

Vegetation Development in a Modified Riparian Environment: Human Imprints on an Allegheny River Wilderness

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Pristine floodplain forests are virtually nonexistent in the eastern United States, requiring that preservation efforts focus on relatively intact representatives of these unique ecosystems, many situated where hydrologic modifications are the norm. This article examines the vegetation dynamics for one such natural area, a wilderness island in northwestern Pennsylvania, to assess how the ecological processes of a riparian preserve are affected by changes to the surrounding environment. Ordination of a vegetation sample identifies several landscape patches on the island; the structure and historical development of these communities are analyzed using tree ring patterns, aerial photography, and the flood regime characteristics preceding and following construction of a large dam upstream. Research on natural riparian sites has emphasized the role of floods as a disturbance that generates early successional habitat. Here, however, moderation of the hydrologic regime has shifted the impact of floods from disturbance to stressor. Peak flows are no longer sufficient to open sites for colonization, while the duration of flooding has increased. Without flood disturbance, later stages of succession become more widely represented, and species regeneration occurs in the context of competitive—rather than open—sites. The altered disturbance regime thus favors species with life history characteristics atypical of the pre-dam environment, including nonnative species, resulting in altered composition and vegetation dynamics. Managerial expectations that natural successional processes will eventually restore degraded riparian habitats in these modified settings are therefore unlikely to be fulfilled. *Key Words:* dam impacts, disturbance regime, flooding, natural area management.

Riparian zones are dynamic landscapes, driven by variation in both local- and regional-scale processes. Much of this environmental variability is integrated by the flood regime, which in natural settings creates a heterogeneous habitat mosaic that maintains the high species diversity associated with riparian ecosystems (Naiman and Décamps 1997). As flood control measures in many watersheds have altered river dynamics, the rivers' patterns of biodiversity have diverged from those typical of unregulated environments (Poff et al. 1997; Ward 1998).

The unique assemblage of species fostered in unmodified riparian habitats is adapted to a frequency of disturbance and set of stresses distinct from that of uplands. The corridor of a free-flowing river is characterized by a mosaic of patches with varied establishment dates and successional stages, structured by both cross-channel and downstream flood impacts (Bendix 1994; Baker and Walford 1995). Spatially, the distribution of species assemblages across a transverse channel profile closely reflects the geomorphic features of floodplain and terraces (Hupp and Osterkamp 1985, 1996). This gradient is driven by the decline in flood frequency and stream

power away from the active channel, producing variation in the extent of erosive scouring and mechanical damage, the duration of anaerobic conditions, and the distribution of alluvial sediments (Bendix 1999). Temporally, succession is initiated when new sites for regeneration are created following disturbances by channel migration and by periodic high magnitude floods (Kalliola and Puhakka 1988; Baker 1990). The result is a shifting mosaic of habitat patches with opportunities for a variety of vegetative life history strategies.

The intermediate disturbance hypothesis is often evoked to explain the importance of flood disturbance in generating high levels of riparian species diversity (Malanson 1993). This model suggests that greatest diversity should be observed when the life histories of both disturbance-adapted (ruderal) species and disturbance-intolerant competitive species are supported (Connell 1978; Huston 1994). At low levels of disturbance, superior competitors exclude ruderals; at high levels of disturbance, only ruderals persist. According to this hypothesis, only with intermediate levels of disturbance do species of both life-history strategies coexist. The validity of this hypothesis has been examined using numerous

interpretations of “intermediate”: intermediate frequency of flooding (Bornette and Amoros 1996; Pollock, Naiman, and Hanley 1998), intermediate site age (Collins, Glenn, and Gibson 1995), intermediate magnitude of disturbance (Bendix 1997), and intermediate positions along the length of a river system (Nilsson et al. 1989). These studies yield mixed results, as the examined variables are interdependent and frequently confounded. Nonetheless, they generally support the concept that species diversity is increased at the landscape scale when there are a variety of successional stages present.

The hydrologic regime generated by dammed rivers is often associated with reduced species diversity (Nilsson and Berggren 2000). A fundamental effect of many dams is a reduction in the variability of stream flow, with fewer large floods leading to greater stability in riparian habitats (Naiman, Décamps, and Pollock 1993). The principal consequence of dams on vegetation is often identified as the maturation of riparian communities to late successional stages. Marston and colleagues (1995) map the increasing homogeneity of Ais River floodplain vegetation that stems from alterations to the hydrologic regime, with pioneer communities succeeding toward greater expanses of alluvial forest. In the western United States, Johnson (1994) and Miller and colleagues (1995) document a similar trend for landscapes along the South and North Platte Rivers, where post-dam cottonwood stands have increased in areal extent and maturity. Little analysis of the downstream impacts of dams on eastern U.S. deciduous forests exists, although Barnes (1997) and Knutson and Klaas (1998) demonstrate that forests along regulated rivers in Wisconsin and Minnesota have shifted in structure and composition from their presettlement condition.

In the eastern U.S., efforts to preserve riparian ecosystems are challenged by reductions in habitat quantity, as well as likely impacts on habitat quality. The quantity of riparian forest has decreased by more than 80 percent in much of this region, due to floodplain development (Noss, LaRoe, and Scott 1995). Beyond such direct loss of floodplain habitat, declines in riparian biodiversity for this region may also be anticipated from the increased modification of fluvial processes. The extent of dam storage and potential impacts reached a high level in this region during the period between 1950 and 1980 (Graf 1999).

This study examines a forested riparian natural area in the Allegheny River managed as a wilderness but situated downstream from a large dam. The preserve represents an attempt to increase the abundance of riparian habitat and prevent direct anthropogenic alteration of it, but the issue of human modification of the surrounding ecological context has not been examined. In this arti-

cle, we analyze the vegetation dynamics of this site as an indicator of the role of dams in affecting the disturbance regime of riparian zones in the eastern deciduous forest region. Specifically, this study identifies the landscape patches present on the site to determine the disturbance-related successional pathways operating in them, the life-history characteristics they favor, and the resultant implications for species composition. Our investigation highlights the dilemmas inherent to natural area policy in the eastern United States, where human influences are inextricably linked with the forested landscape.

Study Area

In an effort to protect regional ecological diversity, the U.S. Forest Service designated seven of the dozens of islands in the Allegheny River of northwestern Pennsylvania as the “Allegheny Islands Wilderness” in 1984 (Wiegman and Lutz 1988). Two of these, Crull’s Island and Thompson Island, are described as possessing among the best examples of riverine forests in Pennsylvania (Smith 1989). This study focuses on the larger of the two islands, Crull’s Island (39 ha).

