian communities and their stability. Field studies include disturbance histories and changes in ages of riparian forest patches for two different types of mountain valleys (fluvial and glacially formed) in the Cascade Mountains of Oregon and Washington, USA. The determination of the relative physical stability of lotic ecotones is approached using geomorphic concepts

of phases of landform change and recovery following disturbance, and time intervals for disturbance recurrence. Recommendations are provided for additional descriptive and quantitative approaches that could be used in managing lotic ecotones.

INTRODUCTION

A major difficulty in defining the role of disturbances in ecological systems is the lack of sufficient paradigms coupling physical disturbance regimes with biological responses (Mooney and Gordon 1983, Sousa 1984, Pickett and White 1985, Forman and Godron 1986). Concepts concerning influences of different scales of disturbance on ecological functions and ecotones and ecosystems are needed in order to develop models at the landscape level (Risser *et al.* 1984, Wiens *et al.* 1985, Forman and Godron 1986, Naveh 1987, Turner 1987, Urban *et al.* 1987). Recent syntheses advancing new concepts for aquatic-terrestrial ecotones within a landscape mosaic give excellent examples of many of these shortcomings (Hansen *et al.* 1988 a, b; Holland 1988, Naiman *et al.* 1988, Resh *et al.* 1988, Reice *et al.* 1990, Pinay *et al.* 1990, Salo 1990).

This chapter examines the assertion that different types and scales of physical disturbances, along with major controls of landform conditions and hydrologic regimes, determine the structure and dynamics of lotic ecotones (lotic-land interfaces) in upland-mountainous landscapes. We focus on landscape disturbances in terms of the influences of fluvial and geomorphic processes on upland lotic ecotones. Other aspects of ecotone disturbance, such as the effects of large animals, fires, tree blowdown, and root rot infestations, on fragmentation of ecotone corridors and patches have been covered elsewhere (Forman and Godron 1981, Burgess and Sharpe 1981, Romme 1982, Dale *et al.* 1986, Turner 1987, Turner and Bratton 1987, Naiman 1988, Décamps *et al.* 1988, Odum 1990, Petts 1990).

We begin by providing definitions of the key terms, which are then treated in more detail in regard to emerging landscape perspectives. These definitions give rise to assertions about the influence of landscape disturbances on lotic ecotones. We examine these suppositions by first describing the role of disturbances within the array of influences on the structure and functioning of ecotones along longitudinal (upstream-downstream) and lateral (stream-landward) gradients. We focus on lotic ecotones that are interfaces of lotic and land systems, either sharp boundaries or gradients depending on position in a river basin and disturbance history. Examples are given of the effects of disturbance on the development of riparian vegetation gradients and patches of lotic ecotones in uplands familiar to us. Conceptual frameworks are presented that could be useful in coupling disturbance regimes with changes in stabilities of ecotones. We

conclude by suggesting approaches that might be used in the management of lotic ecotones.

DEFINITIONS

An *ecotone* can be defined according to a SCOPE/MAB working group definition (Holland 1988) as a zone of transition between adjacent ecological systems having a set of characteristics uniquely defined by space and time scales and by the strength of interactions between adjacent ecological systems.

Lotic ecotones can be defined, in the same manner, as fluvial boundaries (e.g. rivers and stream ecotones; Naiman *et al.* 1988). This definition follows that of Holland (1988) with the exception that resource patches are separated by both longitudinal (upstream-downstream) and lateral (landward) ecotones that operate over various spatial and temporal scales. The definition of Naiman *et al.* (1988) draws upon the river continuum concept (Vannote *et al.* 1980) and related inferences of processes of fluvial ecosystems involving downstream flows of water and materials (Elwood *et al.* 1983, Ward and Stanford 1983, Minshall *et al.* 1985, Statzner and Higler 1985, Naiman *et al.* 1987).

Patches adjacent to ecotones in fluvial systems can be defined as spatial units (e.g., biological communities and ecosystems) determined by patch characteristics and their interactions over various scales (Pringle *et al.* 1988). For example, riparian patches of lotic ecotones have relatively uniform vegetation composition and structure that contrast with neighbouring patches. Topography, substrate conditions, organisms, and disturbance influence patch composition, size, location, and shape (Forman and Godron 1981).

The term *landscapes* usually designates areas, on the scale of hectares to many square kilometres, that contain multiple patches. Landscapes are composed of landforms and ecological units such as patches (Forman and Godron 1986).

Landforms are land areas on a smaller scale than landscapes; they are individual elements of landscape topography, such as landforms created by landslides or gravel bars formed in streams by sediment deposition (Swanson *et al.* 1988).

A *disturbance*, from a landscape ecology perspective, is an event that causes a significant change from the 'normal pattern' in an ecological system (Forman and Godron 1986) – for example, an event creating an area of riparian vegetation distinctive in comparison to previous and neighbouring patches. Another useful definition (Pickett and White 1985) that has recently been applied to stream ecosystems (Resh *et al.* 1988) considers a disturbance as any relatively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratum, or the physical environment. For ecotones, this definition needs to emphasise irregular events, over temporal and spatial scales, that cause abrupt structural alterations in biological communities and the physical environment. Attention should also be given to disturbances occurring under nonequilibrium conditions (Sousa 1984).

DISTURBANCE AND AQUATIC ECOTONES

Aquatic ecotones appear to be highly sensitive to landscape changes caused by physical and biological disturbances (Holland 1988, Naiman *et al.* 1988). Such landscape level conditions suggest that the stability of aquatic ecotones depends on disturbance events (e.g. landslides that dam lotic systems) and related interactions between hydrologic regimes and landform-edaphic features that form, maintain, and disrupt them. Examples of important responses of aquatic ecotones include alterations in surface water-groundwater exchanges and retention times, fragmentation of riparian zones, and woody debris accumulations (Peterjohn and Correll 1984, Pinay and Décamps 1988, Ward and Stanford 1989, Gibert *et al.* 1990). Aquatic ecotones where such disturbances are especially obvious include frequently disrupted (1) riparian areas and shallow waters of streams, rivers, floodplains, and lakes, and (2) landward portions of wetlands (Swanson and Lienkaemper 1982, Hupp and Osterkamp 1985, Wissmar 1986, Turner 1987, Agee 1988, Hook *et al.* 1988, Wissmar *et al.* 1988, Holland *et al.* 1990).

Lotic ecotones of uplands are the product of two interacting landscape functions: forest distribution patterns controlled by limiting factors, and the development of landforms, forest, and aquatic environments in various phases of recovery following disturbance. In uplands, where the mountains are steep and precipitation is high, we consider that periodic disturbances are more important than limiting factors in creating and maintaining lotic ecotones.

Disturbances may directly influence lotic ecotones at the landscape scale. Direct influences may be viewed as variations in ecotone and landscape configurations from 'normal conditions' for edaphic gradients, hydrologic regimes, and energy and material fluxes. Examples of direct influences of disturbances include removal of riparian vegetation by flash floods and landslides, and edaphic and vegetative modifications by large animals and man. Indirect influences, such as altered concentrations in gradients of various dissolved chemical constituents, and pathways of chemical reactions, may result from changes in edaphic and vegetative properties following direct impacts to a system.

LOTIC ECOTONES OF UPLANDS

We hypothesise that ecotones of upland streams of mountainous areas are less stable than those downstream because they are subject to more frequent, random, and diverse landscape disturbances and stronger landform controls. Topographic effects can be more complex because aspect and steepness of slopes influence gravity-driven flows of materials from hillslopes to valley floors and stream channels. Dissected, high relief landscapes focus surface and subsurface flows and consequently the availability of water and energy to transport sediment, large rocks, and organic debris. Water and material transport patterns are also influenced by interactions of landforms and the channel geomorphology of lotic systems. For example, variable sequences of constrained (e.g. landslides and canyons) and unconstrained channel reaches can alter erosional and depositional patterns of sediment. These features, when combined with hillslope disturbances and narrow valleys, exert lateral control on lotic ecotone functions. In contrast, downstream ecotones tend to be more stable because they are influenced less by frequent, random, and diverse disturbances. The broader topographic settings of lowlands allow longer periods for surface and subsurface water flows and patterns of soil development and movement. Persistent, nonrandom fluvial processes permit the development of more stable lotic ecotones. Lotic systems of lowland floodplains usually have low gradient channels and are affected, within fairly long time frames, by disturbances such as infrequent, large floods and modifications caused by agriculture, navigation, and urbanisation (Décamps *et al.* 1988).

