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Observed and modeled directional change in riparian forest composition at a cutbank edge

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Abstract

Lateral migrations of river meanders create transient, spatially transgressive edges where the advancing cutbank edge encroaches upon interior floodplain forest communities. This spatial movement of edge toward the forest interior should initiate directional changes in species composition within a forest plot as it is affected by a changing microclimate and hydrological regime. We found that cutbank edge and forest interior sites in an Iowa floodplain contained markedly different plant assemblages. Species commonly associated with later stages of succession dominated interior sites while cutbank edge sites favored secondary, successional species. Assuming that the cutbank edge sites once contained vegetation similar to that surveyed in the floodplain interior, the observed changes in community structure accompanying channel migration are suggestive of retrograde succession, or retrogression. To link cutbank erosional processes with retrogressional processes, we modified a computer simulation model already in use for floodplain environments. We incorporated the changing edge effects and compared model projections with the data collected from the field sites using detrended correspondence analysis. Without changes, the simulation projected a site compositionally similar to the sampled interior forest. When the changes were initiated, the simulated site progressively took on compositional characteristics similar to the riparian edge sites. Because we included only those forcing functions that would be initiated by cutbank erosion, the model supports the hypothesis that the spatially progressive edge effect results in a directional change in forest community composition analogous to retrogression. Our results demonstrate an interesting linkage between successional and fluvial-geomorphic processes and indicate that site dynamics may be controlled differently in landscapes where sites are progressively created and destroyed than where recurrent disturbances affect the same site.

1. Introduction

Recent studies in landscape ecology have begun to examine the structures of ecosystem boundaries and their role in landscape functioning (*e.g.*, Wiens *et al.* 1985; Holland *et al.* 1991; Hansen and di Castri 1992). We are interested in how the processes associated with the paradigm of succession may drive population and community dynamics along forest edges in a shifting mosaic landscape. At edges, autogenic and allogenic processes affect the interaction of individual plants with site conditions, the basic determinant of succession as proposed by Finegan (1984). Edges contain species displaying a range of life history and physiological traits which Huston and Smith (1987) proposed could explain the variety of population and community dynamics described as succession. Therefore, the study of dynamic edges should illuminate the effects of landscape structure on population and community processes and inform concepts of succession.

The purpose of this study is to examine vegetation dynamics in a riparian forest initiated by an allogenic agent, channel migration. In riparian zones, the linkage between landscape dynamics and ecological processes is especially close (Malanson 1993). Gregory *et al.* (1991) outlined the important relations and dynamics of the riparian zone, defining it as the area 'of direct interaction between terrestrial and aquatic ecosystems'. This definition is a spatially broad interpretation of common dictionary definitions and is a usage now widespread in ecology. We propose that the spatial movement of a cutbank edge towards a forest interior plot will initiate directional changes in species composition as the plot is affected by a changing microclimate and hydrological regime. Specifically, we examine the applicability of the concept of retrograde succession, or retrogression, as the driving mechanism in community-level directional change along a riparian edge.

Retrogression occurs when the effects of chronic stress reduce community structure or change species composition in ways suggestive of succession in reverse (Whittaker and Woodwell 1973). Cases of retrogression have been cited for several environments and been shown to result from numerous factors (*e.g.*, Gordon and Gorham 1963; Woodwell and Whittaker 1968; Woodwell 1970; Young *et al.* 1975; Johnson 1985). Comparisons of disturbed and undisturbed riparian wetland stands in South Carolina by Firth and Hooker (1989) also show vegetational patterns suggestive of retrogression. In this paper, we explicitly test the hypothesis that community composition differs between forest interior and cutbank edge sites. We also hypothesize that the underlying process responsible for the development of a unique riparian edge community is that of a directional but short-lived change which is analogous to retrogression and initiated by meander migration. Support for this directional change would reinforce the interactive concepts of succession proposed by Finegan (1984) and Huston and Smith (1987).

1.1. Riparian forest edges

Floodplain forests serve as an interface between two very distinctive ecosystems, terrestrial and aquatic, across which energy and matter (in the form of nutrients, sediment, and water) regularly move in both directions. Fluvial geomorphic processes make floodplains a highly dynamic and rapidly changing landform surface, characterized by numerous microrelief features such as levees, meander scrolls, sloughs, oxbows, and backwater depressions (*e.g.*, Leopold *et al.* 1964; Kalliola and Puhakka 1988). The end result is a complex plant community with species distributed in response to their tolerances to soil moisture conditions dictated by flood regime and sedimentation patterns.

