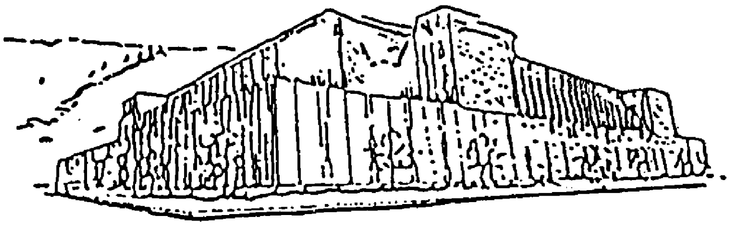
1997

The process of mid-channel alluvial island formation as inferred from plant distribution patterns on islands of the Swan River northwest Montana

Michael S. Cooperman
The University of Montana

Recommended Citation

Cooperman, Michael S., "The process of mid-channel alluvial island formation as inferred from plant distribution patterns on islands of the Swan River northwest Montana" (1997). *Graduate Student Theses, Dissertations, & Professional Papers*. 6939.
https://scholarworks.umt.edu/etd/6939



THE PROCESS OF MID-CHANNEL ALLUVIAL ISLAND FORMATION AS INFERRED FROM PLANT DISTRIBUTION PATTERNS ON ISLANDS OF THE SWAN RIVER, NORTHWEST MONTANA.

by

Michael S. Cooperman
B.S. Tufts University, 1991
presented in partial fulfillment of the requirements
for the degree of
Master of Science
The University of Montana
1997

Approved by:

Chairperson

Dean, Graduate School

12-19-97

Date

Cooperman, Michael S., M.S., September 1997 Organismal Biology and Ecology

The process of mid-channel alluvial island formation as inferred from plant distribution patterns on islands of the Swan River, northwest Montana.

Director: Carol A. Brewer

The pattern of primary succession on fourteen mid-channel alluvial island of the Swan River was studied to evaluate a model for the process of river island development. At the scales of the entire basin and within representative river reaches, tree and shrub species were organized in a linear gradient of seral stages. Pioneering species (i.e., *Populus trichocarpa* Torr. & Gray and *Salix exigua* Nutt.) were most abundant at the downstream ends of the islands. Early seral species (*Alnus tenuifolia* var. *incana* Nutt. and *Salix candida* Fluegge) were most abundant in the middle of the islands. Late seral and climax species (i.e., *Picea engelmannii* Parry ex Engelm. and miscellaneous fruiting shrubs (including *Rubus idaeus* L. and *Rosa* spp.) were most abundant at the upstream ends of the islands. At the scale of individual islands, there was high variability in tree and shrub distribution patterns. Islands in the reach of the smallest catchment area had more late seral species than islands in reaches with larger catchment areas. Islands in the reach with the largest catchment area were uniformly dominated by pioneering species. It appears that an important period for tree germination were 1978-1980. The lowest peak discharge volume on record for the Swan River was in 1978. There was no correspondence between most abundant plant species at a given location and surficial sediment types.

These results suggest that basin scale forces (i.e., fluvial dynamics) exert primary control over the development of plant communities on river islands, but that site-specific influences (i.e., local channel morphology, amount and organization of large woody debris) can modify basin scale forces. Furthermore, based on the linear gradient of seral organization, these results suggest that mid-channel alluvial islands grow incrementally, where each increment has a unique age and collection of edaphic and hydraulic conditions. The addition of new increments is probably related to flood deposition of alluvial sediments.

Table of Contents

Abstract....................ii

Table of Contents....................iii

List of Tables....................v

List of Figures....................vi

Acknowledgments....................viii

Chapter

I Literature review.

Introduction....................1

Ecological Significance of Alluvial Islands....................2

Origin of Alluvial Islands....................4

Evolution of an Alluvial Island from a Gravel Bar....................8

Role of Hydraulic Connectivity and Edaphic Condition in Structuring Plant Communities....................10

Patterns of Vegetation of Gravel Bars and Islands....................15

Other Examples of Primary Succession, and the Plant Characteristics that Dictate Seral Role....................18

Conclusions....................23

Literature Cited....................25

II Plant Distribution Patterns on Alluvial Islands of the Swan River, Northwest Montana, and the Link to Fluvial Dynamics

Introduction....................31

Materials and Methods....................40

Results....................51

Discussion....................63

Conclusions..80
Tables...81
Figures 88
Literature Cited 131

III Reading an Island: The Interplay of Physical and Biotic Forces..........136
Bibliography..143

Appendicies

A. Equations...144
B. Sketches of Study Islands and Reaches....................................146
C. Dendrochronology Investigation Results...................................155
D. Soil Profiles and Photographs...160

List of Tables

2.1. Principle and alternative hypotheses..81

2.2. Description of tree species occuring on Swan River islands.........................82

2.3. Morphological features of study islands..84

2.4. Shrubs occuring on islands of the Swan River...85

2.5. Number of occurances as most abundant tree or shrub per surficial soil type......86

2.6. Percent similarty results..87

C1. Location, species, and age of adult trees (n=67)....................................155

C2. Mean sensitivity results (n=21)...156

List of Figures

2.1. Key 88
2.1. ABC. Hypothesized process of island development....................89
2.2. Hypothesized structure of a mature island....................90
2.3. A recently emerged gravel bar formed downstream of a piece of large woody debris 91
2.4. A gravel bar in the initial stages of colonization by plants....................92
2.5. Sediment rich flood waters inundate and island surface....................93
2.6. A river island at low water....................94
2.7. Map showing location of Swan Lake and the Swan River sub-basin in the Flathead River catchment basin in Montana, U.S.A. and Bristish Columbia, Canada....................95
2.8. Swan River Basin....................96
2.9. Overview of the Swan River and two study islands....................97
2.10 AB. Relative abundance of the principle tree species at the whole basin scale....................98
2.11 AB.Density of trees at the whole basin scale....................100
2.12 ABC. Relative abundance by lifestage....................102
2.13 AB. Mean basal area of con-specifics at the whole basin scale.............. ..103
2.14 AB. Percent basal area at the whole basin scale....................105
2.15 AB. Importance values at the scale of the whole basin....................1107
2.16. Relative abundance of principle tree species at the whole basin scale arranged by distance from the heads of the islands....................109
2.17 ABC. Relative abundance of principle tree species by catchment area....................110
2.18 ABC. Density of principle tree species by catchment area....................111
2.19 ABC. Mean basal area of con-specifics by atchment area....................112

2.20 ABC. Percentage of basal area of principle tree species by catchment area.......113
2.21 ABC. Importance values of principle tree species by catchment area.............114
2.22 ABC. Relative abundance of principle tree species by surface area...............115
2.23 ABC. Densities of principle tree species by surface area..........................116
2.24 ABC. Percentage of basal area of principle tree species by surface area..........117
2.25 ABC. Importance values of principle tree species by surface area.................118
2.26 ABC. Mean basal area of principle tree species by surface area..................119
2.27. Relative abundance of principle tree species on individual islands ordered by surface area...120
2.28. Shrub patterns at multiple spatial scales......................................122
2.29 ABC. Abundance of shrubs at the whole basin scale..............................124
2.30 AB. Abundance of shrubs in the reach with the smallest catchment area.......128
2.31 AB. Abundance of shrubs in the reach of medium catchment area.............129
2.32 AB. Abundance of shrubs in the reach with largest catchment area.............130
B-1-B-8. Sketches of study islands and reaches..146
C.1. Distribution of tree ages on fourteen islands of the Swan River (n=67)...........157
C.2. Tree ages by distance from the tails of islands.......................................158
C.3. Mean sensitivity values by distance from the tails of islands.......................159
D.1-5. Soil profiles...160
D.6. Soil column from a study island...165
D.7. Soil profile of a river island expoed at a cut-bank..................................160

Acknowledgments

This study was funded in part by NSF Grant number NSF-OSR-95540 to Jack Stanford. Dr. Chris Frissel and Dr. Marc Hendrix provided valuable insight and guidance during this project. I greatly appreciate their serving on my thesis committee. I sincerely appreciate the advice and assistance provided by the Yellow Bay Biological Station faculty, staff, and students, and Andy Sheldon and his "Wet Lunch Group." Taxonomic assistance was provided by Bill Thompson, James Hall, Diane Pavek, and Brad Cook. Clark Watry and Eric Bergman assisted in the field. I also thank Tom Thompson for advice on data analysis. Joe Yates and Glenn Gray provided valuable information on the history and ecology of the Swan Valley. Dan and Sheri Burden provided access across their property to several study sites, saving me considerable energy and time. Finally, I wish to thank Dr. Carol Brewer for doing all the things an advising professor does for their students and for giving me enough slack rope so I could hang myself, but never allowing me to choke. Dr. Brewer opened my eyes to the wonderful world of plants.

The number and constant succession of these islands, all green and richly wooded; their fluctuating sizes, some so large that for half an hour together one among them will appear as the opposite bank of the river, and some so small that they are mere dimples on its broad bosom; their infinite variety of shapes; and the numberless combinations of beautiful forms which trees growing on them present: all form a picture fraught with uncommon interest and pleasure.

Charles Dickens (after Malanson 1992)

This day I completed my thirty first year, and conceived that I had in all human probability now existed about half the period which I am to remain in this Sublunary world. I reflected that I had as yet done but little, very little, indeed, to further the happiness of the human race or to advance the information of the succeeding generation. I viewed with regret the many hours I have spent in indolence, and now soarly feel the want of that information which those hours would have given me had they been judiciously expended. But since they are past and cannot be recalled, I dash from me the gloomy thought, and resolved in future, to redouble my exertions and at least indeavour to promote those two primary objects of human existance, by giving them the aid of that portion of talents which nature and fortune have bestoed on me; on in future, to live for *mankind*, as I have heretofore lived *for myself.*

Meriwether Lewis, Sunday, August 18th, 1805.

CHAPTER I

LITERATURE REVIEW

INTRODUCTION

The purpose of this study was to develop and test a conceptual model of how emergent mid-channel alluvial islands are formed. The model is largely dependent upon interpretation of the distribution pattern of trees and shrubs on river islands. Numerous studies on plant distribution patterns within aquatic-terrestrial transition zones (i.e., floodplains, riparian zones, back waters, abandoned river channels and dead arms, and/or alluvial islands; Décamps 1996) have demonstrated that plants can serve as "functional describers" of site conditions (Amoros et al. 1986), as plant species are differentially distributed across an alluvial landscape in response to a complex gradient of environmental conditions including the physical and chemical characteristics of alluvial sediments, and the level of connectivity between a land surface and a river (Hupp and Osterkamp 1985; Harris 1986). Random events also contribute to structuring plant communities on alluvial landforms (Baker 1990). Several researchers have documented that the edaphic and hydraulic characteristics of an alluvial landform often change predictably as the landform matures. Older land surfaces typically have smaller median grain sizes (Brierley and Hickin 1992), higher nutrient levels (Kalliola et al. 1991), less frequent and less intense periods of inundation (Chauvet and Decamps 1989), and a host of other differences, relative to younger land surfaces within the same drainage basin. This suggests that alluvial surfaces of different ages will support different plant communities.

The proposed model of emergent island formation is based on the principle that sediment movement in river systems is controlled largely by discontinuous and unpredictable flood events, i.e. a flood-pulse (Junk et al. 1989). This creates the potential for a distinct "banding" of sediments, where each band has a unique age, and therefore, potentially, a unique collection of edaphic and hydraulic conditions. Based on the presence of such characteristic banding, I hypothesized that each sediment "band" would support a distinct vegetation community type. Moreover, I predicted vegetation patterns could be used to illustrate the process of emergent island development because plants serve as a living record of landform history (e.g., plants are a functional describer of site conditions that vary predictably with time since deposition). The apriori prediction was that mid-channel alluvial islands grow incrementally because of the deposition of new sediments on the downstream side of existing islands by floods. This process of incremental island growth would be reflected in the vegetation patterns of these islands as a successional gradient from late seral species on older sediments that are closer to the upstream end of islands (island head) to pioneering species on the newest sediments at the downstream end of each island (island tails). This model of island development is shown in Figures 1 and 2, Chapter 2. Furthermore, based on the premise that island development is a response to a combination of sediment dynamics and hydraulic conditions that are both initiated and regulated by flood events (Green 1982; Abbe and Montgomery 1996), I hypothesized that development of mid-channel alluvial islands is controlled by fluvial dynamics originating at the scale of the entire drainage basin. This suggests that all islands within a basin are developing in response to similar forces, and not to unique site-specific conditions. For these purposes, I defined an island as "emergent" if it was formed by the deposition of sediments within the active river channel and then emerged above the water level of the river. Islands formed by the capture of a portion of the floodplain, for example by meander loop cut-off, were not considered emergent islands, and therefore excluded from this analysis.

Ecological Significance of Alluvial Islands

Only a limited amount of research has been done on alluvial islands, despite their prominence within some river systems and their ecological importance. Significant gaps exist in the understanding of how islands form and the forces that regulate their continued development.

Islands play several ecological roles in riverine systems. By retaining sediments and large organic matter, alluvial islands help tighten the "nutrient spiral" of a river system (Gregory et al. 1991). Islands may be temporary "sinks" for limiting compounds such as organic carbon, nitrogen, and phosphorous, which otherwise would be transported down-channel and therefore lost to the local system (Malanson 1993). Sediments not sequestered into alluvial landforms either are transported downstream or they may remain within the active river channel, potentially clogging the interstitial spaces that exist between the cobbles and gravel of the river bed and/or causing river bed aggradation. Interstitial spaces are habitat for a broad array of aquatic invertebrates, which, in turn, are food for a variety of fish and bird species. Excessive loads of free sediments within an active channel may negatively impact fish reproduction by trapping and suffocating eggs and fry that develop within the interstitial spaces of clean river gravels (Hartman et al. 1996). River bed aggradation increases the likelihood of flooding (Coleman 1969; McCarthy et al. 1992), and may limit exchanges between surface waters and hyphorheic waters (Creuze Des Chatelliers and Reygrobellet 1990).

Plants on alluvial islands may filter contaminants suspended in the water column, as has been documented for floodplain vegetation (Gregory et al. 1991; Décamps 1996). Moreover, island vegetation also provides habitat and food for diverse mammalian and avian communities (Johnson 1994). Through leaf litter, inputs of woody debris, and insect fall, islands provide inputs of organic matter and nutrients to many aquatic systems (Swanson and Franklin 1992; Ward and Stanford 1995b; Wallace et al. 1997). The overhanging branches of island vegetation shade portions of the river channel, potentially providing thermal refugia for aquatic organisms during low water conditions in late summer months and protection from overhead predators.

Because islands are terrestrial habitats fully contained within an aquatic medium, they provide several beneficial services to the riverine ecosystem that riparian zones and floodplains may not. Fish and other organisms can shelter from high velocity flood waters in areas of reduced river current created by islands, such as where flow divergence occurs at the upstream portion of an island, within the eddy of re-circulating currents at the downstream end of an island, and within the numerous small eddies that form behind the vegetation of an inundated island (Triska 1984). Also, many organisms (i.e., juvenile fish, invertebrates) can shelter within the interstitial spaces common throughout the gravel apron that surrounds river islands (Beschta and Platts 1986).

Surplus energy from river currents is dissipated as the current erodes the banks of an island. Without such roughness features within the active channel, the energy of the current would be directed at either the river bottom or floodplain. Down-cutting of the river channel may result in a lowering of the regional watertable, as happened on the Missouri River of eastern Montana (Scott et al. 1996). Floodplain erosion may cause significant damage to local human and natural infrastructure.

Sometimes islands become part of the floodplain, creating a habitat patch of unique origin, age, sediment condition, and successional stage (Abbe and Montgomery 1996). This happens when a river channel relocates. As an island is incorporated into the floodplain, the abandoned channel often maintains a measure of connectivity with the river. If subsurface flow upwells within the abandoned channel, it may develop into a floodplain springbrook or backwater zone (Keller and Swanson 1979). Both of these are important juvenile fish rearing sites (Cavallo 1997).

River islands become even more important in mainatining the functional integrity of a river system when anthropogenic influences isolate a river from its floodplain. River dyking, snag removal, floodplain development, and de-watering are just a few examples of how anthropogenic effects reduce the level of connectivity between a river and the floodplain (Sedell and Froggatt 1984; Ward 1989; Ward and Stanford 1995a). It is more difficult to sever the connectivity between a river and an island.

Origin of Alluvial Islands

While data on the specific mechanisms of mid-channel alluvial island formation are relatively scarce, existing studies are consistent in their description of the process. Basically, there are two ways islands form. In one scenario, a secondary channel diverges from the main channel, encircling a portion of the floodplain before returning to the main river. A meander loop cut-off via formation of an over-flow chute is an example. A second mechanism of island formation is when a gravel bar within the boundaries of the active channel emerges above the water level of the river as a result of sediment deposition.

Emergent gravel bars form in two ways. The first mechanism relies on the interaction of zones of scour and deposition at high flow levels. In base flow conditions, pools are sites of flow-pathway divergence and therefore sediment deposition. Riffles are sites of flow convergence and therefore erosion. When flow levels approach bankfull, the relationship reverses, and sediments are scoured from pools and deposited on the crest of downstream riffles (Keller 1971 as cited in Green 1982). As the river level falls, the top of such riffles may emerge as a gravel bar .

A second method of mid-channel bar formation starts when a piece of large woody debris (LWD), usually a tree trunk with an attached root-wad, lodges within the river channel (Keller and Swanson 1979; Nakamura and Swanson 1993; Abbe and Montgomery 1996). The root-wad serves as a barrier to flow, thus the flowing water must diverge around the obstruction. At the point where the current diverges around the root-wad, current velocity decreases and sediment deposition can occur (Abbe and Montgomery 1996).

The ultimate size of gravel bars formed behind LWD accumulations is linked to the size of the wood jam, the volume of discharge during peak flow events over the lifespan of the wood jam, and the sediment supply rate (Abbe and Montgomery 1996). Because the size of the eddy that forms downstream of a large woody debris jam is proportional to discharge (Rubin et al. 1990), larger peak flow events produce larger gravel bars. Furthermore, recruitment of new woody debris into an existing jam usually occurs only during high water events, since many alluvial rivers do not have enough energy to move LWD at base-flow levels. High discharge levels are also important in supplying the sediments that are incorporated into the developing gravel bar. Thus, there is a synergistic relationship between recruitment of woody debris, sediment supply rates, and the rate of gravel bar growth. As more wood is accumulated into a jam, the gravel bar grows larger. The larger the gravel bar grows, the more wood it can trap (Malanson and Butler 1990). This suggests that sediment accumulation on a gravel bar is not continuous, but instead is an incremental process tied to the arrival of new wood pieces to the woody debris jam, and the recurrence of significant high water events. Both of these processes of mid-channel gravel bar formation occur when river discharge volumes approach or exceed bankfull volume. In temperate zone rivers not significantly impacted by civil engineering works, bankfull discharges occur with an average recurrence interval of 1.4 to 2 years (Leopold et al. 1964).

Abbe and Montgomery (1996) also report progressive colonization by vegetation on a developing gravel bar downstream of a large woody debris jam. Moreover, they suggest tree height decreases as one moves downstream on a gravel bar (or developing island), but they did not study this pattern specifically.

The relationship between gravel bar formation and bankfull discharge is nicely summarized by the Flood-Pulse Concept (Junk et al. 1989), which emphasizes the primary role of hydrology in structuring floodplain biota (Ward and Stanford 1995b). The Flood-Pulse Concept is quite similar to the "Theory of Kinematic Waves" (Langbien and Leopold 1968 as cited in Green 1982). The Flood-Pulse Concept states that at flow levels less than bank-full, the sediments of the river bottom and banks are relatively stable; however, as flow levels approach the bankfull volume, the bed and sides of gravel bed rivers are mobilized (Buffington 1995 as cited in Abbe and Montgomery 1996). The flood pulse is that period of time when the majority of sediments of the river system are in transport. More than 95% of the total sediment load moved by a river during a one year period may move during less than 5% of the year (MacDonald and Hoffman 1995).

Sediments transported during the flood pulse typically do not reach their ultimate destination (i.e., the ocean or inland lake) the first time they are entrained by the current. Instead, each individual particle moves in pulses. Particles maybe incorporated into the floodplain, gravel bars or islands (Kelsey et al. 1987 as cited in Malanson and Butler 1991), where they are stored temporarily, sometimes for thousands of years, until they are again entrained and resume the journey downstream. Thus, there is a recurring cycle of capture and release (Nakamura and Swanson 1993).

One example of how rapidly local deposition can build an emergent bar or island was reported by Shull (1922). Following the grounding of a barge in the Mississippi River, local deposition occurred immediately downstream of the barge. By the sixth year, enough sediment had accumulated for a man to relocate to the developing island and to start a farm. Unfortunately for the farmer, the island was inundated by a flood the following year which buried his bedroom up to the level of his bed springs in silt. The man promptly left the island.

There is little relationship between the size of sediment particles transported and river discharge. Instead, research on gravel bed rivers has shown that the majority of sediment size classes available within a river will be entrained within a relatively narrow band of flow volumes (Andrews 1983). This suggests that either the bed of a river is relatively stable, or almost all size classes of sediments are in motion together. During transport, hydraulic sorting (smaller particles are separated from larger particles) can occur, such that smaller sediments are preferentially deposited on the highest portion of a developing gravel bar or island, while larger sediments do not reach these sites, as more energy is required to transport larger particles (Miller and Schroeer 1987). Coarse, large sediments are more likely to accumulate at low elevations (e.g., along the river bed immediately down channel from topographic high points that serve as barriers to flow). Hydraulic sorting can account for both upward fining (i.e., vertical accretion) and longitudinal (i.e., down channel) particle grading (Allen 1965; Smith and Smith 1980; Brierley and Hickin 1992). Regardless of the proximal cause of bar formation, the emergent bar formed typically will produce an elliptical bar, notably longer than wide (Green 1982; Abbe and Montgomery 1996). Eventually, either of these bar formation mechanisms can lead to island development, providing the sediment surface reaches an elevation greater than the bankfull level of the river channel, and a host of other conditions are meet (Kellerhal et al. 1976; Abbe and Montgomery 1996).

At the same time that particles are being deposited, erosion also can occur on a portion of a gravel bar or island. Through bank undercutting, dissection of the bar tops by distinct overflow channels, or planation of island tops by uniform, shallow, rapid flow, sediments can be entrained and transported downstream (Blodgett and Stanley 1980 as cited in Green 1982).

A final point worth noting is that while the research results and examples discussed above focus on the deposition of alluvial sediments downstream from an obstruction to flow, this is not always the case. The gradient of the river bottom and valley floor, the current velocity, and the volume of sediment transported by a river determine whether or not deposition will be upstream or downstream from a barrier to flow. In channels with moderate to low gradients, deposition tends to be downstream of barriers to flow. In steeper channels (i.e., first to third order mountain streams) or in rivers of near zero gradient (i.e., coastal plain rivers), sediments typically are stored upstream of barriers (Keller and Swanson 1979).

Evolution of an Alluvial Island from a Gravel Bar

Regardless of the specific mechanism of gravel bar formation, eventual island formation requires colonization of a gravel bar by vegetation (Green 1982). Establishment of vegetation initiates a number of processes that are vital to island development. First, developing root layers of colonizing plants stabilize the bar, making it more resistant to erosion (Maddock 1972; Keller and Swanson 1979; Beschta and Platts 1986; Kalliola and Puhakka 1988). For example, Smith (1976) found that river bank sediments with 16-18% roots by volume were > 20,000 times more resistant to erosion than comparable bank deposits devoid of roots in anastomosing reaches of the gravel and cobble bed Alexandra River in Banff National Park, Alberta, Canada.

Secondly, the above ground structure of plants (e.g., trunks, branches, leaves) contribute to island development in several ways. Plants increase the roughness of the land-surface (Johnson 1994), which accelerates the rate of sediment deposition by slowing the velocity of the floodwaters that periodically inundate the gravel bar or island. Often, fine particles that normally would remain in suspension are "filtered" out of the water column (Beschta and Platts 1986; McCarthy et al. 1992). Islands originally are formed by the deposition of predominantly coarse particles (cobbles, gravels, and sands) transported as bedload, while the filtering effect traps finer particles such as fine sand, silts, and clay. The net effect is a reduction in the median grain size of the land-surface. Church (1995) reported that newly created gravel bars in the Peace River of Canada were quickly colonized by cottonwoods (*Populus balsamifera* Michx.) and various annuals. Fine particles were trapped and held within the cottonwood stands, with a resulting reduction in the median particle size of the bars.

Reduced grain size often is associated with other changes in the composition of sediments on developing islands, including increased levels of nutrients and organic matter, reduced porosity, and elevated levels of soil moisture and water retention capacity. Also, as more sediments are filtered out of the water column, the land-surface elevation rises higher above the water level (Strahan 1984 as cited in Harris 1987; Church 1995). This increases the depth to the water table of the land-surface (Schnitzler 1997), and reduces the level of connectivity between the river and the land surface. These changes promote the establishment of more plants, and the dominant species change. A positive feedback loop develops as additional plants further increase the roughness coefficient of the land surface, resulting in enhanced filtering of finer and finer particles (Osterkamp and Hupp 1984). Also, slower water velocities during peak flows are less erosive than fast moving water, so the land-surface is more protected from flood scour by the developing plant community (Bornette et al. 1994; Dietz (no year provided) as cited in Malanson 1993).

A third way that vegetation influences the development of islands from gravel bars is through the contribution of organic matter to the sediments (Abbe and Montgomery 1996). An initial phase of soil development is the formation of a humus layer as fallen leaves, twigs, flowers, and fruits begin to decay (Longwell and Flint 1963).

Developing vegetation provides important habitat for wildlife, including perching locations for birds and shelter for rodents. Animals that feed on seed-bearing plants disperse seeds on developing islands (Willson 1993), and their metabolic wastes contribute to the nutrient content of the sediments.

The early growth of islands occurs mostly in two dimensions, longitudinally (parallel to current) and vertically. An island will not grow significantly wider until vegetation density and/or LWD volume increases along its flanks. Once sufficient structural complexity develops along the flanks of the island, current eddies can form and promote deposition on the sides of an island (Green 1982). Such localized deposition leads to lateral growth and a reduction in the length to width ratio. Mertez et al. (1996) hypothesized that length to width ratio may be used as a measure of the age of an island.

Role of Hydraulic Connectivity and Edaphic Condition in Structuring Plant Communities

Hydraulic connectivity is a measure of the level of interaction between an alluvial landform and the river that created it. High connectivity implies frequent inundation by relatively high energy flood waters; low connectivity implies only sporadic flooding by low energy flood waters. The level of hydraulic connectivity usually is inversely related to the elevation of the land surface above the base flow level of the river. As elevation increases, connectivity decreases (Pautou and Decamps 1985).

Increases in elevation of a land surface over the river channel occur through sediment deposition on top of an existing alluvial surface or down-cutting of the channel into the river bed. An example of the former is the filtering of fine particles and resulting land surface aggradation (Johnson 1994), and an example of the later is the creation of a river terrace by channel down-cutting (Hupp 1997). Typically, elevation, and therefore the level of connectivity, is proportional to the age of the land surface (i.e., time since deposition; Friedman et al. 1996). Younger land forms are more connected to their associated rivers.

Many changes in the physio-chemical properties of alluvial sediments have been shown to co-vary with level of connectivity. Areas of low connectivity typically have smaller median particles sizes (Bornette and Amoros 1996), higher surface moisture levels (Rostan et al. 1987), and higher organic and nutrient concentrations (Rostan et al. 1987). Soil pH, density, and cation exchange potential also change as a function of connectivity (Kalliola et al. 1991).

Many studies have implicated the co-varieties of hydraulic connectivity, sediment condition, and depth to ground water, either singularly or in various combinations, as the primary structuring agent of plant communities on alluvial landforms (Osterkamp and Hupp 1984; Hupp and Osterkamp 1985; Baker 1989; Tabacchi et al. 1996; Friedman et al. 1996). Dirschl (1972), using principle component analysis, concluded that soil moisture, nutrient status, and soil pH were the principle parameters explaining vegetation patterns of the Saskatchewan River delta. Fonda (1974), after studying six different fluvial surfaces (gravel bars, near-channel flats as a portion of the active floodplain, and four different river terraces) of the Hoh River, Olympic National Park, WA, concluded soil formation and development were the greatest environmental events taking place in relation to forest succession. Soils on young land surfaces (gravel bars and near-channel flats <50 yr old) were scarcely differentiated into horizons. These surfaces were dominated by *Salix* and herbs. Older near-channel flats (50-100 yr old) had emerging B horizons. These surfaces were mono-cultures of *Alnus rubra* Bong. Terraces <400 yr old were dominated by *Picea spp.* and those >400 yr were dominated by *Tsuga spp.* Soil structure changed from single-grained stands on the youngest surfaces to subangular blocky with accumulations of clays on the older surfaces. Soil nutrient levels and soil moisture content were positively correlated with age of the land surface. Nanson and Beach (1977) reported increased concentrations of phosphate, nitrogen, sediment clay content, soil moisture, and organic matter content with increasing distance from the active channel on meandering river point bar deposits. Distance from the active channel co-varied with the age of the land-surfaces. Soil pH decreased along the same distance/time gradient. Strikingly similar patterns have been reported by Rostan et al. (1987), Kalliola et al. (1991), and Puhakka et al. (1992).

Nanson and Beach (1977) also found high fidelity between sediment conditions and plant communities on the point bars of the Peace River (Canada). Surfaces <20 yr old had no trees. Between 20 and 30 yr after formation, a balsam poplar stand developed. Fifty years after formation, meander bars were covered by a mixture of willows, poplars and alders. Spruce seedlings began to establish and poplar levels began to fall approximately 60 yr after bar formation. Between 100 to 200 yr after formation, spruce reached its highest densities. Similarly, Pautou and Decámps (1985) reported that certain alluvial plains plants showed high fidelity for specific soil conditions along the Rhöne River of France. Bornette et al. (1994) studied river side channels of varying levels of connectivity to the main channel of the Rhöne River of France. High-connectivity resulted in a coarser substrate and more pioneering plant species, compared to low-connectivity side arms. Low connectivity channels had thick layers of fine sediments and they supported plant communities with higher species richness and diversity. Because many plant species have high fidelity for a particular habitat type, Amoros et al. (1986) suggested plants can be used as "functional describers" of site conditions.

Studies by Pautou and Decamps (1985), Rostan et al. (1987), Chauvet and Decamps (1989), Bornette et al. (1994) and others support the idea of "fluvial reset". Fluvial reset occurs when frequent flooding leads to a slowing or reversal of the successional changes in vegetation from pioneering to late seral stages. Fluvial reset may be caused by removing nutrients and/or fine particles from the sediments and/or increased mortality of plant species not capable of surviving inundation.

Fluvial reset may be an important factor in the development of vegetation on riverine islands. For example, Auble et al. (1991) attributed the segregation of vegetation cover types of the riparian zone of the Black Canyon of the Gunnison River, CO, to a combination of inundation frequency and sediment particle size, which were co-variates. Clearly, physio-chemical conditions of sediments are linked to the connectivity of an island to a river, and together, these factors influence the species composition and plant distribution pattern across a fluvial landscape (e.g., Ellenberg 1988 as cited in Schnitzler 1997; Schnitzler 1997).

Despite the work on sediments, many studies have implicated hydraulic conditions alone as the principle structuring agent of plant communities. For example, Hupp and Osterkamp (1985) found that 92% of the plant species in Passage Creek Gorge, VA, showed a strong affinity for a single geomorphic landform type or two adjacent landforms. Each geomorphic surface had a unique level of hydraulic connectivity but all surfaces had similar size classes of sediments. Therefore, Hupp and Osterkamp concluded that in Passage Creek Gorge, plant distributions were controlled to a greater degree by hydraulic factors (e.g., flood frequency, duration, and intensity) rather than by sediment size class. Other workers (Sigafoos 1961 as cited in Hupp 1983; Harris 1986, 1987; Decamps et al. 1988; Hughes 1988) also point to the dominant influence of hydraulic forces.

The effect of flooding has been implicated as a causative mechanism for the zonation patterns of riverine wetland plants. Bornette and Amoros (1996) found that flood events were able to slow down, stop, or even reverse the successional pathway, principally through changing the dominant size of substrate through deposition or scour. Frequently flooded regions were held in an early successional state, while a reduction in flood frequency led to the development of a late seral/climax community with few of the early colonizing species. Whether or not intermediate levels of disturbance created maximum levels of species richness (i.e., Connell 1978) depended on whether the geomorphology of the site led to a reduced velocity of flood waters, thereby causing deposition. Deposition lead to higher species richness while scour resulted in lower species richness.

Sub-surface hydrology also has been identified as significant in structuring plant communities on alluvial surfaces. Frye and Quinn (1979) found depth to the water table, as well as depth and type of soil, best explained vegetation structure along the Raritan River of New Jersey. Neither flood frequency nor duration were good predictors of the distribution of tree species distribution along the Raritan. Data of Pautou and Décamps (1985) suggested the segregation of species within floodplain forests of the Rhöne River primarily depended on depth to the water table, the amplitude of its seasonal fluctuation, and substrate grain size.

At the scale of an entire river basin, current velocity, flood magnitude and frequency, and mean discharge may be important influences on species richness of riparian zones, suggesting that the structure of riparian zone plants derives from a combination of forces originating at the scale of the entire drainage basin and site specific conditions (Tabacchi et al. 1996; Nilsson et al. 1991). Hupp and Osterkamp (1985) also implicated drainage basin size as a significant influence on alluvial vegetation. This same study found depth to the water table insignificant in explaining vegetation patterns. Baker (1989) identified several important factors at the scale of the drainage basin which influenced distribution patterns of riparian species in several watersheds of western Colorado, including drainage basin area, topographic relief, elongation ratio, and drainage density (i.e., the length of stream channels per unit surface area) as important macro-scale variables.

Another large-scale influence on the structure of the riparian vegetation is climate. Lindsey (1961) examined fluvial, edaphic, and climatic conditions as well as flooding history. He concluded recent fluvial dynamics and regional climate were the principle agents structuring plant communities. Baker (1990) also implicated climate as a principle agent in plant distribution patterns, noting that while fortuitous soil conditions for cottonwood establishment in Colorado occurred roughly every two years (the same recurrence interval for bankfull flow), new age classes of cottonwoods were produced every five years, on average. The reason for the discrepancy, Baker argues, is that regional climatic conditions (timing of flood water recession, rainfall, and solar irradiance levels) were not appropriate for cottonwood establishment at the same time scale as soil conditions. Only in years when both edaphic and climatic conditions was a new year class of cottonwoods formed.

Patterns of Vegetation on Gravel Bars and Islands

During his investigations of sediments on four mid-channel alluvial islands in the Great Bend Region of the Wabash Valley, Green (1982) found consistent patterns in the stratigraphy of sediments amongst each of the islands. Each island was underlain by a basal deposit of coarse gravel and sand, overlaid by a layer of sand, and then capped with a surface of silt or silty sand. Each layer displayed a sequence of fining upwards as well as fining down-channel.

Green divided his islands into zones based on the following characteristic patterns of vegetation: 1) Gravel Aprons - vegetated by aquatic plants (i.e., emergent macrophytes); sediments were the coarsest of any island region; 2) Lower and Upper Emergent Zones - sparsely vegetated scrub trees and grasses; during high flow (up to bankfull) area between the lower and upper zone was subjected to intense scour and fill processes; and 3) Core

Area - heavily vegetated by trees, weeds, and grasses; inundation only occurred during large flood events. Based on his observations of island plant communities, Green (1982) wrote, "zonation of the plant species on the islands is clear and commonly striking, with an aquatic and emergent community of the apron, consisting of transitional plants, grading into the climax community of the core zone, consisting of a forested stand." However, Green did not discuss the pattern of the vegetation of the core area nor if the size of the core area was stable or variable (fixed, growing, or eroding).

Hupp (1983) studied species composition of plant communities on alluvial bars and islands compared to the floodplain of Passage Creek, VA. Species composition changed from predominantly herbaceous in the mid-channel regions, with replacement by shrubby and then woody species with increasing distance away from the active channel. The change in species composition mirrored changes in the destructive power of flood waters. The decline in the volume and velocity of flood waters with increasing distance away from the active channel was attributed to either loss of current energy at higher elevations, the buffering effect of intervening vegetation, or both.

Barnes (1985) evaluated population dynamics of woody plants on an island in the Chippewa River, WI. This island had a surface area of 48,000 m^2, and a maximum elevation over the baseflow river level of less than two meters. Historical records, aerial photographs, and elevation surveys showed that the island was growing incrementally. The upstream end of the island was the youngest portion of the island and had the lowest elevation; the downstream region was the oldest and had the highest elevation. The only variable significantly correlated with age in this study was elevation of the land surface. Overflow channels were frequent on the lower part of the island, but not the higher portion. *Salix interior* Rowlee (sand bar willow), a species capable of clonal reproduction, was common across the entire land-surface, but most abundant at low elevations, and it readily colonized recently deposited sediments or recently flood scoured sites. River birch (*Betula nigra* L.) and cottonwood (*Populus deltoides* Marsh) were the next most abundant species.

Both of these species can re-spout from stumps following flood damage. *Fraxinus pennsylvania* Marsh (green ash), *Acer saccharinum* L.(silver maple), and *Ulmus americana* L. (american elm) were restricted to older portions of the island. They are slower growing and more mesophytic than the willows, cottonwood, and birch, and can resprout from damaged stumps. A change in the age structure of populations of con specifics, from many young individuals to fewer older individuals, corresponded to an increased island age and surface elevation. The majority of ash, birch and cottonwood were in smaller size classes, while elm and maple had more individual sprouts in the larger size classes. The abundance of small individuals of ash, birch, and cottonwood was attributed to selective felling of larger individuals by beaver. Analysis of age structure revealed no continuous input of seedlings. Rather, it appeared seedlings established at irregular intervals as pulses of recruitment, probably when prevailing hydraulic and environmental conditions were appropriate. Barnes did not describe the trends in abundance and size of each species in terms of successional dynamics; however, because changes in species dominance paralleled the age/elevation gradient, seral succession seems likely.

MacBride and Strahan (1984) designed a study to identify the various factors that regulated the establishment and survival of woody riparian species on newly formed gravel bars in an intermittent stream in Sonoma County, CA. They found that sediment size class correlated best with species composition. Sediments of mean particle sizes of 0.2 to 1.0 cm supported *Salix* communities, while coarser sediments had *Baccharis viminea* L. Depth to the water table was of secondary importance.

In a study on the Middle Fork of the Flathead River, MT, Malanson and Butler (1990) examined the relationship between woody debris, sediment, and riparian vegetation on gravel bars. They determined that: 1) maximum differences between topographic high and low points averaged 100 cm per gravel bar; 2) overflow channels can dissect the surface of developing gravel bars at high flow levels; 3) sediment depth and organic content varied proportionately with elevation, probably due to flood frequency and/or magnitude; 4) organic content of the sediments also was positively correlated with distance from the head (upstream end) of the island and proximity to LWD jams; 5) plant diversity was positively correlated with distance from the head of the gravel bar and elevation and, therefore sediment depth and organic content. They found that sediment conditions varied along the length of the gravel bar, with the more developed condition (higher organic content, greater plant diversity, higher elevation, etc.) typically at the downstream end of the bar. They concluded that, "given the basic statistical relationships, it is clear that sediment, woody debris, soil, and vegetation do interact in affecting the episodic transport of sediment in subalpine rivers and the composition and cover of pioneer vegetation. No data are yet available, however, that would allow us to model the relationship in a way that would provide information on the temporal storage of sediment in vegetated gravel bars nor on the rate of succession."

In a companion study, Malanson and Butler (1991) used the same data set (Malanson and Butler 1990), to focus more closely on the floristic composition of the gravel bars. The two most dominant species (*Populus trichocarpa* T.&G.and *Salix spp.*) established on similar sediments, but they often grew in distinct patches. Evidence suggests this segregation is due to the timing of flood water recession and species-specific seed release. This work sheds additional light on our understanding of the forces that structure vegetation on islands by adding environmental stocasticity, such as founder's effect (Malanson and Butler 1991), to a list that includes numerous other parameters. Evidence on the role of environmental stocasticity (timing of flood water recession, drought, ice) in structuring alluvial land form plant communities also has been presented by Baker (1989); Melancon et al. 1981 as cited in Malanson 1993; and Kalliola et al. (1991).

Other Examples of Primary Succession, and the Plant Characteristics that Dictate Seral Role

Because studies on the patterns of plant colonization and development on emergent gravel bars and islands in rivers are scarce, additional insight on succession on new sediments comes from literature describing changes on analogous landforms such as point bars and glacier forelands (i.e., land recently exposed by glacial retreat). Point bars (also called scroll or meander bars) occur along the inside banks of curves in rivers. In these regions, sediments are deposited at the point where the deepest, fastest portion of the channel (i.e., the thalwag) moves away from one bank (the upstream end of the inside bank of the river bend) and crosses over to the outside bank of the river channel (the cut-bank). As the river channel slowly migrates across the floodplain, point bars are left behind. Over time, a chronosequence of abandoned bars may develop, such that bars close to the active channel are younger than bars further away. Thus, it is possible to use meander bar sequences to reconstruct successional changes.

Kalliola et al. (1991) presented a general view of primary succession on a chronosequence of meander bars based on work in the Amazon basin. The high portions of recently exposed meander bars were occupied by species that could reach these locations by seeds or vegetative means, and the most abundant colonizers were able to endure severe flood disturbance (e.g., deposition of several meters of sediment during their lives). Seedlings established on low points between successive meander bars crests were unlikely to survive their first year because of a combination of breakage and other physical stresses, excessive surface moisture, and potentially anaerobic soil conditions associated with prolonged inundation. Meander bars close to the river were dominated by juveniles of each species, and older bars further from the river channel had more adults. Diversity of woody species increased with increasing age of the point bar.

By comparing vegetation patterns of different river reaches in the Amazon basin, Puhakka et al. (1992) found that successional sequences on meander bars were much more distinct (clear zonation according to sediment age) than in either braided or anastomosed reaches. Two possible explanations are: 1) the sediments of braided and anastomosed river reaches typically deposited in gravel bars, islands, and levees are not arranged sequentially according to time since deposition; or 2) seral organization does exist, but the methodology used was not appropriate for detecting a pattern. This raises the interesting question of whether or not a more detailed study of these depositional bodies could detect seral patterns.

Each of the studies reviewed above implicate allogenic forces (i.e., forces originating outside of the habitat unit of concern) such as flood scour, deposition, and the resulting changes in edaphic conditions as the primary mechanism maintaining community structure. Autogenic forces (i.e., those originating internally to a habit unit) such as competitive interactions between individual plants also have been shown to be important in driving successional changes. For example, Chapin et al. (1994) tested the idea of facilitation, where one species modifies the environment in some way that improves site conditions for later successional species as the primary mechanism of succession on recently deglaciated forelands of Glacier Bay, AK. They chose glacier forelands because the newly exposed areas have low nutrient and organic content, sediments are principally coarse grained, and soil development (e.g., a humus layer) is typically absent. Interestingly, these conditions are quite similar to those of recent alluvial deposits. Moreover, the time since exposure of the land surface was well documented at Glacier Bay. Succession involved four stages, beginning with the development of a blue-green algae crust on the soil (0 to 30 yr). This was followed by limited recruitment of cottonwood, willows, and spruce. After approximately 30 yr, Dryas (*Dryas drummondii* Richards), a nitrogen fixing moss, was dominant. Alder (*Alnus sinuata* Regel), another nitrogen fixing plant, become dominant after approximtely 50 yr. All along, cottonwood, willow and spruce persisted. Approximately 100 yr following deglaciation, a climax stand of spruce (*Picea sitchensis* Bong.) developed. The soils exposed during glacial retreat varied in chemical and physical condition with time since exposure, where soil organic content, bulk density, moisture level, and total nitrogen values were low for the first 30 yr, intermediate for the next 50-70 yr, and highest after 100 yr. An earlier study on the soils of the Glacier Bay forelands found similar results except that soil nitrogen levels were lowest 100 yr after deglaciation (i.e., during the spruce stage; Crocker and Major 1955). Soil pH declined over time. Silt content of the sediments increased in each successive sere, although Dryas -dominated sediments were sandier than during any other stage. Thus, similar successional and sediment development trends are found following deglaciation as on alluvial landforms.