Similar differences in lotic ecotones of upland terrains and lowland floodplains are noted by Pinay *et al.* (1990) in this chapter. They suggest that smaller floodplains reduce the development of riparian vegetation patches. These observations suggest that lotic ecotones of mountainous terrains can be expected to have smaller spatial features and reduced capacities to function because of lateral controls exerted by the surrounding topography and diverse disturbances (e.g. landslides and channel change). Effects of other disturbances on lotic ecotones, such as fire and wind, can be highly variable. This variability relates to the intensity and type of disturbance and to influences of topography. For example, steep slopes may favour the spread of fire while sharp, rocky ridges and wide, wet valley floors may retard the spread of fires.

The following sections discuss paradigms that couple disturbance regimes and biological responses at the landscape level. Important attributes include topographic scaling factors (e.g. channel slopes and landform shapes), disturbance regimes (temporal, spatial, and magnitude), and the stability of lotic ecotones. Examples show the roles played by stream channel slopes and fluvial and geomorphic disturbances in influencing lotic deposits and lateral gradients of riparian vegetation. The scale is then expanded to larger dimensions of the landscape by discussing concepts useful in modelling temporal and spatial influences of fluvial and geomorphic disturbances on the development of riparian patches and ecotone stability.

Channel slopes and colonisation by riparian vegetation

Geomorphic and vegetative characteristics of upland streams and ecotones can be influenced by abrupt changes in channel slope and associated hydraulics. Channel slope (the slope or gradient of the stream along a given reach) influences channel width and depth, water velocity, and discharge rates (Leopold *et al.* 1964). Flood events and movements of debris near slope discontinuities of narrow valleys can create morphometric adjustments at tributary confluences, alter main channel and floodplain geomorphologies, and stress animals and plants (Bull 1979, Statzner *et al.* 1988, Statzner and Higler 1985, Hupp 1982, Hickin 1984, Roy and Roy 1988).

In many steep, high-energy streams of uplands, spatiotemporal heterogeneity of lotic ecotones reflects fluvial patterns of erosion and deposition driven by variations in discharge and related debris inputs from landward disturbances (Benda 1985). During floods and debris flows, flow velocities can increase in reaches with increased slopes and cause considerable flood damage to adjacent riparian and floodplain vegetation. Such conditions may be especially apparent in narrow valleys above and below landform-constrained channels (e.g. gorges and canyons with steep slopes) where high flow velocity has most extensive contact with vegetated areas (Hupp 1982). The cumulative effect of channel shapes, valley floor widths, and disturbances in the narrow floodplains of upland valleys can be expected to increase the instability and ephemeral character of many lotic ecotones.

Insights about influences of channel disturbances on the stability of lotic ecotones have been gained from studies of the development of riparian vegetation along high energy streams (Smith 1976, Teversham and Slaymaker 1976, Hickin 1984). The magnitude, frequency, and duration of flooding and other disturbances in these systems provide excellent information on how disturbance events can influence most aspects of the vegetation life history patterns in lotic ecotones (Swanson and Lienkaemper 1982, Hupp 1982, 1983). Floods can affect vegetation patterns by destroying and subsequently excluding plants, by creating new areas for vegetation colonisation, and by forming elevational gradients where plants show varying tolerances to flows and sediment movements.

Recent studies of upland streams in northern California (USA) have attempted to define relations between sediment transport, colonisation by riparian trees of channel margins, and streambank recovery (Lisle 1989, Trush *et al.* 1989). The streams examined had experienced large floods that mobilised broad areas of valley floors, removed riparian vegetation, and widened channels. Trees such as alder (*Alnus* spp.) colonised at the low

flow level in order to obtain adequate moisture during the dry season. However, these riparian stands became established only when the magnitude of flood-induced sediment transport declined and the width of the mobile channel bed was confined to low flow conditions. When such conditions occurred, the trees became established on the active-channel shelf and were thereafter resistant to typical annual high flows (Fig. 5.1). Lisle (1989) described the mobile bed as the channel area where bedload transport of sediment occurs and the active-channel shelf as the area between the active channel (bankfull discharge width) and mobile bed widths.

This information suggests a simple hypothesis that describes how channel slope influences fluvial and geomorphic processes and the development of riparian vegetation of lotic ecotones. The hypothesis is that the colonisation and density of riparian trees on the active-channel shelf increase with decreasing stream channel slope and corresponding decreases in bedload transport of sediment in the mobile bed (Fig. 5.2). A useful feature of this concept is that it may provide a means to identify the relative stabilities of different lotic ecotones. While studies of Lisle (1989) and Trush *et al.* (1989) suggest that this assertion might be testable at the landscape level, other factors in addition to channel slope need to be considered, such as threshold values of available stream power where channel deposits become subject to erosion and deposition (Bull 1979), the degree of channel curvature and constraint, and the rate of plant colonisation along lotic-riparian elevational gradients.

Lotic deposits and lateral gradients of riparian vegetation

Riparian vegetation of upland lotic ecotones can extend from the active-channel shelves (Fig. 5.1) to higher terrace deposits. Such riparian gradients and patches develop in response to frequent discharge and debris flow disturbances that alter channel and ecotone deposits. An excellent landscape

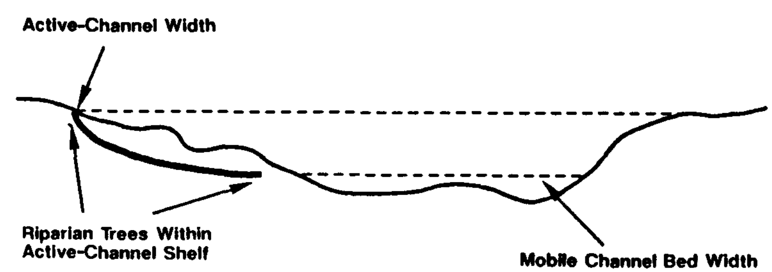

Figure 5.1 Diagram of a stream's mobile channel bed and active-channel width and shelf. The active-channel width is the area, largely unvegetated, where riparian stands can begin colonisation. The lower limit of plant endurance is the mobile channel bed width at low flow conditions

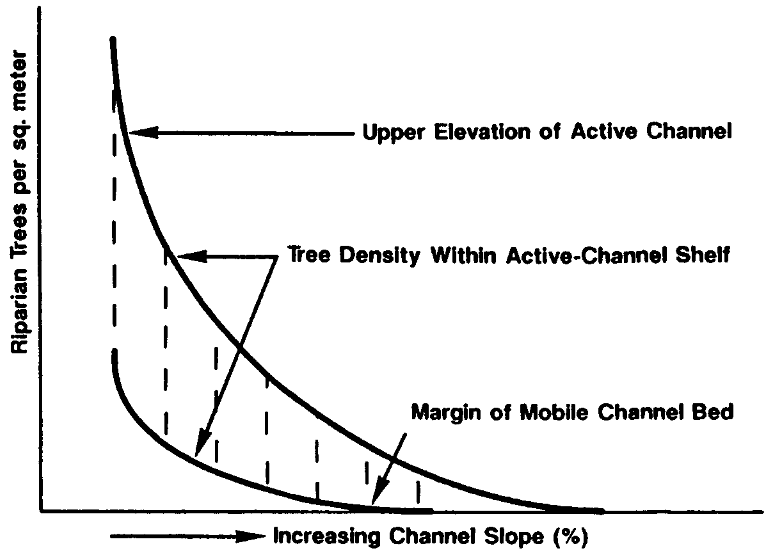

Figure 5.2 Concept of how channel slopes influence the development of riparian vegetation along streamsides. The hypothesis is that the colonisation and density of riparian trees on the active-channel shelf increase with decreasing stream channel slope and corresponding decreases in bedload transport of sediment in the mobile bed