Studies of succession on floodplains have focused primarily on the progressive development of vegetation on newly deposited sediments of prograding and aggrading point and channel bars (*e.g.*, Baker 1988, 1990; Malanson and Butler 1990, 1991). Successional processes on the opposite side of the river, the cutbank edge, have been ignored. The structure and composition of these riparian edges may in fact be shaped by dynamic processes initiated by floodplain erosion caused by the lateral migration of the river channel. Sites initially located in a forest interior become edge sites as the floodplain surface is eroded along a cutbank, thereby initiating changes in site microclimate and hydrologic regime. These changes should hypothetically lead to the development of a unique plant community along the river channel much as upland forest edges bordering agricultural fields differ from adjacent forest interiors.

Based on the existing literature, it is clear that edge creation has a major effect on the flows and exchanges of energy, materials, and species along the newly created edge (*e.g.*, Ranney 1977). Steep microclimatic gradients (*i.e.*, available light, wind speed, temperature, and potential evapotranspiration) develop at the interface between the forested and non-forested habitats (Geiger 1965; Wales 1967). Successional dynamics along the forest edge are in turn impacted by the altered microclimatic regime resulting in the development of a forest edge community with distinct structural and compositional characteristics (Gysel 1951; Wales 1972; Ranney *et al.* 1981). The extent to which edge microclimate is affected by edge creation can be modified by several factors, including edge aspect (Wales 1967), latitude (Forman and Godron 1986), age (Ranney *et al.* 1981), and maintenance (Ranney 1977). This modification of forest structure and composition along the margins of forest patches is commonly termed the edge effect (Forman and Godron 1986).

While induced forest edges are typically the result of human activities (*e.g.*, edges bordering agricultural fields, power-line rights-of-way, logging clear-cuts, and roads), they can also be formed by natural processes. One such example is the edge created along river cutbank by the erosive power of the adjacent river. Microclimatic shifts will occur along both upland and riparian edges, but riparian edge dynamics should also be impacted by flooding effects and changing patterns of sediment deposition. It has been noted that the rate of sediment deposition and the mean particle size deposited are both inversely related to distance from the channel edge (Allen 1970). This results in a differential rate of floodplain development, the creation of natural levees alongside the river channel, the sorting and segregation of sediments across the floodplain, and the creation of different potential habitats for plant species (Frye and Quinn 1979; Parsons and Ware 1982). Cutbank edge levees are higher and better drained than the floodplain basin, less frequently inundated, flooded for shorter durations, and have drier soil moisture regimes. These changes, in turn, alter successional processes and lead to differences in the respective plant communities of levees and the floodplain basin due to the varying tolerances of species to saturated soil conditions (Brinson 1990).

1.2. Successional dynamics of forest edges

In the absence of disturbance or environmental change, classic directional succession (*e.g.*, Odum 1969) is an autogenically-driven process culminating in the establishment of a stable, mesic climax community that is buffered from the macroenvironment. Edge creation, however, is a major disturbance caused by an allogenic agent which dramatically alters environmental conditions. As a result, it does not fit neatly into traditional successional models. The successional mechanism (*sensu* Pickett *et al.* 1987) driving the development of a unique edge community from the previous interior community has not, in fact, been addressed. The process of edge creation by cutbank erosion presents a natural experiment for assessing the applicability of the concept of retrogression to riparian edges. Edge sites currently situated on a cutbank would have once been part of the forest interior and supported an interior plant community. As the river channel migrated laterally, the floodplain was eroded, and sites that were once part of the forest interior eventually came to be located along the river edge. Forest structure and composition should undergo changes as individuals respond to the newly introduced conditions based upon their specific life histories and physiological traits. The differential responses of edge and interior individuals to changing environmental conditions should thus have observable results at the level of community structure and function. We argue that this change is retrogressive because strongly edge-oriented species tend to be early successional species.

2. Methods

2.1. Field study

We sampled 25 quadrats on the floodplain of the Cedar River in southeastern Iowa to assess differences in forest composition between edge and interior riparian habitats. The areas studied included a forest-river cutbank edge (10 quadrats) and the forest interior (10 quadrats). We also sampled five quadrats along an agricultural field-forest edge on the floodplain to identify differences that may exist between human- and naturally-created edges on the floodplain.

2.1.1. Study site

The forest interior and river cutbank sites were located in Red Cedar Wildlife Area (RCWA) on the

Fig. 1. Location of cutbank edge (A) and forest interior (B) study sites in Red Cedar Wildlife Area, Iowa. Sites are 5 km southeast of Nichols, Iowa, in Pike township, T.77N, R.4W, S.24 and 25, Muscatine County.

west side of the Cedar River, Muscatine County, Iowa (Fig. 1). Owned by the Iowa Conservation Commission since 1971, RCWA contains roughly 1.5 km^2 of continuous forest and is currently accessible to the public for recreational purposes. While many of the remaining bottomland forests along the Cedar River have been heavily fragmented by human land use, the forest extent in the vicinity of the interior and cutbank edge sites is similar to that in 1875 (Andreas 1875). Although logging is now prohibited, parts of RCWA were selectively logged for oak, cottonwood and elm when under private ownership. None of the sites examined in this study, however, contained noticeable indications of logging. Grazing in RCWA is prohibited.