Chapin et al. (1994) found that facilitation, competitive interactions, and life history traits were all important in defining the successional dynamics at Glacier Bay, but that life history traits (i.e., dispersal ability, final height, and lifespan) alone were sufficient to generate the observed successional pathway. Pioneering species had small, easily dispersed seeds and were short in stature. Later seral species had larger, poorly dispersed seeds, but were taller and had longer lifespans. The fact that the some early species (principally Dryas and alder) could inhibit the establishment of later succesional species prolonged the period during which they were dominant, but could not prevent their eventual replacement. Conversely, increased nutrient levels associated with maturing soils accelerated seral replacement, but were not needed for a successional sequence to develop (i.e., spruce would eventually established with or without nitrogen fixers). The work of Chapin et al. (1994) demonstrated that if a late seral species was able to reach and germinate on the soils dominated by earlier seral species, it grew well.

The nature of seed rain (was important in another study of primary succession on glacier forelands (Stöcklin and Bäumler 1996) at the foot of the Morteratsch glacier of Switzerland. Seed rain onto recently exposed land near the glacier was heavily skewed. Only five of >300 species known to inhabit the region were common. Each of these five species had distinct morphological adaptations for wind dispersal (i.e., plumes or wings). Moreover, the five species had higher survivorship on the cold, wet soils near the edge of the glacier compared to the other species of the region, and clonal growth strategies were common. Later seral species displayed many fewer morphological adaptations for dispersal, had very low survivorship in cold and wet conditions, and clonal growth strategies were rare. Conversely, the later seral species had higher survivorship on the warmer, better drained soils further from the retreating glacier than did the pioneering vegetation. The benefits of clonal growth strategies included the ability to quickly occupy new sites (thereby inhibiting the establishment of potential competitors), and the ability to withstand common physical stresses (e.g., shifting sediments).

Like glacier forelands, alluvial deposits were more readily colonized by species with small seeds that were readily dispersed large distances by wind and/or water. This was consistent with conclusions from many different studies on dispersal of pioneering species from many different ecosystem types (Walford and Baker 1995).

Plants of mid-seral stages often produce berries (Fenner 1987), which were consumed by birds and mammals. Thus, seeds were dispersed as animals moved. Because animals were not likely to enter an area unless their habitat requirements were met (i.e., sufficient shelter from predators and adverse weather), these species were slow to colonize new land surfaces (i.e., alluvial deposits and glacier forelands). Late seral species were characterized by larger seeds dispersed by both wind and animals. Many seeds were adapted for wind dispersal via “wings”, but due to the large seed size, they did not tend to move as far as seeds from pioneering species.

A study that addressed the role of seed dispersal mechanisms in primary succession was done by Rydin and Borgegårdin (1991) on approximately 30 islands which emerged after the water level of Lake Hjälmaren (Sweden) was lowered between 1882 and 1886. The abundance, timing of arrival, and disappearance of 112 species from herb, shrub, and tree communities was tracked over a 100 yr period. Each species was categorized into a seral stage based on the time at which it first reached 50% of its maximum abundance level, and the time at which it declined to <50% of its maximum abundance. The results showed distinct differences in the characteristics of pioneering species compared to all other species. Eight of the 13 pioneers were annuals, all of which were predominantly autogamous (allows for rapid population growth). As annuals, these pioneering species reproduced via seeds each year; competitive exclusion by later establishing species may account for their lack of persistence within the sere. Dispersal via water was important for transporting the seeds to the islands and seed size was a good predictor of the time of arrival for shrubs and trees. There was no correlation between seed size and floatability. Moreover, the ability to reproduce vegetatively was important for pioneering species such as *Populus tremula* Michx. to persist over time. Johnson (1994) found similar patterns for populous on the gravel bars of the Platte River, NE.

Nilsson et al. (1991) designed a study to specifically address the role of water dispersal in structuring the riparian community of a river. They released wooden cubes into the current of the Sävar River (Sweden) as seed mimics and recorded their final destination. Their results supported the idea that water was an efficient means of dispersal for seeds with long floating times, as these seeds were the only species reaching remote locations. Also, this work suggested that fluvial dynamics (e.g., the rise and fall of flood waters, and the pattern of inundation of near river lands) were important in structuring small-scale patterns of plant communities on alluvial landforms.

CONCLUSIONS

The literature suggests hydraulic forces, plant ecology, sediment chemistry, environmental variations, and stocasticity all structure plant communities on alluvial islands. Despite this wide variety of influences, general patterns occur. River islands are subjected to periodic sediment deposition and scouring by floods, which may yield a “banding” of sediments based on age since deposition. Hydraulic sorting results in fining upwards and longitudinal sorting. The physio-chemical condition of alluvial sediments changes predictably over time and the connectivity between a river and an alluvial land-surface is reduced over time. Distribution patterns of plants are controlled largely by a combination of physio-chemical conditions of sediments and connectivity between the landform and the river. Plant life history strategies can be used to accurately predict the seral stage a species occupies. To be a successful pioneer in these newly emerging habitats, a species needs to possess some or all of the following traits: large, consistently produced seed crops; small seeds which are easily dispersed by wind or water; rapid, early growth; ability to spread clonally or resprout following damage; ability to function in a high light environment/shade intolerance; tolerance of low nutrient levels; and the ability to survive on unstable land surfaces (Scott et al. 1993; Scott et al. 1996). Wiens et al. (1985) concluded, "All other things being equal, the edaphic pattern of a landscape will determine the spatial pattern of the biota in a system." Because an alluvial island may have a distinct arrangement of edaphic conditions that co-vary with time since deposition and connectivity to the river, I hypothesize the physical process of island development can be inferred from the pattern of seral development of plant communities on them. In other words, plants may serve as a proxy for site conditions.

In Chapter 2 of this thesis, I describe my research question and the purpose of the study. A hypothesized mechanism of mid-channel alluvial island formation and apriori predictions of expected plant distribution patterns are proposed for the principle hypothesis and several alternative hypotheses. The study islands from the Swan River are described, and how plant successional patterns help us understand river island development is described.

The third chapter incorporates the results of my thesis into the broader field of aquatic ecology and conservation. It includes a non-technical integration of the existing fields of fluvial geomorphology, plant ecology, and river ecology and concludes with suggestions on how this research project and related works can help develop better ways to manage fluvial systems so that they can meet the needs of society while still maintaining a high level of ecological integrity.

LITERATURE CITED

Abbe, T. B. and D. R. Montgomery (1996). Large woody debris jams, channel hydraulics, and habitat formation in large rivers. Regulated Rivers: Research and Management 12: 201-221.

Allen, J. R. L. (1965). A review of the origin and characteristics of recent alluvial sediments. Sedimentology 5: 89-191.

Amoros, C., A. L. Roux and J. L. Reygrobellet (1986). A method for applied ecological studies of fluvial hydrosystems. Regulated Rivers 1: 17-36.

Auble, G.T., J.M. Friedman, and M.L. Scott (1991). Relating riparian vegetation to present and future streamflows. Ecological Applications 4: 544-554.

Andrews, E. D. (1983). Entrainment of gravel from naturally sorted riverbed material. Geological Society of America Bulletin 94: 1225-1231.

Baker, W. L. (1989). Macro- and micro-scale influences on riparian vegetation in Western Colorado. Annals of the Association of American Geographers 79: 65-78.

Baker, W. L. (1990). Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. Journal of Biogeography 17: 59 73.

Barnes, W. J. (1985). Population dynamics of woody plants on a river island. Canadian Journal of Botany 63: 647-655.

Beschta, R. L. and W. S. Platts (1986). Morphological features of small streams: Significance and function. Water Resources Bulletin 22: 369-378.

Bornette, G. and C. Amoros (1996). Disturbance regimes and vegetation dynamics: role of floods in riverine wetlands. Journal of Vegetation Science 7: 615-622.

Bornette, G., C. Amoros and D. Chessel (1994). Effect of allogenic processes on successional rates in former river channels. Journal of Vegetation Science 5: 237-246.

Brierley, G. J. and E. J. Hickin (1992). Floodplain development based on selective preservation of sediments, Squamish River, British Columbia. Geomorphology 4: 381 391.

Cavallo, B.J. 1997. Floodplain habitat heterogeneity and the distribution, abundance, and behavior of fishes and amphibians in the Middle Fork Flathead River, Montana. M.S. Thesis, The University of Montana.

Chapin, F. S. I., L. R. Walker, C. L. Fastie and L. C. Sharman (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs 64: 149-175.

Chauvet, E. and H. Decamps (1989). Lateral interactions in a fluvial landscape: the River Garonne, France. Journal of the North American Benthological Society 8: 9-17.

Church, M. (1995). Geomorphic reponse to river flow regulation: Case studies and time scales. Regulated Rivers: Research & Management 11: 3-22.

Coleman, J. M. (1969). Brahmaputra River: channel process and sedimentation. Sedimentary Geology 3: 129-239.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. Science 199: 1302 1310.

Creuze Des Chatelliers, M. and J. L. Reygrobellet (1990). Interactions between geomorphological processes, benthic and hyporheic communities: First results on a by passed canal of the French Upper Rhone River. Regulated Rivers: Research & Management 5: 139-158.

Crocker, R. L. and J. Major (1955). Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Journal of Ecology 43: 427-448.

Décamps, H. (1996). The renewal of floodplain forests along rivers: a landscape perspective. Verh. Internat. Verein. Limnol. 26: 35-59.

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

Dirschl, H. (1972). Geobotanical processes in the Saskatchewan River delta. Canadian Journal of Earth Sciences 9: 1529-1549.

Fenner, M. (1987). Seed characteristics in relation to succession in Colonization, Succession, and Stability. 26th Symposium of the British Ecological Society.

Fonda, R.W. (1974). Forest succession in relation to river terrace development in Olympic National Park, Washington. Ecology (55): 927-942.

Friedman, J. M., W. R. Osterkamp and W. M. Lewis (1996). Channel narrowing and vegetation development following a Great Plains flood. Ecology 77: 2167-2181.

Frye, R. J. and J. A. Quinn (1979). Forest development in relation to topography and soils on a floodplain of the Raritan River, New Jersey. Bulletin of the Torrey Botanical Club 106: 334-345.

Green, W. N. (1982). Mid-Channel islands: Sedimentology, physiography, and effects on channel morphology in selected streams of the Great Bend Region of the Wabash Valley. Masters Thesis, Dept. of Geology, Purdue U. 111 pgs.

Gregory, S. V., F. J. Swanson, W. A. McKee and K. W. Cummins (1991). An ecosystem perspective of riparian zones: Focus on the links between land and water. Bioscience 41: 540-550.

Harris, R. R. (1986). Occurance patterns of riparian plants and their significance to water resource development. Biological Conservation 38: 273-286.

Harris, R. R. (1987). Occurrences of vegetation on geomorphic surfaces in the active floodplain of a California alluvial stream. The American Midland Naturalist 118: 393 405.

Hartman, G. F., J. C. Scrivener and M. J. Miles (1996). Impacts of logging in Carnation Creek, a high-energy coastal stream in British Columbia, and their implications for restroring fish habitat. Can. J. Fish. and Aquat. Sci. 53: 237-251.

Hughes, F. M. R. (1988). The ecology of African floodplain forests in semi-arid and arid zones: a review. Journal of Biogeography 15: 127-140.

Hupp, C. R. (1983). Vegetation pattern on channel features in the Passage Creek Gorge, Virginia. Castanea 48: 62-72.

Hupp, C. R. (1997). Riparian vegetation, channel incision, and ecogeomorphic recovery., in *Managment of Landscapes Disturbed by Channel Incision*, The Center for Computational Hydrocience and Engineering, Oxford campus, U. of Mississippi.

Hupp, C. R. and W. R. Osterkamp (1985). Bottomland vegitation distribution along Passage Creek, Virgina, in relation to fluvial landform. Ecology 66: 670-681.

Johnson, W. C. (1994). Woodland expansion in the Platte River, Nebraska: Patterns and causes. Ecological Monographs 64: 45-83.

Junk, W. J., P. B. Bayley and R. E. Sparks (1989). The flood pulse concept in river - floodplain systems., in Proceedings of the International Large River Symposium, Canadian Special Publication of Fish and Aquatic Sciences.

Kalliola, R. and M. Puhakka (1988). River dynamics and vegetation mosaicism: a case study of the River Kamajohka, northermost Finland. Journal of Biogeography 15: 703 719.

Kalliola, R., J. Salo, M. Puhakka and M. Rajasilta (1991). New site formation and colonizing vegetation in primary succession on the western Amazon floodplain. Journal of Ecology 79: 877-901.

Keller, E. A. and F. J. Swanson (1979). Effects of large organic material on channel form and fluvial processes. Earth Surface Processes 4: 361-380.

Kellerhal, R., M. Church, and D.I. Bray (1976). Classification and analysis of river processess. Journal of the Hydraulics Division, ASCE 102: 813-829.

Leopold, L. B., M. G. Wolman and J. P. Miller (1964). *Fluvial Processes in Geomorphology*. W.H. Freeman. San Francisco.

Lindsey, A. A. (1961). Vegetation and environment along the Wabash and Tippecanoe rivers. Ecological Monographs 31: 105-156.

Longwell and Flint (1963). Weathering and Soils. in *Introduction to Physical Geography*. L. A. Flint editor. NY. J. Wiley and Sons Publishing.

MacDonald, L. H. and J. A. Hoffman (1995). Causes of peak flows in Northwest Montana and Northeast Idaho. Water Resources Bulletin vol. 31. pgs. 79-96.

Maddock, T. J. (1972). Hydraulic behavior of stream channels. Thirty-Seventh North American Wildlife Conference: 366-374.

Malanson, G. P. (1993). *Riparian Landscapes*. Cambridge University Press.

Malanson, G. P. and D. R. Butler (1990). Woody debris, sediment, and riparian vegetation of a subalpine river, Montana, USA. Artic and Alpine Research 22: 183-194.

Malanson, G. P. and D. R. Butler (1991). Floristic variation amoung gravel bar in a subalpine river, Montana, USA. Artic and Alpine Research 23: 273-278.

McBride, J. R. and J. Strahan (1984). Establishment and survival of woody riparian species on gravel bars of an intermittent stream. The American Midland Naturalist 112: 235-245.

McCarthy, T. S., W. N. Ellery and I. G. Stanistreet (1992). Avulsion mechanism on the Okavango fan, Botswana: the control of a fluvial system by vegetation. Sedimentology 39: 779-795.

Mertes, L. K., T. Dunne and L. A. Martinelli (1996). Channel-floodplain geomorphology along the Solimoes-Amazon River, Brazil. Bulletin of the Geological Society of America 108: 1089-1107.

Miller, F. J. and D. Schroeer (1987). *College Physics.* sixth. Harcourt Brace Jovanovich.

Nanson, G.C., and H.B. Beach (1977). Forest succession and sedimentation on a meandering-river floodplain, Northeast British Colombia, Canada. Journal of Biogeography (4): 229-251.

Nakamura, F. and F. J. Swanson (1993). Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. Earth Surface Processes and Landforms 18: 43-61.

Nilsson, C., G. Grelsson, M. Dynesius, M.E. Johansson, U. Sperens (1991). Small rivers behave like large rivers: effects of postglacial history on plant species richness along riverbanks. Journal of Biogeography 18: 533-541.

Nilsson, C., M. Gardfjell and G. Grelsson (1991). Importance of hydrochory in structuring plant communities along rivers. Canadian Journal of Botany 69: 2631-2633.

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

Pautou, G. and H. Décamps (1985). Ecological interactions between the alluvial forests and hydrology of the Upper Rhone. Archives of Hydrobiolia 104: 13-37.

Puhakka, M., R. Kalliola, M. Rajasilta and J. Salo (1992). River types, site evolution and successional vegetation patterns in Peruvian Amazonia. Journal of Biogeography 19: 651-665.

Rostan, J. C., C. Amoros and J. Juget (1987). The organic content of the surficial sediment: a method for the study of ecosystems development in abandoned river channels. Hydrobiologia 148: 45-62.

Rubin, D. M., J. C. Schmidt and J. N. Moore (1990). Origin, structure, and evolution of a reattachment bar, Colorado River, Grand Canyon, Arizona. Journal of Sedimentary Petrology 60: 982-991.

Rydin, H. and S. Borgegard (1991). Plant characteristics over a century of primary succession on islands: Lake Hjälmaren. Ecology 72: 1089-1101.

Schnitzler, A. (1997). River dynamics as a forest process: Interaction between fluvial systems and alluvial forests in large European river plains. The Botanical Review 63: 40-60.

Scott, M. L., J. M. Friedman and G. T. Auble (1996). Fluvial process and the establishment of bottomland trees. Geomorphology.

Scott, M. L., M. A. Wondzell and G. T. Auble (1993). Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation, in Proceedings of the 13th Annual American Geophysical Union Hydrology Days., Hydrology Days Publications.

Sedell, J. R. and J. L. Froggatt (1984). Importance of streamside forests to large rivers: The isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. Verh. Internat. Verein. Limnol. 22: 1828-1834.

Shull, C. A. (1922). Formation of a new island in the Mississippi River. Ecology 3: 202 206.

Smith, D. G. (1976). Effects of vegetation on lateral migration of anastomosed channels of a glacier meltwater river. Geological Society of America Bulletin 87: 857-860.

Smith, D. G. and N. D. Smith (1980). Sedimentation in anastomosed river systems: examples from alluvial valleys near Banff, Alberta. Journal of Sedimentary Petrology 50: 157-164.

Stöcklin, J. and E. Bäumler (1996). Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. Journal of Vegetation Science 7: 45-56.

Swanson, F. J. and J. F. Franklin (1992). New forestry principles from ecosystem analysis of Pacific Northwest forests. Ecological Applications 2: 262-274.

Tabacchi, E., A. Planty-Tabacchi, M. J. Salinas and H. Décamps (1996). Landscape structure and diversity in riparian plant communities: A longitudinal comparative study. Regulated Rivers: Research & Management 12: 367-390.

Triska, F. J. (1984). Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: A historical case study. Verh. Internat. Verein. Limnol. 22: 1876-1892.

Walford, G. M. and W. L. Baker (1995). Classification of the riparian vegetation along a 6-KM reach of the Animas River, Southwestern Colorado. The Great Basin Naturalist 55: 287-303.

Wallace, J. B., S. L. Eggert, J. L. Meyer and J. R. Webster (1997). Multiple trophic levels of a forested stream linked to terrestrial litter inputs. Science 277: 102-104.

Ward, J. V. (1989). The four dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8: 2-8.

Ward, J. V. and J. A. Stanford (1995a). Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research &

Management 11: 105-119.

Ward, J. V. and J. A. Stanford (1995b). The serial discontinuity concept: extending the model to floodplain rivers. Regulated Rivers: Research & Management 10: 159-168.

Weins, J.A., C.S. Crawford, and Gosz, J.R. (1985). Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos (45): 421-427.

Willson, M. F. (1993). Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107/108: 261-280.

CHAPTER II

Plant Distribution Patterns on Alluvial Islands of the Swan River, Northwest Montana, and the Link to Fluvial Dynamics

INTRODUCTION

River islands are part of the aquatic-terrestrial transition zone (ATTZ) (i.e., floodplains, riparian zones, back waters, abandoned river channels and dead arms, and/or alluvial islands; Décamps 1996). Fluvial, climatic, and biotic forces integrate within ATTZ's and produce exceedingly high levels of biotic diversity (Salo 1986). Indeed, these areas maybe some of the most species-rich and productive ecosystems of temperate regions (Tabacchi et al. 1996). However, anthropogenic influences such as river damming, water withdrawals, and floodplain development have a deleterious impact on the ecological integrity of river systems (Bravard et al. 1986; Dynesius and Nilsson 1994, Stanford et al. 1996). The purpose of this study was to develop and test a conceptual model of how emergent mid-channel alluvial islands are formed and to enhance our understanding of the link between fluvial dynamics and alluvial landform development. An improved understanding of how processes such as fluvial dynamics and sediment transport influence the structure of riverine ecosystems is imperative if river management strategies which consider both the needs of societies and the ecological integrity of the system are to be developed.

Scientific research on alluvial islands has been limited, which is surprising considering the ecological importance of islands to some river systems. For example, islands are repositories of alluvial sediments. Sediments, if not incorporated into islands or other alluvial landforms, may clog the interstitial spaces of a river bed, impacting food webs as well as population dynamics of fish species that require clean gravel for successful spawning (i.e., salmonids). Excessive free sediments in a river may cause localized river bed aggradation and, therefore, increase the likelihood of flooding (Coleman 1969; McCarthy et al. 1992). Alluvial islands contribute to food web dynamics of riverine systems by contributing nutrients through leaf and insect fall (Swanson et al. 1988; Wallace et al. 1997). Islands also tighten the "nutrient spiral" of the river by prolonging the retention time of limited nutrients such as organic carbon, nitrogen and phosphorous (Malanson 1993).

Mid-channel islands contribute structural complexity to the fluvial system. Islands are geomorphic agents in fluvial systems. They can cause local alterations in channel gradient and the depth to width ratio, and they are sources of large woody debris (LWD), an important geomorphic agent in alluvial rivers (Nakamura and Swanson 1993; Abbe and Montgomery 1996). Fish and other organisms can find shelter from high-velocity flood waters where flow divergence occurs at the upstream portion of islands, within the eddy of re-circulating currents at the downstream end of islands, and within the numerous small eddies that form behind the vegetation on inundated islands (Triska 1984). Islands may provide thermal refugia for aquatic species through localized upwelling of hyphoreic waters that have percolated through the sediments of the island, although this function is not well documented.

River islands also contribute to the productivity and diversity of the terrestrial component of fluvial ecosystems. They provide habitat and food for a diverse avian community (Knopf 1986 as cited in Johnson 1994), and numerous small mammals. As river channels relocate, islands may be incorporated into the floodplain as a vegetated patch of distinct origin, age, and successional stage (Abbe and Montgomery 1996). When one side channel along an island is abandoned via the formation of an alluvial plug a floodplain springbrook may form (Keller and Swanson 1979; Stanford and Ward 1993). Springs are important habitats for a broad array of invertebrates, amphibians, fishes, and birds (Cavallo 1997).

Green (1982) and Abbe and Montgomery (1996) addressed the mechanisms of mid-channel gravel bar formation as the first step in the evolution of an emergent river island. Both studies identified flood events as vital components of the process of gravel bar formation. It is only at times when river flows approach or exceed bankfull discharge that appreciable quantities of sediments are transported and, therefore, available for deposition.

Previous studies of plant communities on alluvial landforms suggest plants are distributed largely in response to the combination of edaphic and hydraulic conditions. Typically, these conditions are interrelated, and their pattern of change across a river bottom is relatively consistent and predictable, and largely determined by the level of connectivity between a land form and the river that created it. Landforms with high levels of connectivity to a river (i.e., mid-channel islands and gravel bars), have lower elevations relative to base flow levels of the river, and are subject to more frequent and prolonged periods of flooding and greater volumes of sediment scour and/or deposition compared to landforms of lower connectivity (e.g., floodplains and terraces). Plants growing on high-connectivity surfaces are subject to more intense physical stresses (e.g., shearing or abrasion by suspended debris, particles or ice, burial by deposited sediments) compared to landforms of lower connectivity (Hupp and Osterkamp 1985; Pautou and Decamps 1985). Commonly, landforms with high connectivity were deposited more recently. Consequently, these deposits have lower organic matter, surface soil moisture, nitrogen, phosphate, sodium, calcium, potassium, magnesium, and conductivity relative to older landforms in the same basin (Rostan et al. 1987; Kalliola et al. 1991; Puhakka et al. 1992). Usually, median grain size and soil pH are greater on landforms with high levels of connectivity to a river (Nanson and Beach 1977; Bornette et al. 1994).

Depth to the water table on alluvial landforms is largely determined by the local shape and geometry of the floodplain (i.e., location of bedrock knickpoints), and the porosity and thickness of the alluvium overlying an impervious substratum (Stanford and Ward 1988). Porosity and thickness of alluvium is primarily determined by the hydraulic condition of a site. Therefore, depth to the water table frequently is correlated with the elevation of the alluvial surface (Friedman et al. 1996).

Sediment physio-chemical condition, strength of hydraulic influences, and depth to ground water have been implicated as the proximal influences creating plant distribution patterns on alluvial landforms, either singularly or in various combination (Frye and Quinn 1979; Conchou and Pautou 1987 cited in Malanson 1993; Décamps et al. 1988; Auble et al. 1994; Schnitzler 1997), and these parameters are determined in large part by the co-variates of time since deposition and level of connectivity. Thus, time since deposition and level of connectivity may combine to create site specific conditions that promote the establishment of a characteristic plant community for that location (Amoros et al. 1986). For example, MacBride and Strahan (1984) found that the species composition of plant communities on gravel bars was best correlated with sediment size class. Hupp (1983) concluded that the change-over in species composition between mid-channel gravel bars and islands and the floodplain of Passage Creek, VA mirrored the change in the destructive power of flood waters. Malanson and Butler (1990) found that plant community diversity on gravel bars was positively correlated with elevation of the land surface, organic content of the sediments, and location of large woody debris accumulations.

Green (1982) identified three distinct island zones based on plant community characteristics. “Gravel Aprons” were always below the baseflow level of the river and were dominated by aquatic macrophytes. The “Lower and Upper Emergent Zone” was the land between the base flow and bankfull levels of the river. This emergent zone was dominated by scrub trees and grasses. The “Core Area” was heavily vegetated by trees, weeds, and grasses, had the highest elevation. Green did not study species distribution patterns within each zone.

Barnes (1985) investigated the age structure of the tree community of one island in the Chippewa River, WI. He determined the island was growing in an upstream direction, and that elevation was correlated with age. *Salix* (willows) dominated the youngest/lowest island substrates, while *Populus deltoides* Marsh (cottonwood) and *Betula nigra* L.(river birch) dominated the intermediate zone. *Fraxinus pennsylvania* Marsh (green ash), *Acer* *saccharinum* L. (silver maple), and *Ulmus americana* L. (american elm) were restricted to the oldest and highest regions of the island. Within each species, a gradient from many small individuals to fewer, larger, individuals occurred commensurately with increased age and elevation of the land surface. While Barnes did not connect plant distribution with successional processes or fluvial dynamics, it was clear that the change-over of dominant species corresponded to an age/elevation gradient on the island. His data suggested that plant community structure might be used to recreate the history of a land surface in cases where detailed historical records and aerial photographs are absent. In 1991, Barnes expanded on his earlier work to look at 25 islands of the Chippewa River. He found a linear relationship between number of species and island surface area, and a correlation between number of tree species and surface elevation. Number of tree species was not correlated with the age of the land surface, substrate type, mode of island origin, or distance to nearest floodplain forest.

These examples, and many others, suggest that plants may be valuable as "functional describers" (Amoros et al. 1986) of site conditions on riverine islands. A certain level of randomness is expected in this process as environmental stocastisity also has been identified as a structuring agent of plant communities on alluvial landform (Malanson and Butler 1991). For example, the successful establishment of cottonwood seedlings requires seed release to occur at the same time flood waters recede, and while climatic conditions (e.g., temperature, humidity, precipitation amounts, rate of fall of ground water level) are appropriate (Baker 1990).

Given the principle that sediment movement in river systems is largely controlled by discontinuous and unpredictable flood events (Junk et al. 1989), accretionary processes on developing river islands may be discontinuous. This creates the potential for distinct "banding" of sediments, where each band has a unique age, possibly a different level of connectivity to the river and, therefore, a unique combination of edaphic and hydraulic conditions. Based on interpretation of aerial photographs, several researchers have presented site-specific examples of the incremental growth of river islands (Green 1982; Barnes 1985; Osterkamp and Costa 1987). The presence of such characteristic banding, led me to hypothesize that each sediment "band" would support a distinct plant community type. Consequently, I predicted patterns of vegetation could be used as a proxy for the process of island development assuming plants serve as a living record of landform history (e.g., plants are a functional describer of site conditions that vary predictably with time since deposition). The apriori prediction was that if mid-channel alluvial islands grow incrementally because of the flood deposition of new sediments on the downstream side of existing islands, the pattern of vegetation on these islands should show a successional trend from late seral species on older sediments that are closer to the upstream end of islands (island head), to pioneering species on the newest sediments at the downstream end of each island (island tails). This model of island development is shown in Figures 1 and 2. Furthermore, based on the premise that island development is controlled by a combination of sediment dynamics and hydraulic conditions that are both initiated and regulated by flood events (i.e., Green 1982; Abbe and Montgomery 1996), I hypothesized that development of mid-channel alluvial islands is controlled by fluvial dynamics originating at the scale of the entire drainage basin, i.e., all islands within a basin are developing in response to similar forces, not unique site-specific conditions.

To evaluate patterns of vegetation as a corollary to explain mid-channel island development, I studied patterns of tree and shrub communities on 14 islands in three different reaches of the Swan River in northwest Montana. Using multi-scale analyses of the distribution patterns of trees and shrubs as a proxy, I explored patterns and processes of riverine island growth and development. An interesting question relates to the presence or absence of micro-scale spatial segregation of plants within non-meandering river reaches in fluvial systems. Despite finding abundant evidence of seral segregation on the point bars of meandering river reaches, Puhakka et al. (1992) failed to find such segregation on the alluvial deposits of anastomsed and braided river reaches within the Amazon basin.

Furthermore, White (1979 as cited in Hupp 1982) and Pickett (1980 as cited in Hupp 1982), suggested that vegetation patterns maintained by disturbance events such as floods should be viewed as non-equilibrium systems. Studies detailing plant organizational patterns of non-equilibrium systems are very scarce, and the question remains if non-equilibrium systems will display patterns associated with seral succession, or some other structuring mechanism such as disjointed patches of random distribution. I will also address this question using data for successional patterns on alluvial islands in the Swan River.

Hypothesized Model of Island Formation

The principle hypothesis evaluated in this study is that river islands grow incrementally in response to the deposition of sediments during high water events, and furthermore, because high water events are basin scale forces, all islands develop similarly. Three alternative mechanisms of river island development are also identified, including: 1) site-specific control of incremental island growth; 2) islands form at their full size, and therefore incremental growth does not occur; and 3) island development is controlled by random events. For each of the four potential models of island formation, predictions of the expected pattern of the plant communities are presented in Table 1.

Figures 1 ABC and 2 illustrate the sequence of events as predicted by my principle hypothesis. Figures 3, 4, 5, 6 are photographs from the Swan River of each stage of the process. The initial stage of island development occurs with the emergence of a gravel bar above the base-flow level of the river (Green 1982; Abbe and Montgomery 1996). First, a piece of large woody debris may lodge within the channel, serving as a local barrier to flow (Figure 1A). Where the flow pathway diverges, a zone of localized deposition develops. As the river level falls, the deposit emerges as a river bar.

The newly exposed gravel bar is available for plant colonization, and pioneering species should be most abundant (Figure 1B). The establishment of vegetation has three significant influences on the continued development of the land surface. First, developing roots consolidate alluvial sediments, making them more resistant to erosion (Smith 1976; Keller and Swanson 1979). Second, seasonal shedding and decay of leaves contributes organic content to the sediments, an initial stage of soil development (Abbe and Montgomery 1996). Third, vegetation increases the roughness of the land surface, which promotes the filtering of sediments from sediment-rich flood waters that periodically inundate all or portions of the island (Johnson 1994; Friedman et al. 1996). These processes combine to increase the land surface elevation and promote several changes in the physio-chemical condition of the sediments, such as a reduction in the median grain size and increased levels of surface soil moisture.

Eventually, a developing gravel bar will accumulate enough organic matter and fine particles for colonization by additional species, and seral replacement occurs. Through time, subsequent flood events deposit new sediments, similar to those of the initial deposit, downstream from the initial deposit. These new deposits are then available for colonization by pioneering species. The evolution of this "band" of sediment is similar to that of the initial gravel deposit (Figure 1C).

Because the edaphic and hydraulic condition of alluvial deposits vary predictably with time since deposition, and plants are distributed largely in response to site specific edaphic and hydraulic conditions, it follows that plant distribution patterns will reflect the depositional history of the alluvial landform. Moreover, because sediments are arranged in a linear gradient according to time since deposition (i.e., more recent sediment deposits lie downstream of older deposits), it follows that plants should also be arranged in a linear gradient, with the newest colonizers closest to the tail of an island.

Island development follows multiple iterations of the processes outlined in Figures 1A-C. Eventually, I predict that a late seral stage or climax community will develop where sediments are the oldest and connectivity of the land surface to the river is the lowest. This should occur first on the upstream portion of islands (i.e., the head of an island). Sites of the most recent deposition and highest connectivity will be dominated by pioneering species on the downstream tails of islands. Sites between the head and tail of islands will be dominated by early- and mid-seral species. Thus, the expected pattern of vegetation is a linear gradient of seral communities, organized along the long axis of the island, and parallel to the direction of river flow (Figure 2). This pattern of vegetation should correspond to the time since deposition of sediments, and thus serve as a proxy for the process of mid-channel riverine island development.

Because a flood pulse is not a stationary event (i.e., it moves through a river system), it follows that all islands within a given river system were subjected to the same flood events. Therefore, the most recent deposits at the downstream ends of all islands within a given river system should be of equal ages. Consequently, for comparison, the vegetation patterns on multiple river islands should be based on distance from the downstream ends of the islands. Thus, each island survey would begin at the same chronological starting point (i.e., time since deposition are all equal at the downstream ends of the islands).

Inherent in this model are the following assumptions: 1) the most recently deposited sediments were incorporated into an island during the last flood event, at the downstream end of the island; 2) Islands studied were not remnants of historically larger islands that have shrunk in size (i.e., partial erosion of the island surface); 3) Islands formed by the capture of a portion of the floodplain, and subsequently reworked by fluvial dynamics, would have the same vegetation patterns as emergent islands, and therefore their inclusion in the study will not adversely affect the study results; and 4) Between the most upstream and downstream islands of the study, the composition and relative abundance of floodplain vegetation is consistant, and therefore, differences in the plant communities on the islands were not caused by differences in the availability or relative abundance of seeds.

MATERIALS AND METHODS

Study Area

The Swan River basin lies in northwest Montana within the headwaters region of the Columbia River system (Figures 7, 8). The Swan River flows northward through the Swan Valley (≈ 64 km long and 10 km wide), bounded by the Mission Mountain Range on the west, the Swan Mountain Range on the East, and the Clearwater River drainage basin to the South. The catchment is approximately 2,070 km^2. The headwaters are near Gray Wolf Lake at an elevation of approximately 2,100 m. The upper portion of the river from its source to Swan Lake is unregulated and largely devoid of civil engineering works. Swan Lake is the dividing point between the upper and lower river. Bigfork dam regulates the flow of the lower Swan River, but does not affect the hydrology of the lake or upper river. From the outfall of Swan Lake, the lower portion of the river flows approximately 13 km to the river's terminus at Flathead Lake (Frissell et al. 1995; Kendy and Tresch 1996).

Elevations within the basin range from 400 m to 3000 m (Frissell et al. 1995). The Swan Valley occupies the southern tip of the eastern extension of the Rocky Mountain Trench, a zone of closely spaced normal faults (Kendy and Tresch 1996). The valley floor consists of variously graded, porous glacial till. Numerous patches of lacustrine, palustrine, and riverine wetlands occupy the valley floor and foothills. The climate is typical of mid-elevation intermontain basins of the northern Rocky Mountains (Frissell et al. 1995). Between 1961 and 1990, the average annual precipitation was 72.2 cm and the average annual temperature was 5.5°C. Dominant land cover on the valley floor is temperate mixed conifer forest (e.g., *Abies* , *Pinus, Thuja, Pseudotsuga, Picea, and Larix*) with patches of deciduous forest (e.g., *Populus, Betula, Salix*; Frissell et al. 1995).

The Swan has a low gradient, cobble bed river. The channel is sinuous and locally anabranched (Frissell et al. 1995) and not deeply incised into the underlying alluvium (Kendy and Tresch 1996). The river grows consistently as it receives the waters of numerous tributary streams with headwaters in the Mission and Swan Ranges, or that upwell as springbrooks on the floodplain. Two USGS gauge stations exist along the main channel. Gauge #12369200 is in the town of Condon, where the Swan River has a drainage area of 179 km^2. This gauge was operated from 1972-1992. Mean annual discharge was 4.8 m^3/s, with a maximum discharge of 46.2 m^3/s on 6/18/74. Gauge #12370000 is on the lower river in the town of Bigfork, just upstream of the confluence with Flathead Lake. The drainage area for this gauge was 1738 km^2, and it operated between 1922 and 1994. The average peak discharge volume for the Swan River was 5,297 cfs (150 m^3/s; USGS Surface Water Gauge data). The record high peak discharge of 8,890 cfs (252 m^3/s) occurred in 1974, and the record low peak discharge of 3,430 cfs (97 m^3/s) occurred in 1977.

Land use patterns are varied within the basin, with timber harvest as the dominant land use. There is limited livestock grazing, agriculture, and residential development. Dominant land managers within the drainage basin include Plum Creek Timber Corporation, Department of State Lands (Swan Valley Sate Forest), U.S. Forest Service (Flathead National Forest and Mission Mountain Wilderness Area), and the U.S. Fish and Wildlife Service. There also is a national wildlife refuge and a Nature Conservancy preserve near the confluence of the upper river with Swan Lake.

Island Selection Criteria

Islands were selected for inclusion in the study only if I could determine (with a high level of confidence) that the islands had formed by the deposition of sediments within the active channel and then emerged above the water level of the river, and based on their accessibility to the required sampling gear. Islands formed by the capture of a portion of the floodplain, for example by meander loop cut-off or new channel formation, were not considered emergent islands and were not included in the study. Selection was based on the following criteria: 1) islands were notably longer than wide; 2) the long axis of the island was at or nearly parallel to the primary channel; 3) islands were completely or nearly surrounded by flowing waters (i.e., water on one side blocked by an alluvial plug behind which there were signs of recent channel activity). Any signs of soil or plant development behind an alluvial plug was sufficient evidence to exclude an island from the study. At no time were vegetation or edaphic characteristics used to evaluate an islands potential for inclusion.

Physical Descriptions of Islands

Island Morphology

Detailed measurements of island perimeters were made using a tape measure and compass. From scaled diagrams of each island, surface area and length to width ratios were determined with a calibrated planimeter. Island length was the longest axis of the island and width was measured at the widest point of the island perpendicular to the long axis.

Sediments

Soil pits were dug at nearly equal distance intervals along the long axis of five islands (PO1, PO 2, PO4, PP 1, and PP 3). Soil pits were attempted on an additional three islands (PO 3, PP2, and PP 5) but were unsuccessful because the majority of the islands were impenetrable due to the presence of a cobble layer within 5 cm of the land surface. Soil pits were not attempted on the remaining islands because of difficulty transporting the sampling equipment to the islands or for safety concerns. The location of each soil pit was referenced from the downstream end of the island.

Soil pits were advanced until further penetration was impossible (i.e., usually upon encountering a layer of large cobbles). Sediments were qualitatively described based on mean particle size (cobble>gravel>sand>silt>clay), cohesiveness, color, moisture content, presence/absence of an organic layer, and any other applicable descriptors (i.e., mottling/gleying/root layers). The location and abruptness of each transition between dominant particle size class layers was noted. When sample points fell at locations where excavation was impossible (e.g., a tree or shrub occupying the spot) the sample point was relocated as close as possible to the predetermined location. One island was selected for replicate sampling.

The surface sediments at 26 different locations on five islands (PO 1, PO 2, PO 4, PP 1, and PP 3) were described and matched with the most abundant tree and shrub species at each locations. Qualitative assessment of the level of fidelity between plant species and surficial sediment type were attempted.

Plant Community Description

Tree Community Distribution Pattern

Tree distribution patterns on the islands selected for study were evaluated along transects oriented parallel to the long axis of the island. At least two transects were measured on each island. Transects were established using the downstream terminus of each island as their starting point (distance from tail of the island = 0). Data were collected using the point-quarter method (Cottom and Curtis 1956). Twenty sample points, spaced equal distances apart, were measured on each transect line. Only the first occurrence of a tree was used in the data analysis. In the event no tree existed within a sample quadrant, or if the nearest tree within a quadrant to a sample point had been previously included in the point-quarter survey, the quadrant was recorded as empty. If one tree fell within two or more quadrants it was placed in the quadrants where the largest portion of the tree was, and the next nearest tree sampled in the "vacated" quadrant. Distance from a sample point to the selected tree were made to the nearest cm. Tree circumference at breast height (CBH) was measured to the nearest millimeter. Tree cores were collected from all trees included in the sampling that had a CBH >10.5 cm, the minimum circumference that could be cored without killing the tree. The lifestage of each tree was determined based on CBH; adult (CBH >10.5 cm), sapling (CBH 0.05 - 10.5 cm), or seedling (CBH<0.05 cm).

Dendrochonological investigation

Sixty-seven cores were collected from trees on the fourteen study islands. Species sampled were *Populus trichocarpa* Torr. & Gray, *Alnus tenuifolia* Nutt., *Picea engelmannii* Parry ex Engelm, *Larix occidentalis* Nutt., *Pinus contorta* Dougl. and *Pseudtsuga menziesii* (Mirbel) Franco. Prior to collecting a core, the borer was sterilized by immersion in 100% bleach, allowed to air dry, and then sprayed with WD-40 grease. Cores were collected at breast height following the procedures of Campbell (1981). All bore holes were sealed with pruning sealer. Storage followed the procedures of Cole (1977). Tree cores were prepared for analysis by gluing them into slotted wooden holders. Cores were sliced length wise at their widest point, thereby exposing the annual growth rings. If needed, the cores were sanded with steel-wool to enhance the contrast between the annual growth rings. Growth rings were counted on prepared cores using a variable power dissecting microscope. Difficulties in counting tree rings were minimized by wetting each core with water and using a spot light directed at a low angle, perpendicular to the direction of the rings. This approach helped to highlight the texture and color differences between summer and winter wood for each year of growth.

The number of annual growth rings from each tree core were counted at least two times, once each by separate investigators. If the results did not match, a third person recounted rings. Tree age was determined by adding a species-specific correction factor (Table 2) to the number of annual growth rings to account for the number of years between germination and attainment of breast height. Because the calculation of mean, median, and 95% confidence intervals for tree ages were sensitive to outlying values, trees considered extreme outliers for age were removed form these calculations according to Barrnett and Lewis (1994; Equation A, Appendix A).

Shrub Community Distribution Pattern

Shrub communities on islands were surveyed using the line intercept technique (McDonald 1980). Patterns of shrub distribution were measured on the same transect lines used during for the tree sampling. Shrub presence was recorded if any portion intersected the plane of the transect line. Species name, starting and ending locations as measured from the end of the island, and length and width at the longest and widest points were recorded to the nearest millimeter. When shrubs were part of a larger clump of conspecifics and the dimensions of an individual could not be delineated, the entire clump was measured, and the number of individuals within the clump recorded. By using dimensions of the clump in subsequent analyses, the likelihood that clonal shrubs were considered more than a single individual were reduced. All measurements were made to the nearest millimeter. Any shrub that could not be positively identified in the field was collected for later identification. At least one representative sample of each species was preserved as a voucher specimen (stored in Dr. Carol Brewer's laboratory at the University of Montana). Pattern analysis was conducted on individual shrub species for each species that represented >5% of the shrub community. Rare species (i.e., <5% of shrub community) were composited into common samples based on seral stage, as determined by life history traits (i.e., all *Salix* not analyzed as individual species, all non-*Salix* shrubs not analyzed as individual species).

Data Analysis

Vegetation Distribution Patterns

Thirty transect lines on 14 different islands were surveyed during the study. Transect lengths ranged from 19.7m to 172.0m. A total of 1,676 quadrants were sampled. Each of the fourteen study islands occurred in one of three river reaches with different catchment areas (414 km^2, 622 km^2, and 842 km^2). Four islands were in the reach of the smallest catchment area, six islands in the intermediate reach, and four in the reach of the largest catchment area.

Tree and shrub patterns were considered from multiple scales of analysis: 1) the entire drainage basin; 2) within three river reaches of different catchment areas (414 km^2, 622 km^2, and 842 km^2); and 3) as individual islands. The tree community also was analyzed following stratification of islands into three surface area size classes (50-404 m^2, 603-988 m^2, and 1700-7958 m^2).