Table 5.1 Fluvial geomorphic relations between valley floor vegetation and deposits. After Hupp and Osterkamp (1985)

*Deposits**	*Vegetation Type*	*%Time Inundated*	*Flood Frequency*
Deposition bar	Herbaceous species	40%	—
Active-channel shelf	Riparian shrubs	0-25%	—
Floodplain	Floodplain forest	—	1-3 yr
Terrace	Terrace assemblages	—	3 yr

* Deposits include depositional bars within the main channel bed, the active-channel shelf, the floodplain above the active channel, and terraces. Terraces are at higher elevations and flooded less frequently than the floodplain. The active-channel shelf is the area between the floodplain and main channel bed that includes the steep bank slope and the lower limit of persistent woody vegetation

study that documents regionally consistent and discrete relations between deposits, flow regimes, and riparian vegetation types was conducted in northern Virginia, USA (Hupp and Osterkamp 1985). Examples of fluvial-geomorphic deposits, vegetation types, percentage of time inundated, and flood frequency are presented in Table 5.1. The depositional bars that experience inundation about 40% of the time were mainly covered with willow. The active-channel shelf, inundated 10 to 25% of the time, exhibited

a riparian shrub forest – for example, red alder (*Alnus serrulata*), winterberry (*Ilex verticillata*), red willow (*Cornus amomum*), and black willow (*Salix nigra*). The floodplain, with a 1-3 yr flood frequency, was covered with a diverse forest dominated by black walnut (*Juglans nigra*), American elm (*Ulmus americana*), silver maple (*Acer saccharinum*), and hackberry (*Celtis occidentalis*). The terraces with 3-yr flood frequency were dominated by upland assemblages including oaks and hickories (Hupp and Osterkamp 1985).

Other investigations in British Columbia, Canada, and Oregon, USA (Teversham and Slaymaker 1976, Swanson and Lienkaemper 1982), demonstrate that certain vegetation types and distributions occur in ecotone patches that correspond with boundaries between geomorphic surfaces on gradients from the channel bed to the terraces. Such ecotones and contrasts in vegetation between patches were apparently controlled by variation in inundation frequency, substrate type, floods, and disturbances by bedload, ice, and debris movements (Yanosky 1983, Hupp 1983, Hupp and Osterkamp 1985).

Additional controls can be exerted by stabilising feedback of plants. Vegetation near channel margins can be very tolerant of channel disturbances, stabilising depositional bars and stream banks. Yanosky (1983) observed that many plant species near channels withstand a high duration of inundation and destructive flooding and exhibit a resilience through rapid sprouting of shrubs from damaged trunks and roots. Such features allow riparian vegetation to affect bank erodibility and lateral migration of channels (Smith 1976), thereby adding stability to lotic ecotones.

Disturbance regimes and developmental pathways of riparian patches

Once concepts of topographic scaling (channel slopes, fluvial deposits, landforms, and vegetative characteristics) have been formulated to describe influences of disturbances on lotic ecotones, attention needs to be given to evaluating temporal and spatial effects of disturbance regimes and biological responses at the landscape level. Perspectives can be examined by considering disturbance history (Décamps *et al.* 1988). Excellent examples are found by examining the role of past disturbances in the development of riparian forest patches in the Cascade Mountains of Oregon and Washington, USA. These studies provide historical information on changes in riparian and valley floor forest patches created by different types of disturbance and frequencies of recurrence. Major natural disturbances affecting the mountain forest include episodic floods, geomorphic changes in stream channels and landforms, fire, wind, and glacial activity (Fig. 5.3). Important landform disturbances include landslides and earthflows in glacial deposits on steep slopes. Human influences include clearcutting and road construction. Many of these events have recurrence intervals ranging from decades to a few

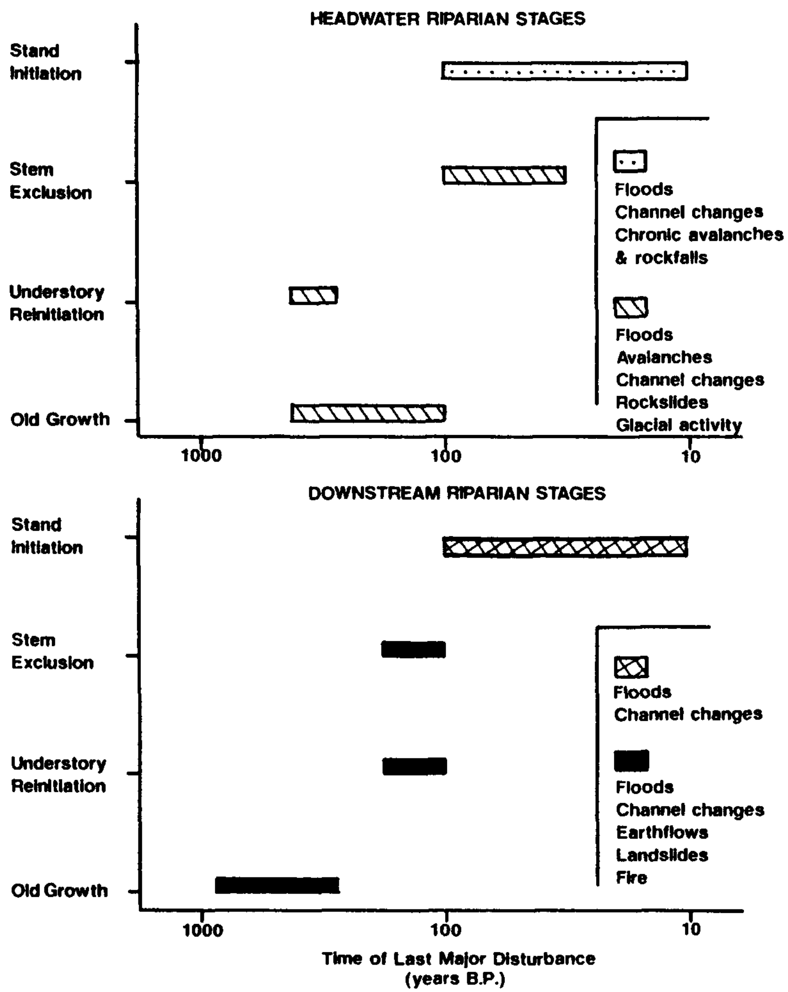

Figure 5.3 Major landscape disturbance and the development of riparian forest patches (successional stages) in downstream and headwater valleys of the Cascade Mountains of Oregon and Washington. The types of disturbance are indicated in the panel boxes. The bars show the length of time B.P. of the last major disturbance and subsequent successional stage. Disturbances that happened more than 1000 years ago include glaciation, volcanism, and tectonic uplift

centuries. Repeated volcanic eruptions also occur in these tectonically active coastal areas on time scales of centuries to millennia.

Examples of changes in the vegetative composition and ages of riparian forest patches in the Cascade Mountain valleys reflect the time of the last major disturbances (yr before present (B.P.)) and types of disturbances (Fig. 5.3). Disturbance regimes and the development of riparian forest patches (successional stages) are presented for an erosionally formed mountain valley in Oregon and a glaciated headwater valley in Washington. The physical and biological organisation of riparian forests in erosional valleys can be attributed mainly to the spatiotemporal characteristics of floods and changes in the geomorphology of stream channels. These alterations appear to affect the distribution, successional stages, and size of forest patches (S.V. Gregory, F.J. Swanson, and W.A. McKee, unpublished data, Forestry Sciences Laboratory and Oregon State University, Corvallis, Oregon, USA). Small patches ($< 100\,m^2$) may be reshaped several times annually by flow events. Larger patches (100-$1000\,m^2$) may be altered by high flows and channel changes (e.g. lateral movements) that recur on the time scale of years to several decades. Much larger landform areas (ha to km^2) can be influenced by geomorphic processes, fire, and wind over hundreds to thousands of years. Large-scale alterations in the valley reflect more infrequent disturbances (10,000–100,000 yr) of volcanism, glaciation, and tectonic uplift. In contrast to erosional valleys, in steeper-headwater glaciated valleys more frequent and diverse types of disturbances are common (Oliver 1981, Oliver *et al.* 1985). The major changes in landforms and lotic ecotones reflect influences of frequent snow avalanches, rockslides, and episodic floods (Figs. 5.3 and 5.4).