Although flooding frequency and duration vary with elevation above river level, the study area is regularly inundated for at least part of the growing season. Based on United States Geological Survey stage data, the study area was flooded in 29 of the 47 years from 1940 to 1986 (Zipp 1988). For years in which flooding did occur, there was an average of two floods per year, with a range of 1–5 floods and average flood duration of 5 days.

The agricultural edge sites were located approximately 8 km downstream from the cutbank sites. Aerial photographs confirmed that the adjacent agricultural field has been under cultivation for at least 35 years but that the edge position has changed only slightly during that time, advancing c. 3–5 m into the field. Even though the area is used for agriculture, the agricultural edge is at a comparable elevation to the cutbank edge and is subjected to similar periods of inundation.

2.1.2. Sampling techniques

We collected data on the species composition and basal area of trees and shrubs using a series of nested quadrats (2, 4, 8, 16, and some 32 m on a side) randomly located along the cutbank and agricultural edges. While there is no abrupt discontinuity in the edge-to-interior gradient that would serve to separate edge from interior communities, Wales (1972) and Ranney *et al.* (1981) estimated functional edge depth to be about 15 m. Miller and Lin (1985) noted that the edge effect along the border of a red maple stand extended roughly one tree height into the forest. Based on preliminary comparisons of data collected in the different sized quadrats, the height of the canopy along the sampled edges, and these authors' estimates on edge depth, we analyzed data from the 16 × 16 m plots. Edge aspects ranged from east to southeast. Rates of channel migration were too slow to be observable from aerial photographs, although the presence of recently downed trees in the river channel indicates that parts of the cutbank are still active (Fig. 2).

We also sampled interior vegetation in randomly located 16 × 16 m quadrats. Sites containing sloughs, oxbows, or other evidence of significant local drainage patterns were not sampled. Levenson (1981) concluded that forest islands smaller than 2.3 ha functioned essentially as edge communities while islands greater than 3.8 ha provided enough macroenvironmental amelioration to permit the development of a mesic core able to sustain the shade-tolerant, mesophytic hardwoods typical of forest interiors. Because RCWA contains approximately 1.5 km^2, the forest interior should be adequately free from undue macroenvironmental influences and represent a true interior habitat.

Fig. 2. A lateral view of the cutbank edge sites. Ongoing erosion along the floodplain edge has resulted in the creation of a sharp boundary between the floodplain forest and the river channel exemplified by steep riverbanks, downed trees in the river channel, and increased growth toward the higher light environment.

We tallied plants with multiple stems as separate individuals if they were connected below the soil surface. We counted those individuals with multiple trunks above ground as one individual and summed the basal area readings for each trunk. Individuals less than 0.5 cm in diameter and shorter than 1.5 m height were counted and classified as saplings. Nomenclature follows Mohlenbrock (1986).

2.1.3. Analysis of field data

We examined between-habitat differences in species composition using detrended correspondence analysis (DCA; Hill and Gauch 1980). Although imperfect, DCA is still one of the most reliable ordination techniques (Gauch 1982; Minchin 1987). The ordinations were based on species importance values calculated by summing the relative frequency, relative density, and relative dominance values for each species in each of the three habitats (McIntosh 1957). Importance values thus ranged from zero (species was absent) to 300 for each habitat.

2.2. Simulation study

While analyses of the field data would reveal differences in the structure and composition of riparian edges, they would not identify the mechanisms or processes responsible. To test the hypothesis that changes in site vegetation instigated by lateral channel migration and cutbank erosion are the result of a process of retrogression within the floodplain community, we modified a computer successional model to simulate the hypothesized environmental and vegetational changes that occur as a site "moves" from the forest interior to the river cutbank.

We used a variant of the FORET model (Shugart and West 1977) because it has been tested and validated for a variety of forest types and for several environmental scenarios. We chose the FORFLO model (Pearlstine *et al.* 1985) because it was specifically designed to simulate successional processes in bottomland forests. FORFLO calculates growth of an individual tree as a function of the species defined growth-rate equation decremented by factors incorporating the effects of shading, temperature, and soil quality. It also incorporates the effects of hydrologic regime on growth through the use of a stochastic flood routine and a depth to water table algorithm modified from SWAMP (Phipps 1979). We used the original coefficients for sensitivity to flooding derived by Phipps (1979) rather than the more sensitive ones used by Pearlstine *et al.* (1985). Plot size in FORFLO is 1/12 ha.

Environmental parameters representative of Iowa riparian habitats were chosen (Hanson 1988). We set flow regime and elevation of the simulated site to create a flood duration of approximately 5% of the growing season. This duration roughly approximates that cited for the RCWA interior sites. We included 23 tree species commonly found on southeastern Iowa floodplains in the simulation and set initial depth to water table at 1.5 m and initial soil type to loam.