Islands were divided into 10m long intervals to facilitate data summary of tree and shrub distribution patterns. Based on the assumption that the most recently deposited sediments were incorporated into the island during the last flood event, and that a flood pulse moves through the river system in a short period of time, it follows that the downstream ends of each island are all of the same age. As such, all plant distribution patterns were analyzed based on distance from the downstream end of the island. Thus, vegetation characteristics at the downstream end of islands were based on the average performance between 0 and 10m from the tails of the islands, and so on for each 10m increment for the length of the island, or the longest island in a composite sample. Because islands varied in length, the number of summary points available for comparison among islands varied. Data were plotted on line graphs with distance away from the tails of the islands on the X axis, and the vegetation characteristic on the Y axis. Curves were smoothed based on a three point moving average.

Plant locations were not standardized in the attempt to make island lengths equal. This would violate the premise of the analysis that distance from the downstream end of an island is a co-variate of time since deposition (i.e., age of the land surface). For example, a plant located at 20 m from the downstream end of a 25 m long island would have a standardized location of 0.80 (i.e., 20/25), while a plant located 96 m from the downstream end of a 120 m long island would also have a standardized location of 0.80 (i.e., 96/120).

Despite the having the same standardized location, the two plants occurring at these locations would not be expected to be the same.

Tree Community Analysis

At each scale of analysis, five summary statistics were calculated for use in the tree community distribution pattern analysis (Relative Abundance, Mean and Relative Percent Basal Area, Importance Value, Actual Density). For each analysis, location of a tree was referenced to the downstream end of the island. The location of each tree was determined according to the following procedure:

For trees in sample quadrants A or B:

Location = distance from tail of island to the predetermined point-quarter sample point - (sample point to tree distance X cosine 45°).

For trees in sample quadrants C or D:

Location = distance from tail of island to the predetermined point-quarter sample point + (sample point to tree distance X cosine 45°).

I only considered species that comprised more than 5% of the tree community in analyses.

Relative Abundance- Relative abundance (RA) is a measure of the number of individuals of a species as a percentage of the total number of individuals within a sample increment. Relative abundance curves are a good tool for comparing the pattern of establishment and survivorship of individuals in a given species and between different species. Relative abundance of a species per 10m interval was calculated as in Equation B, Appendix A. Typically, locations for all lifestages of trees (seedling, sapling, adult) were referenced to island tails. However, I also checked for bias in interpretation by referencing locations to the heads of the islands.

The variance of the data was analyzed at the scale of the whole basin. A standard deviation was calculated for each 10 m increment of transect length from the range of values for a species' abundance within a specified 10 m increment from individual islands.

Mean Basal Area and Percentage of Basal Area - Basal area is an estimate of the biomass of an individual. The basal area of each tree was calculated from data on CBH. Mean basal area (MBA) is a measure of the average size of con-specifics within a 10 m increment. Because calculation of a mean is sensitive to individuals of unusual size, extreme outliers were removed from this calculation (Barnett and Lewis 1994). Mean basal area was calculated as in Equation C1, Appendix A.

Percentage of basal area (PBA) provides an index of how dominant a particular species is in a given community. Only trees > 0.05 CBH were included in these analyses. PBA analysis was calculated based on the sum of the basal areas for all trees and all con-specifics within each 10 m interval (Equation C2, Appendix A); thus, the results are sensitive to trees of unusual size. Trees of great size (cottonwood BA > 88.3 cm^2, alder BA > 97.4 cm^2, spruce BA > 77.6 cm^2) were removed from this analysis (Barnett and Lewis 1994). The rule for identifying extreme outliers is shown in Equation A, Appendix A.

The variance of the data was analyzed at the scale of the whole basin. A standard deviation was calculated for each 10 m increment of transect length from the range of the species' MBA and PBA within a specified 10 m increment from individual islands.

Importance Value - The Importance Value (IV) was calculated as the sum of the RA and PBA for each species within a 10m interval. This is a composite measurement that combines the number and size of individuals of a species into a single index. Potential importance values range from 0 to 200. This index allows for comparisons of the relative contribution of a particular species to the entire community. The variance of the data was analyzed at the scale of the whole basin. A standard deviation was calculated for each 10 m increment of transect length from the range of the species' IV within a specified 10 m increment from individual islands.

Actual Density - Actual density is a measure of the number of individuals of a species growing within a given area. Density calculations were based on the mean distance from each point-quarter sampling point to the nearest tree. Density values are influenced by both the number and size of trees. Actual density values were calculated as in Equation D, Appendix A. The results of the density and relative abundance analyses were compared to determine if relative abundance results provide an accurate interpretation of tree distribution patterns. The variance of the data was analyzed at the scale of the whole basin. A standard deviation was calculated for each 10 m increment of transect length from the range of the species' densities within a specified 10 m increment from individual islands.

Location of Rare Tree Species

A tree species was considered rare if it represented less than 5% of the tree community at the scale of the entire basin. The mean location based on rank of the rare tree species was compared to the mean location of all trees to determine if the rare trees were randomly or differentially located relative to the common tree species. Ranked location was based on distance from the tail of islands. When the sample size of rare tree species was too small for inclusion in quantitative analysis, the mean locations of rare and common trees were compared qualitatively. Because tree locations could not be normalized, ranked locations were used in the analysis.

Dendrochronology Investigation

Correlation analysis was used to explore possible relationships between the age of trees and their location on islands, CBH, and the surface area of the island they occurred on.

Mean sensitivity analysis was conducted only for the spruce trees sampled as part of the dendrochronology investigation. This analysis provides a unitless value that measures the variation in annual tree growth each year (Keller and Hendrix 1997). Mean sensitivity was calculated as in Equation E, Appendix A. Values > 0.30 suggests trees are stressed, while values < 0.30 suggest that a tree is "complacent" in its environment (i.e., has not been subjected to stresses since the time it achieved breast height). The location of complacent and stressed trees was compared to search for potential trends in distribution pattern.

Shrub Community Analysis

Shrub distribution patterns were analyzed by direct gradient analysis at each scale of investigation where location on an island was determined as the distance from the downstream end of the island to the mid point of the shrub's long axis. Shrubs were assigned into 10m intervals based on the location of the midpoint along the transect line (Equation F, Appendix A). Summary values used in interpreting shrub distribution patterns were based on the percent of the available transect length occupied by each species per 10 m interval (Equation G, Appendix A). The calculated value will be referred to as abundance in subsequent descriptions. It is important to stress that this value is not a measure of cover by a particular shrub, nor is it a relative value based on the sum of all shrubs within a sample increment. It is computed from the abundance of a shrub species relative to a fixed length of transect line for all transect increments at the specific scale of analysis. Because islands varied in length, sample sizes were often uneven, particularly for intervals >85m. The variance of the data was analyzed at the scale of the whole basin. A standard deviation was calculated for each 10 m increment of transect length from the range of the species' abundances within a specified 10 m increment from individual islands.

Comparisons of Islands From Different Reaches

A percent similarity index (Pielou 1975) was calculated to test the assumption that islands from a river reach high up in the river drainage basin would be more dissimilar to each other relative to the level of similarity between islands in a reach further downstream in the catchment basin. Percent similarity was calculated as in Equation H, Appendix A. Percent similarity values were calculated for each possible combination of islands within the reach of the largest catchment area and the reach of the smallest catchment area. Both reaches had four study islands, and therefore six percent similarity values were computed per reach (Table 6).

RESULTS

Physical Characteristics of Islands

The fourteen islands selected for inclusion in this study are described in Table 3. Surface areas ranged from 51 to 7959 m^2, and length to width ratios ranged from 1.6:1 to 8.3:1. Graphic representations of the study islands are presented in Appendix B. Four islands were in the reach of smallest catchment area, six in the middle reach, and four in the largest catchment reach. Four islands were in the smallest surface area size class, and five in each of the other two size classes.

The sediments of islands PO 1, PO 2, and PP 3 showed trends of fining upwards and fining upstream (Appendix D). The surficial sediments of these islands progressed from sand at the tails of the islands through sandy silt, to silt, and eventually became an organic soils at the heads. There was no discernible pattern for surface or subsurface sediments on the other two islands sampled (PO 4, PP 1). Inter-bedding, where coarse particles over-laid finer particles, was common. Often the smallest surfical sediments were found in close proximity to the largest.

Dendrochronology Investigation

Sixty seven tree cores were collected as part of the dendrochronology investigation. The location, species, and age of each tree, as well as, frequency distribution data on tree ages and the results of the mean sensitivity analysis are presented in Appendix C. The mean age of all adult trees on study islands was 16.2 yr (95% CI = 14.99 to 17.32), indicating that most of the trees established in, or shortly after, 1978. Three spruce trees were considered extreme outliers based on their age (44, 95, and 115 yr old) and were removed from further analysis. The outliers occurred on two different islands. Their locations on these islands were not similar, and the tree distribution patterns of these islands were not similar.

Tree age was only weakly correlated with location from the tail of an island (r^2 = 0.113). Age was moderately correlated with circumference at breast height (r^2 = 0.305). Tree age was not correlated with surface area of the host island (r^2 = 0.0042).

There was no correlation between mean sensitivity values and the location of the trees on the islands (r^2 = 0.018). Nine spruce were identified as having been stressed (mean sensitivities > 0.30) at some time after attaining breast height. There was no identifiable pattern to the distribution of the stressed trees, as they were randomly distributed on four islands from two different river reaches.

Distribution Pattern of Trees

Eleven species of trees were found on sampled islands (Table 2). Out of 1,676 quadrants surveyed, 374 quadrants were empty (no tree or a previously scored tree). *Populus trichocarpa* (black cottonwood), *Alnus tenuifolia* (mountain alder), and *Picea engelmannii* (Engelman spruce) occupied 1,284 quadrants, and the remaining 16 quadrants were occupied by “rare” species. Cottonwood was found on 12 islands, while alder and spruce were found on 9 islands. Two islands had no trees.

Tree Distribution Patterns at the Whole Basin Scale

Based on relative abundance (RA) data (referenced by distance from the tails of the islands), the downstream portions of the islands were dominated by cottonwood (Figure 10 A). The middle sections of the islands were dominated by alder, and areas near the upstream ends of the islands were co-dominated by spruce and cottonwood. The distribution pattern of cottonwood was U-shaped with peak RA of ≈70% at the tails of the islands and ≈50% at 145 m. The distribution of alder was uni-modal with a peak RA of ≈61% at 85 m. Spruce was almost completely absent from the areas closest to the tail of the islands, but RA increased persistently with increasing distance upstream. Spruce RA peaked at ≈45% at 155 m from the tails of the islands. There was a large degree of variability between islands (Figure 10 B). Tree distribution patterns based on density levels were very similar to patterns based on RA data (Figure 11 A,B). Cottonwood had the highest density from the tail of islands to 65 m upstream. Alder was most dense from 65 m to 115 m, and spruce was the most dense tree species from 115 m to 135 m. From 135 m to the heads of the islands, cottonwood and spruce were nearly equal in density.

Cottonwood seedlings occurred predominantly between the downstream ends of the islands to 65 m, and in a small zone at the heads of the islands (Figure 12 A). Alder recruitment, as seedling RA, was limited in amount and location. Recruitment was concentrated from 45 m to 85 m (Figure 12 A). Alder seedlings were completely absent at distances beyond 105 m. Spruce seedlings occurred predominantly from 75 m to 135 m (Figure 12 A). The pattern of sapling distribution (Figure 12 B) closely matched the overall pattern of tree distribution. The RA of cottonwood saplings was highest in the areas closest to the tails of islands, alder sapling RA peaked in the middle of islands, and spruce saplings were largely restricted to the heads of islands. Adult alders were most abundant in the middle of the islands and adult spruce were most common at the heads of the islands (Figure 12 C). It is difficult to interpret the distribution of adult cottonwood due to their scarcity.

The largest average size of each of the three principle tree species were attained in the middle of the islands. Particularly for alder and spruce larger specimens occurred on the upstream halves of islands relative to the downstream halves of islands, although a large degree of variance existed between islands (Figures 13 A, B). On average, cottonwood were the smallest of the principle tree species. The PBA of cottonwood never exceeded 25% (Figure 14 A). Alder constituted approximately 80% of the total tree basal area on islands between the downstream ends of islands and 85 m. Beyond 85 m, the PBA of alder declined commensurately with an increased in the PBA of spruce. Only between 145 m and the heads of the islands did spruce replace alder as the primary contributor of biomass (as PBA) within the tree community of these islands (Figure 14 A). The variance between islands was very high (Figure 14 B).

The importance values (IV) for cottonwood were highest at the ends of islands (Figure 15 A). The IV of alder reached a maximum in the middle of the islands. IV of spruce increased with distance away from the downstream ends of the islands. Alder was the most important tree across the majority of the island surfaces, due to its larger average size and PBA. As with the other analyses, inter-island variablility was high (Figure 15 B).

When tree locations were referenced from the upstream ends of islands, the distribution of cottonwood and alder, based on RA values, were bi-modal (Figure 16). RA for spruce was consistent across most of the island surfaces, but reached a peak abundance in areas closest to the tails of islands.

Patterns at the Scale of River Reaches for Principle Tree Species

Based on RA values, the distribution pattern of each species is rather consistent from reach to reach, particularly for islands in the reaches of smallest and largest catchment areas (Figures 17 ABC). In all three reaches, the peak abundance of cottonwood occurred at the ends of the islands, usually the downstream ends, and the abundance of alder peaked between 75 m and 95 m, regardless of the actual size of the islands. The RA of spruce in all three reaches was low at the tails of the islands and had their greatest rates of increase between 75 m and 125 m.

In the reach of the smallest catchment area, alder and spruce reached their highest density levels (Figure 18 A), and these species also dominated these islands based on RA values (Figure 17 A). This was the only reach where the RA of cottonwood did not exceed 50%. Within this reach, the MBA of cottonwood peaked in the middle of the islands, the average size of alder was greatest at 135 m, and the MBA of spruce was bi-modally distributed (Figure 19 A). The largest spruce were in the middle of these islands and there was a secondary peak of large spruce at the upstream ends of these islands.

In the reach of medium catchment area (622 km^2), cottonwood was the most abundant tree on the downstream halves of the islands, particularly at the tails of islands. Alder was the most abundant on the upstream halves (Figure 17 B). Patterns derived from density values were similar (Figure 18 B). The MBA of cottonwood on these islands remained near zero, while the largest alders occurred in the middle of these islands (Figure 19 B). Spruce was scarce in this reach. However, within the other two reaches, spruce abundance and density rose most rapidly between 75 m and 115 m and no island in this reach exceeded 95 m (Figures 17 B, 18 B). Therefore, I could not determined if the scarcity of spruce was related to island size or reach catchment area.

Based on RA and density levels, islands in the reach with the largest catchment area (842 km^2) were uniformly dominated by cottonwoods (Figures 17 C, 18 C). Alder and spruce were relatively rare in this reach. The highest density for cottonwood occurred at the tail ends of these islands, the highest density of alder occurred in the middle of these islands, and the highest density of spruce was at the heads of the islands.

Each tree species reached its greatest MBA in the reach of the smallest catchment area, and the lowest MBA values of each species occurred in the reach of the largest catchment area (Figures 19 A, 19 C). There were no consistent patterns in the location of the largest trees. In some cases, they were in the middle of the islands, and in others they were close to the upstream ends of the islands. Regardless of the size of the catchment area, alder had the highest PBA on the study islands, with the exception of the most upstream areas of the islands within the smallest and largest basins (Figures 20 ABC). In the 414 km^2 catchment area, the greatest PBA for spruce was found from 155 m to the heads of these islands. On islands of the largest catchment area, cottonwood had the highest PBA between 135 m and 145 m.

IV results (Figures 21 ABC) were very similar to PBA results, and emphasize the overwhelming contribution of alder to the biomass of the tree community. In general, the IV of cottonwood reached its maximum at the ends of the islands, in each river reach. Maximum IV for alder occurred in the middle of the islands, and the IV of spruce was greatest at the upstream heads of islands.

Influence of Island Size

Within all three island size classes, RA and density analysis gave very similar tree distribution patterns (Figures 22 ABC, 23 ABC). On the largest islands, cottonwoods were dominant at the tails of islands, alder was dominant in the middle of the islands, and spruce and cottonwood were equally dominant at the heads of the islands. The medium sized islands (604-988 m^2) were uniformly dominated by cottonwood. Islands in the smallest size class were dominated by alder. In all size categories of islands, cottonwood abundance and density increased within 10 m of the heads of islands, while abundance of alder decreased. The pattern of alder density also was relatively consistent across islands in each of the three surface area size classes. Beginning at the tail end of the islands and moving upstream, alder density increased gradually, but consistently, to 30 m from the heads of the islands, at which point it declined. Spruce densities were near zero on the medium sized islands. However, on the smallest and largest islands, the density of spruce consistently increased with increasing distance from the tail of the island.

With a few exceptions, alder was almost uniformly dominant in terms of PBA and IV across all islands, regardless of island size (Figures 24 ABC, 25 ABC). However, there were no consistent patterns for peak values of PBA, MBA (Figure 26 ABC), or IV for each species in the different size class strata. On islands of the smallest size class, MBA for cottonwood and spruce was always near zero. Alders on these islands were largest at the tail of the islands and smallest at the heads. On medium sized islands, MBA for cottonwood increased slightly with increasing distance form the tails of the islands. Alder increased substantially with increasing distance form the tails of these islands, and MBA for spruce peaked in the middle of these islands. On the largest islands, the largest cottonwoods occurred in the middle of the islands, the distribution of alder MBA was bi-modal, and MBA for spruce increased with increasing distance away from the tails of these islands. On medium sized islands (603-988 m^2), cottonwood had the greatest PBA from 15 m to 25 m, and on the largest islands (1700-8000 m^2), spruce had the greatest PBA at distances > 115 m. On the large and medium islands, IV for cottonwood had a U-shaped distribution. The IV for alder on these islands consistently increased from the tail end of the islands up to 65 m, at which point it decreased. The IV for spruce on the medium sized islands peaked in the middle of the islands, but the peak value was quite low (<50). On larger islands, the IV of spruce increased with increasing distance from the tail end of the islands. Spruce reached its maximum importance near the upstream ends of the largest islands.

Patterns at the Scale of Individual Islands for Principle Tree Species

For each island, RA and IV analysis produced similar results. Only results from the RA analyses are presented graphically (Figure 27). The fourteen islands were arranged according to the catchment size of the reach they occupied, surface area, and length-to-width ratio. No consistent patterns were found regardless of how islands were organized. The tree communities on some islands were very similar, while they were unique on others. Some islands had distinct zones of different dominant species while other islands were dominated by a single species across their entire length.

Location of Rare Tree Species

Sixteen individual trees belonged to rarely encountered species (Table 2). There were two deciduous trees (*Betula papyrifera* Marsh, *Prunus virginiana* L.) and 14 conifers (*Abies grandis* (Dougl.) Lindl., *Abies lasiocarpa* (Hook.) Nutt., *Larix occidentalis*, *Psetuga menziesii*, *Pinus contorta* var. *latifola*, *Pinus monticola* Dougl.). While the mean rank for all trees was 648, the mean rank for individuals of rare species was 871. Due to the extreme disparity of sample sizes (n=1284, n=16), I did not test if these mean ranked locations were statistically significantly different. However, visual interpretation of the data suggests that rare species were located nearer to the upstream ends of the islands relative to the three most common species.

Shrub Community Distribution Patterns

During the study, 27 species in 13 genera were identified (Table 4). Shrubs were placed into one of seven categories. Five shrub categories were single species: *Salix exigua* Nutt., a combination of the sub-species *Salix exigua exigua* and *Salix exigua melanopsis*; *Salix drummondianna* Barratt.; *Salix candida* Fluegge; *Cornus stolonifera* Michx.; and *Rubus idaeus* L. The sixth shrub category, rare *Salix*, was a combination of all other *Salix* species observed. The seventh shrub category was ‘miscellaneous shrubs.’ It included all rare shrubs not in one of the previous six classes. Species of the genus *Rosa* and *Lonicera* were the most abundant shrubs in this class. A generalized view for the distribution patterns of each shrub class at each scale of analysis is presented in Figure 28. All shrub locations are referenced from the downstream end of the islands.

Shrub Patterns at the Scale of the Whole Basin

Salix exigua was the most abundant shrub from the downstream ends of the islands to 75 m upstream (Figure 29 A). *S. candida* was the most abundant shrub between 75 m and 125 m from the tails of the islands. From 125 m to 145 m from the tails of the islands, *S. exigua* again was dominant. Beyond 145 m, *S. exigua, S. candida*, and miscellaneous shrubs were co-dominant. Abundance of *S. exigua* peaked at 25% from 10 m to 20 m, and gradually declined with increasing distance from the tails of islands. Peak abundance for *S. candida* was 23% at 105 m, and this pattern resembled a weak bell-shaped curve.

The distribution pattern of *Salix drummondianna* was very similar to that of *S. exigua* (Figure 29 A). The abundance of *S. drummondianna* peaked at 18% at the downstream end of islands and decreased with increasing distance upstream. Other *Salix* species on these islands were rare. The peak abundance of rare *Salix* occurred at the tail ends of the islands and fell to near zero at locations > 35 m upstream.

Cornus stolonifera was absent at the downstream ends of the islands, but increased in abundance to ≈10% by 55 m and remained at or near this level across the remainder of the islands (Figure 29 B). The abundance of *Rubus idaeus* also increased with increasing distance from the tails of the islands, but never exceeded ≈5%. From the tails of the islands to 30 m upstream, miscellaneous shrubs were scarce. From 40 m to 130 m, miscellaneous shrubs rose to, and maintained, between 6% to 10% abundance. Beyond 130 m, the abundance of miscellaneous shrubs rose sharply to a peak of ≈17% near the heads of the islands.

There was a high degree of inter-island variability in the abundance of each species at similar distances from the downstream end of islands (Figure 29 C).

Patterns at the Scale of Three River Reaches of Different Catchment Areas

In the reach with the smallest catchment area (Figures 30 AB), *Salix exigua* was the most abundant shrub from the downstream ends of the islands to 95 m upstream. The abundance of *S. exigua* peaked at 42% at 35 m. The abundance of *S. exigua* was notably lower on the upstream halves of these islands, despite an increased abundance near the upstream ends. From 95 m to 135 m from the tails of the islands, *S. candida* was the most abundant shrub. The distribution of *S. candida* was roughly uni-modal with a peak abundance of 24% at 85 m. From 135 m to the heads of these islands, *S. exigua* and the miscellaneous shrubs were co-dominant, reaching peak abundances of ≈18%. The pattern for *S. drummondianna* was very similar to that of *S. exigua*. *Cornus stolonifera* and *Rubus idaeus* were relatively scarce on islands in this reach. Abundance of these species peaked at 19% and 11% respectively from 35 m to 85 m. Miscellaneous shrubs were rare near the downstream ends of the islands, reached intermediate levels from 45 m to 135 m, and peaked in abundance from 135 m to the heads of islands.

On the islands from the medium catchment area reach (Figures 31 AB), *Salix drummondianna* was the most abundant shrub on areas near the tail ends of the islands, reaching an abundance of ≈14%. Not withstanding a slight resurgence in abundance at the heads of these islands, the abundance of *S. drummondianna* fell sharply with increasing distance upstream. *S. exigua* also was relatively abundant at the tails of these islands. The distribution pattern of *S. exigua* was U-shaped. On the most upstream portions of these islands, *S. exigua* and *Rubus idaeus* were the most abundant shrubs, reaching abundance levels of ≈14% and ≈11% respectively. The abundance of *R. idaeus* was related to distance away from the tails of the islands. In the middle of the islands, several shrubs were equally abundant. The abundance of rare *Salix* declined as distance upstream increased, and the distribution of *Cornus stolonifera* was uni-modal with a peak abundance of ≈ 5% at 35 m from the tails.

In the reach with the largest catchment area (Figures 32 AB), shrub distribution patterns were somewhat less distinct than in the other two reaches. The entire land surfaces of these islands were a jumble of *Salix exigua*, *S. drummondianna*, and *S. candida*, without any clear zonation between these species. *Cornus stolonifera* was the only non-*Salix* species that was common. The distribution pattern of *C. stolonifera* showed a nearly linear increase with increasing distance upstream, and its abundance peaked at 25% at the heads of these islands. The increase in abundance of *C. stolonifera* was not mirrored by a decrease in the abundance of any other species. *Rubus idaeus* and miscellaneous shrubs were rare on these islands. Their presence increased with increasing distance from the tails of islands, but they never exceeded 3% abundance. Some rare *Salix* species were present near the tail end of the islands but they were absent from these islands at distances > 55 m from the downstream ends.

Patterns at the Scale of Individual Islands

At the scale of individual islands, there was a significant level of inter-island heterogeneity in the distribution pattern of shrubs. Comparisons of each of the seven shrub classes across all 14 islands yielded no detectable patterns in shrub community organization, regardless of how islands were classified (surface area, length-to-width ratio, catchment area). Inter-island heterogeneity was greatest amongst the six smallest islands. Some of the shrub classes did have a certain level of consistency in their distribution patterns when data from only the largest eight islands were considered.

On the larger islands, trends in the distribution of each of the non-*Salix* shrub classes were relatively distinct and repeatable. In almost all cases, *Cornus stolonifera*, *Rubus idaeus*, and the miscellaneous shrubs increased in abundance with increasing distance away from the tail of an island. Furthermore, each of the *Salix* species typically, but not unanimously, reached their peak relative abundance level at or near the ends of the islands, most often at the downstream ends of the islands.

Correlation Between Surficial Sediment Texture and Plant Abundance

Associations of trees and shrubs with surficial sediments was highly variable (Table 5). No plant species was restricted to a single surficial sediment type, nor to a small group of similar sediment types.

Percent Similarity Analysis

The four islands in the smallest catchment area reach had an average percent similarity of 61.3 (Table 6). The four islands from the largest catchment area reach had an average percent similarity of 51.7.

DISCUSSION

Based on our existing knowledge of the inter-relationship between hydraulic connectivity, soil development, and age, and the physiological ecology of floodplain trees and shrubs, I found that plant distribution patterns were a useful proxy for understanding the process of alluvial land surface development. My results strongly suggest that basin wide fluvial dynamics are important forces in the creation and maintenance of mid-channel alluvial islands, the plant communities that develop on them, and the alpha (# of species) and beta (# of habitat types) diversity within a fluvial ecosystem.

Physical Characteristics of Islands

The investigation of sediments provided valuable insight to the physical structure of the study islands. The sediment profiles of three islands matched the prediction of decreasing mean particle size with increasing distance upstream. In each of these cases, sediment inter-bedding was mostly absent, suggesting that the sediment profile developed in the absence of recurrent periods of sediment scour and back-filling (Brierley and Hickin 1992). This suggests that the larger median particle size on the downstream regions of these was due to the lack of fine particle accumulation, not the eroding away of fine particles. Fine particle accumulation is an important step in the development of both A and O horizons, a process that takes time to complete (Longwell and Flint 1963). The observation that the upstream portions of islands had more well developed soil profiles (i.e., maturing humus layers) suggests that these portions of the islands were older then the downstream regions where fine particles had not accumulated, or that the upstream portions of these islands had lower levels of connectivity to the river than the downstream portions of the islands. Because the age of a land surface and the level of connectivity between the land and a river are often correlated (Puhakka et al. 1992), both of these conditions may be true. These similarities strongly suggest that island sediment profiles on these three islands develop in response to forces originating at a scale larger than that of site-specific conditions (i.e., the scale of individual islands). However, the sediment profiles from the other two islands do not follow a similar trend. The sediments on these islands were not arranged in an upward fining nor up-channel fining sequence, and inter-bedding of different size classes of sediments was common. Moreover, the pattern of sediment inter-bedding was not the same on both islands. This suggests that these islands are subjected to periodic scour and fill events and that these processes are influenced by site-specific variables which may mask the influence of forces originating at larger scales of resolution.

Overall, these data suggest that in the absence of scour and fill events, the sediment profile of islands developed as predicted by the hypothesis of the basin wide control of island development. Coarse particles occur downstream of finer particles, and the organic content of sediments decreased downstream. However, scour and fill events, probably mediated by local conditions, can create significant levels of within island heterogeneity in sediment distribution patterns. Two possible variables creating site-specific variability are local channel and floodplain morphology (i.e., gradient, sinuosity, and depth to width ratio) and the geometry of local accumulations of large woody debris. This study did not address the mechanisms regulating where, when, and with what level of intensity, over-island flow, and scour and fill processes could occur.

Correlations Between Sediment Profile and Plant Communities

I found no relationship between sediment texture and plant distribution. The absence of any level of fidelity between plants and surficial sediments suggests that plant distribution patterns are not solely determined by the texture of surficial sediments. Yet, a high level of fidelity between sediment type and the plant communities growing on them was anticipated, because plant distributions and surfical sediment type were hypothesized to be co-variates of a complex gradient of site conditions largely determined by site age and connectivity. Patten (1968 as cited by Freidman et al. 1996), Osterkamp and Hupp (1984 as cited by Freidman et al. 1996), and Harris (1987 as cited by Freidman et al. 1996) found that plant distribution patterns on alluvial surfaces were more responsive to a complex gradient of variables associated with elevation than with surfical sediment size. Because each of the plant species observed on the islands of the Swan River did have identifiable distribution patterns (i.e., spruce was largely restricted to the heads of islands, *Salix exigua* to the tails of islands), my results support the earlier findings that plants are non-randomly distributed on alluvial surfaces but that surfical sediment texture is not a good indicator of prevailing environmental condition. It is possible that nutrient status of sediments would be more correlated with vegetation patterns than sediment texture. Also, these results provide good support for the claim that plants can serve as "functional describers" of prevailing site condition (Amoros et al. 1986) and, possibly, site history, because surfical sediment condition does not overwhelm the influence of other variables.

Tree Growth Ring Investigation

Based on historic peak discharge records of the Swan River and age distribution of sampled trees, there appears to be a very strong link between fluvial dynamics and the establishment of trees. The record high peak discharge for the Swan River was 8,890 cfs (252 m^3/s) occurred in 1974, and the record low peak discharge of 3,430 cfs (97 m^3/s) occurred in 1977. The majority of adult trees established between 1977 and 1980, and strongly suggests the following scenario. In 1974, the flood of record scoured away most of the existing vegetation cover on the alluvial islands of the Swan River, either leaving freshly scoured island surfaces, or completely removing the mid-channel structures. Very few trees on river islands survived the flood, as evidenced by the presence of only three trees (ages 44, 95, 115 yr) established prior to 1974. Trees that may have germinated between 1974 and 1977 did not persist to the time of this study, perhaps because climatic conditions were inappropriate for tree establishment (e.g., the land surfaces were inundated by flood waters at the same time seeds of the pioneering trees were released, and/or inappropriate precipitation volume or pattern, inappropriate solar irradiance; Baker 1990). In the low water year of 1977, tree seeds successfully reached the mid-channel deposits and germinated.

Based on this scenario, the tree and shrub community on islands of the Swan River are in a recovery phase following a significant disturbance event. As such, the plant communities of these islands are an example of a non-equilibrium system, as defined by White (1979 as cited in Hupp 1982) and Pickett (1980 as cited in Hupp 1982). These data reflect the importance of both floods and low water events in promoting the establishment of trees. Floods create the freshly scoured land surfaces needed for successful germination of pioneering species such as cottonwoods (Scott et al. 1993), and the low flow years ensure that the land surfaces are accessible for colonization at the time seeds are released. Bradely and Smith (1986 as cited by Freidman et al. 1996), Baker (1990), Johnson (1994), and Scott et al. (1996) all reported similar scenarios of low peak flow years promoting the establishment of cottonwoods.

Based on mean sensitivity analysis, there was no consistent pattern in the location of stressed and complacent trees (Table C2, Figure C3; Appendix C). Both stressed and complacent trees were located on the upstream and downstream halves of islands, and in several cases, stressed and complacent trees occurred on the same island, and in close proximity to each other. The lack of consistency in these results suggests that spruce growth is influenced by site-specific conditions, not forces originating at a larger scales, such as a river reach or drainage basin. Examples of site specific conditions that could cause stress of a tree are shading by a larger neighbor and water and nutrient availability during the growing season.

Plant Community Distribution Patterns and Island Development

When plant locations were referenced based on distance from the upstream end of the islands, no new patterns became evident. Both *Populus trichocarpa* and *Alnus tenuifolia* had bi-modal abundance patterns that were exceedingly difficult to interpret. The absence of distinct patterns when viewing distributions relative to the head of islands, combined with the presence of strong patterns when plant locations were referenced from the tails of the islands, indicates that, for this study, it was appropriate to use locations referenced from the downstream ends of these islands.

Location of Rare Tree Species

The observation that rare tree species were located closer to the upstream ends of islands provided evidence supporting the conclusion that the upstream ends of islands are older relative to the downstream ends of the islands. Plant abundance in fluvial systems has been related to dispersal ability (Nilsson et al. 1991), and late seral and climax species are typically poorer dispersers than pioneering and early seral species (Walker et al. 1986). Each of the 16 rare trees are mid- to late-seral species or climax species. These species would be expected to occur more frequently on older land surfaces relative to younger surfaces, either through chance events such as the increased likelihood of a seed reaching an older land surface relative to a younger surface, or because the older surfaces provide environmental conditions more suitable for these species. Site specific conditions such as level of connectivity (i.e., seral and climax species will not commonly occur on frequently disturbed areas), or competitive exclusion by more well established pioneering and early seral species (Chapin 1994) may lead to differential distribution of rare species verses common species.

Seral Stage of Principle Plant Species

Many of the plant species observed on the study islands posses a unique collection of life history traits that relegate them to a distinct seral role (Table 2). Pioneering species have evolved a number of characteristics that allow them to quickly reach, colonize and thrive on recently exposed, disturbed, and/or deposited land surfaces. A typical pioneering plant produces many small seeds that often have morphological adaptations such as papyrus (tufts of small hairs that increase surface area), and the seeds are well dispersed by wind and water (Fenner 1987). Many plants can spread by clonal means (i.e., well spaced ramets and/or adventurous roots; Stocklin and Baumler 1996), tolerate low nutrient levels (Kalliola et al. 1991), and are not shade tolerant (Walker et al. 1986; Rydin and Borgegard 1991; Chapin et al. 1994). Furthermore, plants that have evolved as pioneering species in fluvial systems typically can resprout from stumps; fallen branches may re-establish by producing new roots. Members of the family *Salicaceae*, including *Populus trichocarpa* and many species of *Salix* posses these traits and are typical pioneers in fluvial systems (Everitt 1968; Nanson and Beach 1977; Scott et al. 1993; Friedman et al. 1995).

The available literature on the genus *Salix* is quite vague on whether or not different species fill different seral roles. For example, relatively little is known about the level of shade intolerance of different willows. Some researchers have shown that micro-site segregation of *Salix* can occur based on site-specific environmental conditions (i.e., Cottrell 1996), and it is possible such segregation may be related to seral role. Within the Swan River, *Salix exigua* (either *Salix exigua exigua* or *Salix exigua melanopsis*), along with *Populus trichocarpa* were uniformly the first plants to colonize recently exposed land surfaces (personal observation), indicating that these species are well adapted as pioneering species. The seral roles of *S. drummondianna* and *S. candida* are less clear.

The majority of research on the genus *Alnus* , suggests alder are seral species (i.e., Cooper 1923, 1931, 1939 as cited in Furlow 1979), that can enter a successional sequence at a relatively early time (Burns and Honkala 1990). However, some researchers have demonstrated that *Alnus* can be a pioneering species (Worthington et al. 1962 cited in Furlow 1979). Research specific to the seral role of *Alnus tenuifolia* is rare, but results consistently suggest it is a seral species (Farjon and Bogaers 1985; Chapin et al. 1994). While none of the shrub species observed on the study islands was specifically identified as an early seral species, it is possible that some of the *Salix* species may fill this role (i.e., *S. candida* or *S. drummondianna*).

The non-Salix shrubs found on the islands of the Swan River (i.e., *Cornus stolonifera, Rubus idaeus*, and members of *Rosa* and *Lonicera*) are typically berry producers. These shrubs rely on animal vectors for seed dispersal, a common trait of seral species (Fenner 1987). These species persist if they can tolerate low light levels associated with the eventual closing of the canopy caused by succession. *Picea spp.* is typically considered a climax species in the Rocky Mountains, although they may exist as persistent late seral species (Burns 1983).

Because the three most abundant tree species and many of the shrub species on islands of the Swan River can be relegated to different seral roles (pioneer, seral, climax), plant distribution patterns seem to be useful as a proxy for the age of a land surface. Recent deposits of alluvial sediments, or those areas recently disturbed by flood waters, should be dominated by *Populus trichocarpa* and *Salix exigua.* As a site matures, and in the absence of disturbance, *Alnus tenuifolia* and potentially *S. drummondianna* or *S. candida* replace *P. trichocarpa* and *S. exigua.* As the successional sequence progresses, *Picea spp.* and the berry producing shrubs become established in increasing numbers, eventually forming a self-sustaining stand where pioneering and seral species are scarce. In this manner, plant community organization reflects the relative age (young, medium, old) of land surfaces. Thus, plant distribution patterns should allows us to re-create the history of island development.

Plant Distribution Patterns

There was a high degree of similarity between the tree and shrub community patterns at each scale of analysis based on results of the abundance analysis. At the basin wide scale both tree and shrub communities were organized in a linear gradient of seral stages on sampled islands. At the scale of different river reaches, there was also evidence of a linear gradient of trees and shrubs arranged by seral stage. The pattern was strong within the smallest catchment area, moderate in the medium catchment area reach, and weak in the reach with the largest catchment area. At the scale of individual islands, there was a high level of inter-island variability in both tree and shrub distribution patterns.

The presence of a distinct linear gradient of plant seral stages at the basin wide scale of analysis provides strong evidence in support of the principle hypothesis that island development is largely controlled by basin scale forces (i.e., islands grow incrementally and plants distribute differentially according to the age/condition of the sediments and/or the level of hydraulic connectivity). It is highly unlikely that a linear gradient of seral stages would develop by chance, ruling out random processes as the principle factor influencing plant community development. Also, such a strong pattern of plant distributions would not be expected if site specific influences (e.g., local channel or floodplain morphology, local geometry of LWD accumulations) were the primary forces driving plant community development. Flood events is an example of a basin wide disturbance that can regulate the incremental growth of river islands, and therefore exert control on plant community organization.

The data presented here strongly suggest the presence of a distinct organizational pattern for both tree and shrubs because plants are not randomly distributed on alluvial islands. Instead, plant establishment, survivorship and/or growth appear to be due in large part to some controlling influence (e.g., nutrient and water availability, solar irradiance level, and/or frequency, duration, and intensity of inundation). Several researchers (Rostan et al. 1987; Kalliola et al. 1991; Puhakka et al. 1992) have demonstrated that these parameters can co-vary with time since deposition, which lends support to the hypothesis that island growth is discontinuous. Based on the high level of conformity between location of peak abundance and the seral role for each plant where seral role was known prior to this study, it is possible to predict seral roles for species not previously documented by other researchers. Based on abundance patterns, *Salix drummondianna* appears to be a pioneering species and *S. candida* an early seral species.

The lifestage analysis of the tree community provides additional strong evidence supporting the principle hypothesis that island development is controlled by forces originating at the scale of the drainage basin. Organization patterns of the various lifestages of the three primary tree species suggests a "wave of colonization" is occurring on these islands. First, within each species, older individuals occur upstream from younger individuals. For example, spruce seedling abundance peaked 105 m from the downstream end of the island, spruce sapling abundance peaked at 135 m, and spruce adults peaked in abundance at 165 m. A similar, yet less distinct, pattern exists for alder. The absence of adult cottonwood makes this analysis impossible for this species. This evidence suggests that there is a gradient of site conditions which regulates the establishment and growth of the various tree species. Each species can only become established, as measured by seedling abundance, where conditions are acceptable. Numerous other researchers (Nanson and Beach 1977, Puhakka et al. 1992, Bornette et al. 1994) have documented that conditions of alluvial landforms change over time, and therefore these results suggest that a temporal gradient exists on these islands, reinforcing the conclusions that the islands of the Swan River are growing incrementally, and that upstream portions are older than downstream portions. Secondly, similar lifestages of the different trees were organized in a linear gradient of seral stages. For example, cottonwood seedling abundance peaked between 5 and 45 m from the tails of the islands, alder seedling abundance peaked 55 to 65 m from the tails of the islands, and spruce seedling abundance peaked 85 to 105 m from the tails of the islands. This patterns is also repeated in the sapling community. The absence of adult cottonwood makes this analysis impossible for the adult tree community. In addition to supporting the hypothesis of a linear gradient of seral organization, this observation suggest that facultative interactions might be occurring. It appears that the recruitment and development of later seral trees is limited to areas immediately upstream from the preceding seral species. Walker et al. (1986) found that surface litter and solar irradiance levels were two environmental parameters that influenced species recruitment to the successional sequence on the floodplain of an Alaskan River. Walker et al. (1986) and Chapin et al. (1994) found facultative interactions were not required to generate the observed successional sequences, but that they could serve to regulate the rate of successional changes. Two potential explanations for why the wave of colonization is not supported by the *Populus trichocarpa* distribution data are that either this species relies on specific environmental conditions (i.e., the preparation of a land surface for successful germination by flood scour) or that selective predation of larger cottonwood by beaver (*Castor canandensis*) may be masking the "wave." Also suggested by the lifestage analysis is that environmental conditions at the heads of the islands prohibit *Alnus tenuifolia* from reproducing itself. The inhibitory effect of alder seedling recruitment may be due to competitive interactions with the developing spruce community or because changes in soil chemistry initiated by the first generation of alder has rendered these areas uninhabitable by a second generation of alder (Cole et al. 1990/91).

In addition to providing strong evidence for the hypothesized linear gradient of seral stages, analyses of abundance data at the scale of the whole basin generated several unanticipated results. The resurgence of pioneering species (*Populus trichocarpa, Salix exigua*) at the upstream ends of the islands was unexpected. One potential explanation for this result is that the heads of the islands may experience relatively high levels of disturbance. River water first impacts an island this area, and it is likely the site of frequent flood scour which preferentially removes accumulations of fine particles and organic matter, while coarse, nutrient-poor sediments are left behind (Bornette et al. 1994). These fluvial forces maybe working to maintain the extreme upstream portions of the islands in a juvenile condition. This idea is consistent with the concept of "fluvial reset" presented by Amoros et al. (1987). Furthermore, established plants in flood scoured areas are subjected to intense physical stresses (Hupp 1982), including anaerobic soil conditions, abrasion by water-borne particles, and/or battering by rafted LWD or ice flows. *P. trichocarpa* and *S. exigua* can both resprout from damaged stumps or re-root from broken limbs and are the most likely species to survive in frequently disturbed areas.

Another unexpected result was that the largest average size of trees was not at the upstream end of the islands. Instead, most often, average size of each of the tree species peaked near the middle of the islands. However, the average size of con-specifics was typically greater on the upstream half of islands relative to the downstream halves of these islands, suggesting that differences do indeed exist between the upstream and downstream halves of islands. The apriori prediction of a linear gradient of dominance by seral stage, as measured by basal area was not born out by the PBA and IV analyses. *Alnus tenuifolia* was the primary contributor of biomass on these islands. However, basal area data for spruce shows a persistent increase in the biomass of spruce with increasing distance away from the tails of the islands. This suggests that areas closer to the heads of the islands are more suited to the environmental requirements of late seral species relative to downstream conditions. These observations provide additional support for the hypothesis that islands grow incrementally. The overwhelming dominance of *A. tenuifolia* may be explained by the fact that members of the genus *Alnus*, through a symbiotic relationship with root-dwelling bacteria, can fix atmospheric nitrogen (Furlow 1979). Therefore, alder may have a competitive edge when growing on alluvial sediments which are often nutrient limited. The results of the density analysis were very similar to the relative abundance results, and support the same conclusions. This suggests that it may be acceptable to use the easier, faster, and less costly methodologies required for relative abundance calculations rather than the more involved procedures required for the calculation of the density of a species.