Crull’s Island is situated near the western edge of the Allegheny National Forest, 14 km downstream from the city of Warren (Figure 1). The island formed from glacial

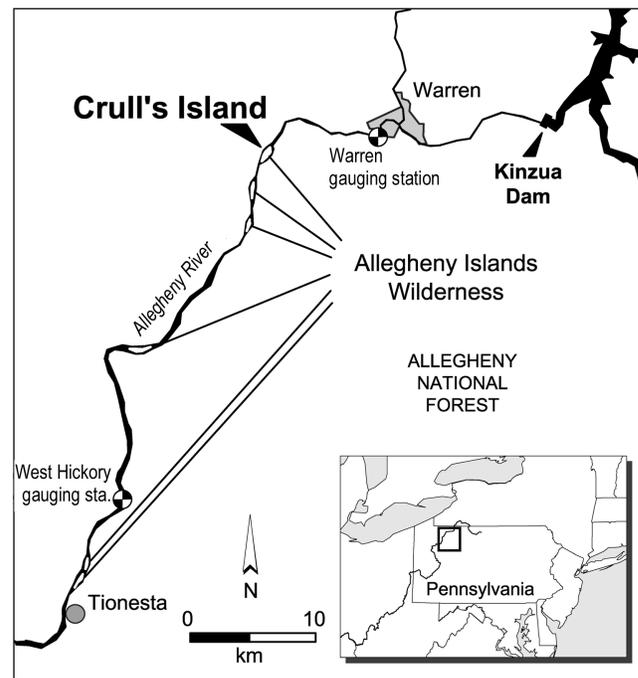


Figure 1. The location of Crull’s Island within the Allegheny National Forest, Pennsylvania.

outwash sediments and Holocene alluvial deposits; its core of sand and gravel is overlain by loam and sandy loam soils (Cerutti 1985). Two primary geomorphic surfaces are present: a floodplain ranging between 0 and 110 m wide and an interior terrace that rises a maximum of 3 m above the channel banks. A steep slope divides these two surfaces in most places, although a more gradual transition at the headward end of the island creates a lower terrace of intermediate elevation. The size and position of the island have remained generally stable since early maps of the river were made (e.g., Babbitt 1855).

Kinzua Dam was built 25 km upstream of Crull's Island in 1965 to limit flooding along the Allegheny River, particularly in urban areas such as Pittsburgh (Rosier 1995). Prior to the dam's construction, the river's annual flow regime (Figure 2) was typified by an early spring peak fed by snowmelt and rains (mean maximum discharge at Crull's Island = 1269 m³/sec), a gradual reduction to its lowest levels by summer (mean minimum = 12 m³/sec), and then a rise during autumn until the river froze for the winter (Way 1942; Cowell and Stoudt 2002). Severe floods occurred during many of the decades prior to the 1960s, with particularly extreme events (those exceeding approximately 1900 m³/sec at Warren since 1806) recorded in 1865, 1873, 1913, 1927, and 1956 (Commonwealth of Pennsylvania 1943; USGS 1998). The dam has stabilized this regime significantly. Median daily flow has increased 57 percent, with seasonal variation moderated to a mean maximum of 688 m³/sec and a mean minimum of 29 m³/sec (Cowell and Stoudt 2002). The level of the highest post-dam flow, recorded in 1972 during Hurricane Agnes, had a recurrence interval of less than two years under the pre-dam regime (Cowell and Stoudt 2002).

Forests throughout the Allegheny River watershed were extensively cleared between 1880 and 1930, with many of the easily accessible stands along the river and streams logged earlier (Whitney 1990). Although most

of the region's uplands now support secondary forest, the riparian zone remains less forested except for the river islands. Walters and Williams (1999) describe the forest of two islands downstream from Crull's as dominated by even-aged stands of silver maple and sycamore, attributing the stands' establishment to the availability of flood-scoured sites. They also note the presence of several non-native herbaceous species in the understory and suggest that their occurrence is the result of human disturbance.

Crull's Island has been utilized for agriculture in the past. Seneca Indian cultivation of nearby floodplain and river island sites is documented, and probably also occurred on Crull's Island (Schenck 1887; Wainwright 1964). The Crull family purchased the island in the nineteenth century, and by 1850 much of the island had been farmed (Babbitt 1855). The flood of 1865 destroyed several buildings on the island, which were never rebuilt, but agricultural use of the island—including livestock grazing—continued into the early twentieth century (W. Crull, personal communication via letter, September 1996). The U.S. Forest Service acquired ownership of the island from the Western Pennsylvania Conservancy in 1973. Since the island was established as a wilderness area in 1984 and as a research natural area in 1988, the only activities permitted there are recreation, education, and research. The management objective for Crull's Island is "to maintain the unique assemblage of species in this natural community," with "no direct management needed to maintain the present ecological conditions" (Wiegman and Lutz 1988, 13).

Methods

We conducted three analyses to examine the controls of the island's vegetation dynamics: the identification of plant community patches, the relationship of flood effects to these patches, and the historical development of each patch. Because riparian vegetation is best explained in terms of both environmental gradients and patchiness (vanColler, Rogers, and Heritage 2000), our methods integrate both approaches.

A vegetation sample was obtained and a topographic survey made along seven 20-m-wide transects across the northern end of the island in June 1996 and 1997 (Figure 3A). These transects were oriented transverse to the channel and spaced 75 m apart, providing representation of the range of conditions found in the portion of the island previously described by Wiegman and Lutz (1988) as the most ecologically important (Figure 3B). Each transect was subdivided into contiguous 20 × 20 m quadrats, wherein all woody stems ≥1 cm diameter at

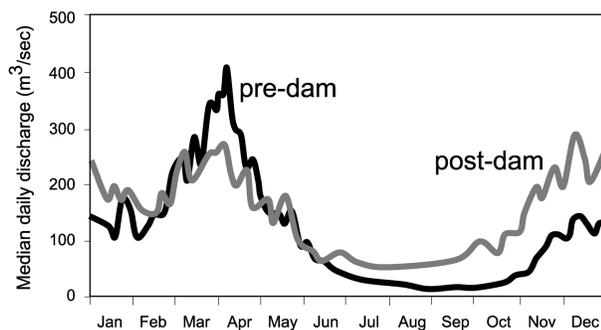


Figure 2. Crull's Island annual hydrographs for the pre-dam (1936–1965) and post-dam (1966–1997) periods.