2.2.1. Simulating riparian edge creation

A number of modifications to the existing FORFLO model were necessary to simulate the changes in site environment that occur as a cutbank approaches an interior site. First, we increased site elevation annually to reflect the development of a natural levee resulting from greater rates of sediment deposition. Long-term data on sedimentation rates at RCWA are not available; therefore, we estimated the rate of accretion based on figures cited in studies of other Midwestern floodplains. Estimates of sedimentation rates range from a low of 0.02 cm/yr for presettlement conditions (Galena River, Illinois; Knox 1987) to a high of 15 cm/yr in the 1930's (Coon Creek, Wisconsin; Trimble 1983). Current rates of sedimentation on floodplains vary widely but estimates generally range from 0.04 cm/yr (Kankakee River, Illinois; Mitsch *et al.* 1979) to 5.0 cm/yr (Galena River, Illinois; Knox 1987). We used a net accretion rate of 1 cm/yr for the simulated site. This figure falls in the range of commonly cited sedimentation rates for floodplains and corresponds with Alexander and Prior's (1971) figure on long-term natural levee growth in the Black Bottom of the lower Ohio River. In addition to raising site elevation, we changed the soil type of the simulated site from loam to sand to represent the deposition of coarser sediments as the river channel nears the site (cf. Allen 1970). We also increased the depth to water table by 1 cm annually to reflect consequences of increased site elevation and better drainage conditions along edges. Flood frequency and duration of the modeled site decreased because of greater site elevation.

To increase the amount of solar radiation reaching the site, we manipulated the PHI-coefficient in the GROW subroutine. The amount of available light that a given tree receives is determined by the equation:

$$\mathrm{AL} = \mathrm{PHI}e^{-\mathrm{k}*\mathrm{SLA}}$$

where AL is the available light, SLA is the "shading leaf area" defined as the sum of the leaf areas of all higher trees on the plot, k is a constant adjusted for reasonable shading beneath a dense canopy, and PHI is "the annual insolation in appropriate units" (Botkin *et al.* 1972). In previous applications of FORET-line models, PHI has been set to a default value of 1.0, indicating that available light for a given tree is strictly a function of the sum of leaf areas of taller trees on the site. In the case of a forest edge, the amount of light available to individuals, especially those in the understory, is considerably greater than that which passes through the canopy because of the effects of side lighting and increased direct and diffuse radiation. Therefore, we incremented the PHI-coefficient by 0.10 annually for 50 years to reflect increased levels of incoming solar radiation along edges. This increase represents a 500% rise in light availability over the course of a 50 year period. While seemingly large, this value is comparable to light levels described by Ranney (1977) and determined by rudimentary field observations. Any values of available light greater than 1.0 (full sunlight) were set equal to one.

Another change in the model involved the establishment conditions for roughleaf dogwood (*Cor-*

nus drummondii) and prickly ash (*Zanthoxylum americanum*). Like the shade-intolerant successional species modeled in JABOWA (Botkin *et al.* 1972), the germination and early survival of these two species are highly dependent upon the openness of the site. Botkin *et al.* (1972) used the total leaf area on the site to determine when shade-intolerant species were able to enter the site. This method stresses the importance of light availability on the establishment processes of the shade-intolerant successional species. The leaf area variable was used because it dictates the amount of light available at the soil surface (when PHI = 1.0) with high site leaf area translating directly into low availability light at the soil surface. Because total leaf area does not necessarily capture the lighting conditions present on an edge site, we used the available light variable instead. If roughleaf dogwood or prickly ash were randomly chosen to enter the site in a given year and AL was greater than 0.40, between 35 and 80 ramets of that species were added. While optimal site conditions for these species are not well known and require better quantification, the AL threshold value of 0.40 and the range of 35–80 new ramets yielded realistic results during trial runs of the model.

The final modification to the model was to increase the number of species entering the site in a given year. Previous FORET-line models, assuming forest interior locations, randomly selected 2–4 species to enter the site per year. Studies have shown that mortality of young plants is lower along forest edges while the growth of saplings and seedlings is better than in the forest interior (Augsburger 1983, 1984; Brokaw 1985). Greater seedling and sapling successes along edges are especially noticeable for shade-intolerant species (Sork 1983), but shade-tolerant species also fare well in the higher light conditions of the forest edge. To reflect this greater seedling establishment and growth along forest edges, we annually added 5–8 species.

2.2.2. Model runs

We ran FORFLO, without any of the changes, for 300 years to generate an initial simulated stand. We then calculated species importance values for each of the species on the computer-generated site based upon their relative density and dominance. Because the importance values were tabulated for specific sites rather than for a group of sites, relative frequency was not a relevant factor; therefore, values ranged only from zero to 200. Importance values for each of the species on the 25 field sites were also calculated using the same formula. We then ordinated the field sites and the computer-generated site using DCA based upon the sites' species importance values to examine the validity of the model. If the computer-generated site is compositionally similar to the RCWA interior sites, the computer site should be located near the interior sites in the ordination space, thereby indicating that the model boundary conditions are adequately defined.