The results stemming from catchment area stratification provide moderate evidence suggesting a linear gradient of seral stages exists. However, the data were not conclusive, and the contribution of site-specific influences or random processes to plant community development on alluvial islands can not be discounted. Within the reach of the smallest catchment area, both the tree and shrub distribution patterns were similar to the patterns at the scale of the whole basin, and there was good evidence of a linear gradient of seral stages. In the reaches with the two larger catchment areas, the seral organization of plants was less distinct. Patterns based on basal area were similarly influenced by catchment size. On islands in the smallest catchment area, the average size of alder and spruce increased with increasing distance from the tails of the islands. However, in the reaches of larger catchment size, there were no distinct patterns based on MBA and PBA. This supports either of the alternative hypotheses of the study (i.e., that tree community development is controlled by either site-specific or random processes).

In both the tree and shrub communities, as discharge volume increased (measured by catchment area), the abundance of later seral species (e.g., *Picea engelmannii*, *Rubus idaeus*, miscellaneous shrubs) decreased, while pioneering species (*Populus trichocarpa*, *Salix exigua*) became more prevalent. The opposite was also true; as catchment area decreased, later seral species became more abundant. The differences are likely attributable to fluvial reset, whereby river dynamics are maintaining islands lower in the drainage basin in a more early successional condition relative to islands further upstream. However, the specific mechanism whereby fluvial reset is occurring is difficult to identify, as there are at least two different potential explainations. The first is that a threshold value of discharge volume must be exceeded before fluvial reset can occur. This threshold discharge would be less frequently exceeded where catchment areas are smaller, hence the limited abundance of pioneering species on islands higher up in the Swan River drainage basin, while the threshold value would be more frequently exceeded in areas with larger catchment areas as reflected by the uniformly high abundance of pioneering species on islands lower in the Swan River drainage basin. The second potential causative agent for the different abundances of seral stages relates to the speed and intensity with which run-off occurs. Typically, river reaches near the headwaters of a system experience a more rapid rise and fall in discharge volume than downstream reaches (i.e., upstream reaches are more "flashy" than downstream reaches). Downstream reaches, while subjected to higher discharge volumes, do not experience as rapid a rise and fall in the peak value of the seasonal hydrograph. These differences are attributable to the de-synchronous nature of run-off from different tributary streams. Because different tribuarty streams have unique physical characteristics (ranges in elevation, slope, aspect, geology, etc), run-off from the different tributaries is unlikely to reach peak levels at similar times. Therefore, the slope of the rising and falling limbs of the local hydrograph in downstream reaches is not as steep as in upstream reaches. The rate of run-off (i.e., flashiness) between upstream and downstream reaches may play an important role in sediment erosion and transport and the distribution of seeds. To further complicate attempts at identifying the specific mechanism causing the observed fluvial reset of the plant communitities of Swan River islands is that in the Swan River system, the downstream reaches maybe more flashy than upstream reaches, owing to the presence of two large lakes (Holland Lake and Lindburg Lake) in the headwaters of the basin. Both of these lakes are glacial moraine dammed lakes (C. Frissell, personal communication) and outflow from each lake does not equal inflow during the spring snow-melt runoff. Each lake “dampens” the flood-pulse moving through these tributary streams, reducing the level of flashiness of the headwaters. Downstream reaches, where tributaries do not emerge from lakes, may be more flashy than the upstream reaches. It may be this difference in flashiness that causes the difference in plant communities from upstream to downstream. A third potential explaination for the differences observed in the plant communities of islands from different river reaches is that the relative abundance of near-by floodplain vegetation is different, and therefore spatially segregated islands (i.e., upstream vs. downstream) are subjected to different availability of seeds. Data, at the necessary scale of resolution, on the distribution and abundance of floodplain vegetation of the Swan River valley is not available.

Inherent in the hypothesis that the observed upstream-downstream differences in plant communities is caused by discharge volume is the argument that islands further downstream in a drainage basin would be more similar to the immediate neighboring islands than to islands higher up in the drainage basin, because the magnitude of the common influence, discharge volume, would be greater relative to site-specific influences. To test this hypothesis, I calculated percent similarity values for multiple pairs of islands from the river reaches of smallest and largest catchment areas (Pielou 1975). The results of the percent similarity analysis did not support the hypothesis that inter-island heterogeneity would be less between islands lower in the drainage basin relative to islands higher up in the basin. The calculated values are very similar for inter-island similarity from both reaches, and in fact, the islands further down in the drainage basin are less similar. However, these results are not completely representative of the islands, as they rely only on the proportion of the plant community a species represents and not the location or organization pattern of the plants. Based on the information available, neither of the two potential explanations for the differences in the plant communities of upstream and downstream islands can be supported or rejected.

Sigafoos (unpublished data cited by Hupp 1982), from his studies on river floodplains, found that frequent flood disturbance led to higher diversity, probably because floods created a mosaic of habitat patches, with each patch being in a different stage of succession. My results suggest that frequent flood disturbance of river islands reduces the diversity of the plant community. Islands in the reach of the largest catchment area were fully dominated by pioneering species (i.e., *Salix exigua, Populus trichocarpa*) suggesting recent flood disturbance. Late seral species were very scarce, and therefore diversity (as number of species present) was quite low. Many more species, most of which are mid- to late seral species, were present on islands in the reach of the smallest catchment area. The discrepancies in these conclusions probably lies in the fact that floodplains have one boundary in contact with the river and one boundary removed from the river, while an island is fully contained within the active river channel. As such, flood waters are more likely to influence the entire land surface of an island than they are to influence an entire floodplain. Therefore, it is more likely that some portion of a floodplain will advance to a more mature vegetation community, while islands are more likely to be reset.

The results of the catchment area stratification lead to a second observation on biodiversity patterns. Because the islands from the different study reaches were characterized by different abundances of pioneer, seral, and climax species, and discharge volume (as measured by catchment area) was the main variable to change between reaches (floodplain and channel slope, climatic conditions, and large scale geologic condition are all assumed to be relatively consistent across the entire length of the Swan River), the importance of maintaining a natural hydrograph becomes evident if the greatest diversity of habitat types is to be maintained (i.e., high beta diversity). For example, if the annual flood pulse of the Swan River associated with snow melt run-off was dampened by upstream river impoundment, the threshold discharge needed to cause fluvial reset may not be reached. Islands that were characterized by a combination of seral stages (i.e., islands from the reach of 414 km^2 catchment area) would mature to a uniform climax community. Animal (birds, mammals, insects, amphibian, etc.) that must exist in close proximity to resources from both pioneering and climax communities would no longer be able to persist on these islands. Likewise, species that can only persist on islands wholly dominated by pioneering plants (i.e., islands of the 842 km^2 catchment area) would also disappear as these islands matured to later seral conditions. In the absence of flood events, no land surfaces acceptable for pioneering species would be created. The reliance of alluvial islands on disturbance events (i.e., floods and droughts) for maintaining long term stability in of habitat availability provides further evidence of why river islands should be considered examples of non-equilibrium systems (White 1979 as cited in Hupp 1982; Pickett 1980 as cited in Hupp 1982).

Stratification of river islands by surface area failed to generate any distinct patterns. On the larger islands (SA=1700-8000 m^2), the predictions of a linear gradient of seral stages are met. However, in the other two size classes (SA=51-404 m^2 and 603-988 m^2) the land surfaces are dominated by a single tree species. This suggests that either each island emerged in its entirety at one time and is evolving as a cohesive unit, or that incremental growth is occurring but each increment is not significantly different from the others. Also, the prediction that smaller islands would be dominated by pioneering species (cottonwood), medium sized islands by seral species (alder), and large islands by climax species (spruce) was not supported. The smallest islands were dominated by alder, the medium islands by cottonwood, and the largest islands had zones of different dominant trees. The lack of consistency in the results suggests that either tree community development is controlled by site-specific forces or random events, or that surface areas are not good predictors of island age or development processes, and therefore not a good way to stratify river islands. Based on the more consistent results stemming from other scales of analysis, I believe surface area is not a good method for stratifying islands into supposedly similar groups. Possible explanations for the failure to observe the expected patterns on the smaller study islands are that because of their small size, and potentially younger age, stochastic events such as seed rain, or island shrinkage caused by erosion, may account for the high variability in plant communities on small islands. Founders effect has also been suggested as an exlaination of the high variability of plant communities on small river islands (Osterkamp and Costa 1987, Barnes 1991).

At the scale of individual islands, there was a high degree of inter-island variability in both tree and shrub distribution patterns. These results indicate that site-specific forces play a role in creating the observed pattern of plant distribution patterns, and therefore island development. Examples of site-specific forces include the unique morphology of the local channel (i.e., radius of curvature of river bends, depth to width ratio), the arrangement of large woody debris deposits, and possibly, competition between individual plants. Environmental stocasticity also is a cause of small scale heterogeneity. Osterkamp and Costa (1987) reported that the smallest islands of their study were also the youngest and that they were the only ones not to follow an otherwise consistent pattern of island development. Barnes (1991), in a study of 25 river islands in the Chippewa River of Wisconsin, found that smaller islands had greater variability in their tree species composition than did larger islands. These results are consistent with the conclusion of this study that small islands are more variable than large islands. Mertez et al. (1996) had hypothesized that the length to width ratio of river islands could be used as a proxy for the age of an island. However, this study fails to support this hypothesis as the individual islands, when arranged based on length to width ratios failed to show any expected trends (i.e., low L:W ratio corresponding to larger surface area, more climax species, smaller median grain size).

CONCLUSION

Overall, the plant community distribution results strongly support the conclusion that seral segregation of plants on alluvial islands is scale dependent. At basin-wide and reach scales, the data support the hypothesis that distinct plant communities have developed along a linear gradient on the alluvial islands of the Swan River. This suggests that the development of mid-channel alluvial islands is controlled largely by the discontinuous movement of sediments within the river during flood events, a basin-scale process. However, the pattern of vegetation between individual islands was highly variable. Thus, the prediction that all islands would have similar patterns of seral development was not supported. These seemingly disparate results suggest that site-specific factors moderate basin scale forces, and they combine to regulate the development of mid-channel river islands. This scale dependent factor may explain why Puhakka et al. (1992) failed to find seral patterns on alluvial deposits within anastomosed and braided reaches within the Amazon basin. They may not have analyzed their data at the appropriate scale to detect such patterns. Stanford et al. (1996), in their protocol for the restoration of regulated rivers, stated that for flood prone rivers, "...ultimately, biophysical structure is controlled by the inexorable, but highly dynamic, scouring process of cut and fill alluviation." I believe my work provides a strong example of these processes and responses in action.

TABLES

Table 1. Principle and alternative hypotheses.

Principle Hypothesis - Basin wide fluvial dynamics control the development of mid-channel islands.

Predictions:

- Linear gradient of seral plant communities, from climax at the upstream end of islands to pioneering at the downstream end of islands.
- Arrangement of seral communities is consistent across all islands in a basin.
- Trend of decreasing basal area of tree species from largest at heads of islands to smallest at tails of islands.

Alternative One - Site-Specific control of island development.

Predictions:

- Seral communities exist but they are not organized along a linear gradient from climax to pioneering community.
- No repeatable patterns of vegetation development amongst islands.

Alternative Two - Islands emerge at full size. No incremental growth.

Prediction:

- Each island will be dominated by one community type across its entire length.

Alternative Three - Random processes control island development.

Predictions:

- No seral community organization
- No repeatable patterns of vegetation amongst islands.

Table 2. Description of tree species occurring on Swan River islands.

Scientific Name	Common Name	Number of occurrences	Years to reach breast height**	Dispersal mechanism †	Dispersal timing	Seed size (grams/seed)	Seed morphological adaptations / typical niche	Seral role
Abies grandis (Dougl.) Lindl.	Grand fir	1	15	1	NA*	NA	very small wing	climax
Abies lasiocarpa (Hook.) Nutt.	Sub-alpine fir	1	15	1	mid. Sept. to Oct.	0.013	small wing	climax
Alnus tenuifolia var. *incana* Nutt.	Mountain alder and Thinleaf alder	417	4	2	Aug. to following spring	0.00067	small wing, good floatability, prefers full sunlight,	early seral, nitrogen fixer
Betula papyrifera Marsh.	Paper birch	1	NA	1	wind	NA	NA	NA
Larix occidentalis Nutt.	Western larch	1	5	1	Sept. to following March	0.01	large wing	mid. seral
Psetuga menziesii (Mirbel) Franco.	Douglas fir	1	9	1	Sept. to Oct.	0.0104	large wing, needs duff layer for germination	climax

* NA = Data not available.

** Elapsed time from germination to reaching breast height assumes no suppression of juvenile.

† 1) wind; 2) wind+water, 3) animal vector, 4) wind and animal vector.

Table 2 cont.

Scientific Name	Common Name	Number of occurrences	Years to reach breast height**	Dispersal mechanism †	Dispersal timing	Seed size (grams/seed)	Seed morphological adaptations / typical niche	Seral role
Populus trichocarpa Torr.&Gray	Black cottonwood	716	3	2	May to June	0.00065	Papyrus, good floatability, needs recently scoured alluvial sediments for germination; shade intolerant; re-sprout from stump and shoots	pioneer
Picea engelmannii Parry ex Englem	Engelman spruce	149	10	1	Sept.to Oct.	0.0033	Seeds have large wing, usually <10% dispersed more than 100m from parent. Best germination in moderate shade , Preferred soils - moderately deep, well drained, loamy sands; alluvial soils also good.	Typically persistant late seral; can be early seral in some areas.
Pinus contorta var. *latifola*	Lodgepole pine	8	14	1	Sept. to Oct.	0.0023	seritonous cones (fire adapted)	determined by site history
Pinus monticola	Western White pine	2	12	4	Aug. to Sept.	0.0167	moderate wing	mid. seral
Prunus virginiana	Chock cherry	1	NA	3	July to Oct.	NA	seed enveloped in edible fruit	NA

* NA = Data not available.

** Elapsed time from germination to reaching breast height assumes no suppression of juvenile.

† 1) wind; 2) wind+water, 3) animal vector, 4) wind and animal vector.

Table 3. Morphological features of study islands

Island	Surface Area (m^2)	Length:Width Ratio	Size of Drainage Basin (km^2)
PCFC 1	966	5.4	622
PCFC 2	904	1.6	622
PCFC 4	2934	2.5	622
PCFC 5	1950	2.0	622
PCFC 6	51	5.0	622
PCFC 7	232	2.2	622
PP 1	2680	5.2	842
PP 2	1728	2.0	842
PP 3	603	8.3	842
PP 5	353	4.0	842
PO 1	988	2.6	414
PO 2	404	3.2	414
PO 3	620	5.8	414
PO 4	7959	2.1	414

Table 4. Shrubs occuring on islands of the Swan River.

Species	Common name(s)	# of occurrences
Arctostaphylos uva-ursi (L.) Spreng.	Bearberry, kinnikinnick	1
Cornus stolonifera Michx.	Red-Osier Dogwood	103
Crataegus douglasii Lindl.	Hawthorn, Thornapple	1
Juniperus communis L.	Common juniper	7
Linus vercillosa	NA*	1
Lonicera ciliosa (Pursh) DC.	Orange honeysuckle	2
Lonicera utahensis Wats.	NA	8
Pachistima myrsinites (Pursh) Raf.	Mountain lover	1
Rhamnus alnifolia L'Her.	Alder buckthorn	2
Ribes setosum Lindl.	Currant, Gooseberry	2
Ribes lacustre (Pers.) Poir.	Prickly currant, Black gooseberry	1
Ribes spp.	NA	1
Rosa nutkana Presl	Rose	3
Rosa spp.	Rose	2
Rosa acicularis Lindl.	Prickly rose	1
Rosa woodsii Lindl.	Wood's rose	10
Rubus idaeus L.	Red raspberry, American raspberry	52
Salix candida Fluegge	Hoary willow	141
Salix drummondiana Barratt	Drummond willow	118
Salix exigua melanopsis (Nutt.) Cronq.	Dusky willow, Gravel bar willow, Coyote willow	232
Salix exigua exigua Nutt.	Sandbar willow, Gravel bar willow, Coyote willow	26
Salix geyeriana Anderss.	Geyer willow	5
Salix lasiandra Benth.	Whiplash willow	2
Salix lutea Nutt.	Yellow willow	3
Salix planifolia Pursh	Planeleaf willow	1
Salix hybrid**	NA	12
Shepardia canadensis (L.) Nutt.	Buffalo-berry, Soapberry	1

* NA - Not applicable or data not available.

** *Salix* hybrids were those specimens showing distinct characteristics of two or more *Salix* species.

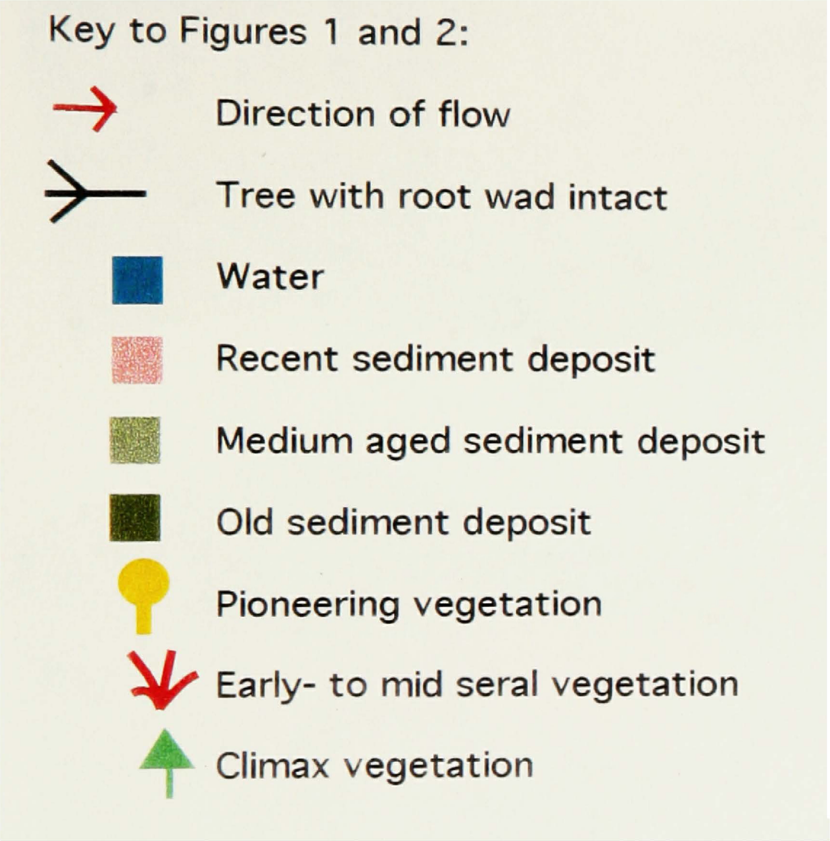
Table 5. Number of occurrences as most abundant tree or shrub per surficial soil type.

Surficial soil type	Organic Soil	SILT	Sandy SILT	Sandy SILT - Silty SAND	Silty SAND	fine SAND	SAND	COBBLE
Dominant tree species	Cottonwood	Alder	Alder (5x)	Alder (2x)	Spruce (2x)	Cottonwood	Alder	Cottonwood (4x)
	Spruce		Cottonwood (3x)		Cottonwood (4x)	Spruce		Spruce (2x)
	Alder (2x)		Spruce		Alder	Alder		Alder (2x)
Dominant shrub species	S. candida	S. drum.	S. exigua (2x)	S. candida (2x)	S. exigua (2x)	S. exigua (3x)	S. drum.	S. exigua (2x)
	Misc. shrubs	S. candida	S. drum. (2x)	S. drum.	S. candida (4x)	S. candida (3x)		misc. shrubs
	S. drum.		S. candida (2x)		S. drum. (3x)			S. candida (2x)
	R. idaeus							S. drum.

Table 6. Percent similarity results.

Catchment Area: 414 km^2		Catchment Area: 842 km^2	
Island Pair	Percent Similarity	Island Pair	Percent Similarity
PO1 - PO 2	63.5	PP1 - PP2	52.6
PO1 - PO3	74.8	PP1 - PP3	71.2
PO1 - PO4	66.4	PP1 - PP5	32.0
PO2 - PO3	61.2	PP2 - PP3	60.4
PO2 - PO4	52.4	PP2 - PP5	41.4
PO3 - PO4	49.8	PP3 - PP5	52.4
Average	61.3	Average	51.7
St. deviation	11.0	St. deviation	16.0

FIGURES



Key to Figures 1 and 2:

→	Direction of flow
≻—	Tree with root wad intact
🟦	Water
🟥	Recent sediment deposit
🟩	Medium aged sediment deposit
⬛	Old sediment deposit
●	Pioneering vegetation
↓	Early- to mid seral vegetation
▲	Climax vegetation

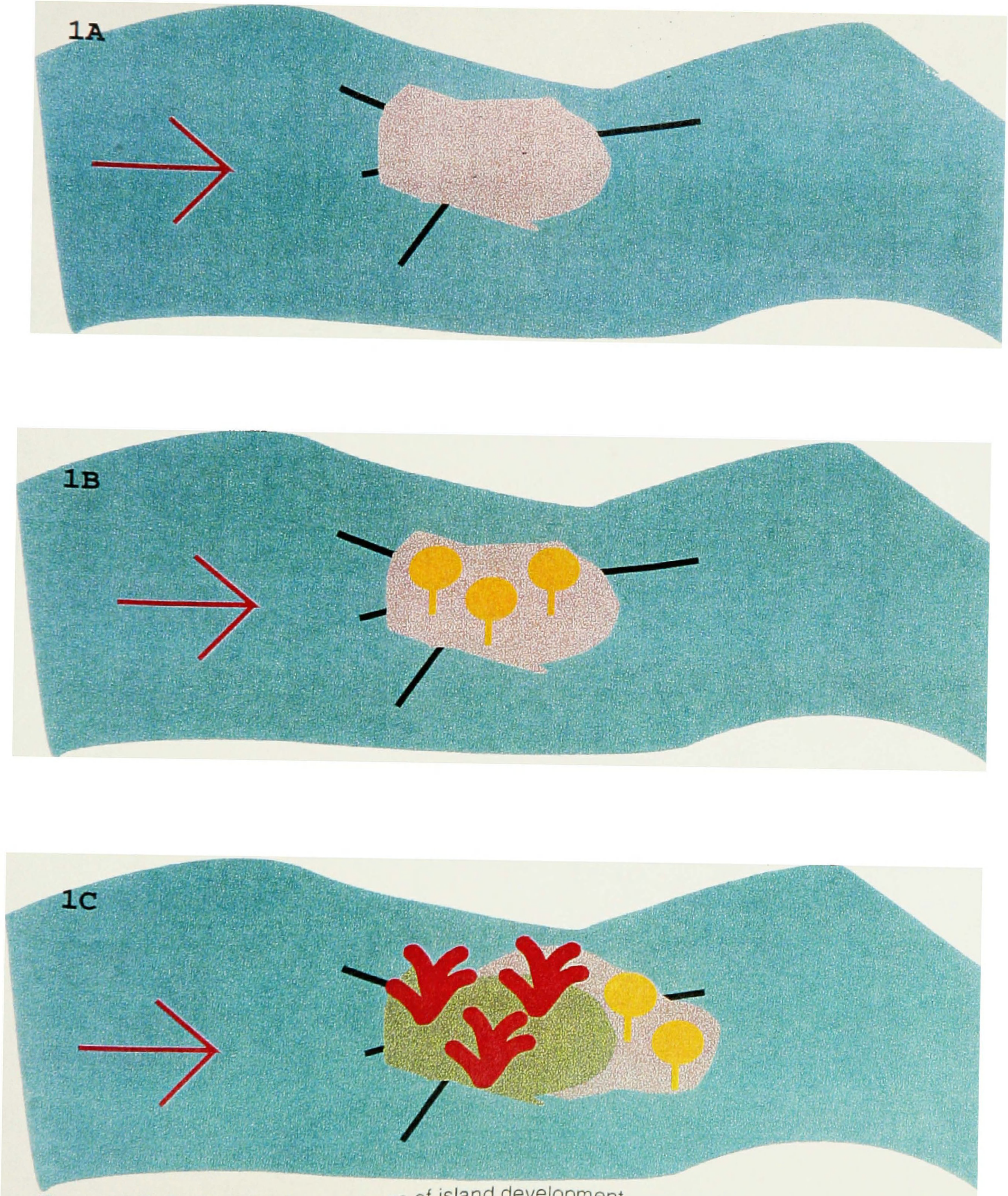


Figure 1A,B,C. Hypothesized process of island development.

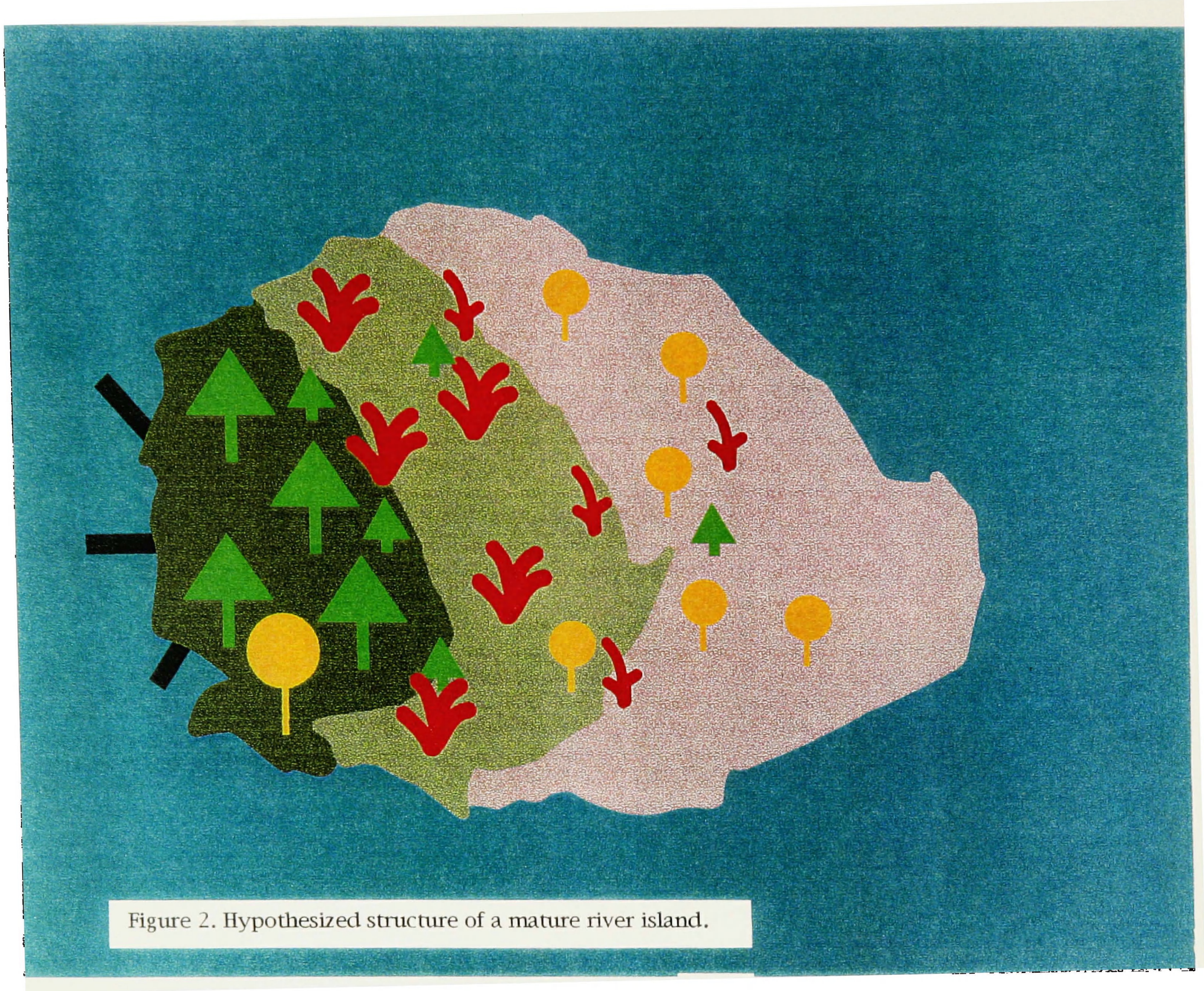


Figure 2. Hypothesized structure of a mature river island.

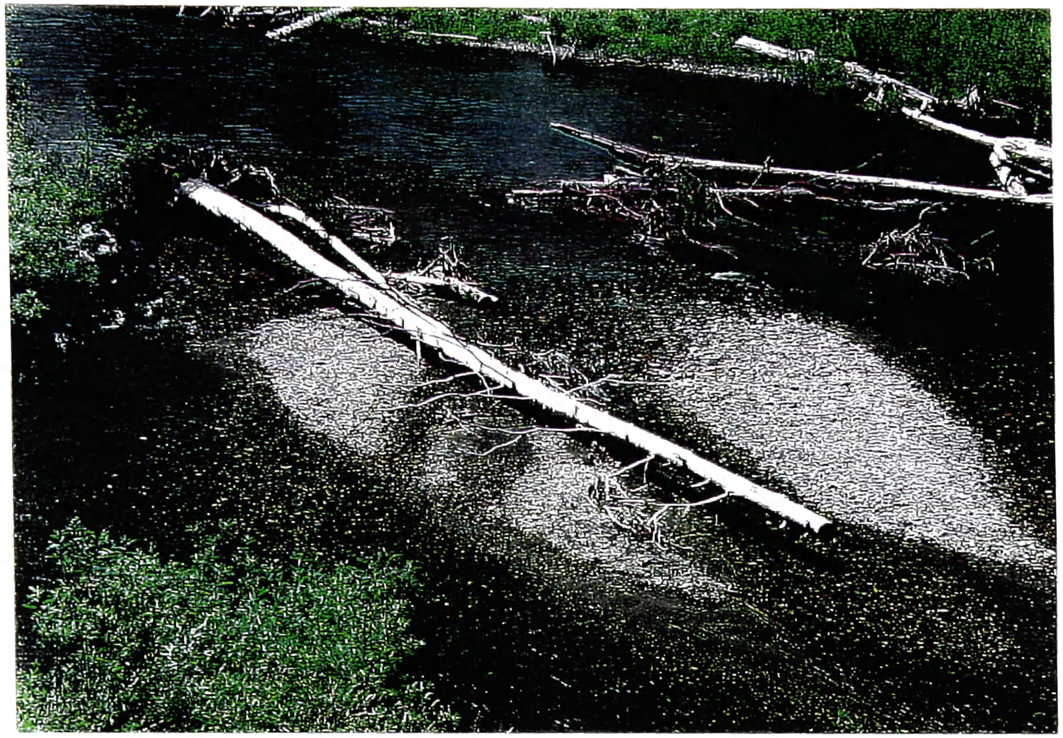


Figure 5. A recently emerged gravel bar formed downstream from a piece of large woody debris.

Figure 4. A gravel bar in the initial stages of colonization by plants.

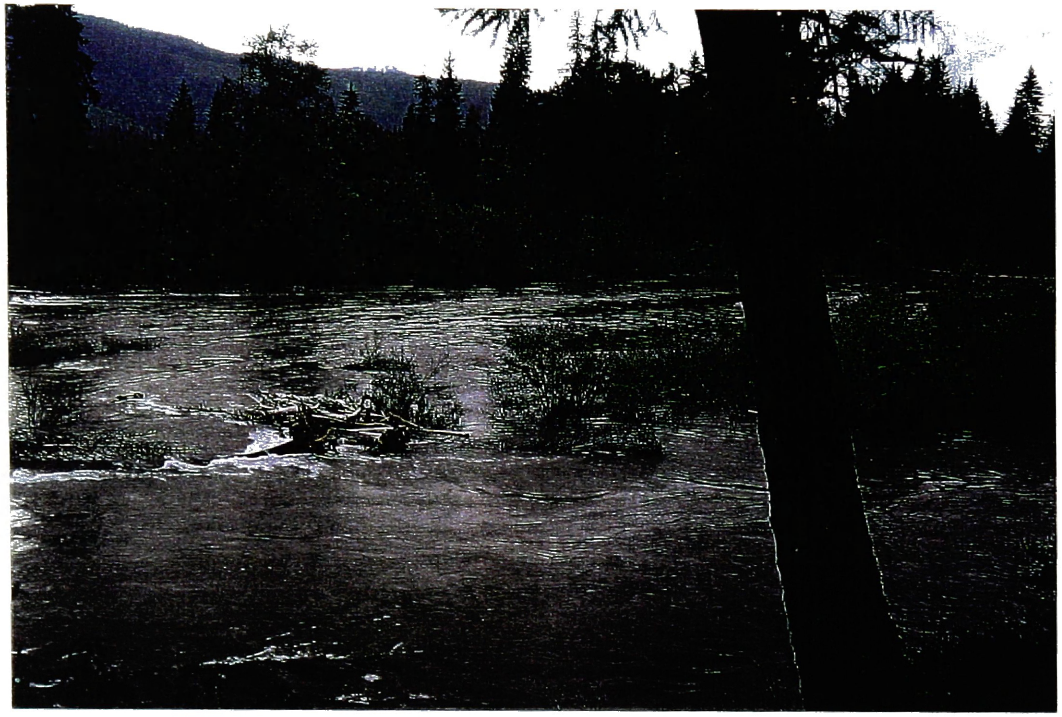


Figure 5. Sediment rich flood waters inundate an island surface. The head of the island is on the right.

Figure 6. A river island at low water. Upstream head of island is on the left.

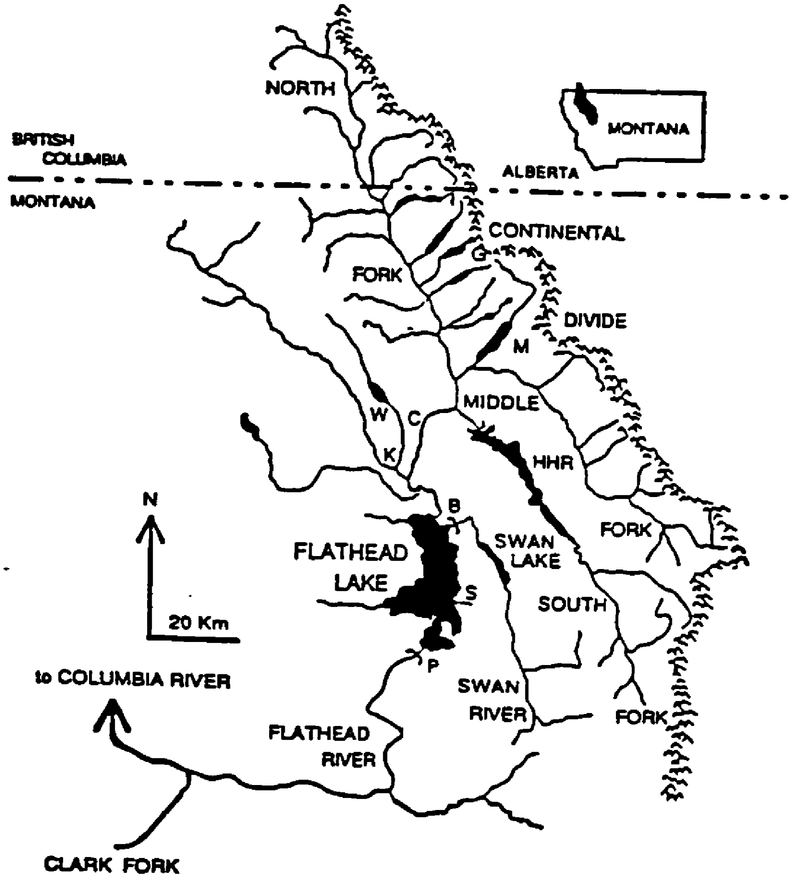


Figure 7. Map showing location of Swan Lake and the Swan River sub-basin in the Flathead River catchment basin in Montana, U.S.A. and British Columbia, Canada.

Map reproduced from Butler, N.M., J.A. Craft, and J.A. Stanford 1995. A diagnostic study of nutrient loading at Swan Lake, Montana. Flathead Lake Biological Station Open File Report 138-95.

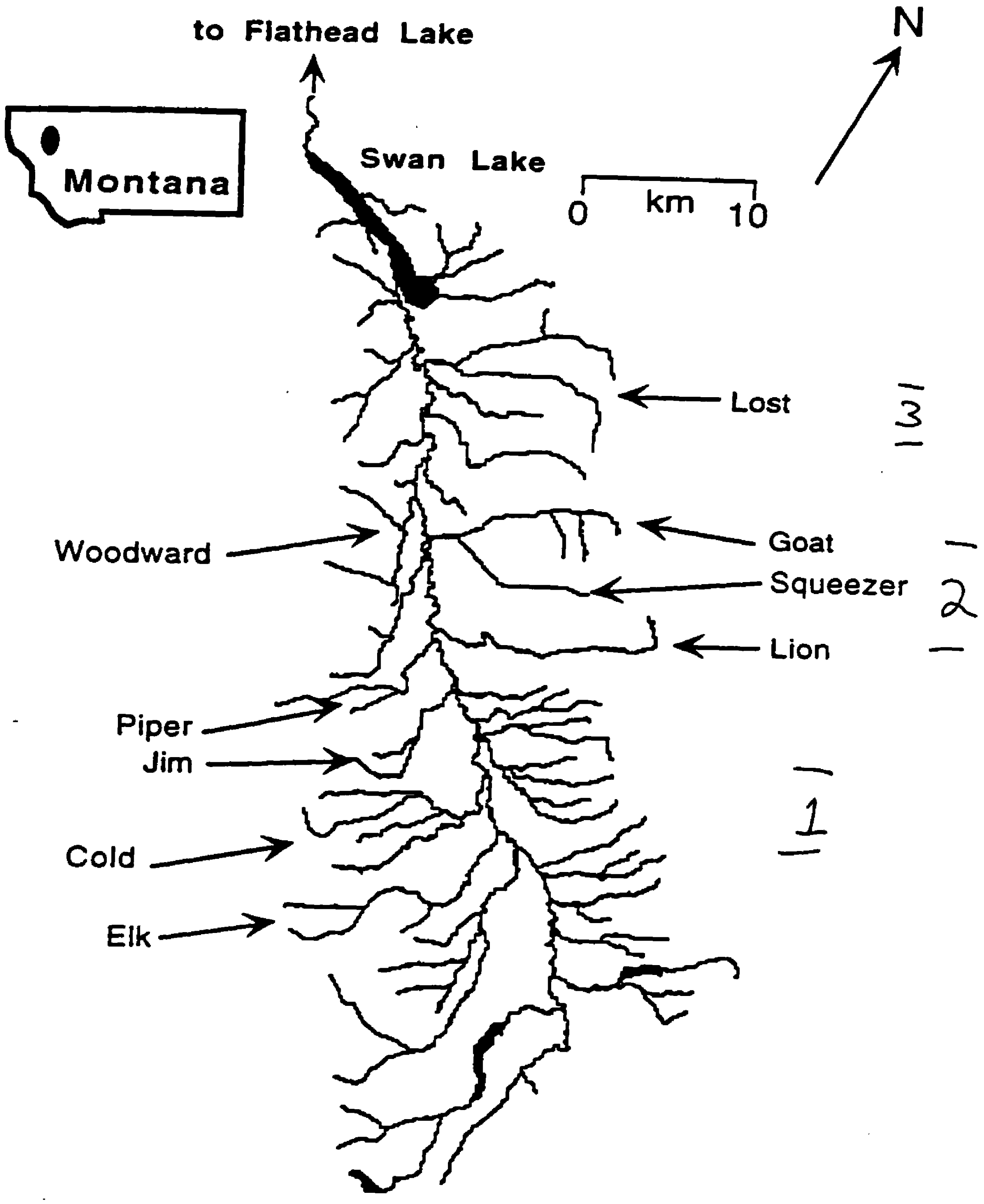


Figure 8. Swan River basin. The three study reaches are identified: 1) catchment area 414 km^2; 2) 622 km^2; 3) 842 km^2. Map provided by C. Frissel, Flathead Lake Biological Station, University of Montana.

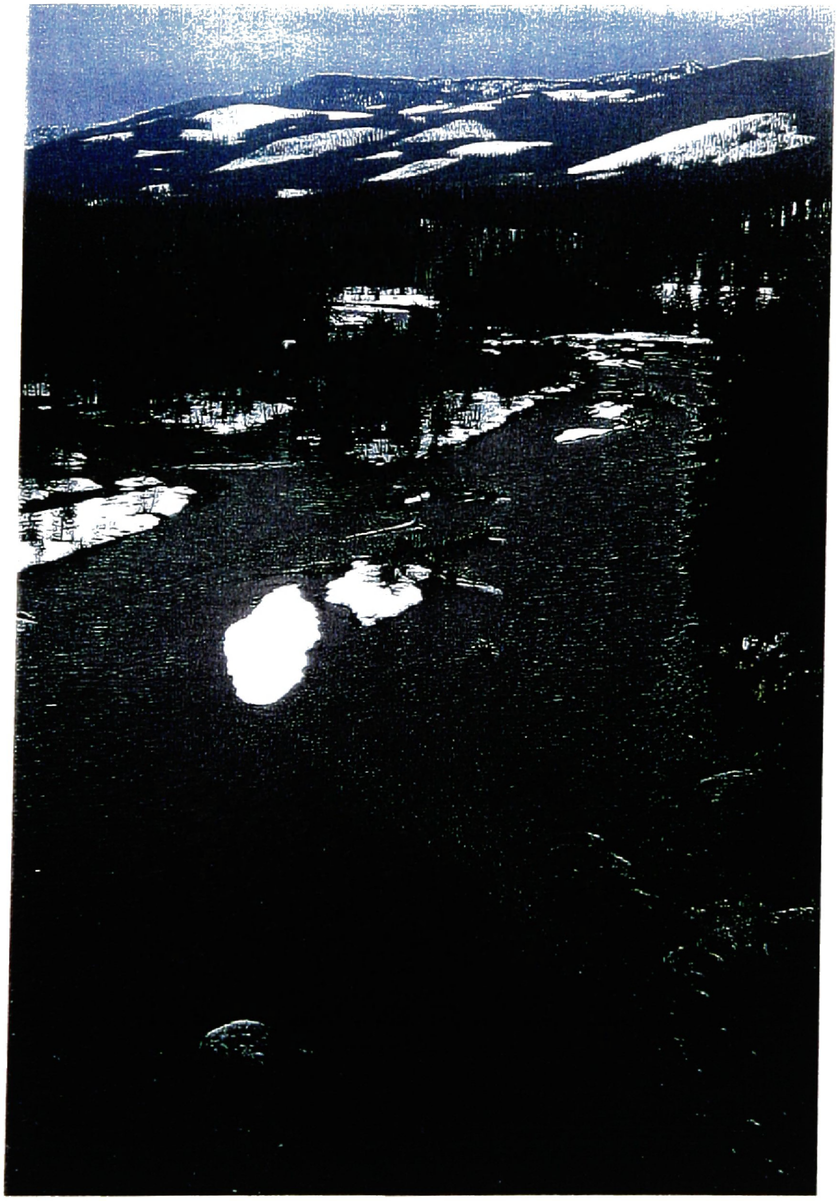


Figure 9. Overview of the Swan River and two study islands. The island in the foreground has been bisected by an overflow channel.