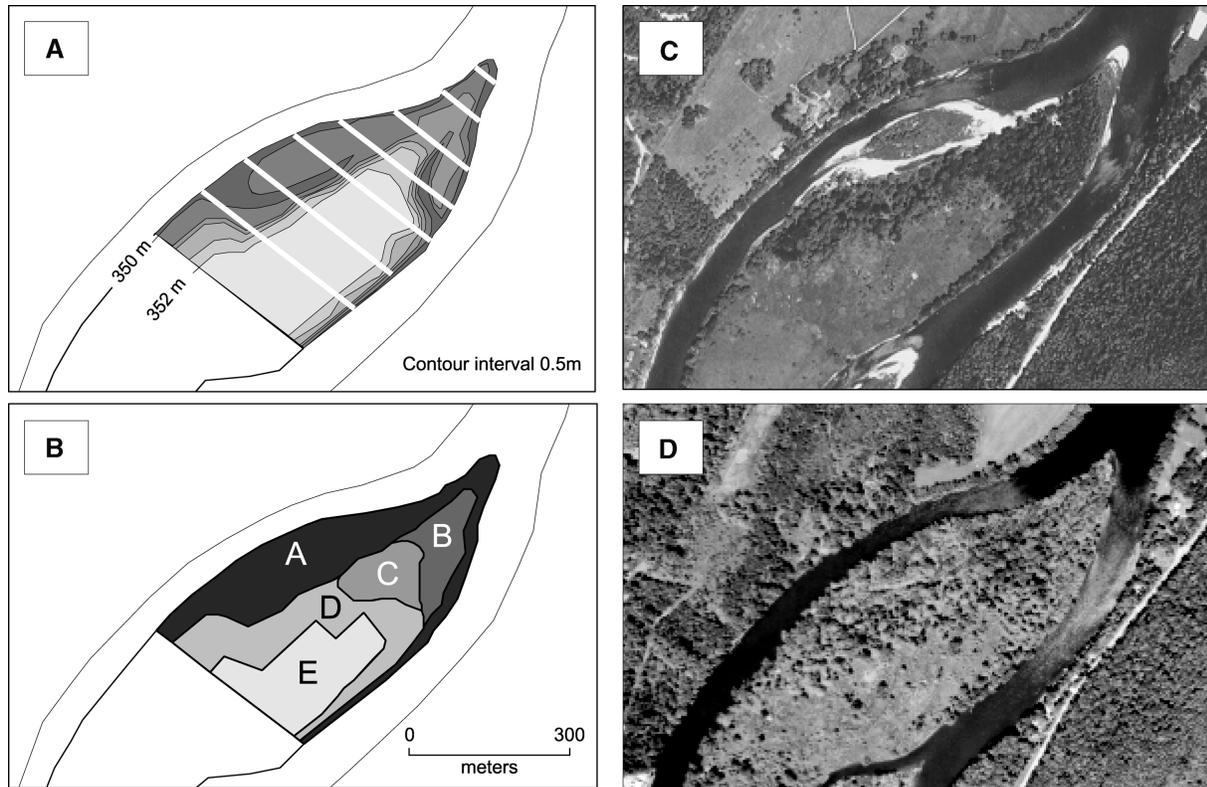


Figure 3. Sampling scheme and landscape patterns on the Crull's Island study area. (A) Survey transects and contours. (B) Landscape patches: A = floodplain, B = low terrace, C = terrace forest, D = terrace edge, E = terrace old field. (C) 1939 USDA aerial photograph. (D) 1994 USDA aerial photograph.

breast height (dbh) were identified and measured and herbaceous species presence recorded. Elevations relative to the channel were measured at 10-m intervals along the transects using an autolevel. Increment cores were taken from the base of trees representative of the range of individuals (species and sizes) and community types present on each transect. Aerial photographs of the island taken in 1939, 1950, 1968, and 1994 were obtained to provide a record of any changes in the extent of community patches.

Landscape patches were identified primarily by an ordination of vegetation composition. Species importance values within each of the 73 quadrats were calculated by averaging the relative density and relative dominance of all stems. These values were used to generate an ordination of sites (quadrats) and species by canonical correspondence analysis (CCA) within the PC-ORD software package (McCune and Medford 1995). CCA is a form of direct gradient analysis, arranging species and sites along axes that indicate the dominant modes of community variation present in the data (terBraak 1994). These compositional axes are constrained to incorporate environmental measures; in this case, quad-

rat elevation is included as an indicator of site relationship to the transverse-channel gradient. Site ordination scores were mapped in a GIS to classify spatial clusters of similar composition. The boundaries of these community types were confirmed and refined by overlays of elevation, air-photo, and tree-ring data so as to demarcate patches with internally consistent geomorphic settings and tree-establishment dates.

The relationship of flood regime to the landscape patches, and the extent to which these patterns have been altered as a result of dam construction, were analyzed using the HEC River Analysis System (USACE 1997). This program models steady-flow water-surface profiles, including estimation of rating curves (discharge–flood stage relationship) for the elevational profile of an area between two stations with directly measured rating curves. Data for the two nearest USGS gauging stations, Warren (upstream) and West Hickory, Pennsylvania (downstream; see Figure 1) were input along with a valley cross-section surveyed at one of the Crull's Island transects. From this analysis, the stream discharge necessary to inundate each of the landscape patches was determined from the estimated rating curve. Daily discharge

values at Crull's Island (USGS 1998; Cowell and Stoutt 2002) were examined for the pre-dam (1936–1965) and post-dam (1966–1997) periods of record to calculate flood duration patterns by patch.

The disturbance history of each landscape patch was analyzed using dendrochronological methods developed by Nowacki and Abrams (1997). Their radial-growth averaging technique detects sustained growth increases characteristic of canopy disturbance, while filtering out climate-related variation. The “percent growth change” index, which compares sequential 10-year running averages of annual ring widths, was applied to each of the 64 usable individual tree-ring series. These tree cores were prepared following standard dendrochronological procedures, visually cross-dated, and measured to the nearest 0.01 mm with an increment-measuring machine (Stokes and Smiley 1968). Due to the highly consistent tree-origin dates within patches and the interspecies similarity of growth responses, all cores within a patch were grouped and percent growth change averaged within groups. To determine whether climatic trends were related to growth releases, the “PDSI difference” (Nowacki and Abrams 1997, 229) was calculated from annual Palmer Drought Severity Index (PDSI) records for the northwestern climate division of Pennsylvania (NCDC 1998). This statistic relates sequential 10-year means in PDSI values, allowing direct comparison with the percent growth change index. Positive peaks in PDSI differences indicate a year during which a climatic change beneficial to tree growth occurred, such as the end of a drought. Growth releases (positive peaks in percent growth change) that do not correspond to years with PDSI peaks are interpreted as resulting from canopy disturbance.