Subsequent to verification, we iterated the model for an additional 150 years while implementing the changes to simulate the incursion of a cutbank toward an interior site. Available light (in the form of the PHI-coefficient) was incremented from years 300–350, elevation and depth to water table were progressively increased from years 300–400, soil type was changed from loam to sand in year 320, and the number of species entering the site was raised in year 310. The timing and the extent of the environmental changes resulting from cutbank erosion in a natural environment would be highly dependent upon the fluvial system being modeled and would undoubtedly affect the rate at which vegetational response occurs. While the extent of differences in conditions between edge and interior sites is relatively well documented, few data exist detailing the rate at which these changes occur. Therefore, the rates at which we implemented the environmental changes in the simulation were estimates based on the limited amount of information that does exist. Because we were more interested in observing the overall changes that occur in community composition rather than the temporal scale at which change occurs, uncertainty in the rate of site condition change should not be a major problem.

We then used DCA to ordinate and compare outputs from the model with the data collected at the field sites. In their study on the resilience of garrigue (*Quercus coccifera*) following disturbance in southern France, Malanson and Trabaud (1987) showed that the trajectory of a site through DCA statistical ordination space could be tracked and used to quantify temporal changes in site characteristics. By observing the location of the same sites in ordination space at different times, they were able to quantitatively examine trends in vegetation through time. We used a similar approach in this study. Outputs from the model detailing species importance values were obtained at five year intervals. We repeatedly performed DCA using the field sites and each of the model outputs, resulting in a time series of ordinations showing where the simulated site stood in relation to the field sites at five year intervals. By comparing the location of the simulated sites with respect to the locations of the field sites, we tracked the trajectory of the site through the DCA ordination space. If the simulated site moves from the cluster of interior sites to the cluster of edge sites as the retrogressive environmental changes are implemented, we would infer a relationship between these processes and the observed pattern. Conversely, if the site trajectory is erratic or exhibits a different pattern of directional movement, we would infer that the observed pattern is not explained by the retrogressive environmental change.

3. Results

3.1. Field study

The field data clearly supported the hypothesis that a distinctive plant community exists along cutbank edges. Comparisons between floodplain edge and interior communities revealed marked differences in site composition. Most notably, the edge sites were typified by a number of species not found in interior sites and decreased importance of species that were common to the interior but still present along the edges. We identified 25 species on the sites, of which 23 occurred along the cutbank edge, 17 along the agricultural edge, and 17 in the forest interior (Table 1). Of the 17 species identified in the interior sites, eight had only one or two individuals on the 10 sites. In contrast, 20 of the 23 species along the cutbank edge had three or more individuals. All of the species observed in the forest interior, with the exception of eastern hop-hornbeam (*Ostrya virginiana*) which occurred on only one interior site, were also found along the edge. Eight species observed in the edge sites were not found in the interior sites.

An examination of the dominant species in edge and interior habitats indicated that edges favor the establishment and growth of shade-intolerant, successional species. Roughleaf dogwood and prickly ash, in particular, are classic early-successional species, characterized by small mature size, short lifespans, vegetative reproduction, highly dispersible seeds, and rapid growth. In contrast, the interior dominant, bitternut hickory, is commonly recognized as a later successional species in southeastern Iowa.

3.1.1. Detrended correspondence analysis

The DCA ordination of field sites accentuated the differences between edge and interior sites in species composition (Fig. 3). The first DCA axis distinctly separated sites based on their location with all of the edge sites grouped on the right end of the axis and the interior sites clustered on the left end. The eigenvalue of the first DCA axis (0.613) indicated a strong ordering of floristic composition. Subsequent axes displayed much weaker correlations (Axis 2 = 0.341; Axis 3 = 0.163; Axis 4 = 0.071). The second DCA axis revealed no clear distinction between any of the three microhabitats (Fig. 3a) and represented an unknown factor(s) not tested for in this study. The third axis, however, differentiated cutbank edge sites from agricultural sites (Fig. 3b). This distinction could have one of two explanations: 1) there was an actual difference between cutbank and agricultural edges which was manifested by the vegetation establishing in the respective habitats; or 2) the results were caused by spurious physical differences in the sample sites not related to edge origin, such as slight differences in site elevation, flood frequency, soil texture, or microtopography.

The DCA ordination also pointed to a greater variation in the composition of edge sites. The forest interior cluster, with the exception of one outlier (site 21), is densely packed, spanning only 94 DCA units on the primary axis and 79 units on

Table 1. Importance values of woody species in cutbank edge, agricultural edge, and forest interior habitats, Cedar River floodplain, Iowa. Values are calculated as the sum of relative density, dominance, and frequency.