Such retrospective information can be useful in designing studies that evaluate influences of frequent and infrequent disturbances on the temporal and spatial dynamics of lotic ecotones. Several biological studies of impacts of disturbances on forests have used transitional probability models of succession (Shugart *et al.* 1973, Romme 1982, Weinstein and Shugart 1983, Dale *et al.* 1986, DeAngelis *et al.* 1986). A diagram appropriate for the glaciated valleys shows how transitional probability models (e.g. Markov models) might be used to examine different developmental pathways of vegetative patches of ecotones in response to disturbances with different frequencies (Fig. 5.5). In mountain valleys, where disturbances are chronic to frequent, the riparian forest patches are commonly young, approaching 60 yr. In this case, Pathway 1 depicts vegetative patch development as being continually reset by disturbances and remaining in the stand initiation and exclusion successional stages during a system's physically disturbed phases (see definitions of reaction and recovery phases in the subsequent section on ecotone stability). Where disturbances are less frequent, development can proceed via Pathway 2. For Pathway 2, the developmental stages following stand initiation stage include stand exclusion (age 41-165 yr),

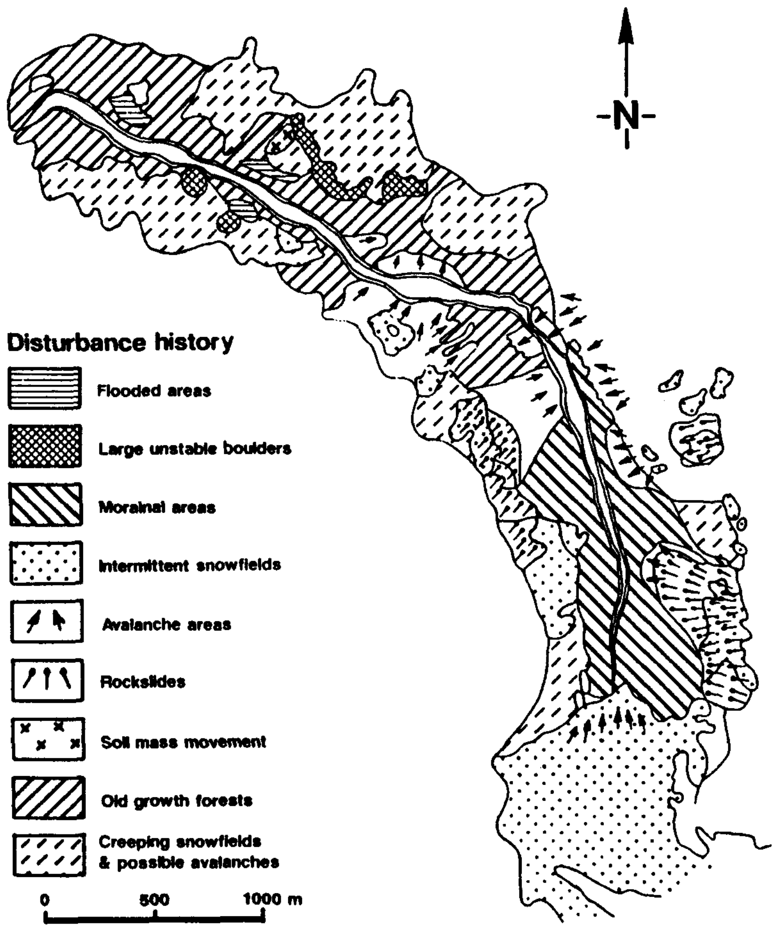

Figure 5.4 Map of major disturbances influencing riparian vegetation of lotic ecotones of a glaciated valley located at the headwaters of the north fork of the Nooksack River in the North Cascade Mountains of Washington, USA. The north end of the valley is downstream. After Oliver *et al.* (1985)

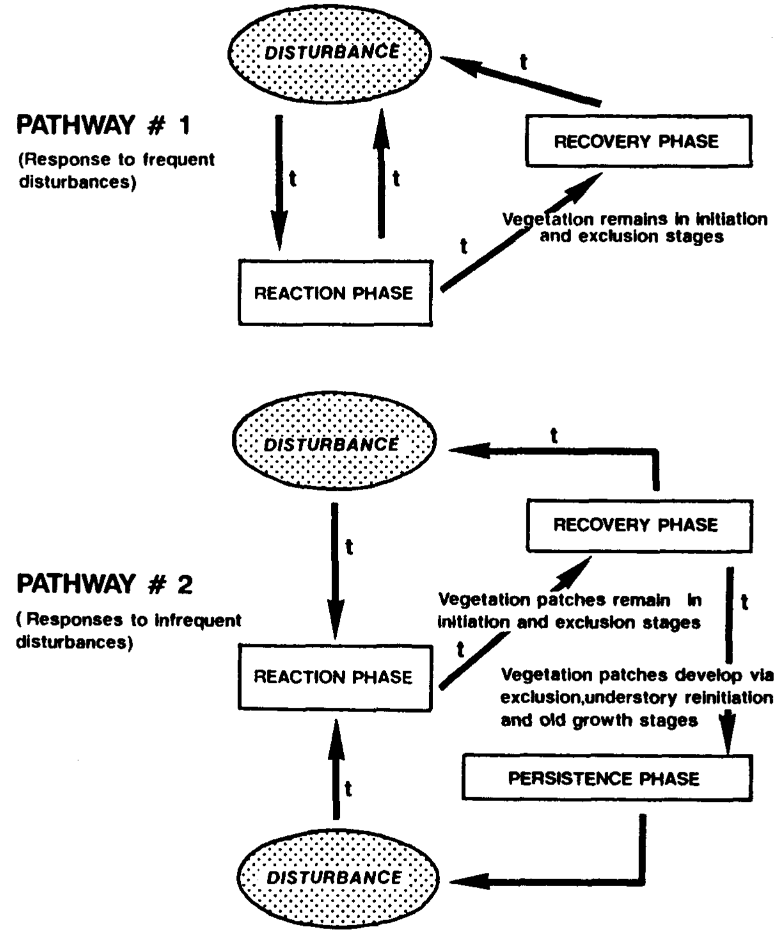

Figure 5.5 Developmental pathways of riparian forest patches in response to frequent and infrequent disturbances. Pathway 1 includes stand initiation and exclusion stages during reactive and recovery phases in ecotones following disturbances. Pathway 2 includes stand exclusion, understory reinitiation, and old growth stages after the recovery and during the persistence phases. See text and Fig. 5.7 for the definitions of reaction, recovery, and persistence phases in ecotones. The letter 't' indicates different transition times for riparian patches (successional stages)

understory reinitiation (age 144-480 yr), and old growth (age > 480 yr) (Fig. 5.5).