Results

The vegetation on Crull's Island is composed of several communities, each shaped by a distinct set of natural and human-induced disturbance processes. The CCA ordination of the transect quadrats (Figure 4) suggests that five vegetation types can be recognized: closed canopy forests occupying the (1) floodplain, (2) low terrace, and (3) upper terrace; (4) a more open canopy edge-habitat forest, transitional between the terrace forest and (5) an old field with scattered trees. Figure 3B maps these types. Two disturbance-related gradients account for 24 percent of the total variance in the species data. The first CCA axis is highly correlated with elevation ($r = 0.89$), and thus is presumably a surrogate for flood-related impacts. The associated compositional gradient ranges from flood-adapted species on the low elevation sites to

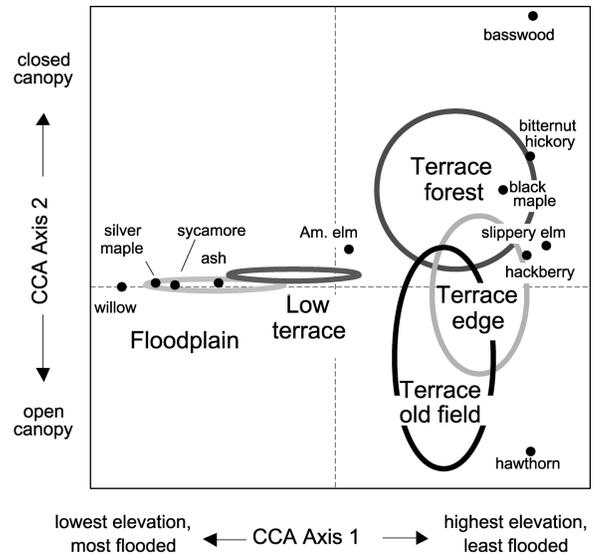


Figure 4. Canonical correspondence analysis ordination of the vegetation data. Ellipses indicate the distribution of quadrat samples, drawn as ± 1 standard deviation from the centroid of each landscape patch type.

the less flood-tolerant species dominant on the terrace. The second axis separates the terrace communities along a gradient reflecting recovery from past agricultural disturbance, distinguishing species associated with the closed canopy forest from those related to the edge forest or the open-canopy old field.

Species composition in the low elevation patches is dominated by sycamore and silver maple (Table 1). Within the floodplain patch, these two species have populations with unimodal size distributions centered on the 10–30-cm dbh classes (Figure 5a, Figure 6). White ash and American elm are abundant as saplings, with the understory typified by a fairly continuous herbaceous cover of reed canarygrass and scattered clusters of dogwood (Table 2). Colonies of Japanese knotweed are also becoming established in this patch. The overstory of sycamore and silver maple on the low terrace is less dense, with individuals distributed over a greater range of size classes. While American elm and white ash occur in the understory at densities comparable to that on the floodplain, they are found in conjunction with very dense thickets of dogwood and an herbaceous layer dominated by ostrich fern and skunk cabbage.

Composition on the terrace differs markedly, with a greater number of tree species prevalent than on the two lower patches (Table 1). The terrace forest is dominated by black maple and basswood, each represented in all size classes, with American elm and bitternut hickory important in small and intermediate classes (Figure 5b, Figure

Table 1. Landscape Patch Composition: Trees (≥ 10 cm dbh)

	A Floodplain	B Low Terrace	C Terrace Forest	D Terrace Edge	E Terrace Old Field
Tree density (stems/ha)	349	244	172	228	96
Tree basal area (m ² /ha)	27.3	26.9	20.3	19.5	3.9
Sycamore (<i>Platanus occidentalis</i>)	50.0	43.9	—	15.6	—
Silver maple (<i>Acer saccharinum</i>)	32.4	33.8	2.2	—	—
White ash (<i>Fraxinus americana</i>)	5.8	1.8	3.5	—	—
American elm (<i>Ulmus americana</i>)	8.9	16.9	16.7	1.0	—
Basswood (<i>Tilia americana</i>)	—	—	20.0	—	—
Black maple (<i>Acer nigrum</i>)	—	—	32.3	3.1	—
Hackberry (<i>Celtis occidentalis</i>)	—	0.7	6.8	9.1	3.4
Bitternut hickory (<i>Carya cordiformis</i>)	0.8	2.2	7.9	10.1	1.4
Slippery elm (<i>Ulmus rubra</i>)	—	—	3.4	20.8	28.1
Hawthorn (<i>Crataegus</i> sp.)	0.7	0.7	7.2	33.1	52.6
Butternut (<i>Juglans cinerea</i>)	—	—	—	—	10.1
Others ^a	1.4	—	—	7.1	4.4

Note: Species values are percent importance [(relative density + relative dominance)/2]; those in bold highlight the dominants within the patch. Nomenclature follows Gleason and Cronquist (1991).

^a Black locust (*Robinia pseudoacacia*), boxelder (*Acer negundo*), choke cherry (*Prunus virginiana*), ironwood (*Carpinus caroliniana*), northern red oak (*Quercus rubra*), willow (*Salix nigra*)

6). Stand density is lower than that on the floodplain and low terrace patches, while the herbaceous cover is near 100 percent (Table 2). Upon transition into the edge forest, the canopy opens, maple and basswood drop out, and the minor constituents of the closed forest become prominent. The edge patch is composed of three distinct size-classes: scattered large individuals of sycamore and hackberry, abundant intermediate size slippery elm and bitter-

nut hickory, and an understory dominated by hawthorn, slippery elm, and choke cherry. The underlying dense herbaceous layer of skunk cabbage is strewn with numerous downed tree stems. The old-field patch in the center of the island (Figure 5c) is distinguished by a shift in herbaceous composition to dominance by reed canarygrass. Widely planted throughout North America for pasturage, this introduced species is able to aggressively invade wetland



Figure 5. Appearance of the landscape patches. (a) The floodplain, dominated by young, even-aged sycamore and silver maple. (b) Terrace forest, comprised primarily of black maple and basswood. (c) The old field, dominated by reed canarygrass and scattered hawthorns; the view is toward the edge forest.