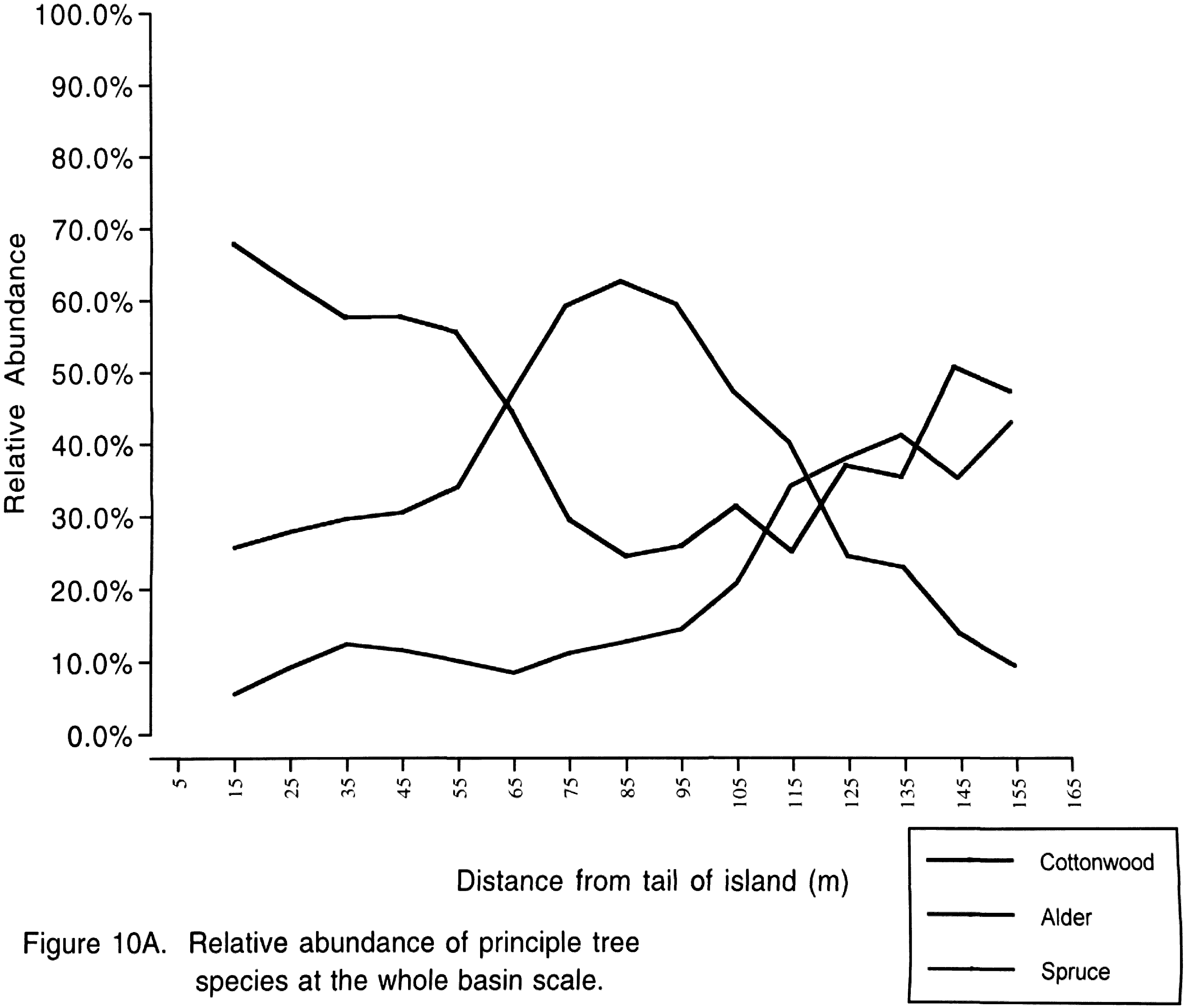


Figure 10A. Relative abundance of principle tree species at the whole basin scale.

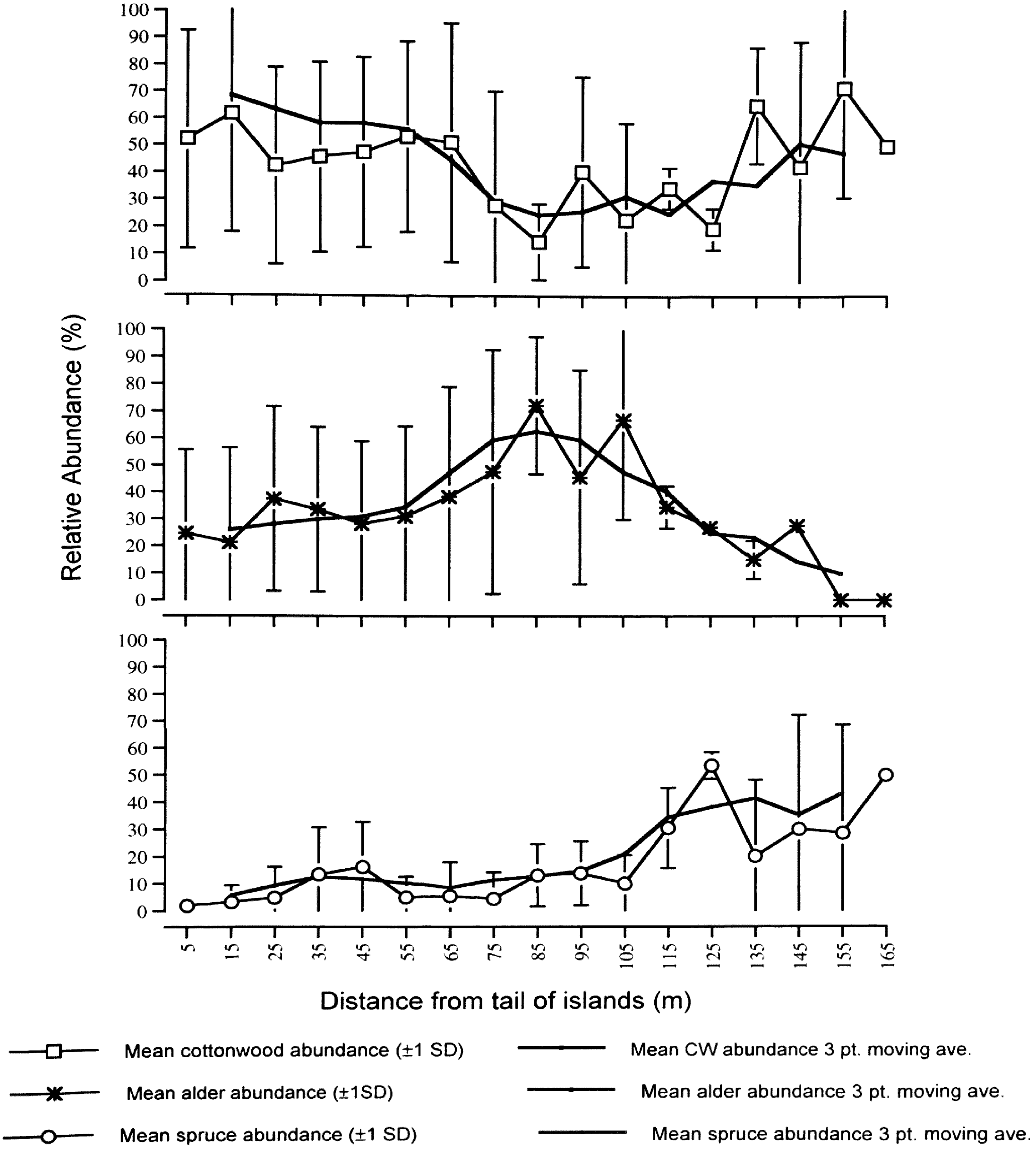


Figure 10B. Relative abundance of trees at whole basin scale.

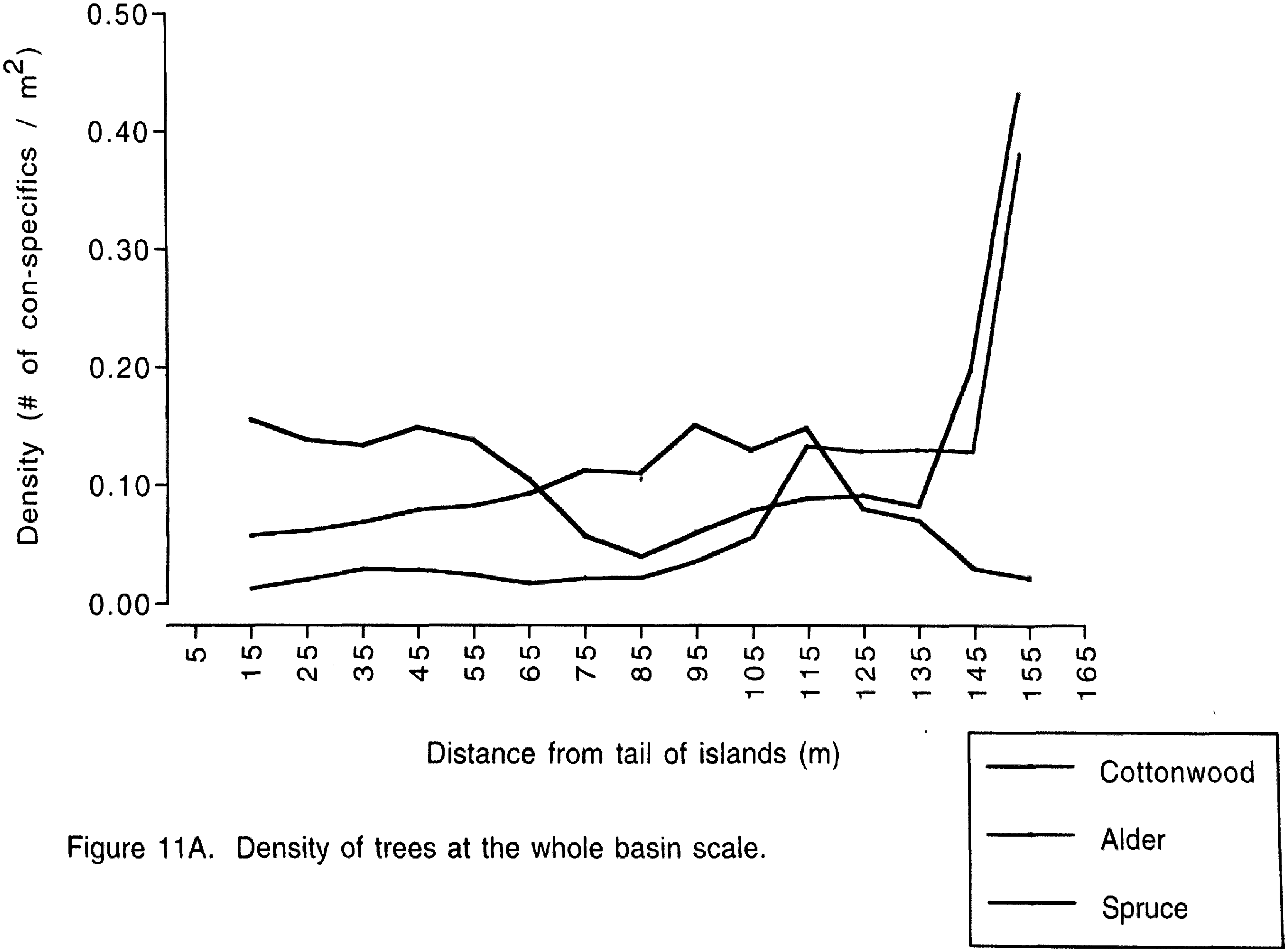


Figure 11A. Density of trees at the whole basin scale.

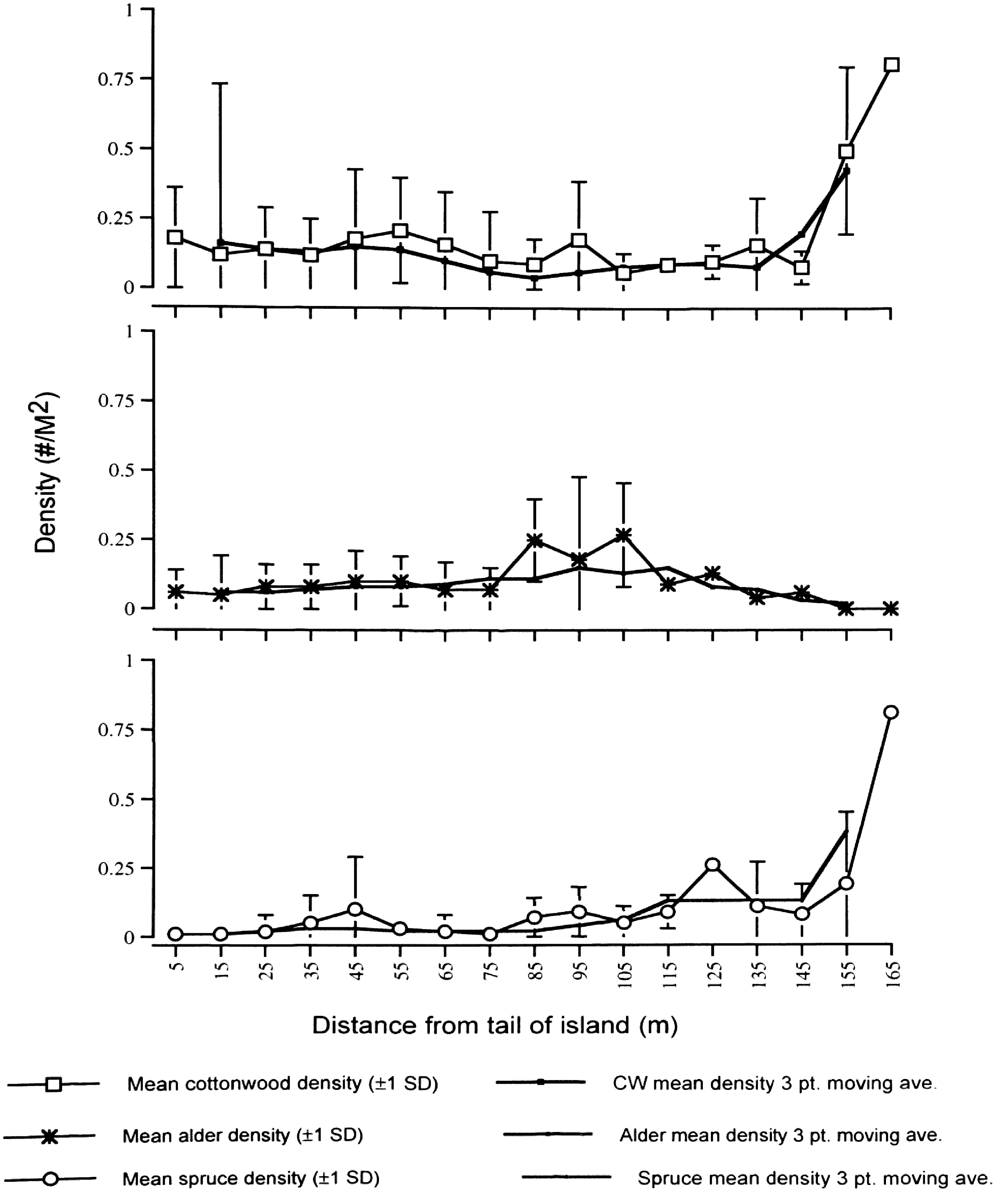


Figure 11B. Density of trees at whole basin scale.

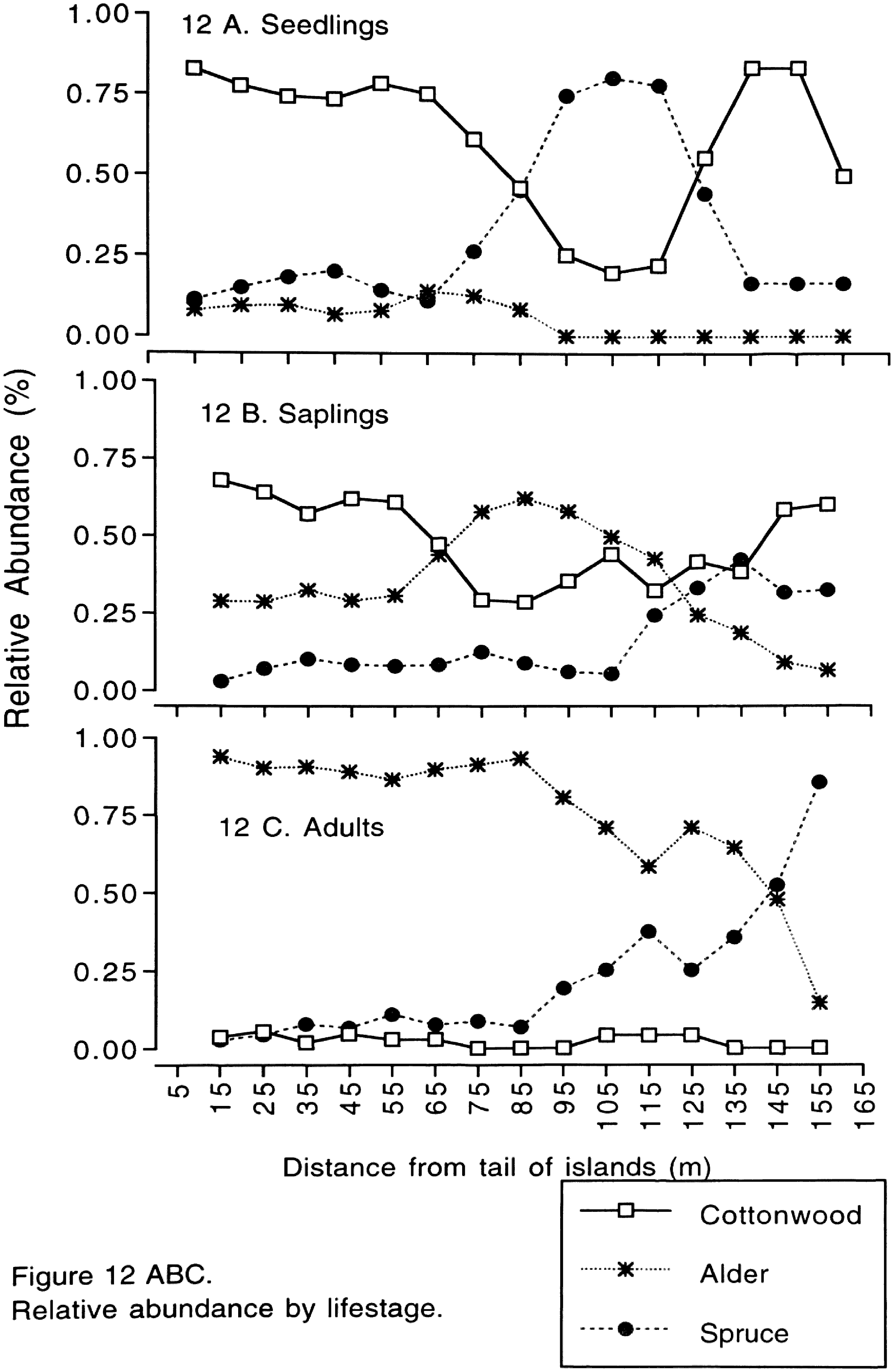


Figure 12 ABC.
Relative abundance by lifestage.

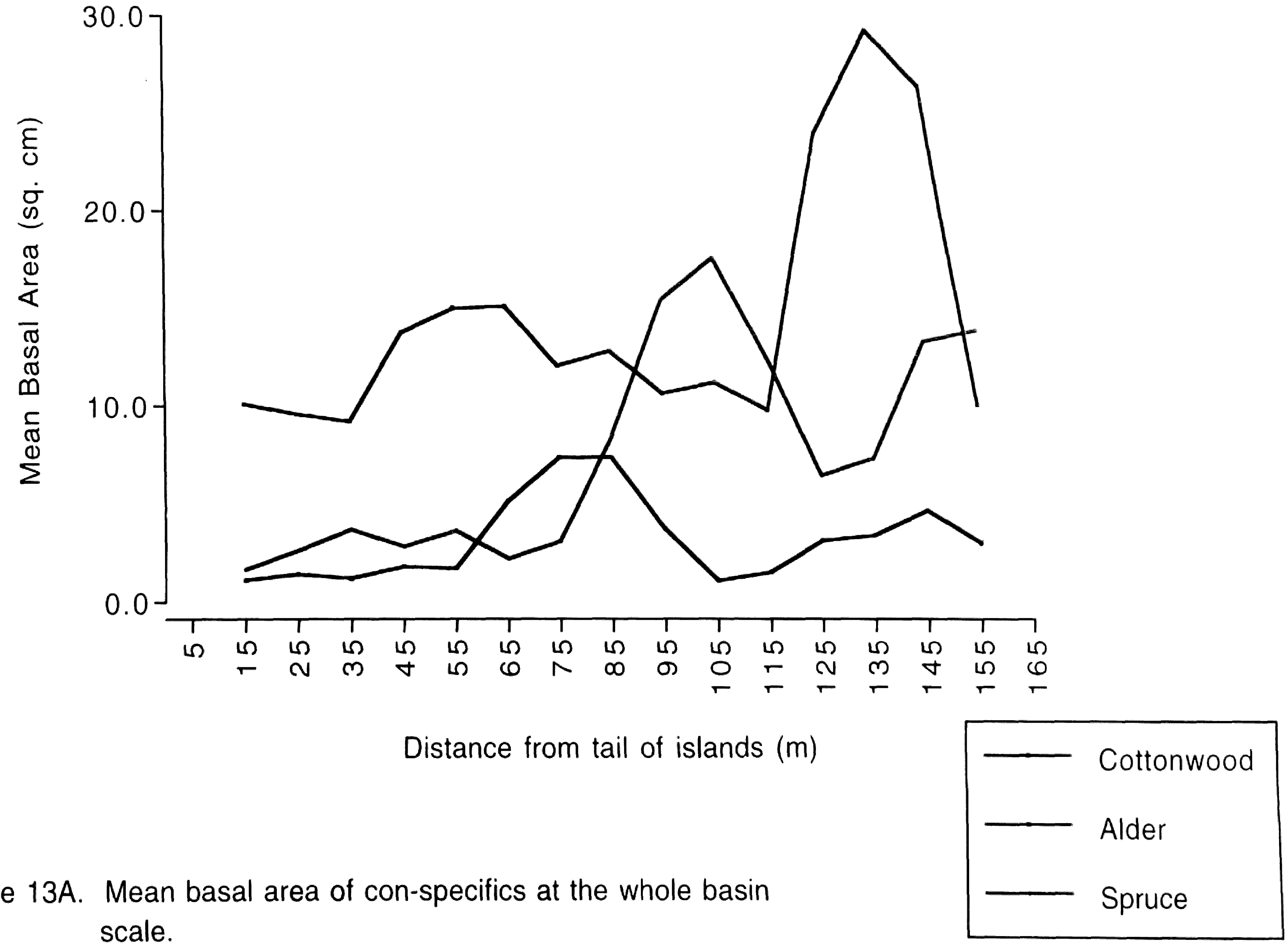


Figure 13A. Mean basal area of con-specifics at the whole basin scale.

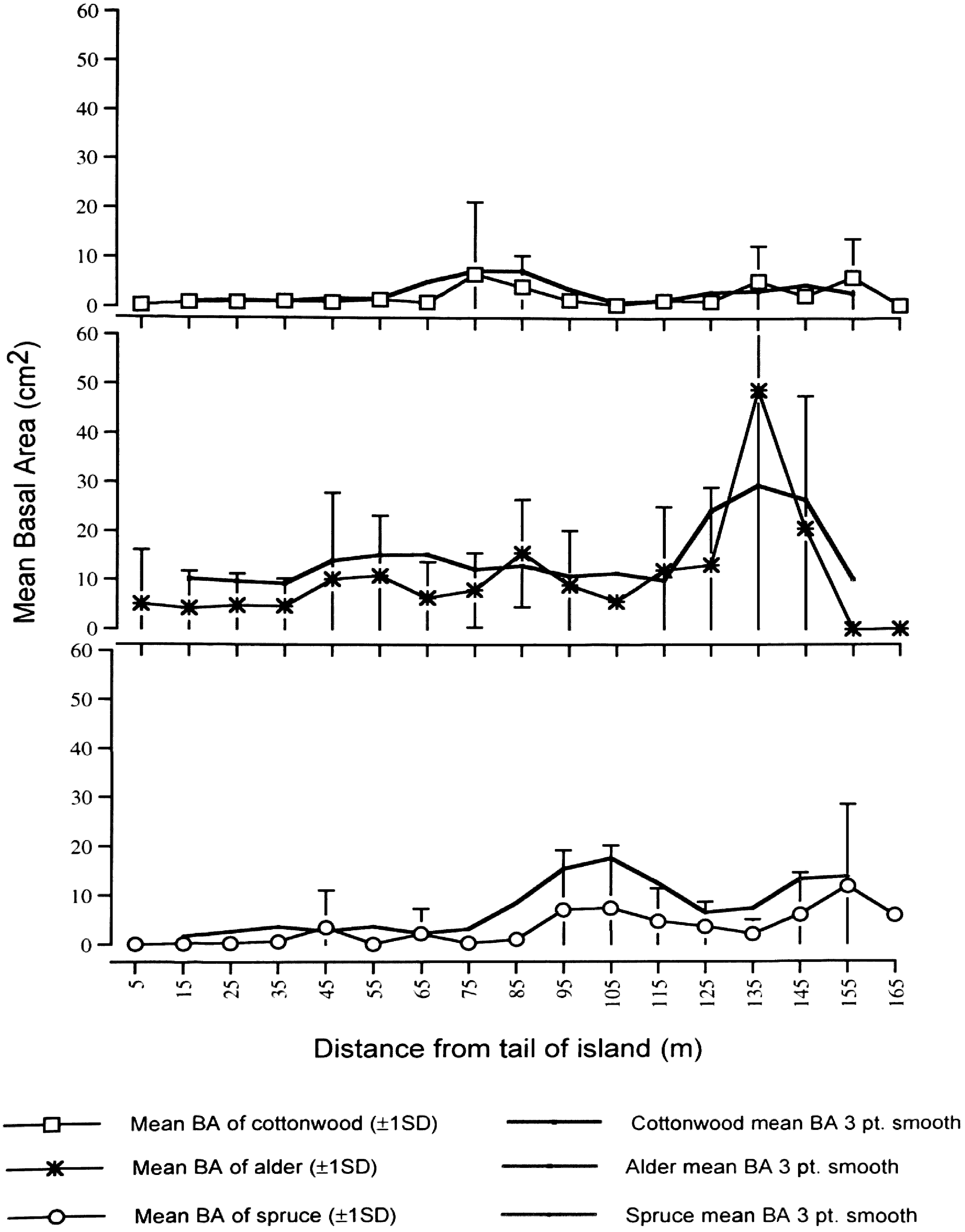


Figure 13B. Mean basal area of trees at the whole basin scale.

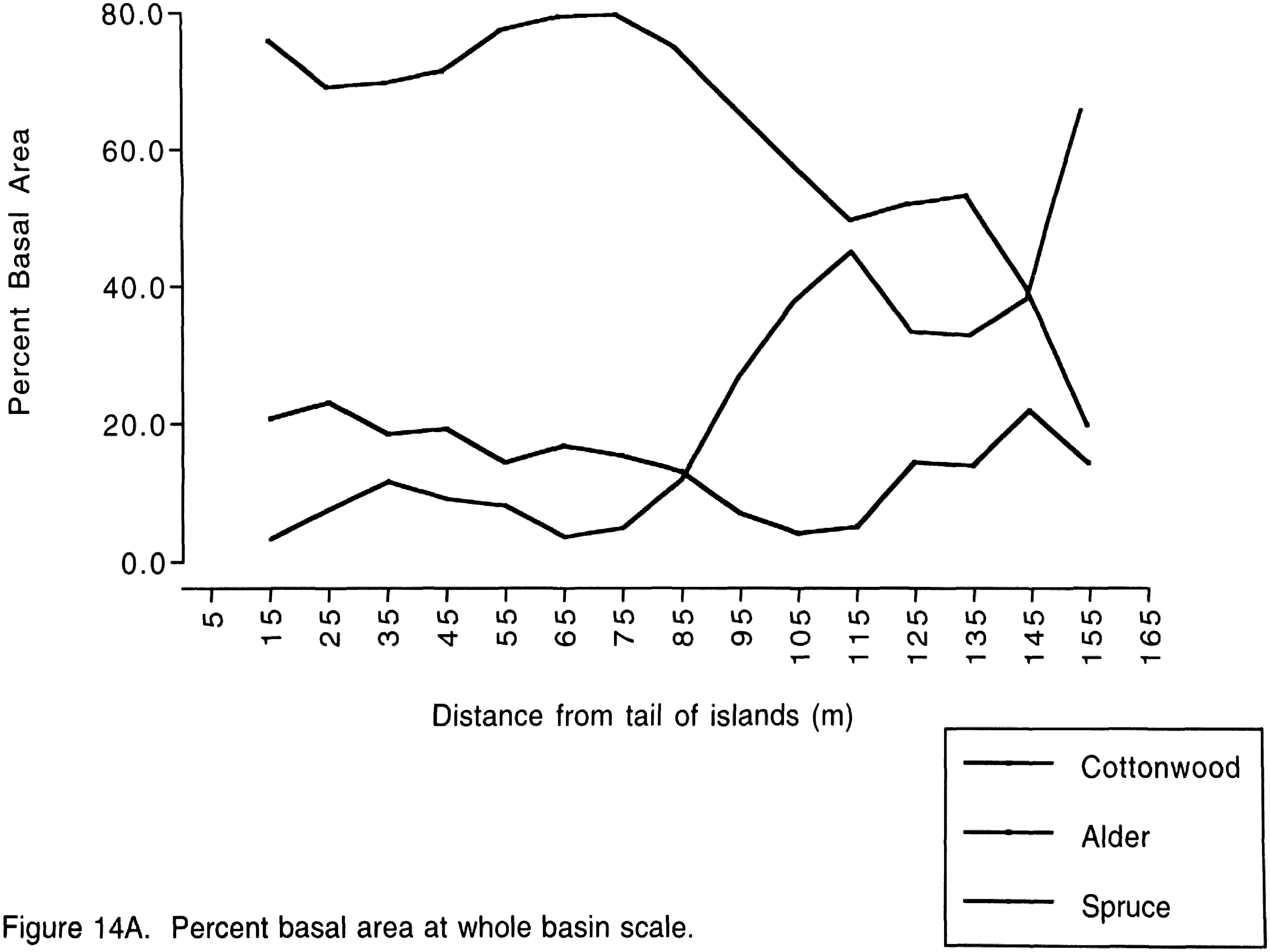


Figure 14A. Percent basal area at whole basin scale.

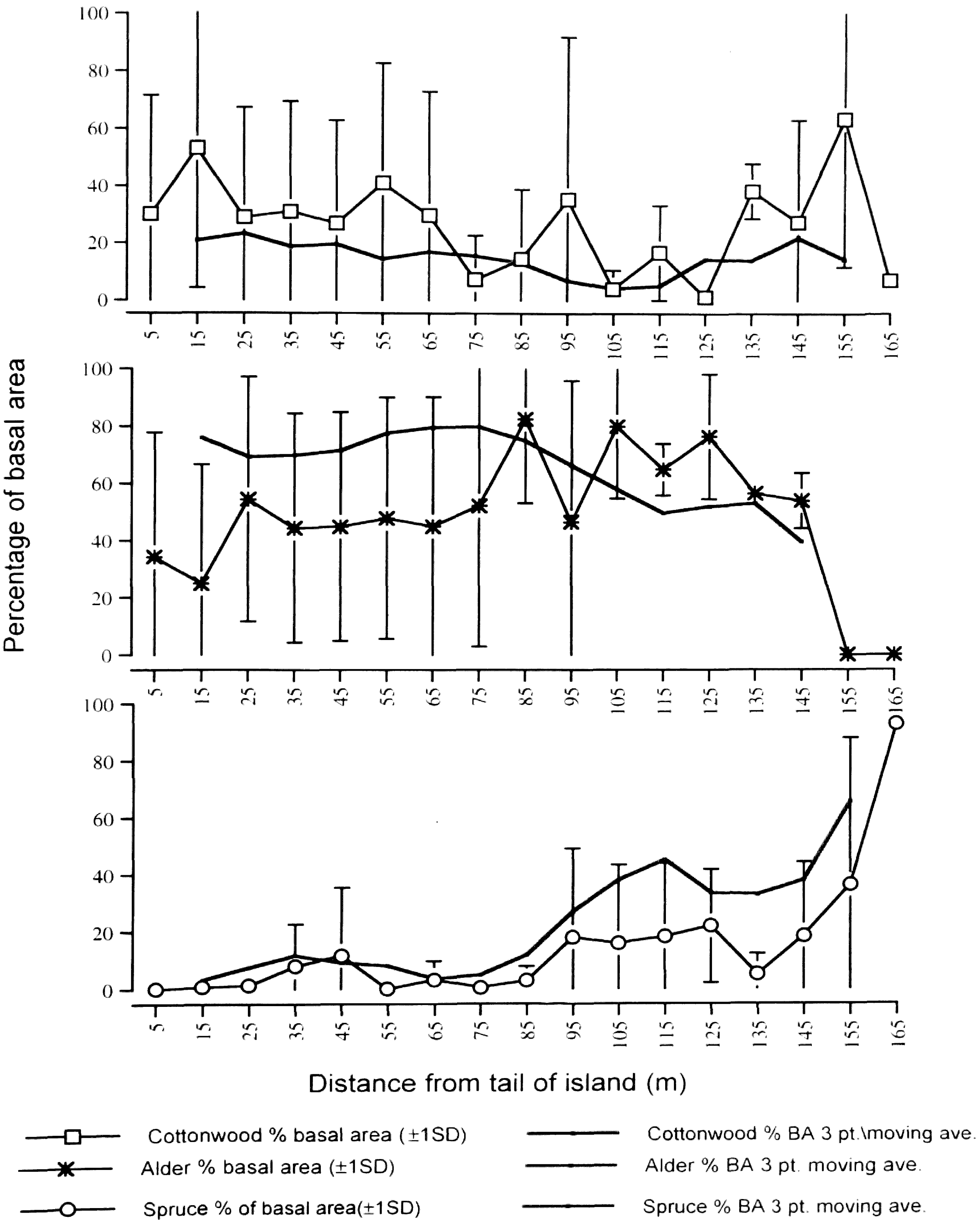


Figure 14B. Percentage of basal area of trees at the whole basin scale.

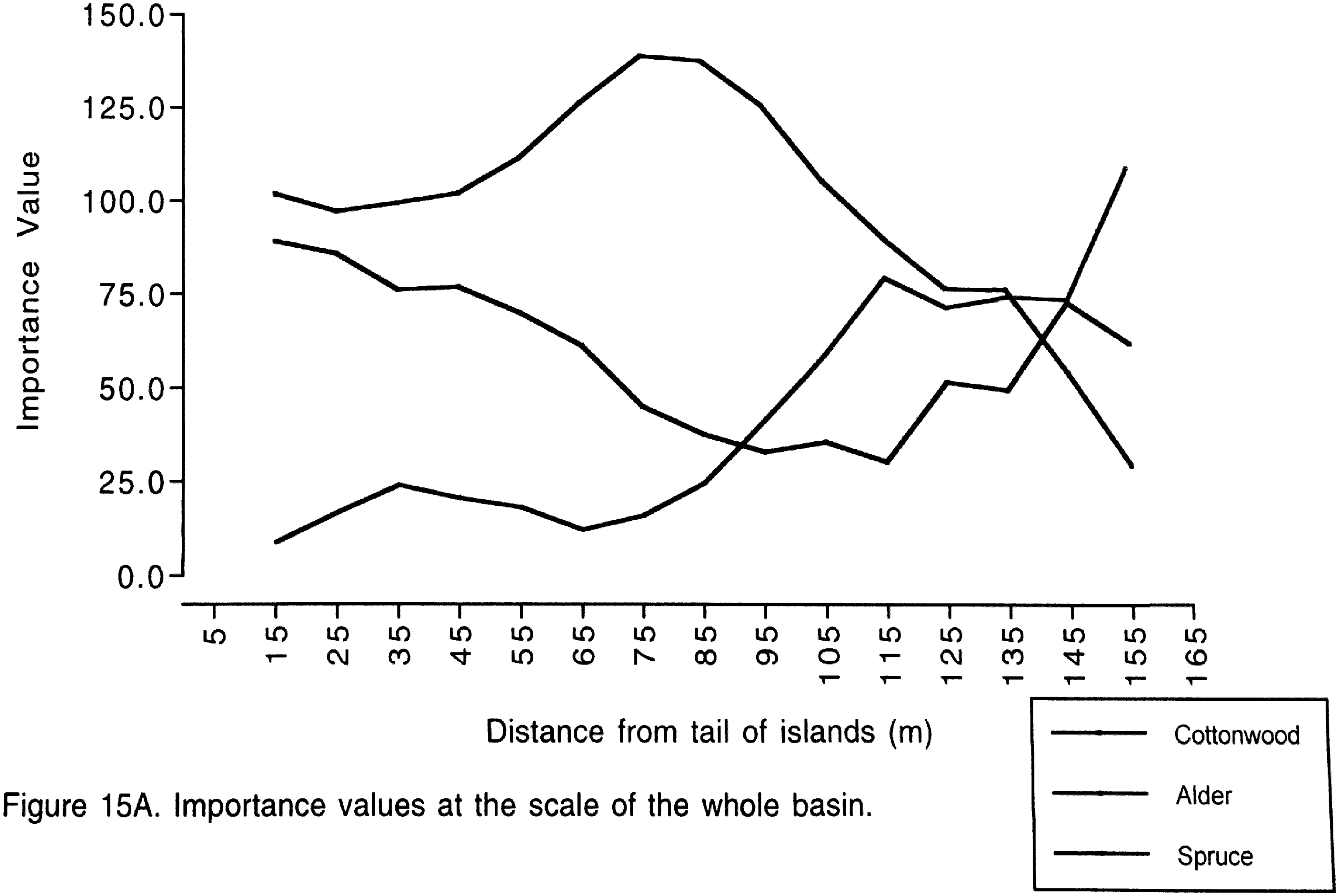


Figure 15A. Importance values at the scale of the whole basin.

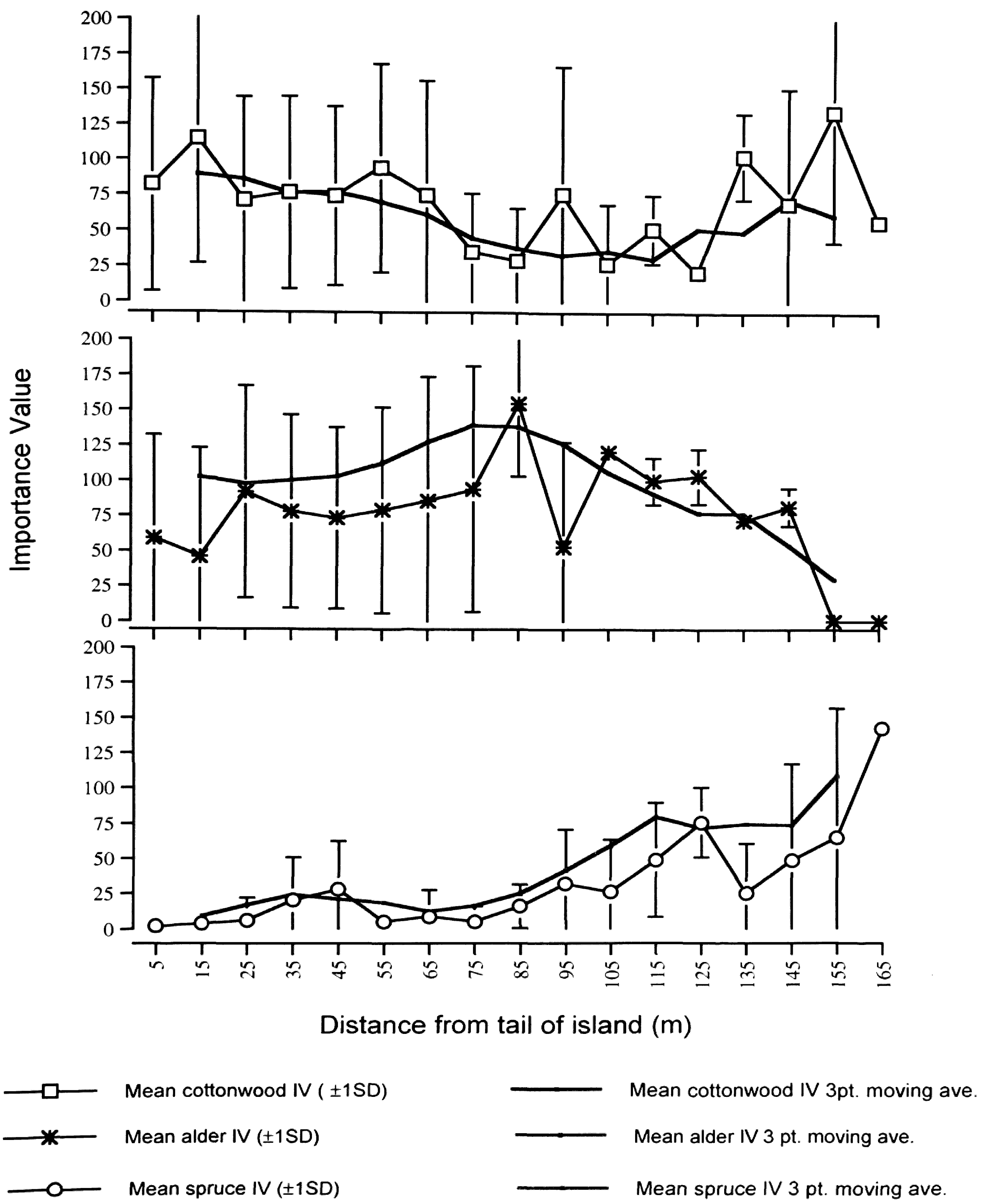


Figure 15B. Importance values of trees at whole basin scale.