Spatial characteristics of disturbances may be considered along with evaluations of the effects of disturbance frequency and biotic responses (Fig. 5.5). One approach to spatially scaling disturbances in landscapes involves using probability models that contain functions describing the phasing of disturbances (Abugov 1982). For example, given the disturbance of a single riparian patch, the probability of that patch being disturbed during various time intervals is viewed as being independent of any probability of juxtaposed patches being disturbed during the same time interval (Fig. 5.6). In this case, biotic responses (Fig. 5.5) to a disturbance would be confined to single patches. Numerous and relatively frequent

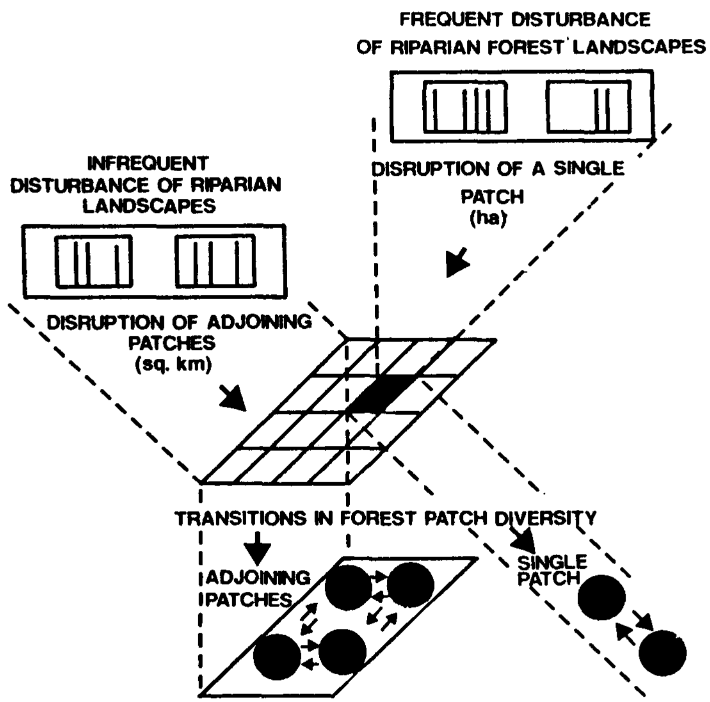

Figure 5.6 Landscape perspective for lotic ecotones that describes disturbance impacts in terms of frequencies and two general spatial patterns. First, given a disturbance rate, the probability of an ecotone being disturbed during each time interval is viewed as being independent of the juxtaposed ecosystems being disturbed during the same time interval. Frequent disturbances are considered typical of this pattern. Second, the influence of patterning of disturbance is viewed as having landscape-wide ramification. Each time a disturbance occurs, the disruptions occur in ecotones and adjoining ecosystems. Infrequent and large disturbance events are considered typical of this pattern

disturbances like flooding, debris flows, and landslides, which can be common in uplands (Fig. 5.3 and 5.4), could be considered typical disturbances affecting single patches. In contrast to single-patch disturbance events, other disturbances may have more landscape-wide ramifications. In this situation, each time a disturbance affects a patch, the modification disrupts adjacent patches (Fig. 5.6). Infrequent and large-scale events such as storms and fires typify these landscape-wide disturbance patterns.

Disturbance regimes and the physical stability of lotic ecotones

Concepts concerning the influences of disturbance regimes in lotic ecotones need to be tested in different landscapes. In order to examine concepts like those presented here (Figs. 5.5 and 5.6), a general framework is needed to define the relative stability of different ecotones. We hypothesise that ecotones differ in physical stability or resistance to changes caused by disturbance. In contrast to other components or patches of a landscape, lotic ecotones might be recognised as transient and unsteady landscape components that appear and disappear in response to disturbances having great frequency. Consequently, ecotones are unstable, having spatial variations leading to transient features in terms of physical structure and biological organisation. Spatially and functionally, ecotones are highly sensitive to disturbances because of low resistance (e.g. steep channel slopes), low storage capacities (e.g. narrow valley floors and high sediment yield), and rapid reaction and recovery times (changes in channel geomorphology and biological recolonisation). Such characteristics would indicate that while the magnitude of disrupting forces that affect lotic ecotones may be less than in other patches of a landscape, the high frequency of disruption could cause greater change. As previously noted, we would expect such attributes to cause the stability of lotic ecotones to vary with respect to locations in a landscape (e.g. headwaters versus lowlands).

In contrast to lotic ecotones, juxtaposed land and water patches may be viewed as occupying 'more stable positions' in a landscape where disturbances are less frequent than the time for patch adjustment to them. As a result, the respective patches would be more insensitive to change than lotic ecotones. For example, in contrast to lotic ecotones, terrestrial patches may be the most stable because they exhibit more persistence of relief, higher resistance and storage capacities, and greater potential for superimposed vegetative patterns.

These concepts can be placed in a framework for use in evaluating the physical stability of ecotones. Here lotic ecotones are viewed as being subject to short-term or frequent disturbances while juxtapositioned patches display long-term responses to less frequent events. Patch structure and functions are considered to be more closely linked to widespread climatic-hydrologic and geomorphic changes. The framework draws upon geomorphic concepts of landform change and recovery (Brunsden and Thorns 1979, Chorley *et al.* 1984). The approach divides time into: *reaction phase* (A), the time taken for ecotones and other patches of landscapes to react to a disturbance; *recovery phase* (R), the time taken for a system to attain a characteristic equilibrium state; *persistence phase* (P), the period following R over which the characteristic state persists; and *disturbance recurrence* (D) time interval.

Within this framework, recovery (R) and disturbance recurrence (D) times have important roles to play in assessing ecotone stability and in determining ecotone adjustment to a wide range of disturbance time scales. The ratio of the recovery to disturbance recurrence (R:D) suggests differences in recovery characteristic of ecotones and ecosystems (Fig. 5.7). For unstable systems, the R:D ratios exceed one. The ratio is greater than one (> 1) because the mean recurrence time of disturbance events capable of producing changes is shorter than the time taken for the system to recover or equilibrate to a characteristic persistence state (P). Ratios greater than one indicate a minimal correspondence between processes of recovery and persistence. High R:D ratios might be viewed as common for predominantly transient systems, like many lotic ecotones in uplands.

For more stable systems, R:D ratios are commonly less than one (< 1). Here, adjustment to new conditions occurs before the next major disturbance. In this case, the characteristic persistent state (P) can exist after the initial recovery phase. The shortness of recovery times in relation to disturbance intervals suggests more predictable process-response relationships (Fig. 5.7).

Examples of apparent diagnostic power of the R:D ratio are shown in Table 5.2. Ratios of < 0.1 to 0.3 for riverine ecosystems suggest stable systems with longer disturbance intervals than recovery times. In contrast, ratios ranging from 0.5 to 10 for an array of small and large landslides in the Alps, Himalayas, and mountains of Japan imply unstable or transient systems with long recovery phases relative to short return periods for disturbance recurrence (Table 5.2). These transient systems can be viewed as having the ability to change but not the ability to always adjust before a new disturbance arrives.

These observations point to the need to view disturbance events and the stability of lotic ecotones as a series of adjustments between processes of disturbance recurrence and a system's responses during physical reactive, recovery, and persistence phases. At present, little is known about system characteristics that might be used to identify the states and pathways of systems during these time sequences. Numerous considerations need to be taken into account when comparing R and D characteristics like those in Table 5.2. For example, attention should be given to instances where disturbance events occur more frequently than recovery can take place. In another situation, the magnitude of a disturbance event might possibly play