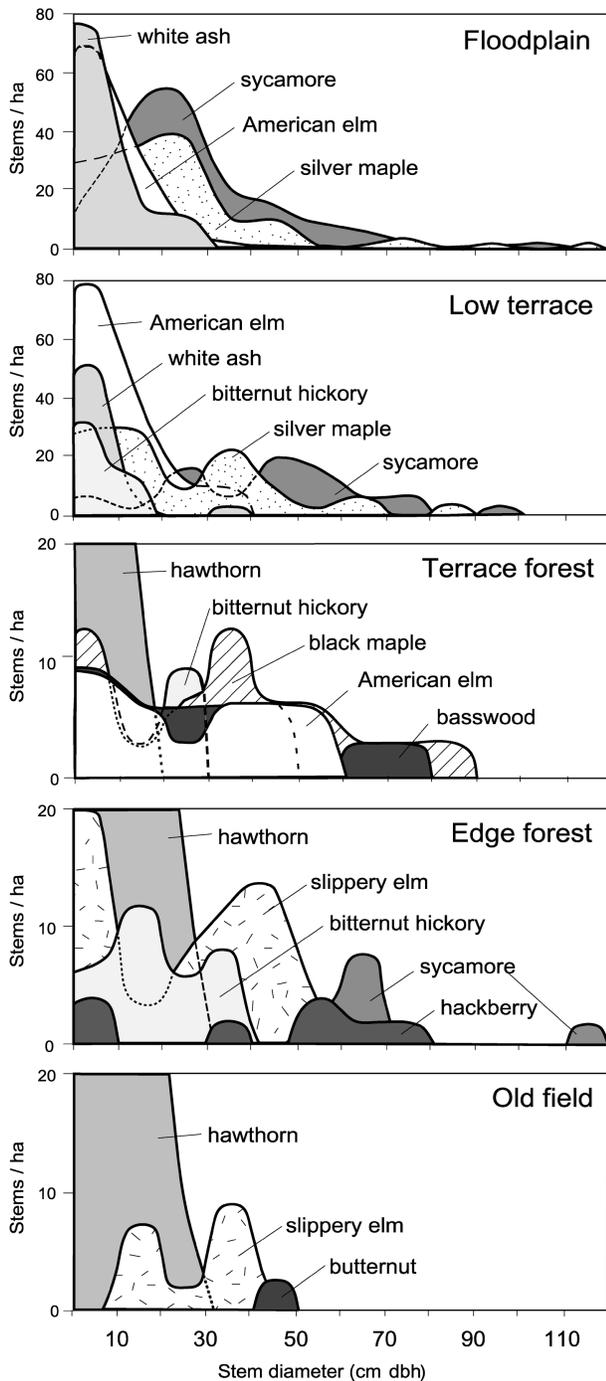


Figure 6. Size-class distribution of species within the landscape patches of Crull's Island.

areas (Lyons 2000). Open-grown hawthorns are dispersed throughout this grassy matrix, with isolated individuals of several other species—particularly slippery elm—present.

As suggested by compositional patterns, the flood regime differs between these five communities, with important changes in the duration of floods since emplace-

ment of the Kinzua Dam (Table 3). The hydrologic model indicates that a discharge of 325 m³/sec is necessary to inundate the floodplain. Prior to the dam, flows of this magnitude occurred an average of 49 days per year; following dam construction this increased by an average of 12 days. Much of this additional inundation happens during the growing season: 19 percent of pre-dam flows above this level occurred in May–November, versus 32 percent under the post-dam regime. Flows of 630 m³/sec are required to flood the low terrace; these occurrences have decreased since dam construction, from an average of 13 to 9 days per year. Floods with discharge of 975 m³/sec will reach the terrace forest, while discharges of 1360 m³/sec are necessary to affect the old field in the center of the terrace. The terrace was commonly flooded prior to the dam (Figure 7) for at least several days during the spring. Since construction of the dam, peak flows have not reached the terrace.

Tree establishment within patches is tied mainly to episodes related to the island's flood history (Figure 8). The earliest establishment date through nearly all of the floodplain patch is 1964; most individuals in this patch established within the following decade. As visible in the 1939 aerial photograph (Figure 3C), much of this floodplain surface was bare in the pre-dam period, with a small zone of scrubby vegetation on slightly elevated ground. The mature individuals on this higher surface date to the early 1940s. Immediately following construction of the dam, the even-aged stand of sycamore and silver maple now dominant on this surface was initiated (Figure 3D). This young stand has had no notable growth releases; instead, its high density has produced a largely negative trend in annual ring increments (Figure 9).

The canopies of the low-terrace, terrace-forest, and edge-forest patches are composed of individuals that largely became established in the late nineteenth century (Figure 8). The dominant sycamores of the low terrace date principally to the 1890s. The growth-change index for this patch (Figure 9) suggests that the 1927 flood may have opened portions of this maturing stand, with several of the larger trees in this patch establishing soon after the flood occurred. The oldest trees on the upper terrace consistently date to the period between 1870 and 1890, corroborating historical accounts that the continuation of agriculture in this patch was foregone following the massive 1865 flood. The stands in the terrace-forest and terrace-edge patches originated after this initial agricultural abandonment; the highest ground (the old field) remained cultivated or pastured until approximately 1930. Most colonization of this old field occurred soon after, particularly by hawthorn, with only limited invasion by other species in the following de-

Table 2. Landscape Patch Composition: Understory

	A Floodplain	B Low Terrace	C Terrace Forest	D Terrace Edge	E Terrace Old Field
Relative density of saplings (%)					
Silky dogwood (<i>Cornus amomum</i>)	51.3	82.8	27.3	—	—
White ash (<i>Fraxinus americana</i>)	14.1	3.5	4.0	1.2	—
American elm (<i>Ulmus americana</i>)	12.7	5.2	3.0	—	—
Silver maple (<i>Acer saccharinum</i>)	5.6	1.7	—	0.6	—
Sycamore (<i>Platanus occidentalis</i>)	3.3	0.4	—	—	—
Black cherry (<i>Prunus serotina</i>)	3.1	0.7	12.1	—	—
Basswood (<i>Tilia americana</i>)	0.2	—	3.0	—	—
Black maple (<i>Acer nigrum</i>)	—	—	4.0	—	—
Choke cherry (<i>Prunus virginiana</i>)	0.6	—	11.1	14.9	—
Slippery elm (<i>Ulmus rubra</i>)	0.3	0.2	—	6.6	—
Bitternut hickory (<i>Carya cordiformis</i>)	1.1	2.2	4.0	1.8	2.8
Hawthorn (<i>Crataegus</i> sp.)	0.3	3.3	29.3	73.2	97.2
Others ^a	0.5	—	2.0	1.7	—
Sapling density (stems/ha)	531	1,437	309	323	126
Dominant Associated Herbaceous Cover					
Mean percent cover	74	81	94	97	98
Japanese knotweed (<i>Polygonum cuspidatum</i>)	•	—	—	—	—
Ostrich fern (<i>Matteuccia struthiopteris</i>)	—	•	•	•	•
Skunk cabbage (<i>Symplocarpus foetidus</i>)	—	•	•	•	•
May apple (<i>Podophyllum peltatum</i>)	—	—	•	•	—
Blackberry (<i>Rubus allegheniensis</i>)	—	—	—	•	—
Grape (<i>Vitis riparia</i>)	—	—	—	•	•
Sedge (<i>Carex</i> sp.)	—	—	—	—	•
Reed canarygrass (<i>Phalaris arundinacea</i>)	•	—	—	—	•

Note: Saplings are woody stems 1–10 cm dbh; • indicates presence of dominant herbaceous cover ($\geq 25\%$ of quadrats in a patch).

^a Serviceberry (*Amelanchier arborea*), box elder, hackberry.

cedes. Hawthorn commonly indicates past grazing (Stover and Marks 1998), and while release from this pressure would normally allow secondary succession to proceed, the aggressively competitive reed canarygrass has precluded forest development.