Species	Cutbank	Agric.	Interior
Cornus drummondii C.A. Mey (Roughleaf Dogwood)	55.61	36.78	12.51
Celtis occidentalis L. (American Hackberry)	38.88	40.58	56.14
Ulmus rubra Muhl. (Slippery Elm)	33.06	27.97	16.55
Zanthoxylum americanum Mill. (Prickly Ash)	23.14	60.13	–
Acer saccharinum L. (Silver Maple)	17.82	–	–
Carya cordiformis (Wang.)K.Koch (Bitternut Hickory)	17.81	18.67	110.22
Quercus alba L. (White Oak)	17.10	4.13	5.10
Fraxinus pennsylvanica Marsh. (Green Ash)	15.06	12.06	3.39
Cercis canadensis L. (Redbud)	14.69	7.10	3.24
Acer negundo L. (Box Elder)	10.58	3.96	–
Carya laciniosa (Michx.f)Loud (Shellbark Hickory)	9.48	–	27.36
Carya illinoensis (Wang.)K.Koch (Pecan)	8.92	–	3.24
Gleditsia triacanthos L. (Honey Locust)	8.20	38.28	–
Quercus rubra L. (Red Oak)	5.32	–	3.60
Crataegus spp. (Hawthorn)	4.00	4.13	8.76
Juglans nigra L. (Black Walnut)	3.40	6.77	8.85
Euonymus atropurpureus Jacq. (Eastern Wahoo)	3.35	3.12	1.62
Quercus velutina Lam. (Black Oak)	2.65	5.43	3.64
Ulmus americana L. (American Elm)	2.97	–	–
Morus rubra L. (Red Mulberry)	2.47	7.66	–
Gymnocladus dioicus (L.)K.Koch (Kentucky Coffeetree)	2.34	–	16.21
Morus alba L. (White Mulberry)	2.12	11.36	–
Tilia americana L. (American Basswood)	1.04	–	17.82
Maclura pomifera (Raf.)Schneid. (Osage Orange)	–	11.86	–
Ostrya virginiana (Mill.)K.Koch (Eastern Hop-hornbeam)	–	–	1.77

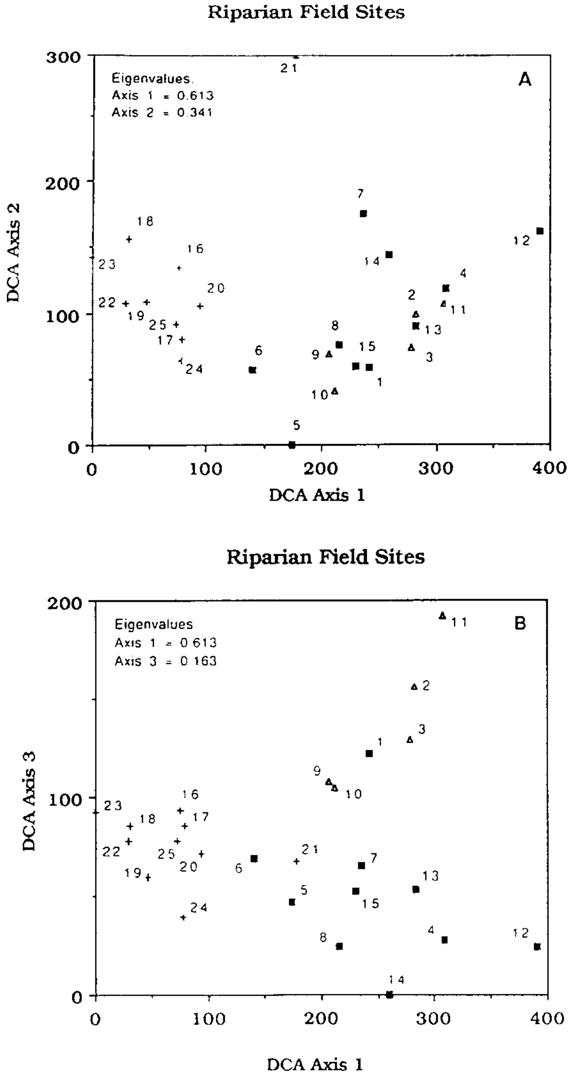

Fig. 3. DCA ordination of field sites. Sites are located along the DCA axes based on importance values of woody plant species. (A) Placement of sites on DCA Axis 1 vs DCA Axis 2. (B) Placement of sites of DCA Axis 1 vs DCA Axis 3. ■ = Cutbank edge; Δ = Agricultural edge; + = Forest interior.