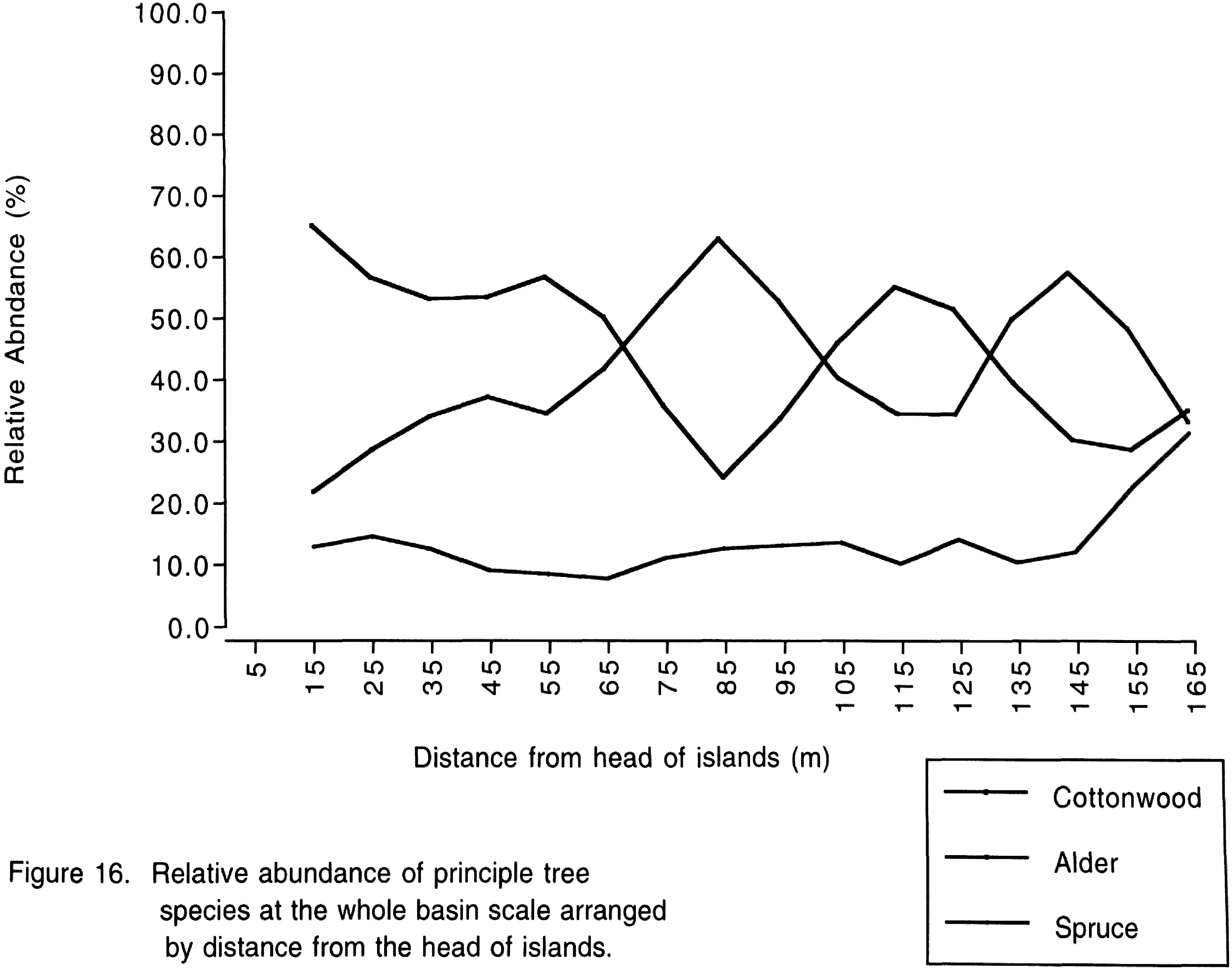
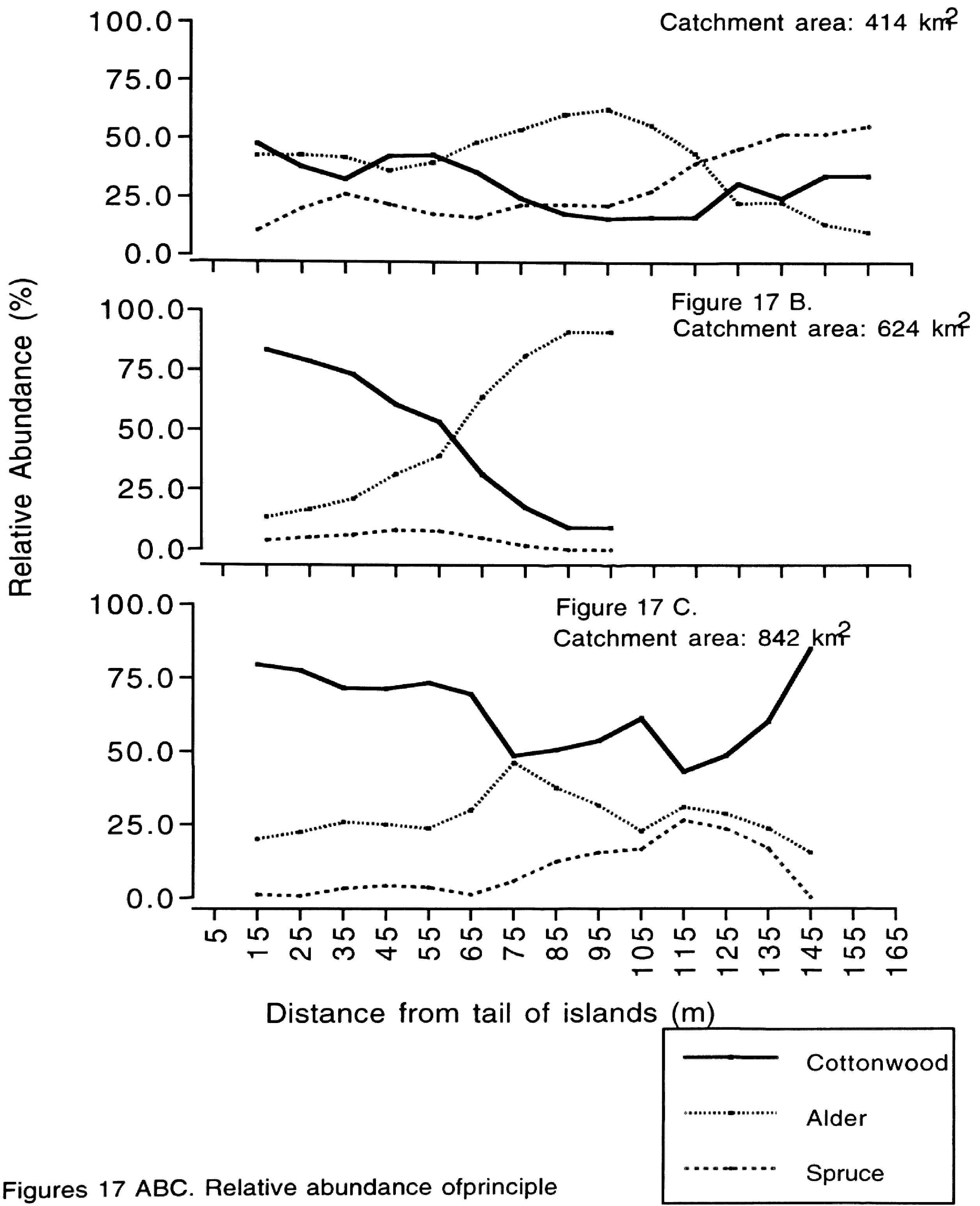
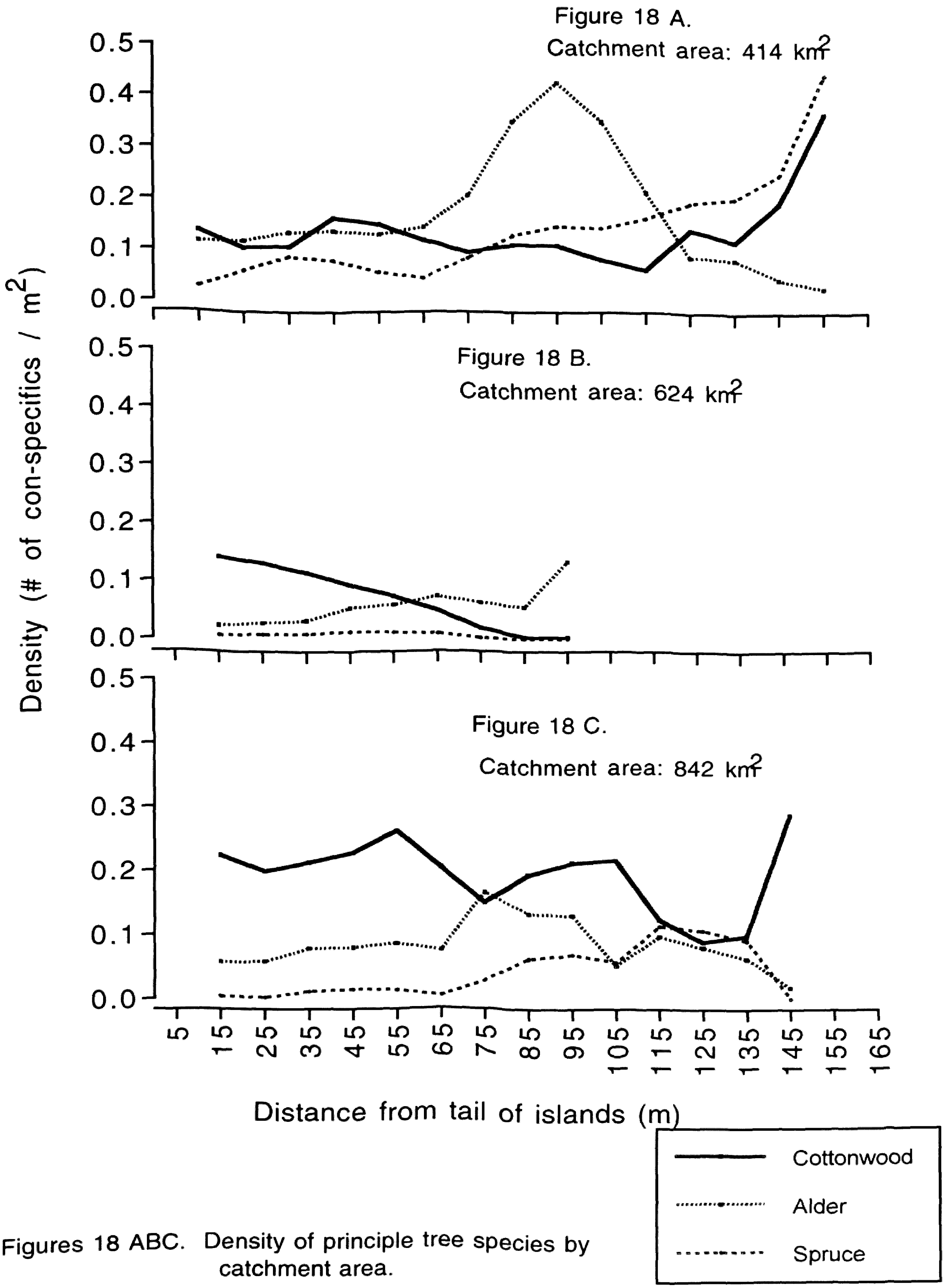


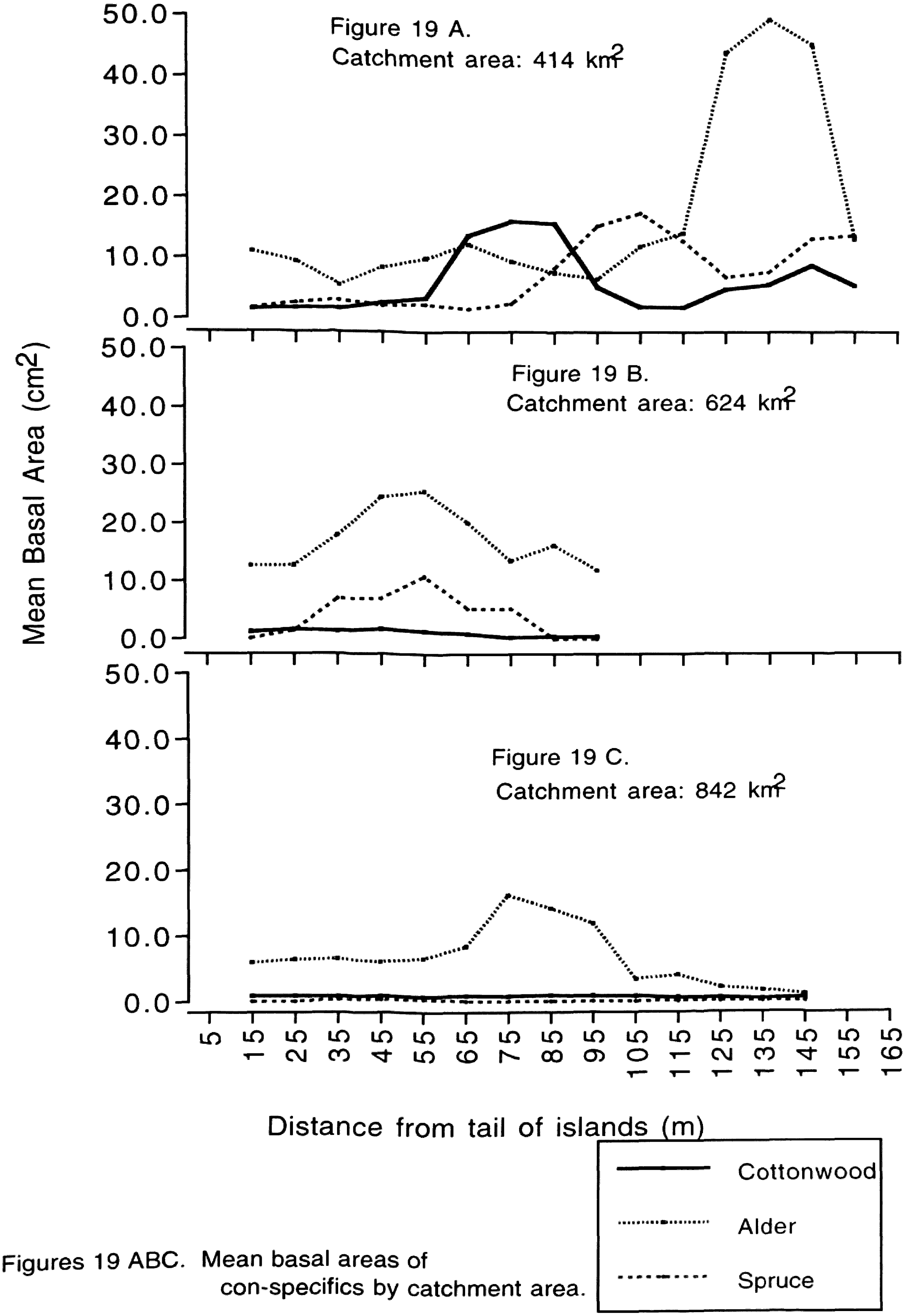
Figure 16. Relative abundance of principle tree species at the whole basin scale arranged by distance from the head of islands.



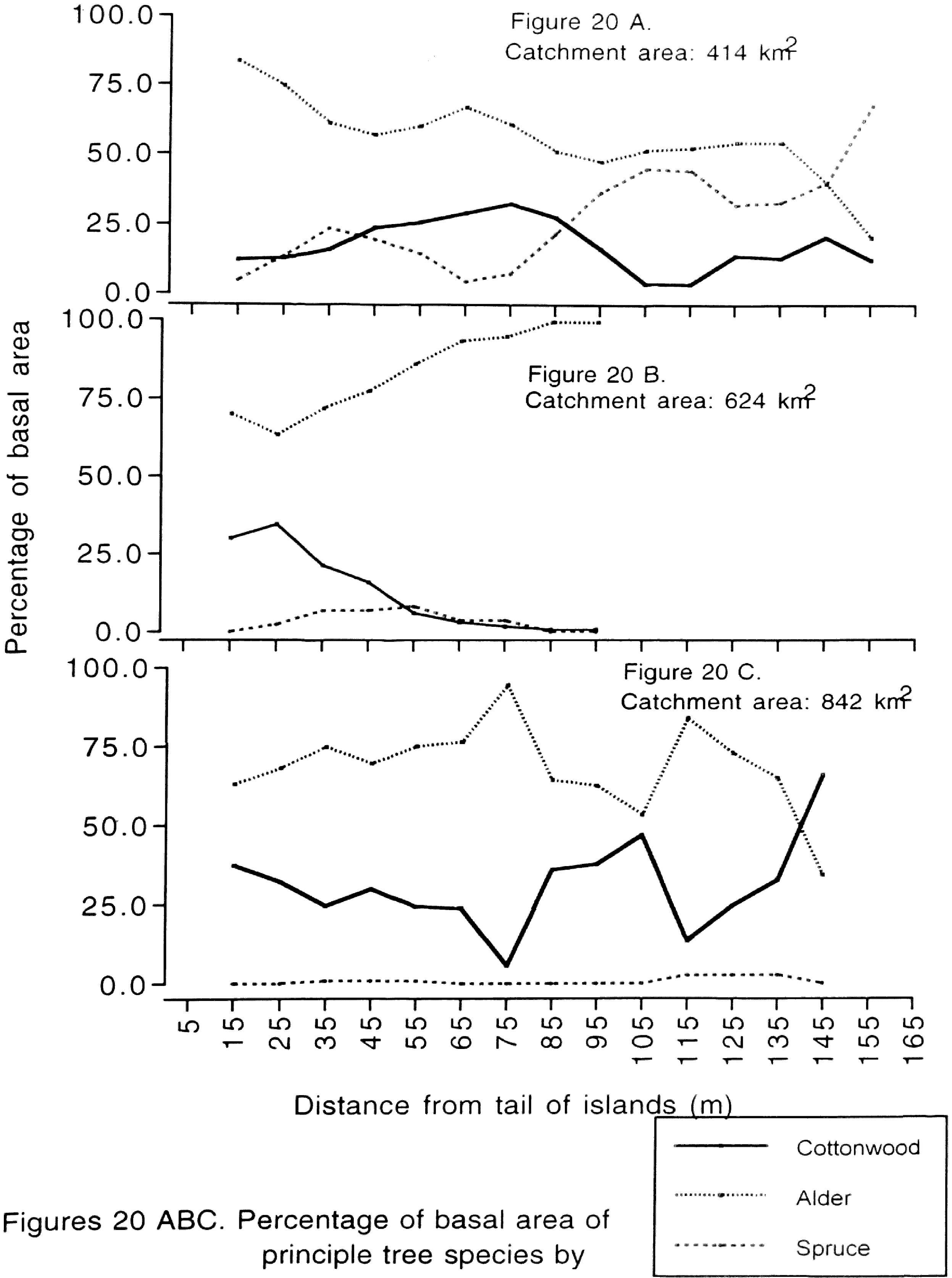
Figures 17 ABC. Relative abundance ofprinciple tree species by catchment area.



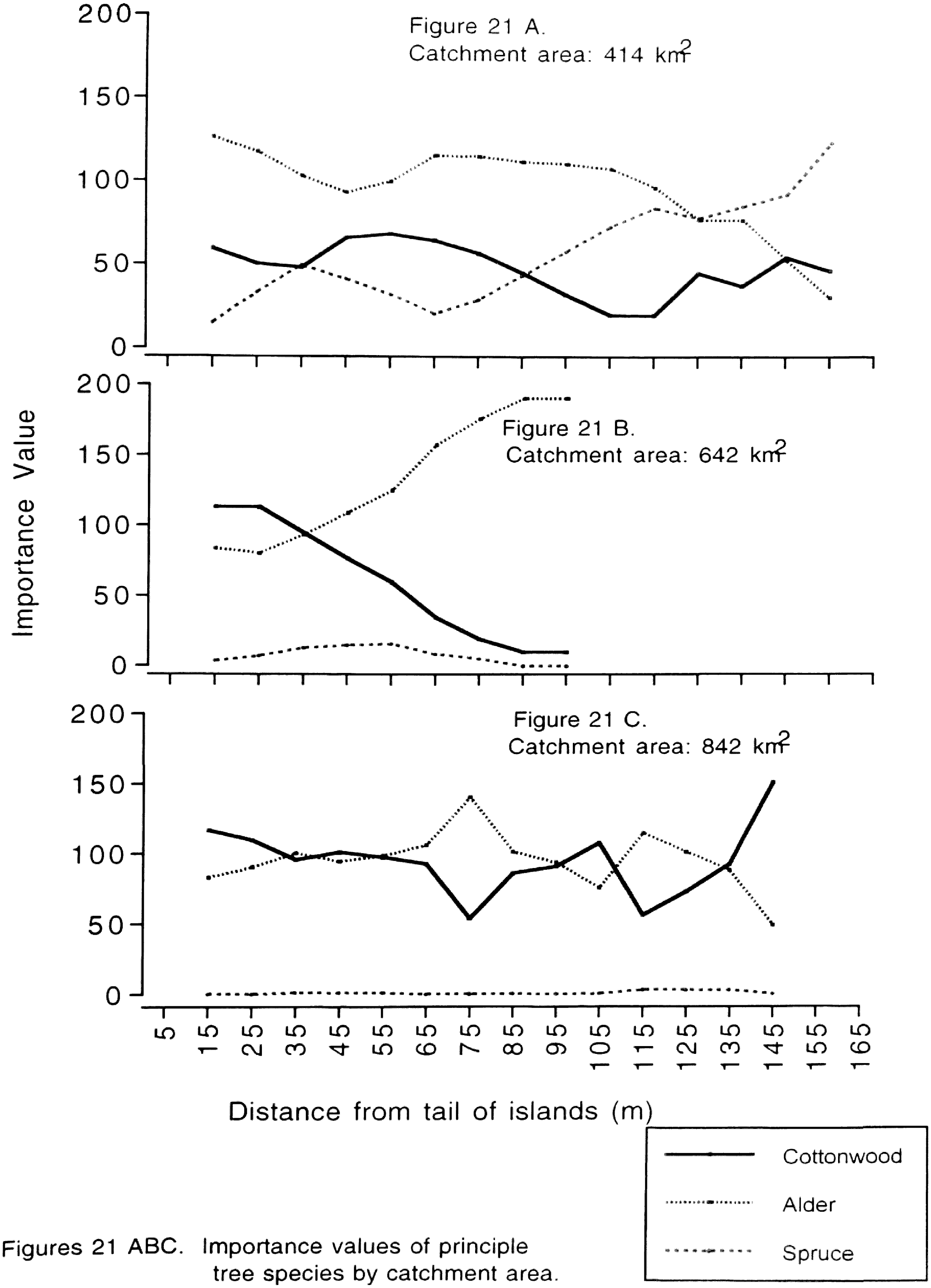
Figures 18 ABC. Density of principle tree species by catchment area.



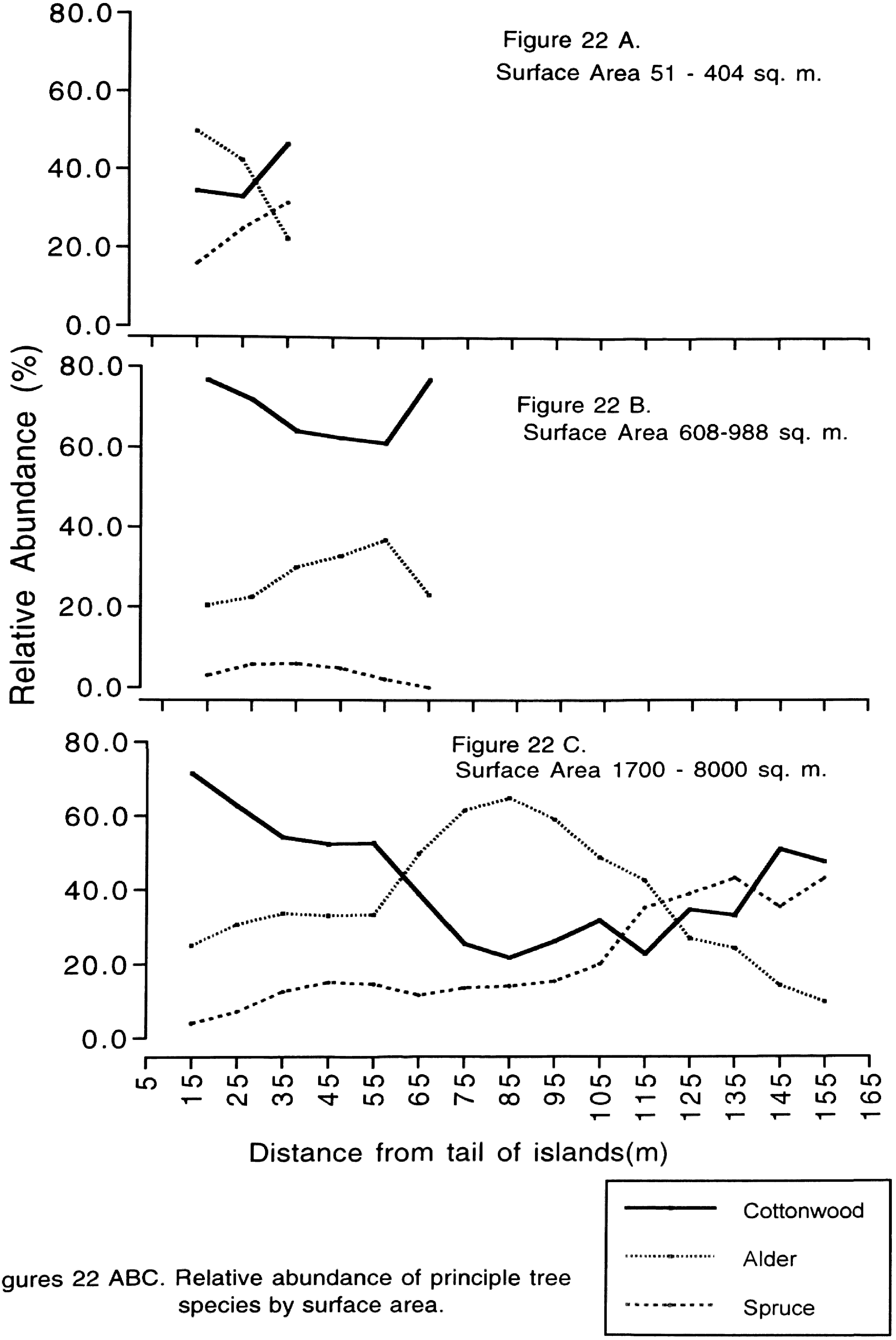
Figures 19 ABC. Mean basal areas of con-specifics by catchment area.



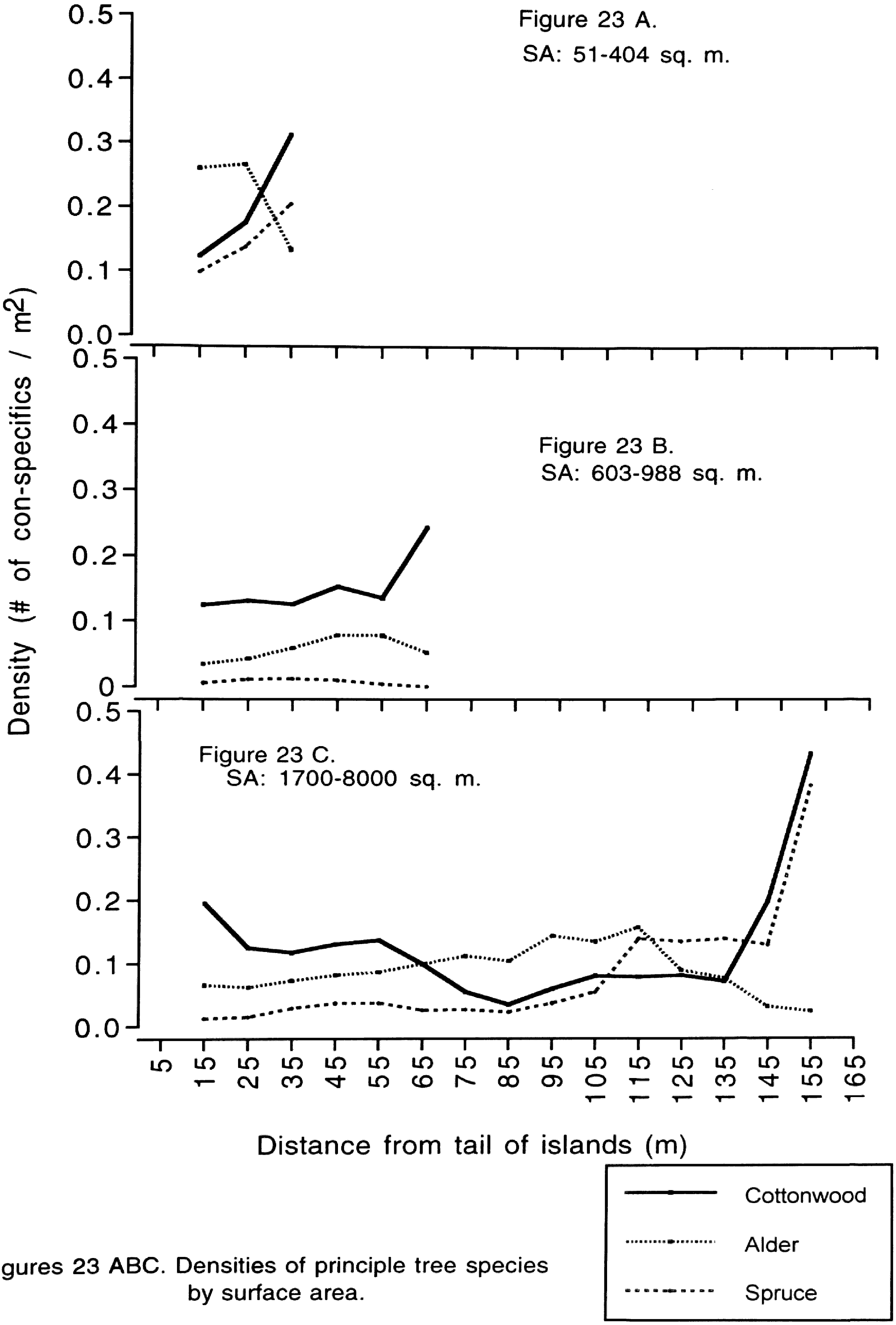
Figures 20 ABC. Percentage of basal area of principle tree species by catchment area.



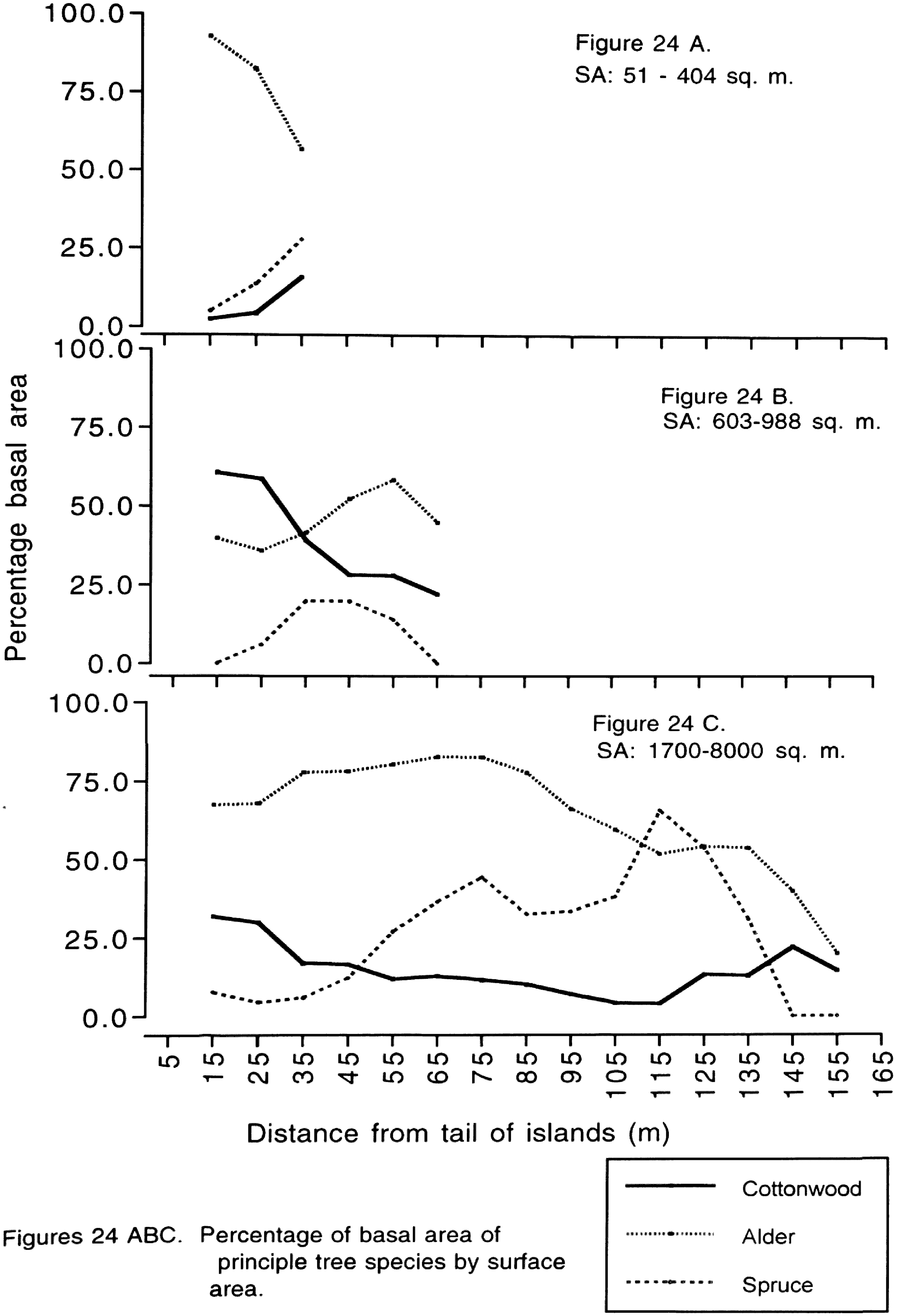
Figures 21 ABC. Importance values of principle tree species by catchment area.



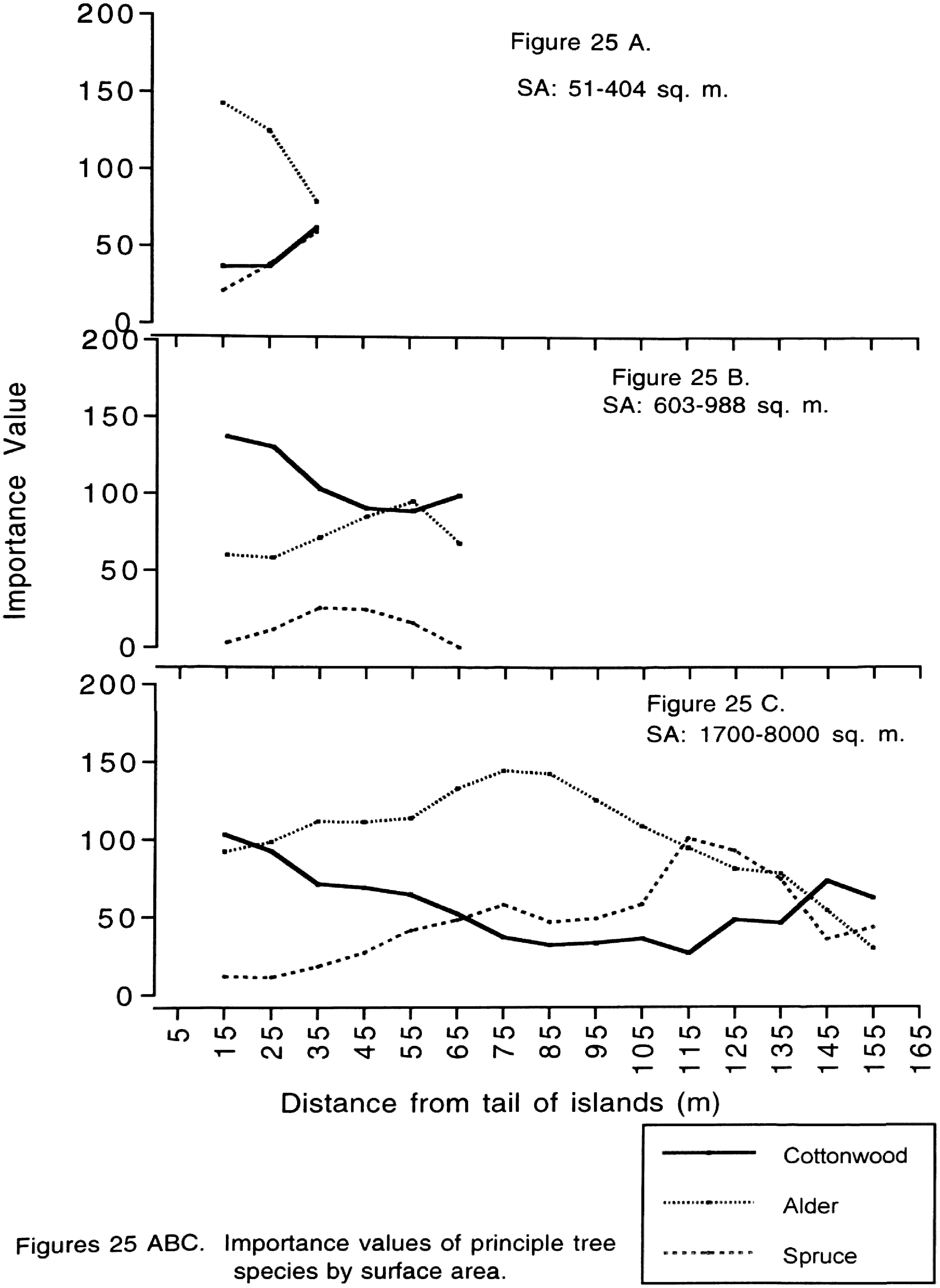
Figures 22 ABC. Relative abundance of principle tree species by surface area.



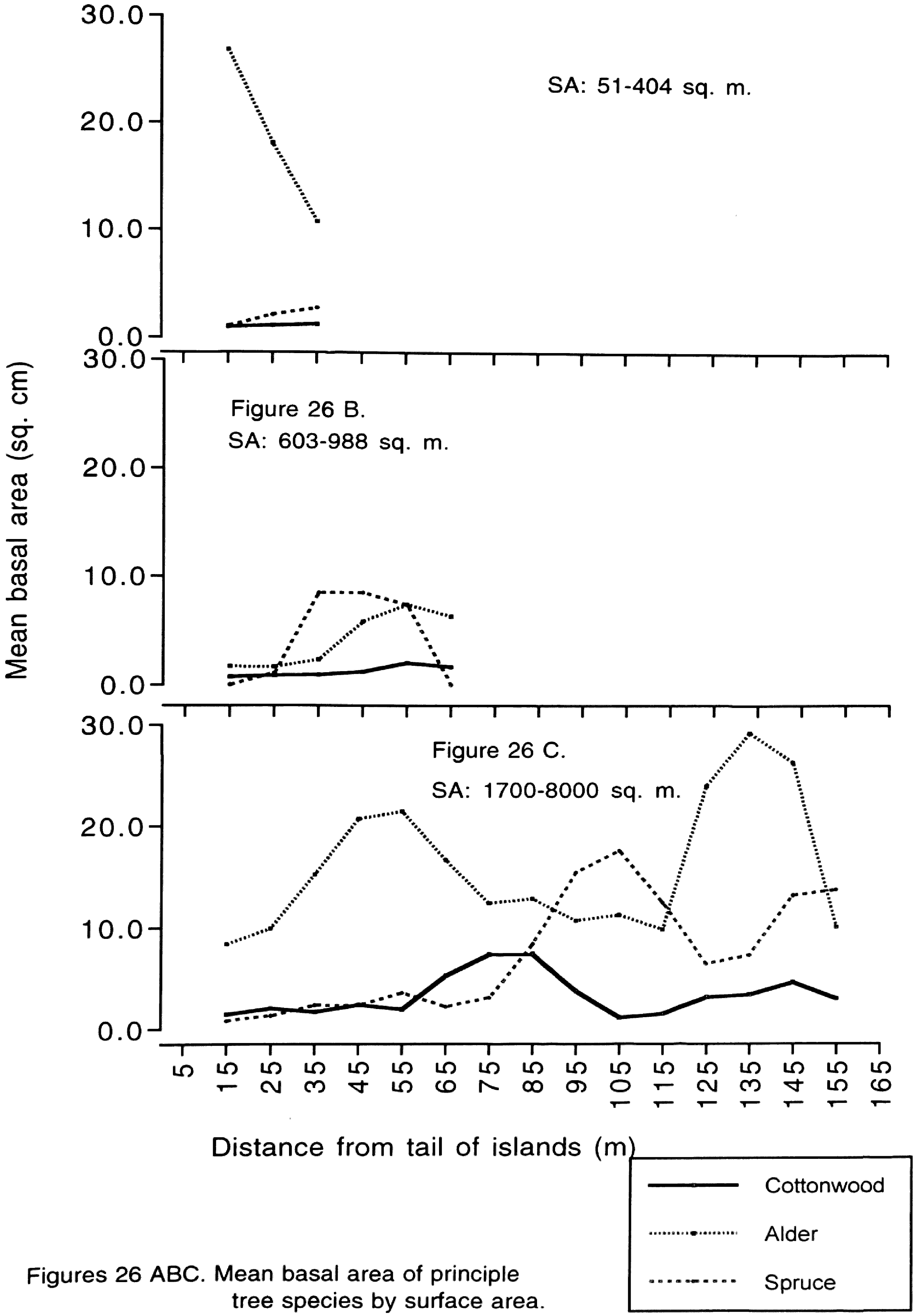
Figures 23 ABC. Densities of principle tree species by surface area.



Figures 24 ABC. Percentage of basal area of principle tree species by surface area.



Figures 25 ABC. Importance values of principle tree species by surface area.



Figures 26 ABC. Mean basal area of principle
tree species by surface area.

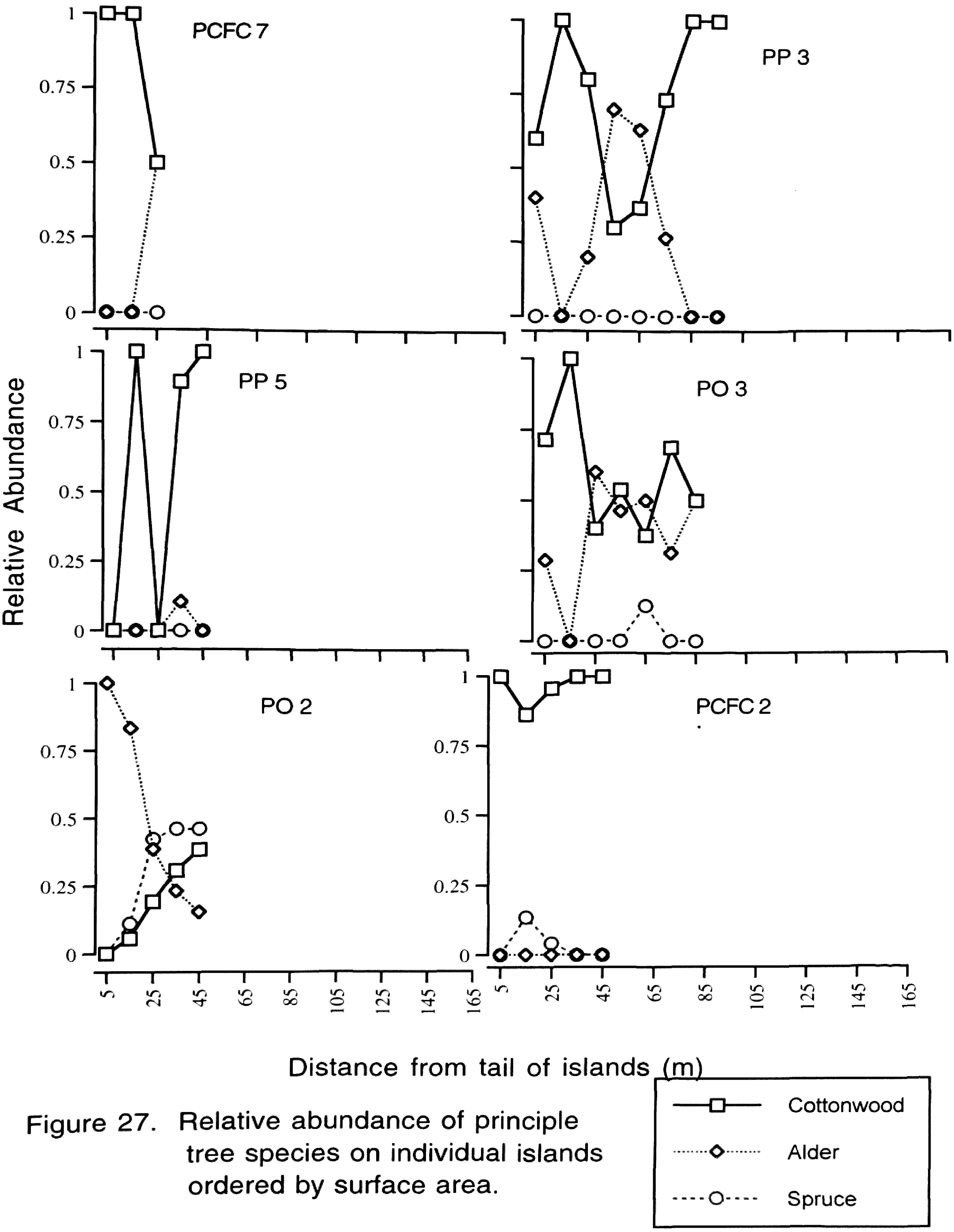


Figure 27. Relative abundance of principle tree species on individual islands ordered by surface area.