The growth index for terrace edge and forest (Figure 9) shows little evidence of patch-wide disturbance prior to 1970, with large increases in growth rates occurring only

during the first decade of succession. Recruitment within the terrace edge stand has occurred continuously since establishment, while regeneration in the terrace forest appears more episodic (Figure 8). The only major increase in tree growth occurred during the late 1970s and does not coincide with precipitation changes. This growth release signals a disturbance event most significantly affecting the edge forest, but also pronounced in the low terrace

Table 3. The Duration of Floods at Crull's Island, by Landscape Patch, Preceding and Following Construction of the Kinzua Dam

Landscape Patch	Surface Height (meters a.s.l.)	Estimated Discharge	
		Necessary to Flood Patch (m ³ /sec)	Mean Pre-dam Discharge Duration (days/year \pm SD)
Floodplain	350.0	325	49.1 \pm 17
Low terrace	350.8	630	12.6 \pm 8
Terrace forest	351.6	975	3.9 \pm 4
Terrace edge	352.1	1250	1.4 \pm 2
Terrace old field	352.3	1360	1.1 \pm 1
			Mean Post-dam Discharge Duration (days/year \pm SD)
			61.2 \pm 25
			9.3 \pm 9
			0.0 \pm 0
			0.0 \pm 0
			0.0 \pm 0

Note: The estimated flood stage/discharge values are obtained from the modeled rating curves; flow durations for these levels are based on measured values for 1936–1965 and 1966–1997.

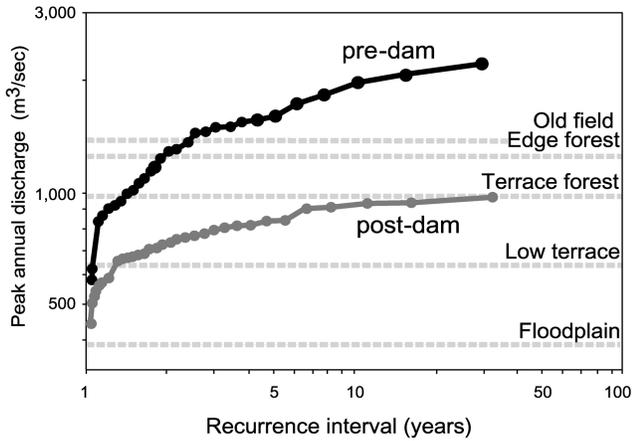


Figure 7. Flood-frequency diagram for Crull's Island, with estimated flood stage for each landscape patch.

and margins of the old field. Several snags and the many downed logs distributed throughout the terrace probably date to this event, although they were too decayed to successfully extract usable increment cores. Wood and bark of these dead trees suggest that many are American elms. Although prevalent in small size classes, this species rarely occurs at diameters greater than 40 cm on the island. Such evidence is in keeping with the impacts of Dutch elm disease, and it was at about the time of the late 1970s that the fungus affected this region (S. Stout, personal communication via email, December 1999). Gaps formed as a result have allowed the encroachment of reed canarygrass from the old field into parts of the neighboring edge forest.

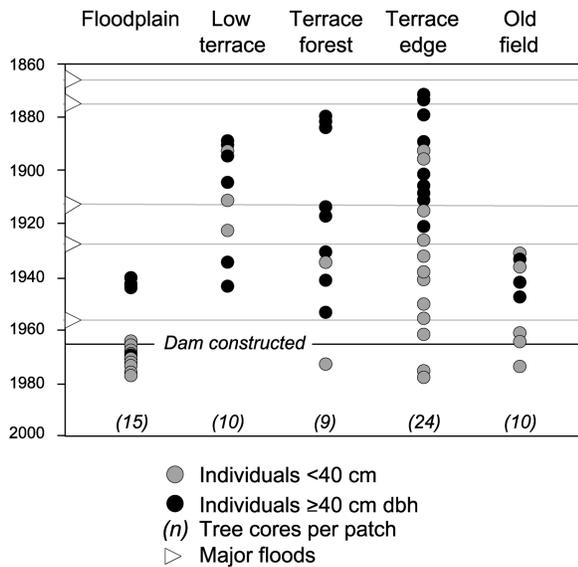


Figure 8. Tree-ring-based reconstruction of establishment patterns within the Crull's Island landscape patches. Each circle represents a sampled individual.

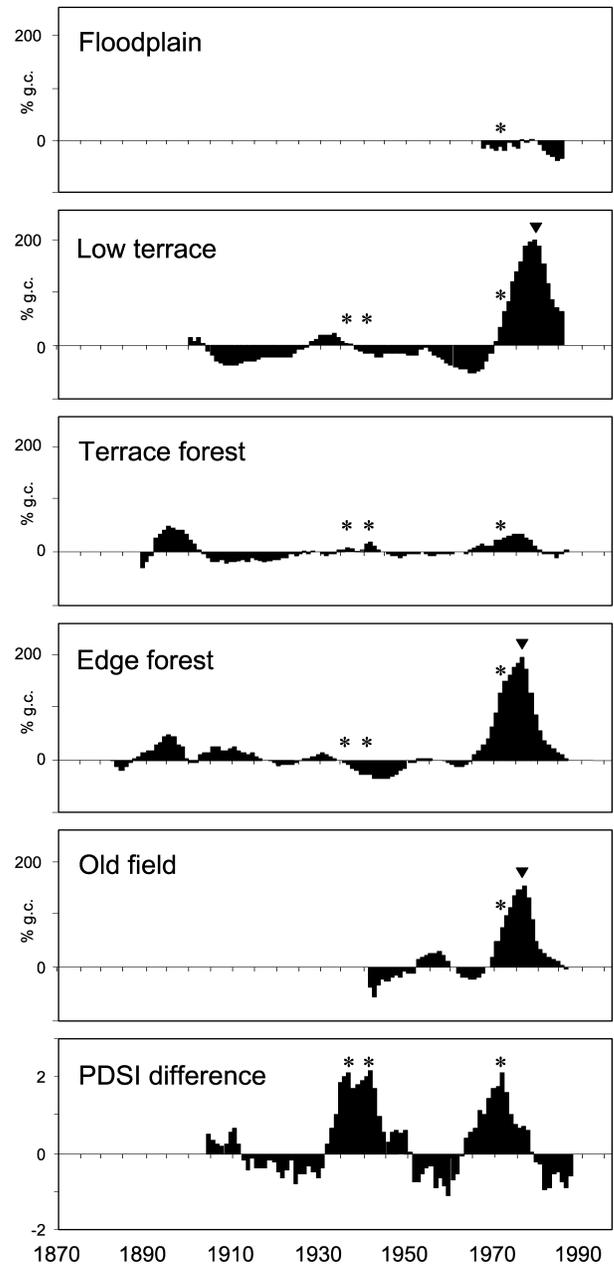


Figure 9. Percent growth change in annual tree rings by landscape patch. Triangles (▼) identify the beginning of a growth release. Asterisks (*) indicate years when climate-related variation is most likely to initiate growth increases (1936, 1941, 1971), based on differences in 10-year sequential means of the Palmer Drought Severity Index (PDSI). A lack of correspondence with climate signal indicates that growth releases are most likely a result of canopy disturbance.