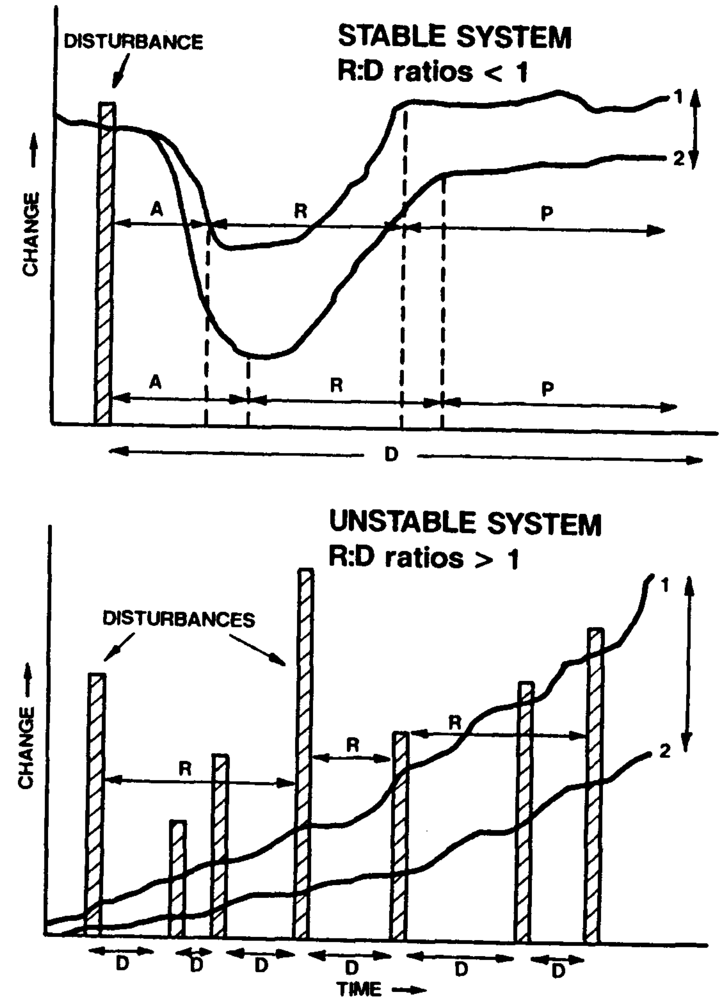

Figure 5.7 Concept of stable and unstable systems that divides time into phases for a system responding to a disturbance. Phases include reaction phase (A); recovery phase (R); persistence phase (P); and the time for disturbance recurrence (D). The stability of a system is recognised by ratios of recovery to disturbance recurrence (R:D). 1 and 2 indicate systems responding to disturbances of different magnitudes

a more important formative role in an ecotone's character than more frequent, smaller disturbance events.

Quantification of the magnitude of a disturbance event and its formative influences in ecotones and ecosystems is clearly an area of major future research. Potential approaches to estimating the magnitude of physical

Table 5.2 Representative disturbance recurrence times (D), recovery times (R), and R:D ratios for disturbed hillslopes and rivers

Disturbed System	*Disturbance Recurrence Frequency (yr)*	*Recovery (yr)*	*R:D Ratio*	*Reference*
RIVER CHANNELS AND BANKS				
Suspended sediments	50-100	5-10	0.1-0.2	Wolman and Gerson (1978)
Channel widths	3-200	1-15	0.01-0.3	Wolman and Gerson (1978)
HILLSLOPE LANDSLIDES				
Himalayas	10-20	10	0.4-1.0	Starkel (1972) Brunsden *et al.* (1989)
Japanese mountains	5	25	5	Wolman and Gerson (1978)
Alps	40-100	100-1000	1-10	Brunsden and Jones (1980)

disturbances have been described for fluvial systems (Wolman and Miller 1960, Chorley *et al.* 1984, Baker *et al.* 1987, Anderson 1988). In a seminal paper, Wolman and Miller (1960) maintain that despite flow variability, discharge of moderate frequency is responsible for determining channel capacity for transport of sediment. They describe the most significant discharge influencing channel capacity, through channel and bank morphologic adjustments, as the discharge that transported the most sediment for its given frequency of occurrence. They assert that the magnitude of the disturbance (the dominant stress or discharge) can be estimated as the product of the rate of sediment transport and the frequency of occurrences (Fig. 5.8). A recent study of different alluvial streams, where channels were both unconstrained (i.e. lateral migration of channels may occur) and constrained (i.e. lateral migration constrained by bedrock), suggests that Wolman and Miller's concept holds true for channel maintenance, recovery, and freedom to adjust boundaries (Carling 1988). These studies provide valuable paradigms for future investigations of disturbance frequency and magnitude in both aquatic and terrestrial ecosystems. Such information should prove useful in predicting influences of both natural and man-induced disturbance regimes on the stability of ecotones.

CONCLUSIONS AND RECOMMENDATIONS

We have recommended several possible approaches for obtaining better information about the effects of different disturbance regimes on lotic

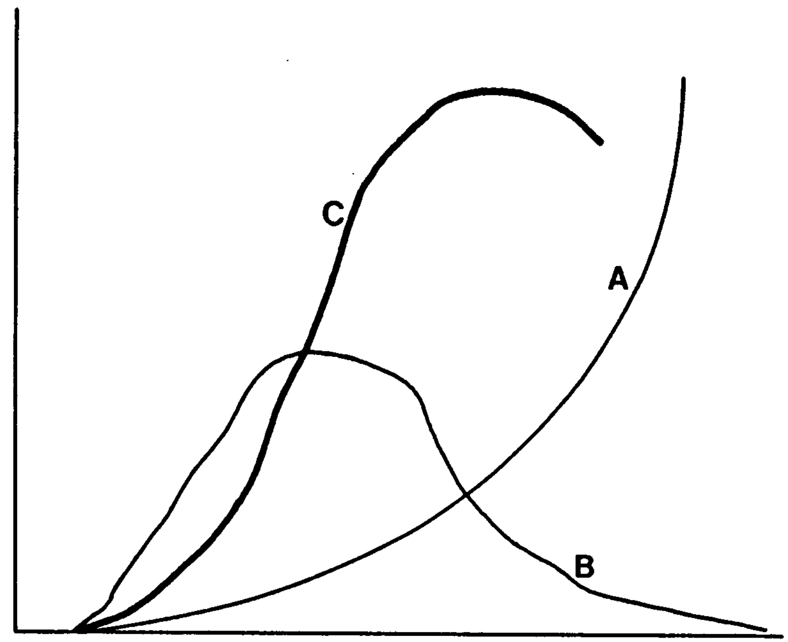

Figure 5.8 Relationship between the rate of bedload movement (A) and the frequency of occurrence (B). The product (C) of the two curves (A and B) defines a maximum used to isolate a dominant stress or discharge. After Wolman and Miller (1960)

ecotones and juxtaposed ecosystems. The physical influences of disturbances on landform stability in natural systems have received much attention (Hack and Goodlett 1960, Swanson and Swanston 1977, Swanson 1981, Swanson *et al.* 1982), but few ecological studies have dealt with the effects of disturbance regimes on communities across regional landscapes (Romme 1982, Risser *et al.* 1984, Pickett and White 1985, Forman and Godron 1986, Turner 1987, Swanson *et al.* 1988). Much of the recent information on disturbance and the ecology of ecotones pertains to smaller-scale systems such as high energy streams and riparian zones (Teversham and Slaymaker 1976, Swanson and Lienkaemper 1982, Yanosky 1983, Hupp and Osterkamp 1985, Lisle 1989, Trush *et al.* 1989).

In the context of landscapes, we have discussed how spatial and temporal information on geomorphic features can be essential to interpreting environmental disturbances and changes in system structure and dynamics. Examples of basic templates have been presented that could facilitate an understanding of natural background disturbance regimes and the sensitivities of ecotones and ecosystems. For instance, the effects of different disturbance regimes, such as spatial patterning and rates of disturbance in hillslope and stream ecosystems, have major implications for understanding how biological communities develop in lotic ecotones of large landscapes (Smith 1976, Osterkamp and Hupp 1984, Hickin 1984, Agee 1988, Lisle 1989). Available information points to the need for studies at the regional landscape scale that facilitate predictions of the effects of disturbances on lotic ecotones and adjacent ecosystems of broad environmental gradients. Such information is fundamental to a better understanding of environmental changes at landscape and global scales.

Disturbance of aquatic ecosystems has been cited as one of the major topics having both fundamental and applied aspects in need of research during the next decade (Resh *et al.* 1988, Reice *et al.* 1990, Gore *et al.* 1990). A basic scientific problem in the evaluation of landscapes and their ecotones is the lack of testable models with short- and long-term predictive capabilities. The difficulty concerns not knowing the extent to which characteristic or repetitive changes in ecotones and ecosystems of a landscape are caused by disturbances of low frequency and high magnitude extremes. We understand that large disturbance events can dominate the main trends of change. Yet we do not know which events will be formative, or how to recognise temporal and spatial sequences of events and the ability of ecotones and ecosystems to recover to characteristic persistent states. Although we have presented information about representative disturbance recurrences and recovery phases for disturbed hillslopes and rivers, such landscape knowledge for both physical and biotic components of ecotones and ecosystems is generally lacking.