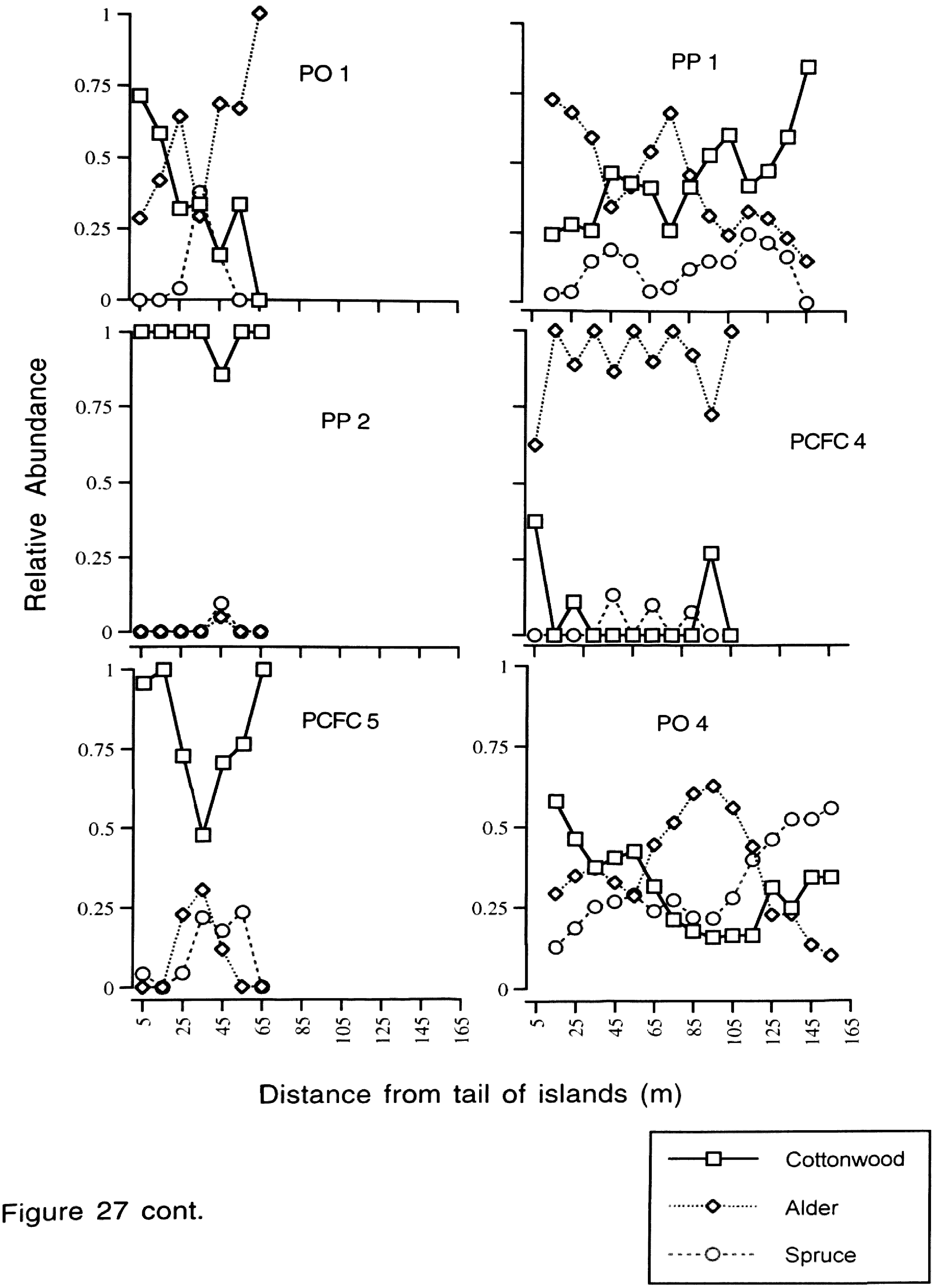


Figure 27 cont.

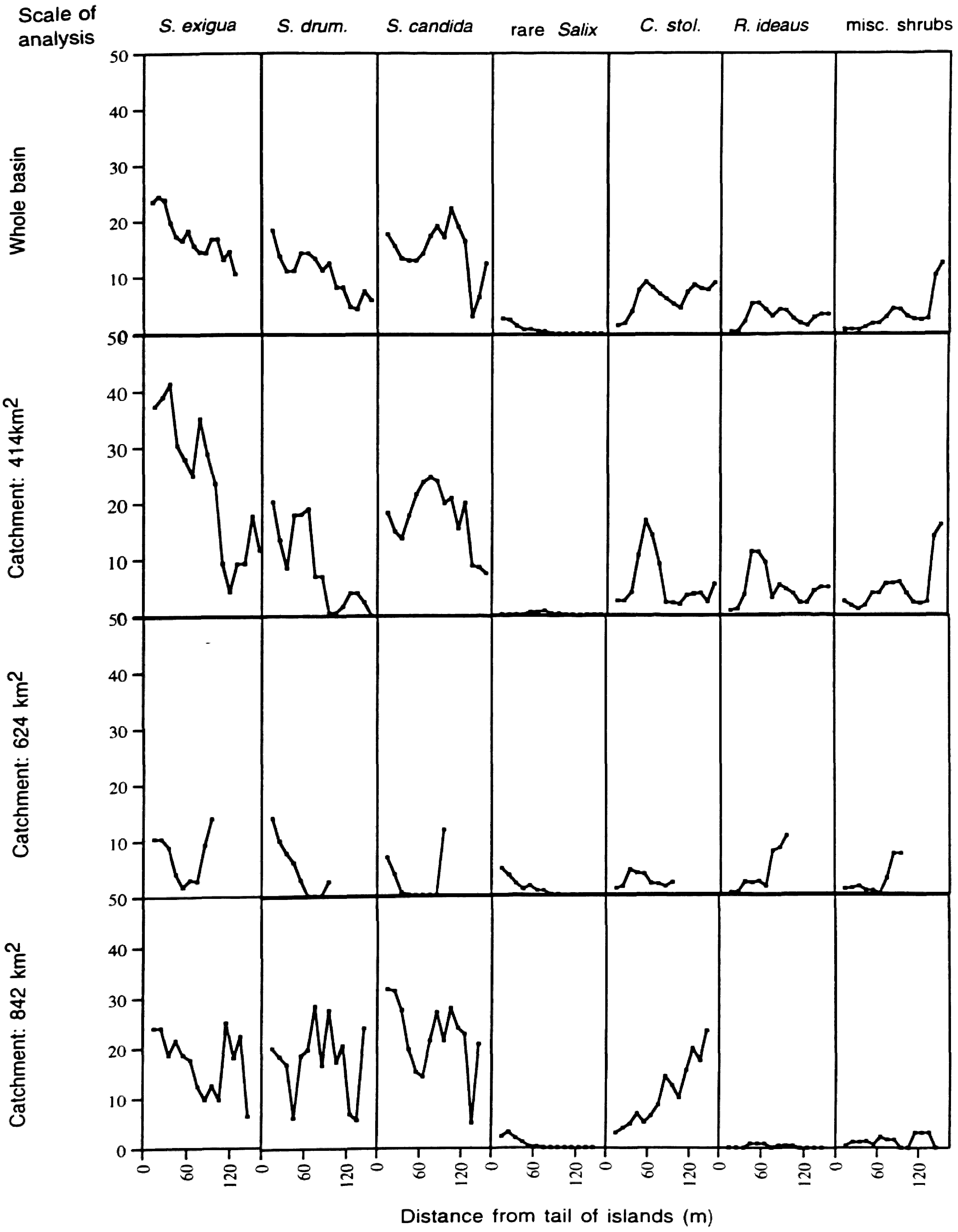


Figure 28. Shrub patterns at multiple spatial scales.

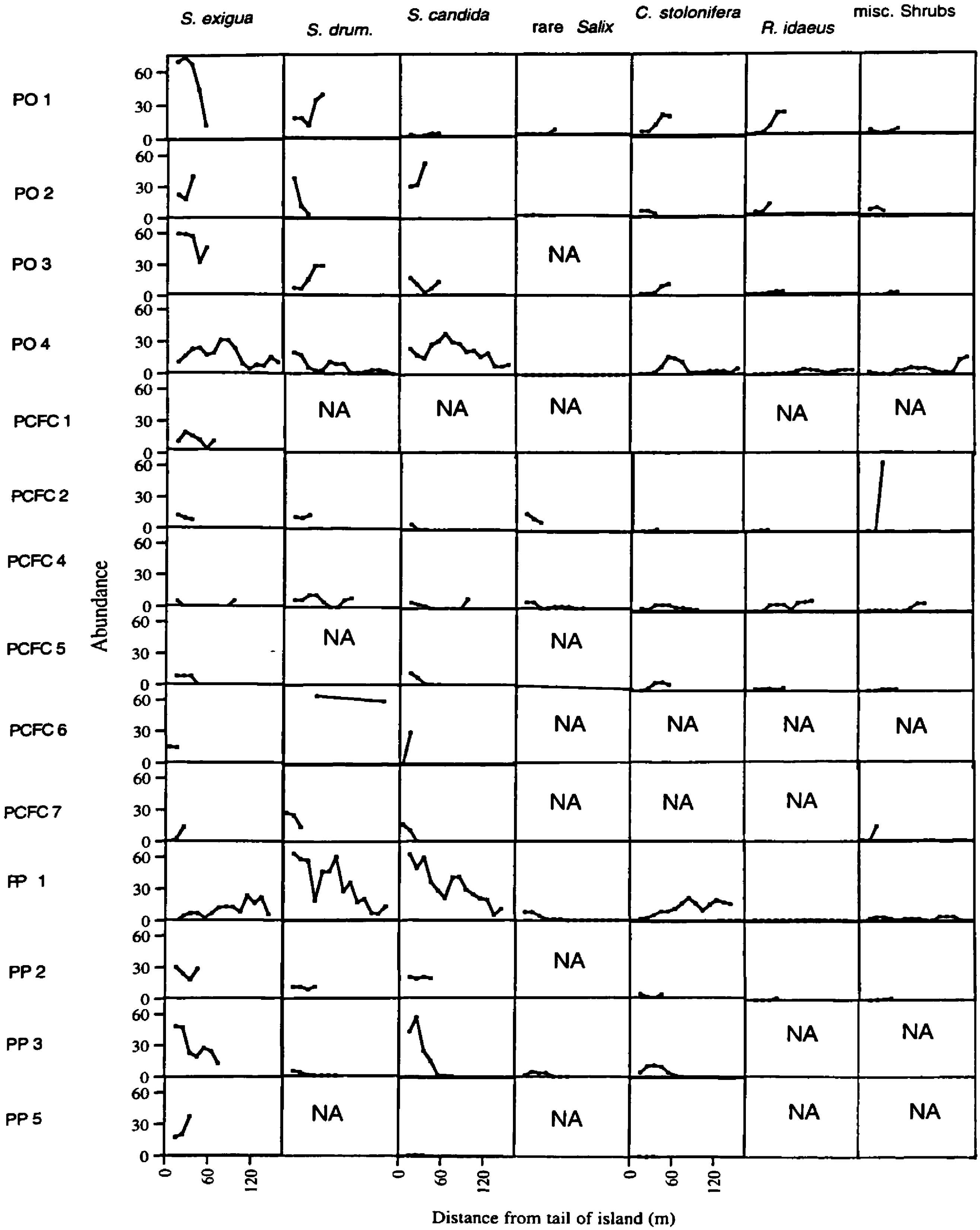
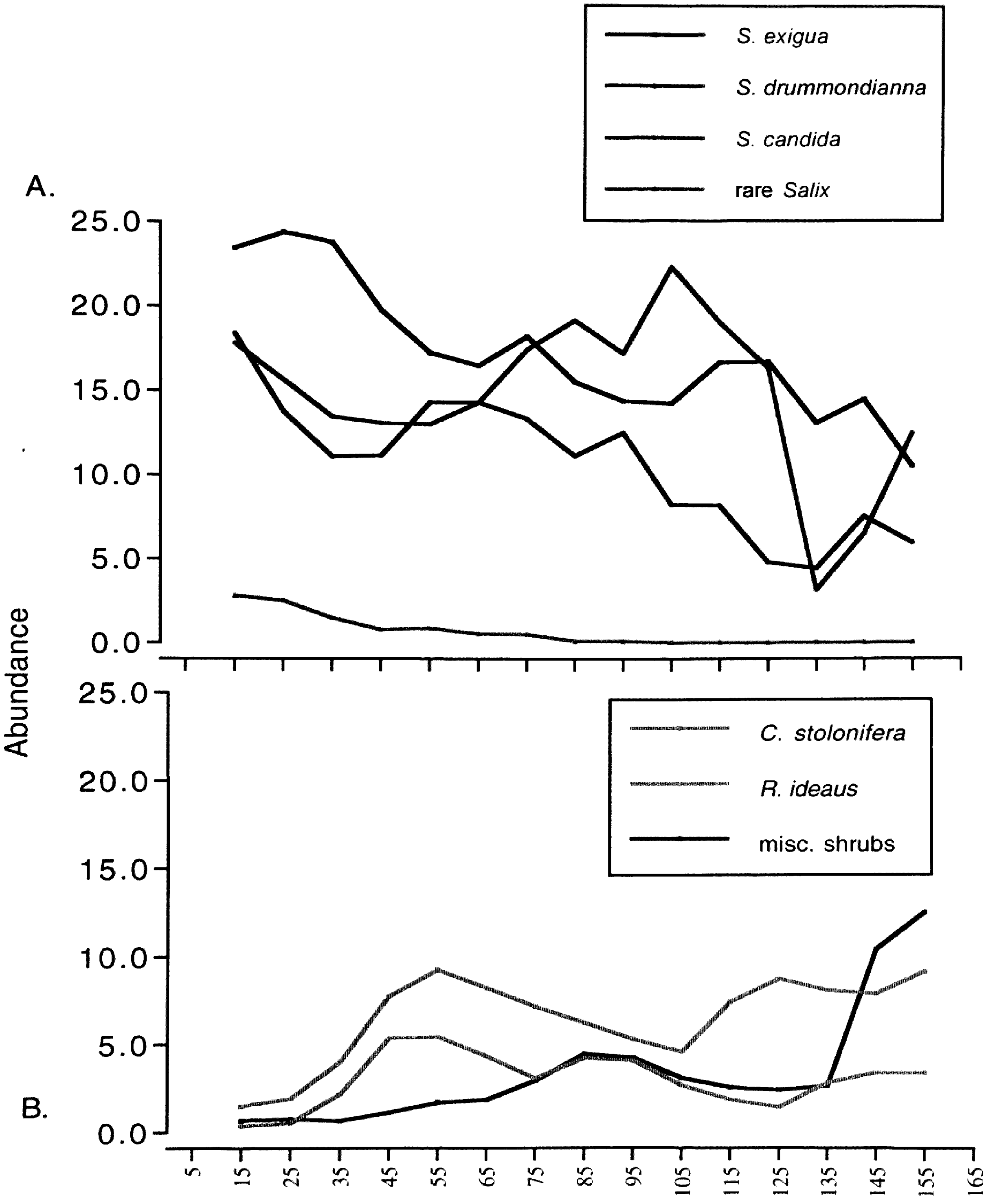


Figure 28 cont. (NA=shrub species not present)



Figures 29 AB. Abundance of shrubs at the whole basin scale.

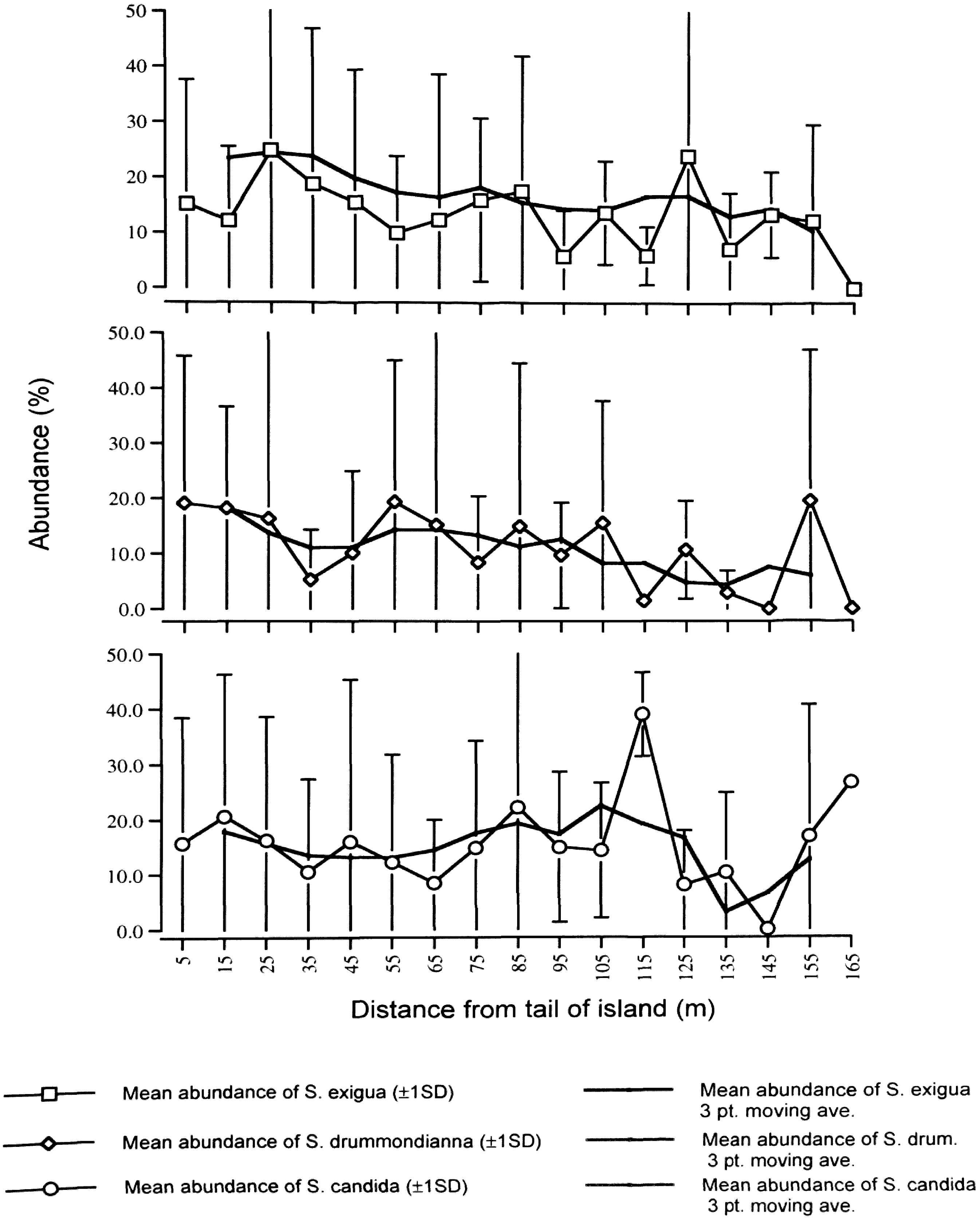


Figure 29 C. Abundance of shrubs at the whole basin scale.

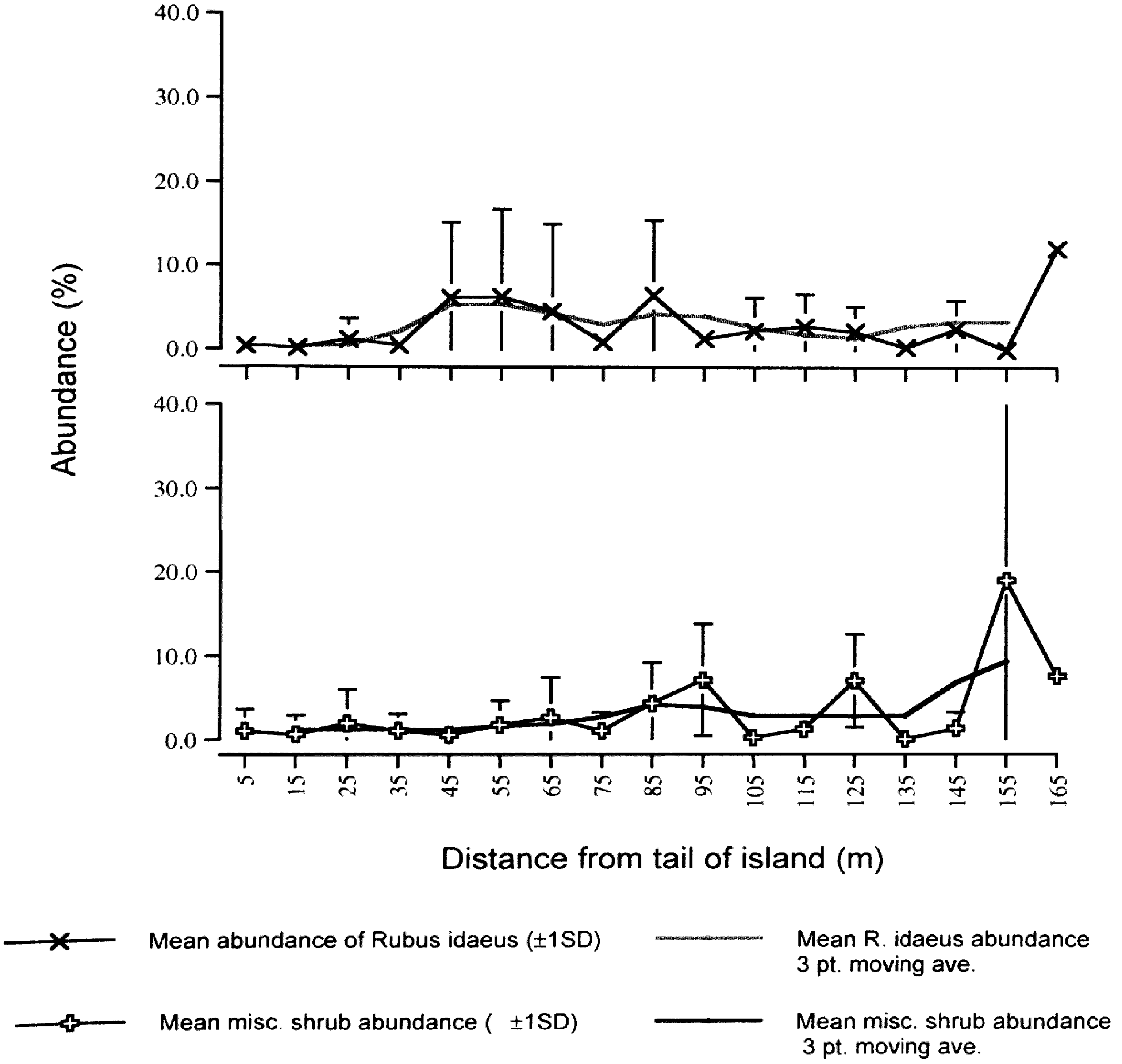


Figure 29 C cont. Abundance of shrubs at the whole basin scale.

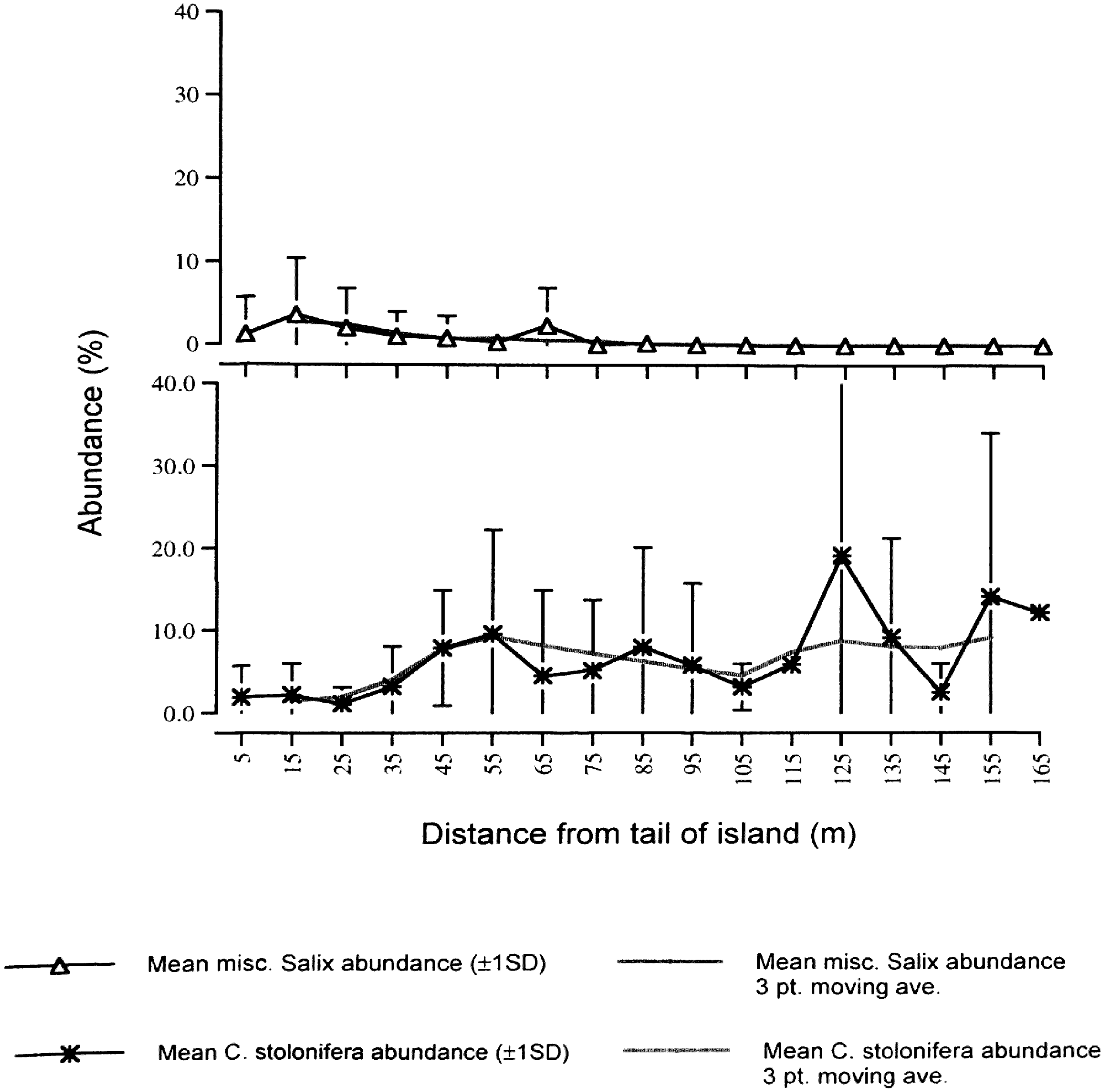
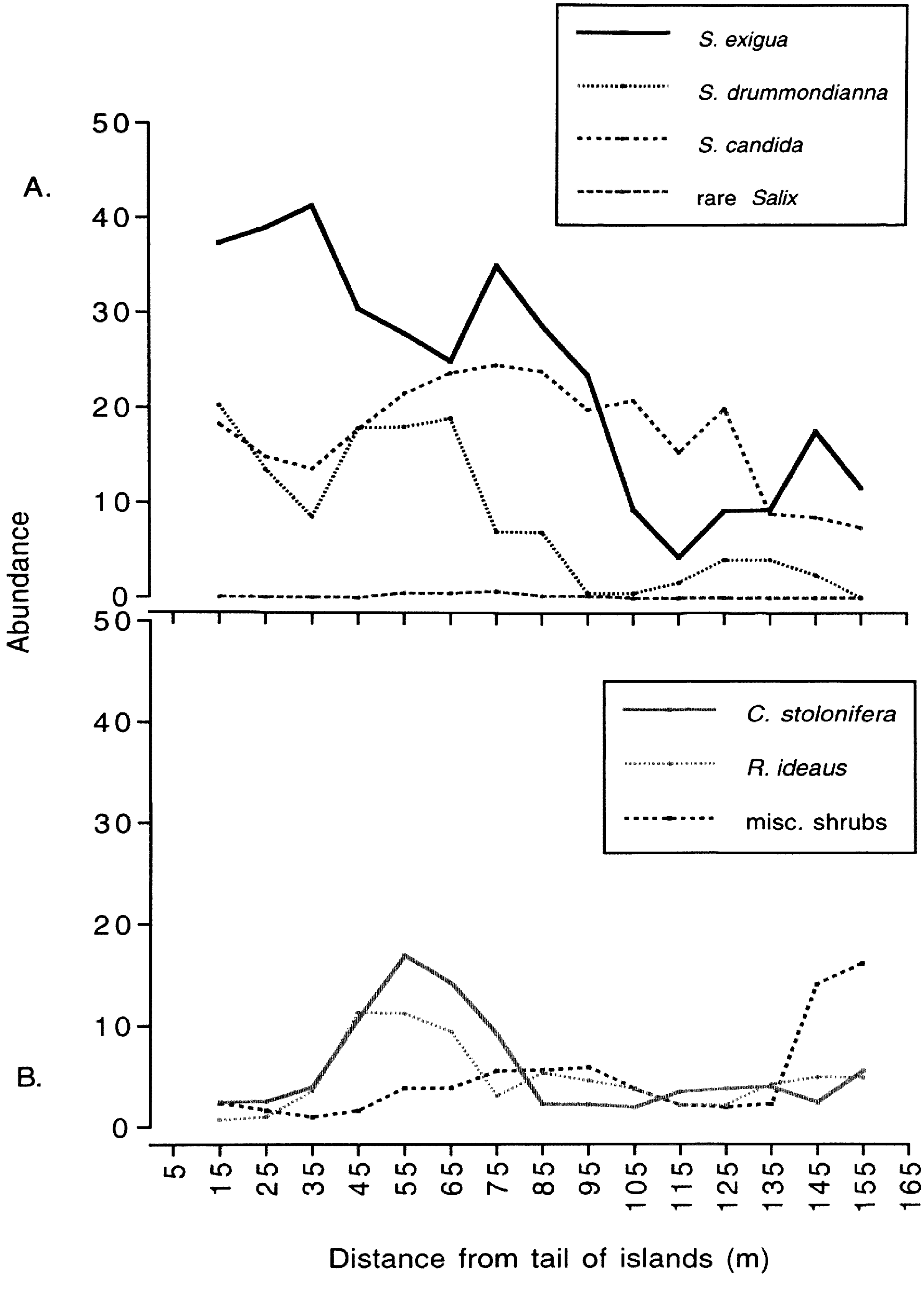
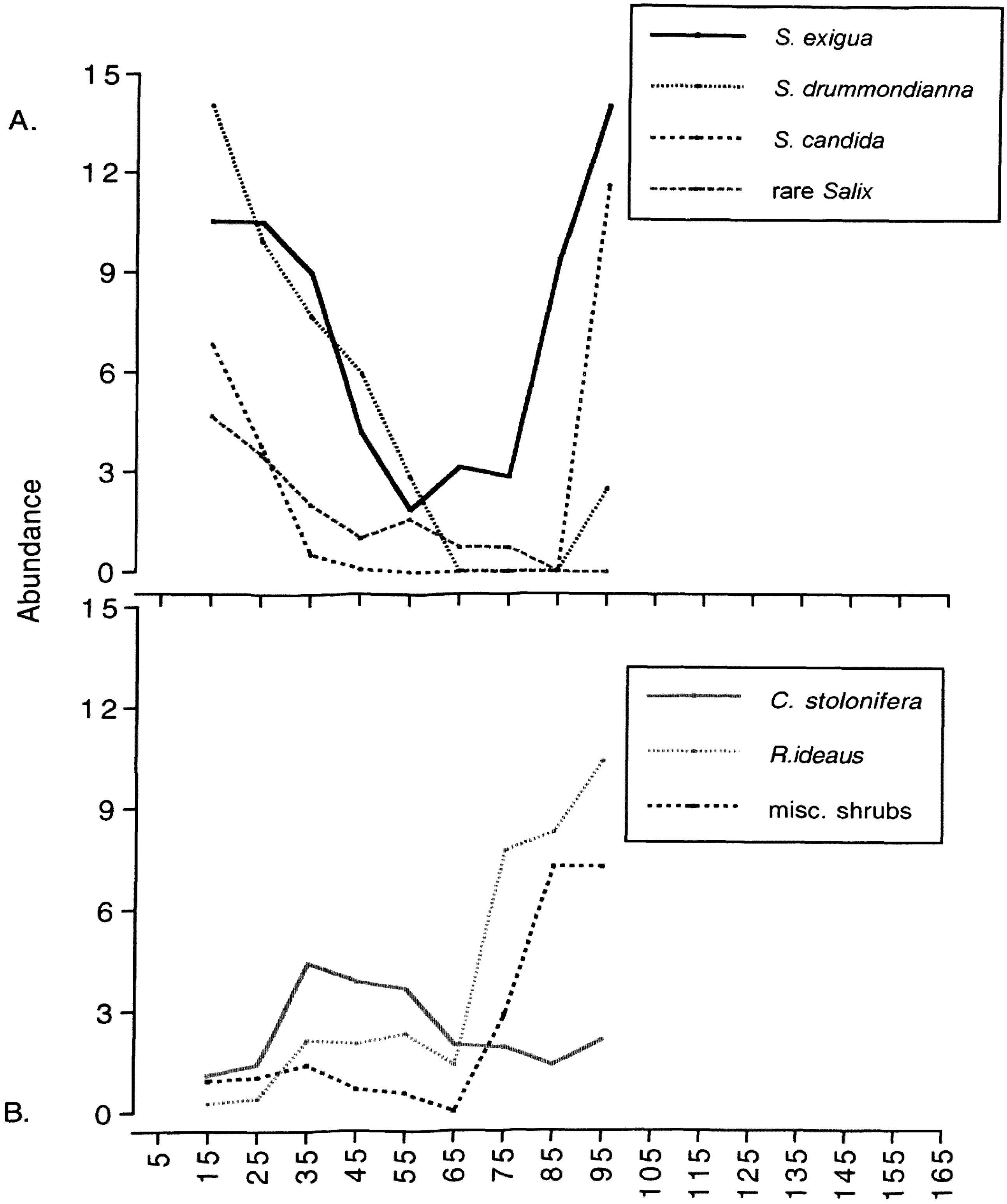


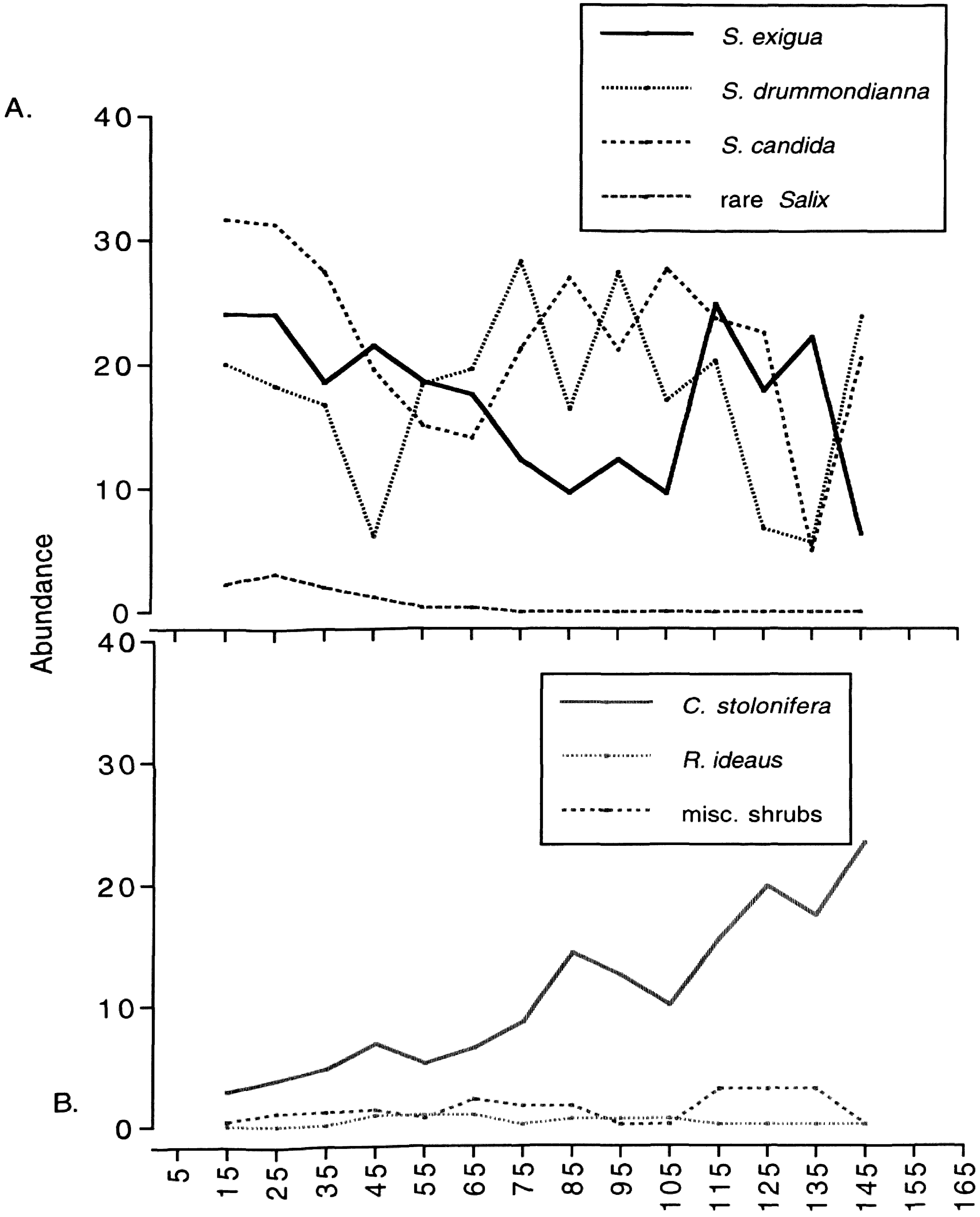
Figure 29C cont. Abundance of shrubs at the whole basin scale.



Figures 30 AB. Abundance of shrubs in the reach with the smallest catchment area (414 km ^{2}).



Figures 31 AB. Abundance of shrubs in the reach of medium catchment area (624 km ^{2}).



Figures 32 AB. Abundance of shrubs in the reach with largest catchment area (842 km ^{2}).

LITERATURE CITED

Abbe, T. B. and D. R. Montgomery (1996). Large woody debris jams, channel hydraulics, and habitat formation in large rivers. Regulated Rivers: Research and Management 12: 201-221.

Amoros, C., J. Rostan, G. Pautou and J. Bravard (1987). The reversible process concept applied to the environmental management of large river systems. Environmental Management 11: 607-617.

Amoros, C., A. L. Roux and J. L. Reygrobellet (1986). A method for applied ecological studies of fluvial hydrosystems. Regulated Rivers 1: 17-36.

Auble, G. T., J. M. Friedman and M. L. Scott (1994). Relating riparian vegetation to present and future streamflows. Ecological Applications 4: 544-554.

Baker, W. L. (1990). Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. Journal of Biogeography 17: 59 73.

Barnes, W. J. (1985). Population dynamics of woody plants on a river island. Canadian Journal of Botany 63: 647-655.

Barnes, W. J. (1991). Tree populations on the islands of the lower Chippewa River in Wisconsin. Bulletin of the Torrey Botanical Club 118: 424-431.

Barnett, V. and T. Lewis (1994). *Outliers in Statistical Data.* 3rd. ed. John Wiley and Sons Publishers. 584 pgs.

Bornette, G., C. Amoros and D. Chessel (1994). Effect of allogenic processes on successional rates in former river channels. Journal of Vegetation Science 5: 237-246.

Bravard, J.-P., C. Amoros and G. Pautou (1986). Impact of civil engineering works on the successions of communities in a fluvial system. A methodological and predictive approach applied to a section of the Upper Rhone River, France. Oikos 47: 92-111.

Brierley, G.J. and E.J. Hickin (1992). Floodplain development based on selective preservation of sediments, Squamish River, British Columbia. Geomorphology 4: 381-391.

Burns, R.M. technical coordinator, Silvicultural systems for the major forest types of the United States (1983). USDA USFS Agricultural Handbook 445.

Burns, R.M., and B.H. Honkala, technical coordinators, Silvics of North America-Hardwoods (1990). USDA USFS Agricultural Handbook 645.

Butler, N.M., J.A. Craft, and J.A. Stanford (1995). A diagnostic study of nutrient loading at Swan Lake, Montana. Flathead Lake Biological Station Open File Report 138-95.

Campbell, J., R.B. (1981). Field and laboratory methods for age determination of Quaking Aspen. U.S. Forest Service research note INT-314. U.S. Dept. of Agriculture.

Cavallo, B.J. 1997. Floodplain habitat heterogeneity and the distribution, abundance, and behavior of fishes and amphibians in the Middle Fork Flathead River, Montana. M.S. Thesis, The University of Montana.

Chapin, F. S. I., L. R. Walker, C. L. Fastie and L. C. Sharman (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs 64: 149-175.

Cole, D. M. (1977). Protecting and storing increment cores in plastic straws. USDA Forest Service research note INT-216.

Cole D.W., J. Comton, H. Van Miegroet, and P Homann (1990/91). Changes in soil properties and site productivity caused by red alder. Water, Air and Soil Pollution 54: 231-246.

Coleman, J. M. (1969). Brahmaputra River: channel process and sedimentation. Sedimentary Geology 3: 129-239.

Cottom, G. and J. T. Curtis (1956). The use of distance measures in phytosociological sampling. Ecology 37: 451-460.

Cottrell, T. R. (1996). Use of plant strategy ordination, DCA and ANOVA to elucidate relationships among habitats of *Salix planifolia* and *Salix monticola.* Journal of Vegetation Science 7: 237-246.

Decamps, H. (1996). The renewal of floodplain forests along rivers: a landscape perspective. Verh. Internat. Verein. Limnol 26: 35-59.

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

Dynesius, M. and C. Nilsson (1994). Fragmentation and flow regulation of river systems in the northern third of the world. Science 266: 753-762.

Everitt, B.L. (1968). Use of the cottonwood in an investigation of the recent history of a floodplain. American Journal of Science 266: 417-439.

Farjon, A. and P. Bogaers 1985. Vegetation zonation and primary succession along the Porcupine River in interior Alaska. Phytocoenologia 13: 465-504.

Fenner, M. (1987). Seed characteristics in relation to succession in *Colonization, Succession, and Stability.* 26th Symposium of the British Ecological Society.

Freidman, J.M., M.L. Scott, and W.M. Lewis, Jr. (1995). Restoration of riparian forests using irrigation, artificial disturbance, and natural seedfall. Environmental Management 19: 547-557.

Friedman, J. M., W. R. Osterkamp and W. M. Lewis (1996). Channel narrowing and vegetation development following a Great Plains flood. Ecology 77: 2167-2181.

Frissell, C. A., J. Doskocil, J. T. Gangemi and J. A. Stanford. (1995). Identifying priority areas for protection and restoration of aquatic biodiversity: A case study in the Swan River basin, Montana, USA. Open File Report Number 136-95. Flathead Lake Biological Station, The University of Montana. Polson.

Frye, R. J. and J. A. Quinn (1979). Forest development in relation to topography and soils on a floodplain of the Raritan River, New Jersey. Bulletin of the Torrey Botanical Club 106: 334-345.

Furlow, J.J. (1979). The systematics of the American species of *Alnus* (*Betulaceae*). Rhodora 81: 1-121.

Green, W. N. (1982). Mid-Channel islands: Sedimentology, physiography, and effects on channel morphology in selected streams of the Great Bend Region of the Wabash Valley. Masters thesis, Geology dept. 111 pgs.

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

Hupp, C. R. (1983). Vegetation pattern on channel features in the Passage Creek Gorge, Virginia. Castanea 48: 62-72.

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

Johnson, W. C. (1994). Woodland expansion in the Platte River, Nebraska: Patterns and causes. Ecological Monographs 64: 45-83.

Junk, W. J., P. B. Bayley and R. E. Sparks (1989). The flood pulse concept in river-floodplain systems in Proceedings of the International Large River Symposium, Canadian Special Publication of Fish and Aquatic Sciences.

Kalliola, R., J. Salo, M. Puhakka and M. Rajasilta (1991). New site formation and colonizing vegetation in primary succession on the western Amazon floodplain. Journal of Ecology 79: 877-901.

Keller, A. M. and M. S. Hendrix (1997). Paleoclimatological analysis of a late Jurassic petrified forest, Southeastern Mongolia. Unpublished paper.

Keller, E. A. and F. J. Swanson (1979). Effects of large organic material on channel form and fluvial processes. Earth Surface Processes 4: 361-380.

Kendy, E. and R. E. Tresch (1996). Geographic, geologic, and hydrologic summaries of intermountain basins of the northern Rocky Mountains, Montana. US Geological Survey report # 96-4025.

Longwell and Flint, eds. 1963. Weathering and Soils in *Introduction to Physical Geology* J. Wiley and Sons Publishers.

Malanson, G. P. (1993). *Riparian Landscapes.* Cambridge University Press.

Malanson, G. P. and D. R. Butler (1990). Woody debris, sediment, and riparian vegetation of a subalpine river, Montana, USA. Arctic and Alpine Research 22: 183 194.

Malanson, G. P. and D. R. Butler (1991). Floristic variation among gravel bar in a subalpine river, Montana, USA. Arctic and Alpine Research 23: 273-278.

McBride, J. R. and J. Strahan (1984). Establishment and survival of woody riparian species on gravel bars of an intermittent stream. The American Midland Naturalist 112: 235-245.

McCarthy, T. S., W. N. Ellery and I. G. Stanistreet (1992). Avulsion mechanism on the Okavango fan, Botswana: the control of a fluvial system by vegetation. Sedimentology 39: 779-795.

McDonald, L. L. (1980). Line-intercept sampling for attributes other than coverage and density. Journal of Wildlife Management 44: 530-533.

Mertes, L.K., T. Dunne, and L.A. Martinelli (1996). Channel-Floodplain geomorphology along the Solimoes-Amazon River, Brazil. Bulletin of the Geological Society of America 108: 1089-1107.