Discussion

Contemporary analysis of vegetation dynamics and species composition in natural riparian sites has been framed by the concept of disturbance regimes, emphasizing the role of floods as disturbance events that generate

early successional habitat by removing standing vegetation, as well as modifying the substrate through scouring and deposition (Bendix and Hupp 2000). This understanding fits well with the definition of disturbances as relatively discrete events that disrupt community structure and alter resource (e.g., light) availability, typically through the destruction of biomass (White and Jentsch 2001). However, disturbances play a diminished role in the altered vegetation dynamics of the post-dam riparian landscape of the upper Allegheny River. Instead, modification of the hydrologic regime has transformed the impact of the river from disturbance to stress.

While the annual volume of water flowing through the Allegheny has remained fairly constant, the temporal displacement of these flows from a pre-dam large spring pulse to a post-dam pattern of moderate flow throughout the growing season (Figure 2) leads to distinctive biological and ecological impacts. The capacity of the river to destroy standing biomass and prevent establishment of new individuals depends on comparatively powerful flood events, as evident from the lack of vegetation on the pre-dam floodplain. The loss of such disturbances is clear from the immediate and sustained colonization of these sites following establishment of the dam. No early successional patches have been initiated in the post-dam period. The tradeoff for decreased flood peaks has been increased duration of inundation, which induces greater stress on established patches by creating anaerobic conditions in the root zone. By definition, these stresses are processes that may affect ecosystem

function (such as reducing productivity) but are more chronic than abrupt and fail to directly remove biomass (White and Jentsch 2001).

This shift from a disturbance-dominated pre-dam regime to a stress-dominated post-dam regime is most pronounced on the floodplain of Crull's Island. This habitat has been altered from one favoring regeneration of the ruderal species adapted to the open sites generated by flood disturbance to one favoring species that tolerate the stresses associated with inundation (Figure 10A). The even-aged sycamore and silver maple canopy that dominates this patch originated with the dam's closure in 1965, under the open-site conditions remaining from the pre-dam flood regime. These species are typical early successional riparian colonists, preferring high light levels and somewhat tolerant of inundation once established (Burns and Honkala 1990). This cohort is likely to maintain its dominance for decades, and—as in Knutson and Klaas' (1998) and Barnes' (1997) Mississippi Valley study areas—can be expected to experience a reduction in density and increase in individual tree size, maturing to a canopy structure comparable to that currently found on the lower terrace.

Unlike the lower terrace however, the floodplain will maintain significantly higher flood stress under the current hydrologic regime, with key implications for future understory recruitment. The open-site conditions favorable to sycamore and silver maple regeneration are tied to the now-absent flood disturbances; these species' relative intolerance of shade makes it unlikely that this stand will be self-replacing. American elm and white ash dom-

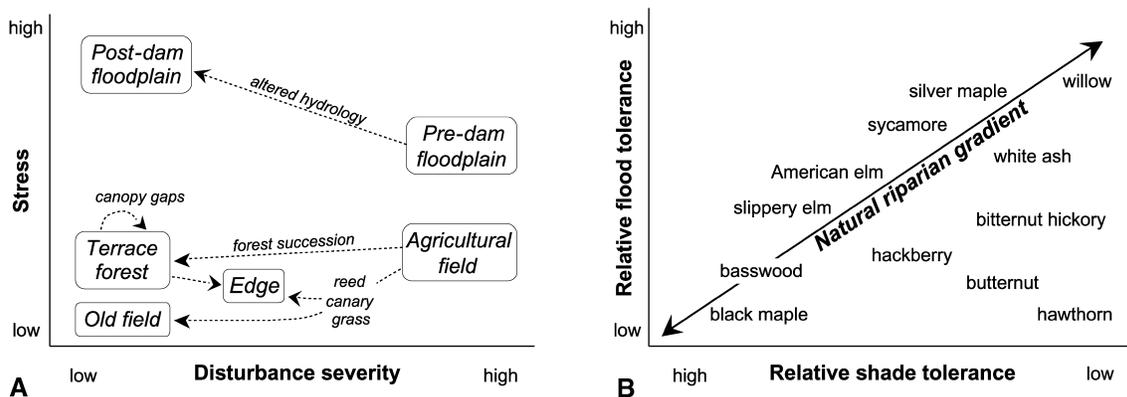


Figure 10. The relative importance of shade and flooding on Crull's Island as controls of succession for the habitat patches, and in relation to life history characteristics (Burns and Honkala 1990) of dominant species. (A) On the floodplain, disturbance severity is reduced with dam construction, to the point that spring scour no longer opens colonization sites; however, these sites now experience longer periods of inundation stress. On the terrace, the introduction of reed canarygrass has prevented normal succession to forest in the agricultural field, which remains open. Additionally, reed canarygrass is extending into the forest areas along its edge. (B) Pre-dam composition varied along a topographic gradient: Species requiring open sites and tolerant of flooding were found on the floodplain, whereas more shade-tolerant species occurred on the infrequently flooded, low-light environments of the post-dam floodplain.

inate the sapling stratum, but neither is ideally suited to eventually assuming canopy dominance under the post-dam regime of flood stress and shade. As American elm seedlings mature, they become susceptible to Dutch elm disease; ash rarely matures beneath closed canopies (Burns and Honkala 1990). In contrast, the nonnative and invasive plants that have recently become important constituents of the understory, such as the expanding colonies of Japanese knotweed, appear to be among the plants best suited to this newly established stress regime. Beyond their ability to persist in stressed environments, these species form dense stands that inhibit regeneration by others (Seiger 1992).

In the terrace communities, the near-elimination of flooding has coincided with a period of increased canopy-gap formation. Successional recovery of these former agricultural fields has proceeded to a point where some century-old members of the original cohort are beginning to die, opening individual canopy gaps. Standard models of successional dynamics (e.g., Oliver and Larson 1996) suggest that shade-tolerant individuals from the understory grow to fill these gaps. This is occurring in the terrace forest, where basswood and black maple are found in all size classes, suggesting that this small stand is capable of maintaining its present composition (Figure 10A). In contrast, the old field shows little sign of successional replacement. Vegetation that colonized this patch upon its abandonment has simply matured: The hawthorns present in the 1939 photograph are the same ones present today, with no further invasion into the surrounding reed canarygrass. Reed canarygrass was probably planted as forage in this old field during the early 1900s, following reforestation of the upstream terrace patch, since the dense colonies it forms preclude the establishment of competing plants (Barnes 1999; Lyons 2000). Such inhibition of succession has clearly occurred in the old field (Figure 10A). Similarly, the larger expanse of edge forest shows little sign of successional maturation, with a distinct boundary remaining between the terrace forest and the encroaching old field. The numerous and often large gaps opened by the loss of mature American elms have become occupied particularly by shade-intolerant species. In addition to trees such as bitternut hickory and slippery elm, species dominating many of these gaps include hawthorn, multiflora rose, and reed canarygrass.