Many of the difficulties in studying landscapes arise from the need to acquire and interpret vast amounts of current and historical environmental information (e.g. dendrochronological and sedimentation records) in terms of their temporal variabilities and responses to episodic disturbance behaviour. Historical data are important because we must take into account the memory of systems. Memory is evaluated in terms of relative changes in a system caused by past disturbances and the ability of the system to adjust to new events. The wealth of information preserved in ecotones (e.g. dendrochronology, river alluvium, peat bogs, lake deposits, and other records) should play an important role in advancing our knowledge. Ecotones, which we have viewed as unstable system components and sensitive to frequent change, may exhibit distinct breaks in temporal and spatial records of a landscape mosaic. For example, ecotones may be important in the recognition of small spatial processes that operate on temporal scales of 10 to 100 yr. Time scales for both geomorphic and vegetative processes are important because they reflect controls on an ecotone's physical structure and patterns that can depend on landscapewide disturbances. In contrast, longer time scales that operate > 1000 yr for other landscape features, such as stable hard rock canyons and low

relief energy plateaus, may have unrecognisable geomorphic processes. Nevertheless, perspectives at both scales have value in understanding ecotone and ecosystem dynamics across landscape gradients and for use in resource planning and management.

A prime example of the demands for landscape management information are those created by the passage in the United States of the National Environmental Policy Act of 1969 (Public Law 91-190; 42 U.S.C. 4321-4347). Federal resource managers must assess disturbances within the context of cumulative and long-term effects of proposed management actions on the environment. Cumulative effects amount to the incremental impact of an action when added to other past, present, and reasonably foreseeable future actions. The monitoring of effects of past and present activities has become an explicit policy requirement for forest and land managers. However, procedures and guidelines for implementing such directives remain vague and are not usually based on sound scientific information.

Considerable information useful for fundamental studies and management purposes can undoubtedly be obtained through evalution of concepts like those presented in this chapter and by development of landscape models that yield indices of landscape patterning. Useful measures for lotic ecotones might include fractal dimensions (O'Neill *et al.* 1988, Turner and Ruscher 1988) and indices of chaos (Naiman *et al.* 1988). Measures of fractals have made it possible to quantify complex boundaries or patch shapes and relate these pattens to the underlying processes (e.g. disturbances) that may affect pattern complexity. Indices depicting chaotic regimes have been shown to be useful where natural and human-induced perturbations push biological populations into chaos (Pool 1989).

Other research approaches could focus on ecological functions of landscapes and their ecotones by applying energy balance methods commonly used in evaluating agricultural landscapes. In agricultural cases, higher variabilities of energy flow and water cycling have been observed for individual ecosystems than for landscapes (Ryskowski and Kedziora 1988). Similar information on the variability of energy fluxes under different forest management and cutting practices (Franklin and Forman 1987) could be useful in pointing to differences in ecological stresses experienced by ecotones and ecosystems across the forest landscape. Many of the approaches advanced in this chapter could be used by resource managers in developing adaptive management programs. Such programs could include both the monitoring of disturbance regimes and their cumulative effects in land-water ecotones, and provisions for information feedback that improve long-term management plans.

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LITERATURE CITED

Abugov, R. 1982. Species diversity and phasing of disturbance. Ecology 63:289-293.

Agee, J.K. 1988. Successional dynamics in forest riparian zones. Pages 31-43 *in* K.J. Raedeke, editor. Streamside management: riparian wildlife and forestry interactions. Contribution 59, University of Washington, Institute of Forest Resources, Seattle, Washington, USA.

Anderson, M.G. 1988. Modelling geomorphological systems. John Wiley and Sons, New York, USA.

Baker, V.R., R.C. Kochel, and P.C. Patton. 1987. Flood geomorphology. John Wiley and Sons, New York, USA.

Benda, L.E. 1985. Delineation of channels susceptible to debris flows and debris floods. Pages 195-201 *in* International Symposium on Erosion, Debris Flow, and Disaster Prevention, Tsukuba, Japan.

Brunsden, D.D., and K.C. Jones. 1980. Relative time scales and formative events in coastal landslide systems. Zeitschrift für Geomorphologie, Supplement 34:1-19.

Brunsden, D.D., K.C. Jones, R.P. Martin, and J.C. Doornkamp. 1989. The geomorphological character of part of the Low Himalaya of eastern Nepal. Zeitschrift für Geomorphologie, *in press*.

Brunsden, D., and J.B. Thornes. 1979. Landscape sensitivity and change. Transactions of the Institute of British Geographers 4:463-484.

Bull, W.B. 1979. Threshold of critical stream power in streams. Bulletin of the Geological Society of America 90:453-464.

Burgess, R.L., and D.M. Sharpe. 1981. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, USA.

Carling, P. 1988. The concept of dominant discharge applied to two gravel-bed streams in relation to channel stability thresholds. Earth Surface Processes and Landforms 13:355-367.

Chorley, R.J., S.A. Schumm, and D.E. Sudgen. 1984. Geomorphology. Methuen, London, England.

Dale, V.H., M. Hemstrom, and J. Franklin. 1986. Modeling the long-term effects of disturbances on forest succession, Olympic Peninsula, Washington. Canadian Journal of Forest Research 16:56-67.

DeAngelis, D.L., W.M. Post, and C.C. Travis. 1986. Positive feedback in natural systems. Springer-Verlag, New York, USA.

Décamps, H., M. Fortuné, F. Gazelle, and G. Pautou. 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecology 1:163-173.

Elwood, J.W., J.D. Newbold, R.V. O'Neill, and W. Van Winkle. 1983. Resource spiraling: an operational paradigm for analyzing lotic ecosystems. Pages 3-27 *in* T.D. Fontaine III and S.M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan, USA.

Forman, R.T.T., and M. Godron. 1981. Interaction among landscape elements: a core of landscape ecology. Pages 35-48 *in* S.P. Tjallingii and A.A. de Veer, editors. Perspectives in landscape ecology. Centre for Agricultural Publication and Documentation, Wageningen, The Netherlands.

Forman, R.T.T., and M. Godron. 1986. Landscape ecology. John Wiley and Sons, New York, USA.

Franklin, J.F., and R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology 1:5-18.

Gibert, J., M.J. Dole-Oliver, P. Marmonier, and P. Vervier. 1990. Surface groundwater ecotones, *this volume*.

Gore, J.A., J.R. Kelly, and J.D. Yount. 1990. Application of ecological theory to determining the recovery of disturbed lotic ecosystems: research needs and priorities. Environmental Management, *in press*.

Hack, J.T., and J.C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. United States Geological Survey Professional Paper 347, Renton, Virginia, USA.

Hansen, A.J., F. di Castri, and R.J. Naiman. 1988*a*. Ecotones: what and why? Biology International, Special Issue 17:9-46.

Hansen, A.J., F. di Castri, and P.G. Risser. 1988*b*. A new SCOPE project. Ecotones in a changing environment: the theory and management of landscape boundaries. Biology International, Special Issue 17:137-163.

Hickin, E.J. 1984. Vegetation and river channel dynamics. Canadian Geographer 28:111-126.

Holland, M.M. 1988. SCOPE/MAB technical consultations on landscape boundaries: report of a SCOPE/MAB workshop on ecotones. Biology International, Special Issue 17:47-106.

Holland, M.M., D.F. Whigham, and B. Gopal. 1990. The characteristics of wetland ecotones, *this volume*.

Hook, D.D., *et al.* (12 editors). 1988. The ecology and management of wetlands. Volume 1: Ecology of wetlands. Timber Press, Portland, Oregon, USA.

Hupp, C.R. 1982. Stream-grade variation and riparian forest ecology along Passage Creek, Virginia. Bulletin of the Torrey Botanical Club 109:488-499.

Hupp, C.R. 1983. Vegetation patterns in the Passage Creek gorge, Virginia. Castanea 48:62-72.

Hupp, C.R., and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology 66:670-681.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial processes in geomorphology. W.H. Freeman, San Francisco, California, USA.