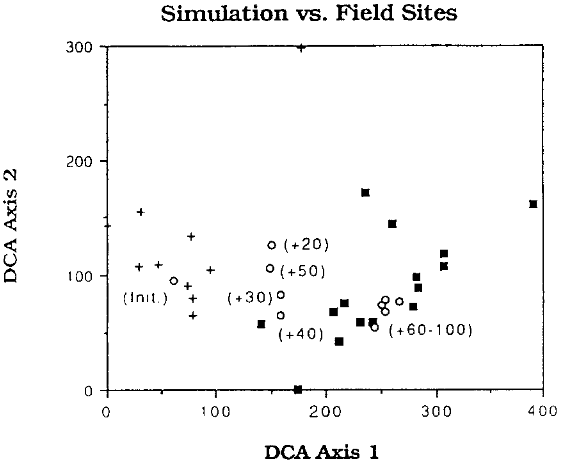

Fig. 4. DCA ordination showing the trajectory of a computer-generated site through time with respect to the Cedar River field sites. Years after the initiation of edge creation are shown in parentheses (+20 through +100). ■ = Edge sites; + = Interior sites; O = Simulated sites.

the second axis. Such a tight arrangement indicates a relatively homogeneous composition among the interior sites. In contrast, the edge sites show much greater heterogeneity in their position in ordination space, spanning a total of 251 units on the primary axis and 175 units on the second. Because DCA axes correspond to actual ecological distances with 100 units being equivalent to one average standard deviation of a species, the 2–3 times greater span of edge sites reflects the considerably greater compositional variability among edge sites than interior sites.

3.2. Simulation study

The preliminary ordination comparing the composition of the field sites with that of the beginning computer-generated site indicated that the modified FORFLO model was adequately calibrated to the environment of Iowa (Fig. 4). When ordinated with the 25 field sites, the computer-generated site was situated in the midst of the cluster of interior sites. Thus the computer site exhibited a species composition, based upon species importance values, indistinguishable from the forest interior sites which we sampled. Given that the standard parameterizations for an Iowa floodplain forest result in projections which match their species compositions, we felt confident in progressing to the next step.

The trajectory of the computer-generated site through the ordination space clearly exhibited a directional progression from the cluster of forest interior sites to the cluster of forest edge sites (Fig. 4). In the first several years, the simulted site began to move away from the cluster of interior sites and briefly stabilized at a position intermediate to the interior and edge sites (years 20–50). At this position, the computer-generated site exhibited characteristics of both the edge and interior sites, indicating that the development of a unique edge community was underway. The initial movement away from the interior cluster can be ascribed to the establishment of edge species with gradually increasing levels of available light, the change in soil texture, and the change in hydrologic regime. However, the site remained between the two clusters because of the continued presence of established interior species which do not die immediately.

In year 60, however, the simulated site shifted to the middle of the cluster of edge sites. This movement was attributable to two factors: 1) a continued increase in the importance of edge species (especially roughleaf dogwood and prickly ash), and 2) a sharp decrease in the importance of interior species as environmental conditions become progressively more favorable for the growth and establishment of edge species. The death of these large, interior trees was especially important in freeing space and nutrients for edge oriented species. Successive years (years 70–150) showed little variation in the location of the computer site in ordination space as the edge microclimate stabilized and the edge community became established.

4. Discussion

4.1. A process of retrogression

Results of the field study clearly exposed the compositional differences between edge and interior communities in a floodplain setting. They also concurred with previous studies that have noted similarities between edges and early successional habitats (*e.g.*, Ranney *et al.* 1981; Taylor 1987). From the higher available light levels to the greater moisture stress to the greater overall impact of the macroenvironment, the riparian edges resembled an earlier successional habitat than the forest interior in nearly every respect. Similarly, the dominant edge species shared many of the life history traits and physiological adaptations commmon to earlier successional species.

The major limitation of the field results is that they only reveal differences in species patterns between edge and interior habitats. They are unable to define the processes or mechanisms directing the development of the compositionally distinct edge community from a floodplain interior community. Specifically, the similarities in characteristics between edge and early successional habitats do not conclusively prove or disprove the hypothesis that the modification of environmental conditions by lateral channel migration leads to a retrogressive process along the forest margin. The field study is thus unable to rule out other possible causes that might instigate retrogression.

To help understand and define the processes responsible for the development of the edge community, we utilized the model results. Simulation models have two distinct advantages in this respect. First, it is possible to define the impacts of a given process on community development by selectively varying only those variables of interest in the model. Second, models can be used to examine ecological processes which normally occur at a scale not conducive to manipulative experiments. This capability to manipulate variables selectively coupled with the ability to simulate the long-term processes of edge development makes the model a particularly powerful tool for examining successional dynamics along the forest edge.

In this study, we used the model to further our understanding of successional processes along the cutbank through selective manipulation of the variables that change as a result of cutbank erosion (available light, site elevation, depth to water table, soil texture, and species immigration rates). The results of the simulation supported the hypothesis that the process of erosionally-induced retrogression is a viable explanation for the development of a distinct edge community. Because the trajectory of the computer site led clearly and directly from the interior cluster to the edge cluster, it can be inferred that the introduction of regimes of light, soil moisture, and soil texture resulting from cutbank incursion was the mechanism driving the development of the riparian edge community.