The impact of the Allegheny River on Crull's Island vegetation can be separated into two dimensions of successional control: disturbance and stress (Figure 10A). In natural riparian zones, the two are correlated: frequently flooded sites are also those with the most severe disturbance. Tree species adapted to these habitats (e.g., wil-

low and silver maple) capitalize on the temporary abundance of resources such as light while tolerating flood stresses. The order of species along this region's typical natural riparian gradient—from sites adjacent to the stream to those on upper terraces (e.g., Hupp and Osterkamp 1985)—thus coincides with the diagonal from upper right to lower left on Figure 10B. Succession is often truncated by disturbance on floodplain sites, conferring few advantages on longer-lived competitive species that both regenerate in shade and endure flood stresses. In these natural sites, disturbance impacts override those of stress during peak flows—eliminating, rather than simply stressing, the vegetation. Successful competitors in this new post-dam floodplain environment must be tolerant of both shade (due to limited disturbance-generated canopy openings) and extended periods of inundation—conditions unlike those in this region's natural settings. Although the species common to terrace habitats (e.g., black maple, basswood) regenerate and compete successfully in shaded conditions while tolerating short periods of flooding, these species are rarely found in settings with higher levels of flood stress (Hupp and Osterkamp 1985; Burns and Honkala 1990). Thus, the direction of environmental change on the floodplain (Figure 10A) cuts across the grain of the normal riparian gradient to conditions of low light and high stress to which few tree species are adapted.

With the introduction of stress as a separate dimension of successional control in the post-dam landscape, the intermediate-disturbance hypothesis is unable to account for the impact of modified hydrology on the species dynamics of the Crull's Island floodplain. Interpreted at the landscape scale, this hypothesis suggests that spatial and temporal variability in disturbance creates patches of varying age, thus maintaining a diversity of sites suitable to a variety of life history strategies (Ward 1998). Since the model assumes a single dimension of vegetation succession, from disturbance-favored to competitive species, it predicts that a lack of disturbance will produce a decline in early successional landscape patches and a corresponding increase in late successional patches. Species diversity should concomitantly decline as ruderal habitats diminish. Our results in this modified riparian corridor show that patch ages are indeed increasing, but both ruderal and competitive tree species are becoming increasingly excluded by stress-tolerant plants. Grime's (1979) triangular model of successional life-history strategies similarly incorporates stress along with disturbance and competition, although our results suggest that in riparian settings it is necessary to distinguish between stresses—particularly those of shade and flooding—that involve different adaptations (Jones et al. 1994).

Nonnative species are successfully colonizing the modified floodplains of the Allegheny Islands Wilderness. Although often interpreted as benefiting from increased human disturbance in riparian settings (Nilsson et al. 1989; Pyle 1995; Planty-Tabacchi et al. 1996), exotic species appear to be particularly responsive to the stress regime maintained on these floodplain sites. Thus, regeneration strategies are of primary importance in determining the current and future successional dynamics here. Those species that can reproduce within the constraints of persistent moderate flows and the shade of established canopy will succeed. The primary invasives on Crull's Island, particularly Japanese knotweed and reed canarygrass, reproduce vegetatively through the spread of rhizomes (Seiger 1992; Lyons 2000), a characteristic well suited to stressful environments (Grime 1979). Once established, these nonnatives strongly preclude establishment by other species.

Modifications of the environmental context have also favored reed canarygrass on the terrace, significantly affecting post-dam dynamics of these patches (Figure 10A). While development of these terrace patches is largely a response to the disturbance initially caused by agricultural clearing, typical patterns of old-field succession have only occurred within the forest patch. There, shade tolerant species dominate, as would be expected in this relatively low-disturbance, low-stress setting. The incidence of disturbance (cultivation) has similarly diminished in the old field, but rather than competition focusing on light, reed canarygrass has forced the competition belowground. Persistent moist conditions—particularly such as those typical of the post-dam period—favor production of dense, impenetrable mats of this species (Lyons 2000). Its expansion into portions of the edge habitat created by large American-elm canopy gaps suggest that this exclusion of tree regeneration will not only persist, but increase over time. As on the floodplain, the life history characteristics of nonnative plants appear best suited to exploit the novel regime of disturbance and stress.

Conclusions

The forest of Crull's Island has been largely perceived and portrayed as old-growth, valued and managed as a riparian community preserved from the effects of human influence (Wiegman and Lutz 1988; Smith 1989; ANF 1996). The results of this investigation indicate that this site is deeply shaped by human activities, particularly the impacts of past agricultural use, the altered hydrology of the Allegheny River, and the presence of introduced species. As a consequence, the ability

of this site to support plant communities representative of the native Allegheny River vegetation has diminished.

While the protection of habitats representing all components of the landscape is crucial to the maintenance of biodiversity (Noss, LaRoe, and Scott 1995), proper understanding of the history and dynamics of preserved natural areas is equally vital. The results presented here demonstrate that preserves do not develop in isolation: This island, while made off-limits to direct human manipulation, remains embedded in a stream of anthropogenic modification. Similarly, it cannot be assumed that successional recovery of previously modified sites (such as abandoned old fields) will return to a state comparable to the predisturbed condition. Alteration of both the prevailing disturbance regime and the landscape context of preserved areas changes their vegetation dynamics and, as a result, their species composition.

The extent of anthropogenic influence on the origin and dynamics of forested landscapes throughout the eastern United States is often unrecognized by the public but increasingly demonstrated by reconstructions of landscape history (e.g., Whitney 1990; Nowacki and Abrams 1994; Cowell 1998; Foster, Motzkin, and Slater 1998; Motzkin et al. 1999). While management of river systems has begun to account for impacts on riparian ecosystems (Sparks, Nelson, and Yin 1998; Graf 2001), few simple remedies exist. In the case of Crull's Island, floods large enough to disturb the floodplain forest are unlikely to be permitted due to their adverse economic impacts. Moreover, were characteristics of the pre-dam flood regime restored, destabilization of the now-established floodplain community would require disturbances of extreme severity. Similarly, direct manipulation of the vegetation is not permitted due to the island's wilderness designation and perception as natural (ANF 1996). Were attempts to control invasive species on the island made, the prime obstacle to their long-term removal would be the persistence of conducive habitats created by anthropogenic change. These dilemmas suggest that greater recognition of the extent to which direct and indirect environmental modifications penetrate the boundaries of conservation areas must inform the managerial goals of biodiversity preservation.

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