Lilse, T.E. 1989. Channel-dynamic control on the establishment of riparian trees after large floods in northern California. California Riparian Systems Conference, September 1988, Davis, California, USA.

Minshall, G.W., K.W. Cummins, R.C. Petersen, C.E. Cushing, D.A. Burns, J.R. Sedell, and R.L. Vannote. 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 42:1045-1055.

Mooney, H.A., and M. Godron. 1983. Disturbance and ecosystems. Springer-Verlag, New York, USA.

Naiman, R.J. 1988. Animal influences on ecosystem dynamics. BioScience 38:750-752.

Naiman, R.J., H. Décamps, J. Pastor, and C.A. Johnston. 1988. The potential importance of boundaries to fluvial ecosystems. Journal of the North American Benthological Society 7:289-306.

Naiman, R.J., J.M. Melillo, M.A. Lock, T.E. Ford, and S.R. Reice. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68:1139-1156.

Naveh, Z. 1987. Biocybernetic and thermodynamic perspectives of landscape functions and land use patterns. Landscape Ecology 1:75-83.

Odum, W.E. 1990. Internal processes influencing the maintenance of ecotones: do they exist?, *this volume*.

Oliver, C.D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management 3:153-168.

Oliver, C.D., A.B. Adams, and R.J. Zasoki. 1985. Disturbance patterns and forests development in a recently deglaciated valley in the northwestern Cascade Range of Washington, U.S.A. Canadian Journal of Forest Research 15:221-232.

O'Neill, R.V., *et al.* (11 authors) 1988. Indices of landscape pattern. Landscape Ecology 1:153-162.

Osterkamp, W.R., and C.R. Hupp. 1984. Geomorphic and vegetative characteristics along three northern Virginia streams. Bulletin of the Geological Society of America 95:1093-1101.

Peterjohn, W.T., and D.J. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65:1466-1475.
Petts, G.E. 1990. The role of ecotones in aquatic landscape management, *this volume*.
Pickett, S.T.A., and P.S. White (editors). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.
Pinay, G., and H. Décamps. 1988. The role of riparian woods in regulating nitrogen fluxes between alluvial aquifer and surface water: a conceptual model. Regulated Rivers 2:507-516.
Pinay, G., H. Décamps, E. Chauvet, and E. Fustec. 1990. Functions of ecotones in fluvial systems, *this volume*.
Pool, R. 1989. Ecologists flirt with chaos. Science 243:310-313.
Pringle, C.M., R.J. Naiman, G. Bretschko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme, and M.J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7:503-524.
Reice, S.R., R.C. Wissmar, and R.J. Naiman. 1990. The influence of spatial and temporal heterogeneity and the background disturbance regime on the recovery of lotic ecosystems. Environmental Management, *in press*.
Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R.C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.
Risser, P.G., J.R. Karr, and R.T. Forman. 1984. Landscape ecology: directions and approaches. Illinois Natural History Survey Special Publication Number 2, Champaign, Illinois, USA.
Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199-221.
Roy, A.G., and R. Roy. 1988. Changes in channel size at river confluences with coarse bed materials. Earth Surface Processes and Landforms 13:77-84.
Ryszkowski, L., and A. Kedziora. 1988. Impact of agricultural landscape structure on energy flow and water cycling. Landscape Ecology 1:85-94.
Salo, J. 1990. External processes influencing origin and maintenance of inland water-land ecotones, *this volume*.
Shugart, H.H., T.R. Crow, and J.M. Hett. 1973. Forest succession models: a rationale and methodology for modelling forest succession over large regions. Forest Science 19:203-212.
Smith, D.G. 1976. Effect of vegetation on lateral migration of anastomosed channels of a glacier meltwater river. Bulletin of the Geological Society of America 87:857-860.
Sousa, W. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:535-591.
Starkel, L. 1972. The role of catastrophic rainfall in the shaping of the relief of the lower Himalaya (Darjeeling Hills). Geographic Polon 21:103-147.
Statzner, B., J.A. Gore, and V.H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7:307-360.
Statzner, B., and B. Higler. 1985. Questions and comments on the river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 42:1038-1044.
Swanson, F.J. 1981. Fire and geomorphic processes. Pages 401-420 *in* Proceedings of the Conference on Fire Regimes and Ecosystem Properties. USDA Forest Service General Technical Report WO-26, Washington, D.C.
Swanson, F.J., R.J. Janda, T. Dunne, and D.N. Swanston. 1982. Sediment budgets and routing in forested drainage basins. USDA Forest Service General Technical Report PNW-141, Portland, Oregon, USA.
Swanson, F.J., T.K. Kratz, N. Caine, and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience 38:92-98.
Swanson, F.J., and G.W. Lienkaemper. 1982. Interaction among fluvial processes, forest vegetation, and aquatic ecosystems, South Fork Hoh River, Olympic National Park. Pages 30-34 *in* E.E. Starkey, J.F. Franklin, and J.W. Matthews, editors. Ecological research in National Parks of the Pacific Northwest. Forestry Sciences Laboratory, Corvallis, Oregon, USA.
Swanson, F.J., and D.W. Swanston. 1977. Complex mass-movement terrains in the western Cascade Range, Oregon. Engineering Geology, Geological Society of America 3:113-124.

Teversham, J.M., and J. Slaymaker. 1976. Vegetation composition in relation to flood frequency in Lillooet River Valley, British Columbia. Catena (Cremlingen-Destedt, Germany) 3:191-201.
Trush, W.J., E.C. Conner, and A.W. Knight. 1989. Alder establishment and channel dynamics in a South Fork Eel River tributary, Mendocino County, California. California Riparian Systems Conference, September 1988, Davis, California. USA.
Turner, M.G. (editor). 1987. Landscape heterogeneity and disturbance. Springer-Verlag, New York, USA.
Turner, M.G., and S.P. Bratton. 1987. Fire, grazing, and the landscape heterogeneity of a Georgia Barrier Island. Pages 85-101 *in* M.G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York, USA.
Turner, M.G., and C.L. Ruscher. 1988. Changes in landscape patterns in Georgia, USA. Landscape Ecology 1:241-251.
Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology. BioScience 37:119-127.
Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.
Ward, J.V., and J.A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29-42 *in* T.D. Fontaine III and S.M. Bartell, editors. Dynamics of lotic systems. Ann Arbor Science, Ann Arbor, Michigan, USA.
Ward, J.V., and J.A. Stanford. 1989. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology. Canadian Journal of Fisheries and Aquatic Sciences, *in press*.
Weinstein, D.A., and H.H. Shugart. 1983. Ecological modelling of landscape dynamics. Page 29-46 *in* H.A. Mooney and M. Godron, editors. Disturbance and ecosystems. Springer-Verlag, New York, USA.
Wiens, J.A., C.S. Crawford, and J.R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45:421-427.
Wissmar, R.C. 1986. Carbon, nitrogen, and phosphorus cycling in Pacific Northwest wetlands. Pages 51-69 *in* R.S. Strickland, editor. Wetland functions, rehabilitation, and creation in the Pacific Northwest: the state of our understanding. Washington Department of Ecology Publication 86-14, Lacey, Washington, USA.
Wissmar, R.C., J.A. Baross, M.D. Lilley, and C.N. Dahm. 1988. Nitrogen cycling in altered and newly created lakes near the Mount St. Helens volcano. Journal of Freshwater Ecology 4:551-568.
Wolman, M.G., and R. Gerson. 1978. Relative rates of time and effectiveness in watershed geomorphology. Earth Surface Processes 3:189-208.
Wolman, M.G., and J.P. Miller. 1960. Magnitude and frequency of forces in geomorphic processes. Journal of Geology 68:54-74.
Yanosky, T.M. 1983. Evidence of floods on the Potomac River from anatomical abnormalities in the wood of flood-plain trees. United States Geological Survey Professional Paper 1296. 1-42.

Key words: Disturbance, ecotone, geomorphic, landscape, lotic, riparian, streams, uplands.