Successional processes along river cutbanks yield interesting insights into models of succession such as those proposed by Connell and Slatyer (1977), Finegan (1984), and Huston and Smith (1987). Retrogression initiated by lateral channel migration includes the major processes, or their inverse, identified by Finegan (1984) as simultaneous or successive and interacting: facilitation – when increased light allows different species to prosper; tolerance – when existing species continue to grow after the initial environmental change; inhibition – revealed by the sudden change when older dominants begin to die; and allogenic forcing – fluvial erosion and deposition. The spatially progressive nature of meanders leads to significant processes of landscape evolution; because sites are continually created and destroyed, each site is on a temporal trajectory of development rather than continuing through recurrent disturbances, as has been the case for most studies of succession (Malanson 1993). In this situation, the spatial relationships of sites change, and so spatial processes should, in part, differentiate species abundance and plant community structure among sites. Furthermore, the spatial progression results in vegetation being in disequilibrium with the environmental setting. The processes of succession and retrogression may usefully be reformulated in terms of disequilibrium, now a feature recognized as common in ecology (DeAngelis and Waterhouse 1987) and geomorphology (Malanson *et al.* 1992). Succession driven by autogenic processes with short time lags is close to an equilibrium processes, but allogenic succession, and retrogression, are responses by the plant species to adjust to a changed environment and so are essentially products of disequilibrium.

4.2. A question of equilibrium

The importance of disequilibrium along the cutbank edge raises a major question left unanswered by the study: what is the relationship between cutbank erosion rate and the development of the edge community? The extent to which site conditions change subsequent to edge creation is relatively well known. The rate at which microclimate changes at the site, however, will be highly dependent on the dynamics of the fluvial system involved. Active cutbank erosion is often an ongoing but uneven process, sporadically reshaping the floodplain, creating new edges, temporarily ceasing to allow a new edge community to develop, then resuming to create a new edge. Changes in site microclimate may be more gradual, again depending on the dynamics of the system, than along human-created edges where environmental conditions literally change overnight.

The total extent of changes in the forest composition evoked by cutback erosion may also be impacted by the rate of channel migration. If the cutback is highly active, edge development might never progress as far along cutbank edges as it does on relatively stable upland edges. Specifically, rapid channel migration may prevent site vegetation from reaching an equilibrium before the cutbank destroys the site. Such repetitive erosional episodes hint at not only a temporal dimension to edge development, wherein sequential vegetational changes occur on a single forest site, but also a spatial one, with edges being continually created and destroyed as lateral channel migration occurs across the floodplain. With each lateral migration and stabilization of a river channel, at least part of the former edge community is destroyed, a new cutbank edge is created, and the edge development process begins anew. Because the relationship between cutbank erosion rate and edge dynamics is unknown but probably integral, this is an area where there appears to be fertile ground for further study. Specifically, linking the rate of cutbank encroachment with the rates of variable change could yield imporant insights into the relationship between fluvial-geomorphic processes and community dynamics.

Whereas the spatial progression of a meander creates a particular local disequilibrium, cutbank edges are just one tessera within a riparian landscape (Fig. 1). Erosion along a cutbank edge, and the accompanying nonequilibrium processes, are complemented by point bar development at the landscape scale (Malanson 1993), leading to a potential dynamic equilibrium (cf. DeAngelis and Waterhouse 1987) for landscapes. Spatially limited nonequilibrium conditions along a cutbank edge may, nevertheless, have significant consequences for regional ecology and biogeography because of the function of these edges as terrestrial-aquatic ecotones (*e.g.*, Risser 1990) and longitudinal corridors (*e.g.*, Tabbachi *et al.* 1990). The complete destruction and recreation of terrestrial conditions may engender landscape-level relations different from those found with other disturbances.

5. Conclusions

By altering the flows of energy and matter within a floodplain ecosystem, the lateral migration of a river channel initiates distinct, directional changes in the composition of a forested site. The integration of field and simulation techniques proved to be an effective method for examining these successional dynamics along an eroding cutbank edge. Ordinations of data detailing woody species composition on the Cedar River floodplain in southeastern Iowa exposed striking differences between floodplain edge and interior sites. Comparisons of species importance values between cutbank edge sites and floodplain interior sites revealed that edges were dominated by successional species, suggesting that they represent an earlier successional phase than the forest interior. Results from the computer simulation support our hypothesis that these changes in community composition initiated by channel migration are retrogressive in nature.

While shedding light on the relationship between successional dynamics and fluvial-geomorphic processes along a cutbank edge, our results also have broader implications at the landscape level. Although we illustrate disequilibrium in only one part of the landscape while a dynamic equilibrium may exist at a coarser scale, the presence of disequilibrium even in subsystems may produce nonlinear dynamics which would make landscape modeling difficult (Malanson *et al.* 1992).

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