Nakamura, F. and F. J. Swanson (1993). Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. Earth Surface Processes and Landforms 18: 43-61.

Nanson, G. C. and H. B. Beach (1977). Forest succession and sedimentation on a meandering-river floodplain, northeast British Columbia, Canada. Journal of Biogeography 4: 229-251.

Nilsson, C., M. Gardfjell and G. Grelsson (1991). Importance of hydrochory in structuring plant communities along rivers. Canadian Journal of Botany 69: 2631-2633.

Osterkamp, W.R., and J.E. Costa (1987). Changes accompanying an extraordinary flood on a sand-bed stream, in *Catastrophic Flooding.* L. Mayer and D. Nash eds. Allen and Unwin publishing. 201-224 pgs.

Pautou, G. and H. Dècamps (1985). Ecological interactions between the alluvial forests and hydrology of the Upper Rhone. Archives of Hydrobiolia 104: 13-37.

Pielou, E. C. (1975). *Ecological Diversity.* John Wiley & Sons, Inc. publishers.

Puhakka, M., R. Kalliola, M. Rajasilta and J. Salo (1992). River types, site evolution and successional vegetation patterns in Peruvian Amazonia. Journal of Biogeography 19: 651-665.

Rostan, J. C., C. Amoros and J. Juget (1987). The organic content of the surficial sediment: a method for the study of ecosystems development in abandoned river channels. Hydrobiologia 148: 45-62.

Rydin, H. and S. Borgegard (1991). Plant characteristics over a century of primary succession on islands: Lake Hjalmaren. Ecology 72: 1089-1101.

Salo, J. (1986). River dynamics and the diversity of Amazon lowland forest. Nature 322: 254-258.

Schnitzler, A. (1997). River dynamics as a forest process: Interaction between fluvial systems and alluvial forests in large European river plains. The Botanical Review 63: 40-60.

Scott, M.L., J.M. Freidman and G.T. Auble (1996). Fluvial processes and the establishment of bottomland trees. Geomorphology (in press).

Scott, M.L., M.A. Wondzell and G.T. Auble (1993). Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation. Proceedings of the 13th annual American Geophysical Union Hydrology Days. H.J. Morel-Seytoux ed.

Smith, D. G. (1976). Effects of vegetation on lateral migration of anastomosed channels of a glacier meltwater river. Geological Society of America Bulletin 87: 857-860.

Stanford, J. A. and J. V. Ward (1988). The hyphoreic habitat of river ecosystems. Nature 335: 64-66.

Stanford, J.A. and J.V. Ward (1993). An ecosystem perspective of alluvial rivers: connectivity and the hyphoreic corridor. Journal of the North American Benthological Society 12: 48-60.

Stanford, J.A., J.V. Ward, W.J. Liss, C.A. Frissell, R.N. Williams, J.A. Lichatowich, and C.C. Coutant (1996). A general protocol for restoration of regulated rivers. Regulated Rivers: Research and Management 12: 391-413.

Swanson, F. J., T. K. Kratz, N. Caine and R. G. Woodmansee (1988). Landform effects on ecosystem patterns and processes. Bioscience 38: 92-98.

Stocklin, J. and E. Baumler (1996). Seed rain, seedling establishment, and clonal growth strategies on a glacier foreland. Journal of Vegetation Science 7: 45-56.

Tabacchi, E., A. Planty-Tabacchi, M. J. Salinas and H. Dècamps (1996). Landscape structure and diversity in riparian plant communities: A longitudinal comparative study. Regulated Rivers: Research & Management 12: 367-390.

Triska, F. J. (1984). Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: A historical case study. Verh. Internat. Verein. Limnol. 22: 1876-1892.

Wallace, J. B., S. L. Eggert, J. L. Meyer and J. R. Webster (1997). Multiple trophic levels of a forested stream linked to terrestrial litter inputs. Science 277: 102-104.

Walker, L.R., J.C. Zasada and F.S. Chapin III (1986). The role of lifehistory processes in primary succession of an Alaskan Floodplain. Ecology 67: 1243-1253.

CHAPTER III

Reading an Island: The Interplay of Physical and Biotic Forces

Have you ever looked at a river island and noticed that the tallest trees were at one end and the shortest at the other? Or perhaps you have observed that one end of an island in your favorite western trout fishing river was dominated by conifers and wild roses but cottonwoods and willows were most abundant at the other end. On islands in eastern rivers the plants you observed may have been elm, maple, or even a hawthorne on one end of an island, while rushes, milkweeds, and perhaps some willows were common at the other end. May Watt, in 1962, provided a very literate, poetic, description of these patterns in a chapter titled "Watching the Islands Go By" in her book Reading the Landscape: An Adventure in Ecology. While walking along the banks of the Swan River of northwest Montana, I also noticed interesting differences in where plants grew on islands. So I set out to learn why plants were arranged in such distinct and repeatable patterns. During my studies, I learned how islands grow and come to be colonized by different plants, and of the interactions between plant establishment and island growth. These finding might be useful in determining how best to balance management processes so a river can maintain a high level of ecological integrity while meeting society's needs.

My field surveys of 14 islands of the Swan River in northwest Montana confirmed that larger trees were more common on the upstream end of the islands and smaller trees were most common on the downstream end of the islands, and that species abundances changed based on location on an island. Downstream ends of islands were almost uniformly dominated by young Black Cottonwoods (*Populus trichocarpa* Torr. & Gray.) and two different species of willow: Gravel Bar Willow (*Salix exigua* Nutt.) and Drummond Willow (*Salix drummondianna* Barratt.). The middle areas were dominated by Thin-leafed Alder (*Alnus tenuifolia* Nutt.) and Hoary Willow (*Salix candida* Fleugge), while the upstream ends of the islands were dominated by conifers, such as Engelmann Spruce

(*Picea engelmannii* Parry ex Engelm), along with a collection of shrubs which all relied on animals for dispersal. The most common shrubs were American Raspberry (*Rubus idaeus* L.), Red-Osier Dogwood (*Cornus stolonifera* Michx.) and wild roses (*Rosa spp.*).

Confident that there was a distinct, predictable pattern, the next step was to determine the cause. Obviously, rooted plants can't move from one location to another. They either live or die depending upon how well their immediate environment meets their unique habitat requirements. It is possible to infer how conditions must differ between locations if we understand the habitat requirements of the different plants we observe. In this way, plants serve as a living record of the history of the site they are growing on. Taller trees are usually older than shorter trees of the same species. This suggests that the upstream ends of the islands, where all the largest trees were aggregated, were older than other portions of the islands. Similarly, the abundance of small trees on the downstream end suggests that these areas are younger.

The observed trend in size also may be attributed to differences in the amount of nutrients that are available in the immediate vicinity of individual trees. Nutrient concentrations in sediments deposited by rivers usually increase as the land surface ages. Therefore, older surfaces have higher nutrient concentrations, allowing plants in these areas to grow faster than the trees on younger surfaces. The difference in nutrient levels between old and young surfaces intensifies the size disparity between plants on old and young surfaces. Many other factors also influence tree size, for example, flood history, depth to the water table, and characteristics of the soil (i.e., size and porosity of the surface and subsurface sediments). All of these factors change as a function of the age of the sediment deposit.

Knowledge of the way seeds disperse to islands also is important for understanding how plant distribution patterns reflect the process of island development. Cottonwoods and willows produce many very small seeds that are well dispersed by wind and water. Plants with these characteristics are very good disperses. They specialize in reaching new land surfaces before other species, and therefore, they enjoy a period of excellent growth before competing species become established. Such plants are considered "pioneering" species, and typically, they are the most abundant plants on newly formed land surfaces. Newly deposited sediments are typically deficient in nutrients because they have no small particles, like clay or silt, to bind onto organic matter. Pioneering species have evolved the ability to tolerate, and even thrive, in low nutrient level environments.

Over time, pioneering species are replaced by "seral" species. Seral species do not disperse as well as pioneers, and therefore, it takes longer for them to reach a site. However, they are better competitors for limited resources such as space, nutrients, and sun light then are pioneering species, and eventually they replace the pioneers as the most abundant plants. Through the process of "seral succession," early arriving species are replaced by later arriving, but more capable, competitors. Over time, if there are no disturbances, a stable plant community, called the "climax community," may develop. On river islands in northwestern Montana, spruce and fruiting shrubs are examples of late seral species, which suggests that the upstream end of the island where they were most abundant was significantly older than the downstream end where cottonwood and willows were most abundant.

The possibility that the presene of young, pioneering plants downstream of older, climax species could be caused in part by sediments of different ages was very intriguing to me. Before accepting this explanation, it was critical to eliminate all the other potential influences that might yield this repeatable pattern amongst islands. For example, because many islands within one river had similar patterns, the cause was not likely to be the result of site-specific factors that were unique to a single island. The factors responsible probably affected all of the river islands. Of all the forces acting within a river system, extreme events such as floods and droughts are amongst the few that will impact the entire length of a river. For example, consider the "crest" of a flood as it moves downstream through a river channel. In the absence of significant engineering works such as dams, the entire river, from the headwaters to the mouth, will experience a peak in discharge volume within a short time frame. Similarly, during low water years, all portions of a river will have reduced discharge levels at the same times. I believe the cycle of floods and droughts is responsible for creating the pattern observed on the islands in the Swan River.

Floods are incredibly dynamic periods for rivers. It is during floods that the majority of sediment movement occurs. High energy flood waters erode river banks and pool bottoms and transport the eroded material downstream. Eventually, as the flood waters recede, the energy level of the river falls and the eroded particles (cobbles, gravel, sand, silt, etc.) are dropped out of transport. One place where sediments frequently are deposited is on the downstream side of river islands. What results is a band of newly deposited sediments lying downstream of older sediments. The older sediments probably were deposited during preceding flood events, and similarly, they lie downstream of an even older band of sediments. A chronological sequence of sediment bands, with older lying upstream of younger, progresses upstream on an island until the original deposit is finally reached. Often, the original deposit formed on a natural high point within the river channel, such as at the crest of a riffle or behind a large obstruction that formed an eddy of low velocity water. For example, a tree trunk with its rootwad intact may lodge within a river channel and catch debris and sediments floating in the river during a high water event, thus initiating the process of island formation.

However, my data, and that of several other researchers, indicated that floods alone could not create the observed patterns of island vegetation. Low water events also are important. More than 95% of the trees on the islands I studied were established between 1978 and 1980, but mostly in 1978. That year featured a drought and the lowest peak discharge volume on the Swan River during the entire 80 year period of record. Prior to that year, the last significant high water event was in 1974.

It is interesting that the timing of seed release by many pioneering plant species coincides with the timing of annual high water events. For example, in my home in the northern Rocky Mountains of Montana, cottonwoods and willows release their seeds in late May and June, the same time when snow-melt swells our rivers. In years with large snow packs, rivers may stay high well into July (in 1997, the Swan River was near flood stage well into August!). During high water years, by the time the discharge of a river falls low enough to expose the surface of river islands, the seeds of the pioneering species have been swept downstream and they may no longer be viable. So, while floods provide the freshly deposited uncolonized sediments favored by pioneering species, they do not provide the appropriate conditions for successful plant recruitment. Thus, it is during the subsequent low water events, when uncolonized sediments are exposed, that successful plant establishment occurs. In the end, it is clear that flood waters prepare the land surface for colonization, but a low water year is needed for significant successful recruitment. Once the pioneering species have become established, they stabilize the newly formed island, and the process of seral succession begins. Moreover, river islands are not the only type of riparian habitats that benefit from water level fluctuations. Many researchers have demonstrated similar sequences for a variety of riparian zones and flood plain forests. Consequently, the maintenance of a naturally fluctuating hydrograph (the rise and fall of discharge volume on a repeatable time scale) is needed if people wish to have aquatic habitats with some level of "naturalness."

In the Swan River, I found that islands that were far upstream in the drainage basin had a significant portion of their surface covered by climax species such as spruce. Further downstream, islands were dominated by cottonwoods and willow. The differences may be attributed, in part, to the increased destructive power of floods in river segments further downstream relative to the flood-waters upstream. Flood-waters raging through a river channel downstream have greater energy because of the added volume of water contributed by tributary streams. The increased energy level in areas further downstream is a disturbance maintaining river islands in a more "juvenile" condition where pioneering species are most abundant. As you move upstream, above where tributary streams join the main-stem, the energy level of flood-waters is lower. Islands in these river segments can progress to a more "mature" condition where alder and conifers are most abundant. Because of the variable power of floods in different portions of rivers, river islands separated by only a relatively short distance (in this example approximately 25 miles) can have very different dominant plant communities.

As plant communities change, so to do the animal communities that live on the islands. Cottonwoods and willows are home to many different species of migratory song birds, as well as beaver. In contrast, spruce- and alder-dominated forest stands support abundant numbers of woodpeckers and perching sites for Bald Eagles and Ospreys. Furthermore, rodent and insect populations are likely to be different between the two habitat types as well.

I've provided just a few examples from my research of how the physical process occurring in rivers can influence biotic processes and the development of an entire ecosystem. Many other researchers have documented other comparable processes. Together, these results suggest that if we want to maintain a river system with its historical level of diversity and functions, then we must ensure that natural processes such as high and low flow events and sediment erosion and transport, are allowed to occur at a time frame more frequent than the life span of the shortest lived organism adapted to these cycles that we wish to maintain. For example, if we wish to ensure the neo-tropical migrant song birds continue to summer in the willow and young cottonwood stands of river islands in a valley where the river is regulated by releases from a dam, then water level management must have some relation to natural hydro-cycles to moderate the conversion of cottonwood stands to alder stands. Otherwise the amount of song bird habitat may change through time.

A river island is like a good novel. If you know the language, it can tell you an intriguing story filled with colorful characters and "disturbing" events. The birth, maturation, and eventual death of a river island is intimately tied to the dynamics of the river. Islands are born out of floods, but don't escape their infancy without a low water period. As they age, they are inhabited by a variety of plant species, which in turn host a variety of animals. Eventually, a future flood event may destroy an island by eroding away all the deposited sediments. However, this same flood probably initiated the start of a new island at some point along the river.

Bibliography

Cooperman, M.S.,(1997). Plant distribution patterns on alluvial islands of the Swan River, Northwest Montana, and the link to fluvial dynamics. Masters thesis, Division of Biological Sciences, University of Montana. Missoula, MT. 180 pgs.

Watts, M. (1957). *Reading the Landscape: An Adventure in Ecology.* The Macmillan Company. 230 pgs.

APPENDIX A

EQUATIONS

Equation A

$$\text{Outlier Test Value} = \left[\left(\begin{array}{c}\text{75th percentile of basal}\\ \text{area values of species A}\end{array}\right) + 3\left(\begin{array}{c}\text{Inter - quartile range}\\ \text{of species A}\end{array}\right)\right]$$

Equation B

$$\text{Relative Abundance} = \left[\frac{\text{\# individuals of species A in 10 m interval Y}}{\text{total \# individuals in 10 m interval Y}}\right]\times 100$$

Equation C1

$$\text{Mean Basal Area} = \left[\frac{\sum \text{Basal areas of species A in 10m interval Y}}{\text{\# individuals of species A in 10 m interval Y}}\right]$$

Equation C2

$$\text{Percent Basal Area} = \left[\frac{\Sigma\left(\begin{array}{c}\text{basal areas of species A}\\ \text{in 10 m interval Y}\end{array}\right)}{\Sigma\left(\begin{array}{c}\text{basal areas of all species}\\ \text{in 10 m interval Y}\end{array}\right)}\right]\times 100$$

Equation D

$$\text{Density} = \left[\left(\frac{\text{\# of species A in 10 m interval Y}}{\text{total \# of individuals in 10 m interval Y}}\right)\times\left(\begin{array}{c}\text{mean point to plant distance}\\ \text{in 10 m interval Y}\end{array}\right)^2\right]$$

Equation E

$$\text{Mean Sensitivity} = 1/n-1 \sum_{t=1}^{t=n-1} \left| 2\left(x_{t+1} - x_t\right) / \left(x_{t+1} + x_t\right) \right|$$

where x equals the width of an individual annual growth ring, and t is the year when the growth ring was produced.

Equation F

$$\text{Shrub location} = \left[\text{Length of transect} - \left(\frac{\text{start location of specimen} + \text{end location of specimen}}{2} \right) \right]$$

Equation G

$$\text{Percent coverage of available space} = \left(\frac{\begin{array}{c}\text{Length of transect line occupied by} \\ \text{shrub class X in distance increment Y}\end{array}}{\begin{array}{c}\text{Total transect length} \\ \text{in distance increment Y}\end{array}} \right) \times 100$$

Equation H

$$\text{Percent Similarity} = 200 \sum_{i=1}^{s} \min\left(P_{ix}, P_{iy}\right)$$

where P_{ix} and P_{iy} are the quantities of species i in sample X and Y as proportions of the quantities of all s species in the two samples combined. Percent similarity can range from 0 to 100 with 100 being complete equality between samples.

APPENDIX B

SKETCHES OF STUDY ISLANDS AND REACHES

Key to Figures :

■	Vegetated Island
▩	Water
▩	Floodplain
■	Unvegetated sand bar, attached to island
▩	Underwater, unvegetated gravel bar
▒	Above water, unvegetated gravel bar
⟋	Tree (Large woody debris)
●	Upwelling water

Scale: 1 cm = approximately 20 m

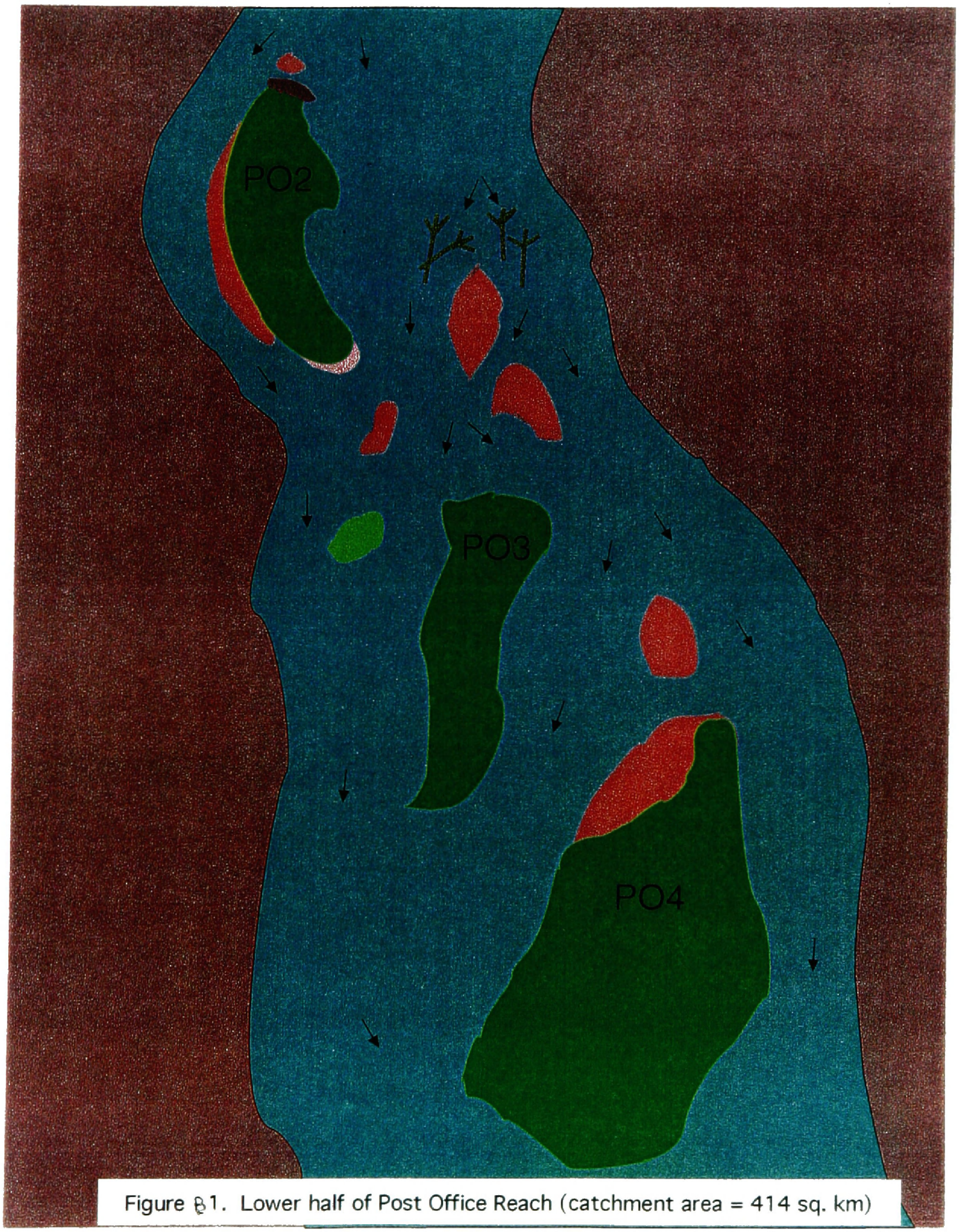


Figure B1. Lower half of Post Office Reach (catchment area = 414 sq. km)

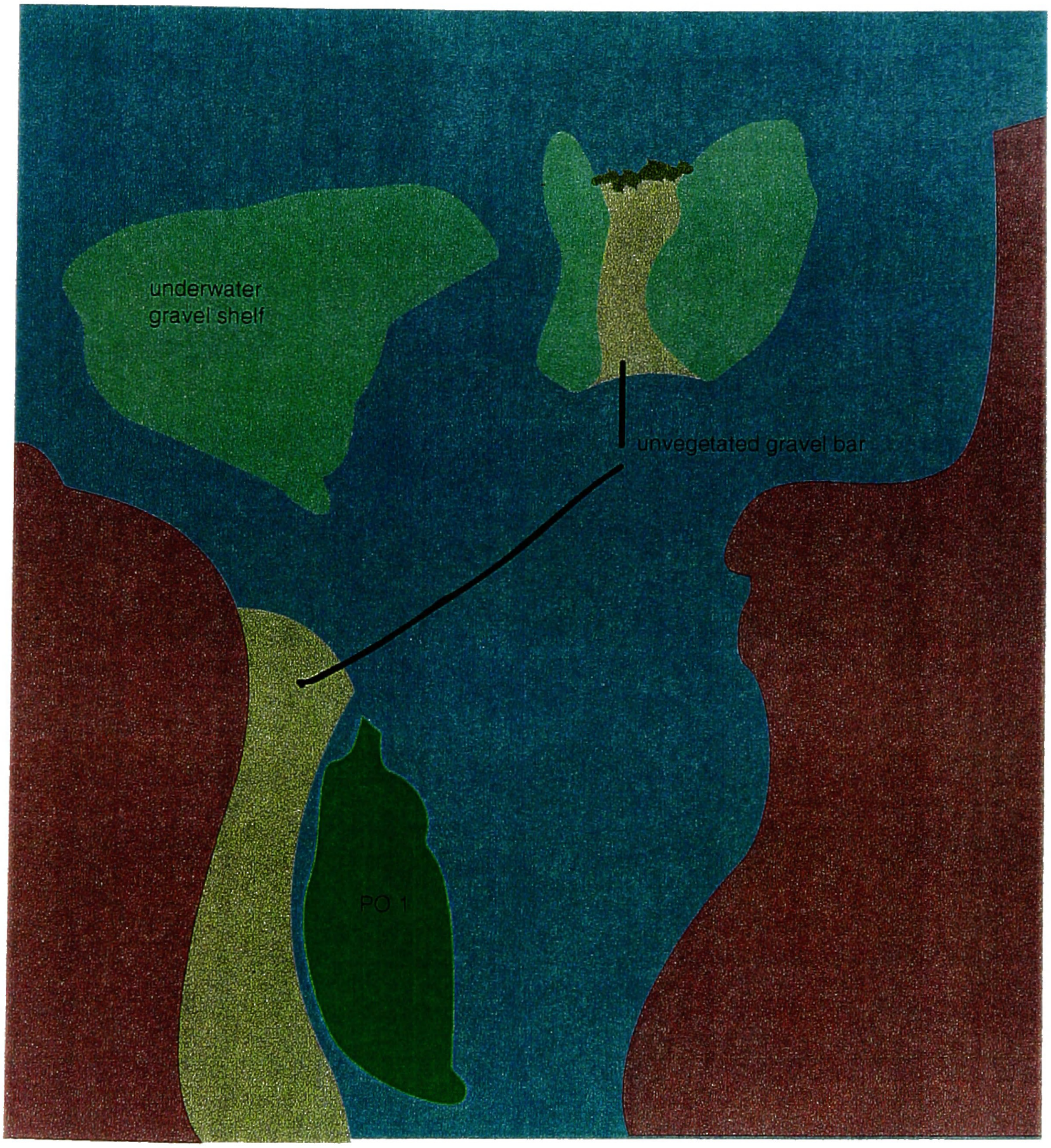


Figure B2.. Upper half of Post Office reach (catchment area = 414 sq. km)

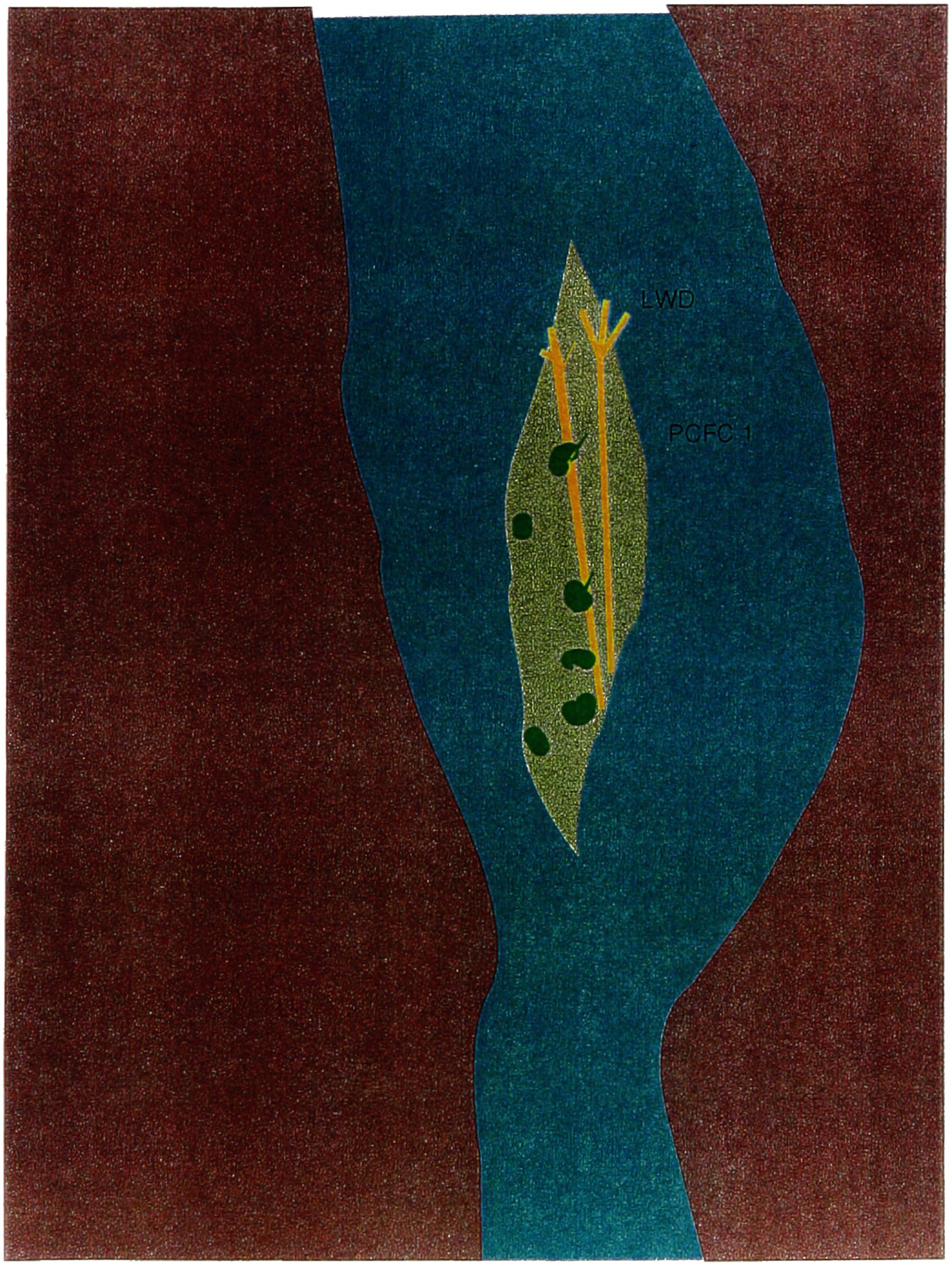


Figure B3. Upper quarter of Piper Creek to Fatty Creek reach
(catchment area = 622 sq. km)

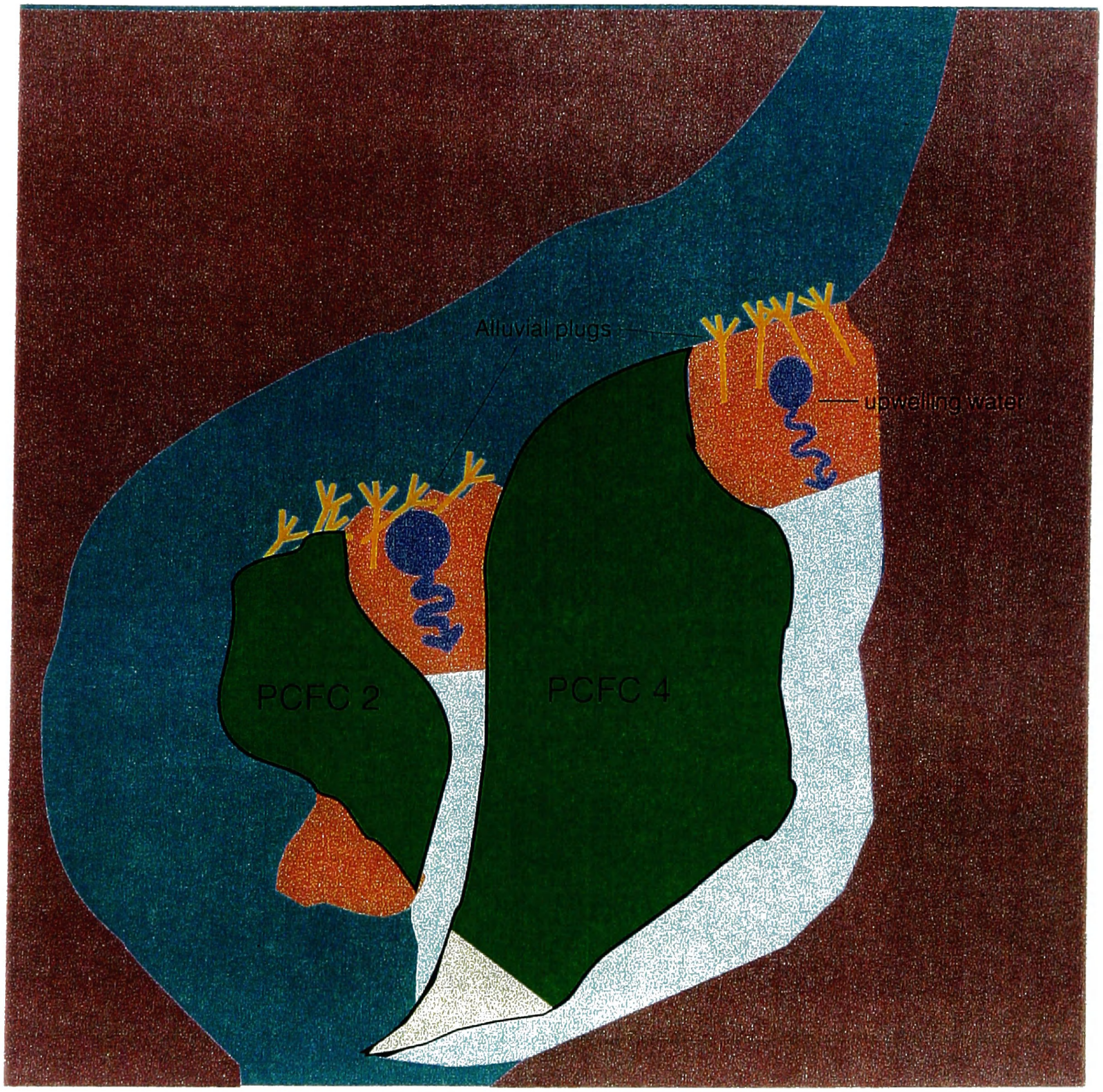


Figure 34. Second of four quarters in the PiperCreek to Fatty Creek reach
(catchment area = 622 sq. km)

Figure B5. Third of four quarters of Piper Creek to Fatty Creek reach
(catchment area = 622 sq. km)

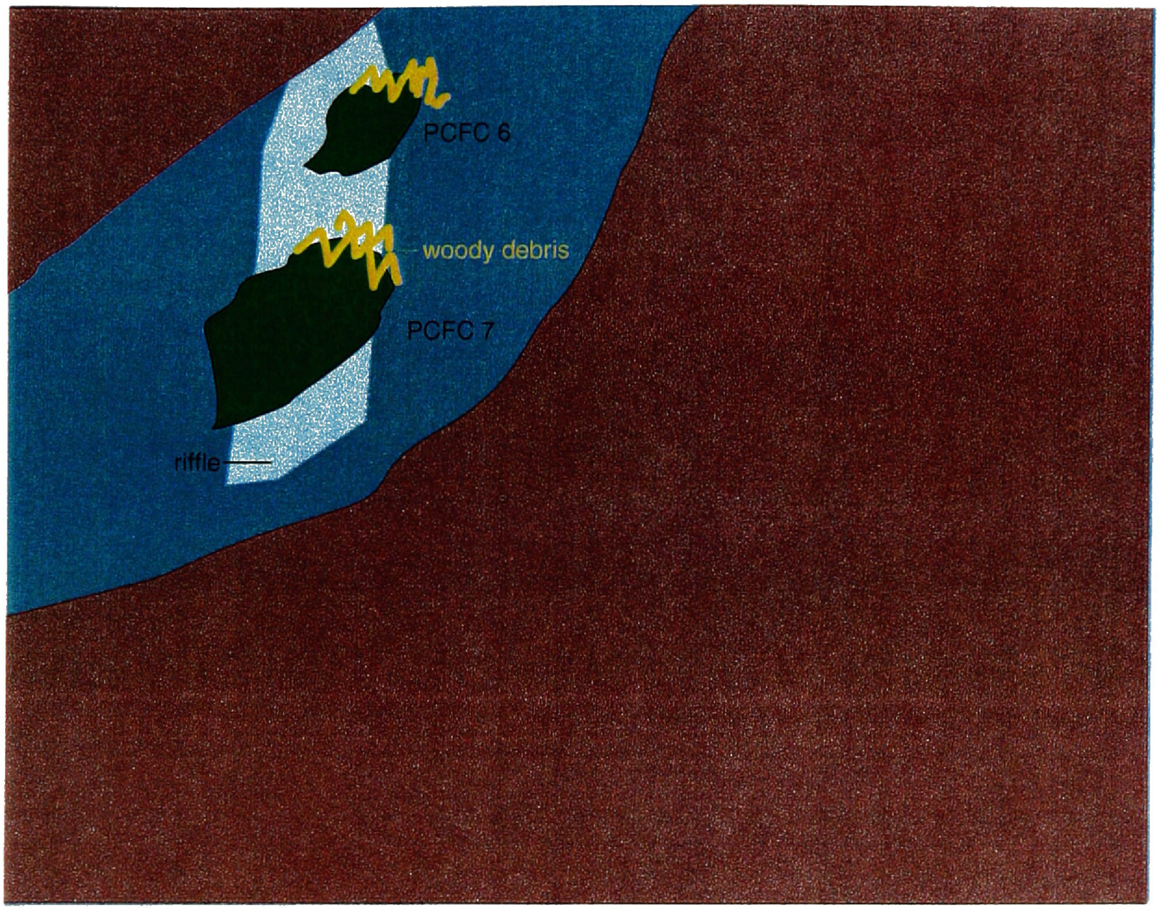


Figure B6. Lower quarter of Piper Creek to Fatty Creek Reach (ch
(catchment area = 622 sq. km)

Figure 87. Upper half of Point Pleasant reach (catchment area = 842 sq. km)

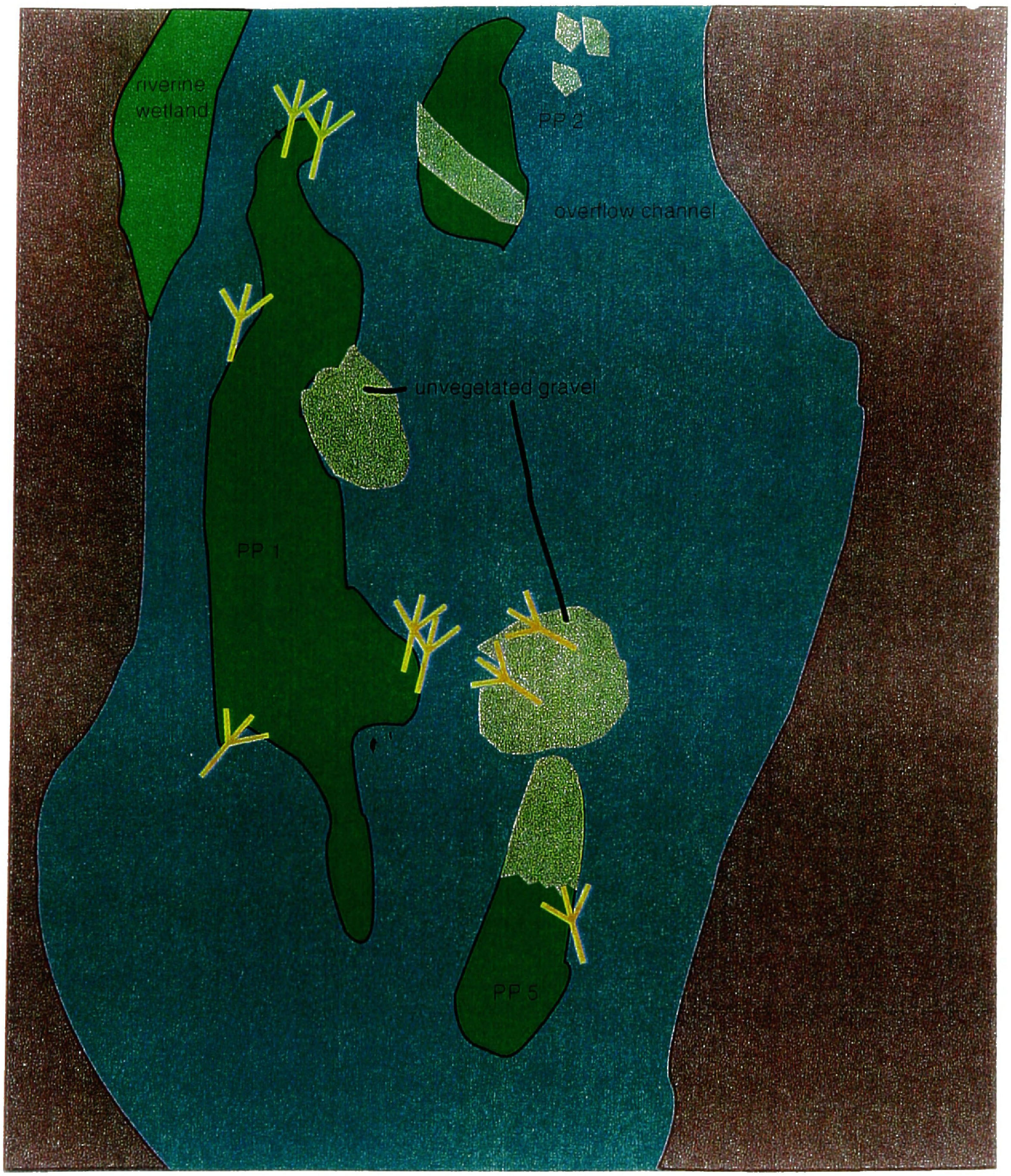


Figure B 8. Lower half of Point Pleasant reach (catchment area = 842 sq. km) km)

APPENDIX C

DENDROCHRONOLGY INVESTIGATION RESULTS

Table C1. Dendrochrolonogy results.

Island	Distance from tail of island (m)	Species	Age
PCFC 4	100.9	*Alnus tenuifolia*	12
PCFC 4	95.7	*Alnus tenuifolia*	20
PCFC 4	85.3	*Picea engelmannii*	44
PCFC 4	69.7	*Alnus tenuifolia*	19
PCFC 4	48.9	*Alnus tenuifolia*	23
PCFC 4	43.7	*Picea engelmannii*	15
PCFC 4	12.5	*Alnus tenuifolia*	15
PCFC 5	50.5	*Picea engelmannii*	94
PCFC 5	47.0	*Alnus tenuifolia*	8
PCFC 5	37.2	*Populus trichocarpa*	6
PCFC 5	24.2	*Populus trichocarpa*	8
PCFC 5	16.2	*Populus trichocarpa*	8
PCFC 5	30.2	*Picea engelmannii*	115
PP 1	85.5	*Alnus tenuifolia*	15
PP 1	15.7	*Alnus tenuifolia*	11
PP 1	112.5	*Alnus tenuifolia*	20
PP 1	118.0	*Populus trichocarpa*	18
PP 1	52.0	*Alnus tenuifolia*	14
PP 1	19.0	*Alnus tenuifolia*	23
PO 1	41.8	*Alnus tenuifolia*	19
PO 1	53.4	*Alnus tenuifolia*	17
PO 1	44.1	*Picea engelmannii*	20
PO 1	34.8	*Populus trichocarpa*	6
PO 1	31.7	*Alnus tenuifolia*	15
PO 1	31.7	*Picea engelmannii*	16
PO 1	38.4	*Picea engelmannii*	20
PO 1	23.7	*Picea engelmannii*	21
PO 1	7.7	*Alnus tenuifolia*	12
PO 1	38.4	*Larix occidentalis*	17
PO 2	46.9	*Picea engelmannii*	17
PO 2	30.0	*Alnus tenuifolia*	18
PO 2	27.6	*Alnus tenuifolia*	10
PO 2	25.2	*Alnus tenuifolia*	15
PO 2	25.2	*Picea engelmannii*	18
PO 2	13.2	*Alnus tenuifolia*	16
PO 2	29.2	*Picea engelmannii*	13
PO 3	62.8	*Alnus tenuifolia*	10
PO 3	52.8	*Alnus tenuifolia*	10
PO 3	49.8	*Alnus tenuifolia*	9
PO 3	42.8	*Alnus tenuifolia*	11
PO 4	147.6	*Picea engelmannii*	17
PO 4	139.9	*Pseudotsuga menziesii*	18
PO 4	124.6	*Populus trichocarpa*	17
PO 4	124.6	*Picea engelmannii*	17
PO 4	117.0	*Alnus tenuifolia*	17
PO 4	117.0	*Picea engelmannii*	19
PO 4	101.7	*Picea engelmannii*	20
PO 4	63.4	*Picea engelmannii*	16
PO 4	40.5	*Pinus contorta*	28

Table C1 (cont.)

Island	Distance from tail of island (m)	Species	Age
PO 4	32.8	*Alnus tenuifolia*	11
PO 4	168.6	*Picea engelmannii*	17
PO 4	159.6	*Picea engelmannii*	20
PO 4	150.6	*Picea engelmannii*	18
PO 4	150.6	*Populus trichocarpa*	16
PO 4	150.6	*Larix occidentalis*	19
PO 4	150.6	*Picea engelmannii*	22
PO 4	141.6	*Alnus tenuifolia*	18
PO 4	96.6	*Alnus tenuifolia*	21
PO 4	69.6	*Alnus tenuifolia*	21
PO 4	60.6	*Alnus tenuifolia*	19
PO 4	42.6	*Populus trichocarpa*	11
PO 4	118.9	*Alnus tenuifolia*	25
PO 4	112.7	*Picea engelmannii*	17
PO 4	100.4	*Populus trichocarpa*	10
PO 4	94.3	*Pseudotsuga menziesii*	16
PO 4	63.5	*Picea engelmannii*	19
PO 4	51.2	*Pinus contorta*	20

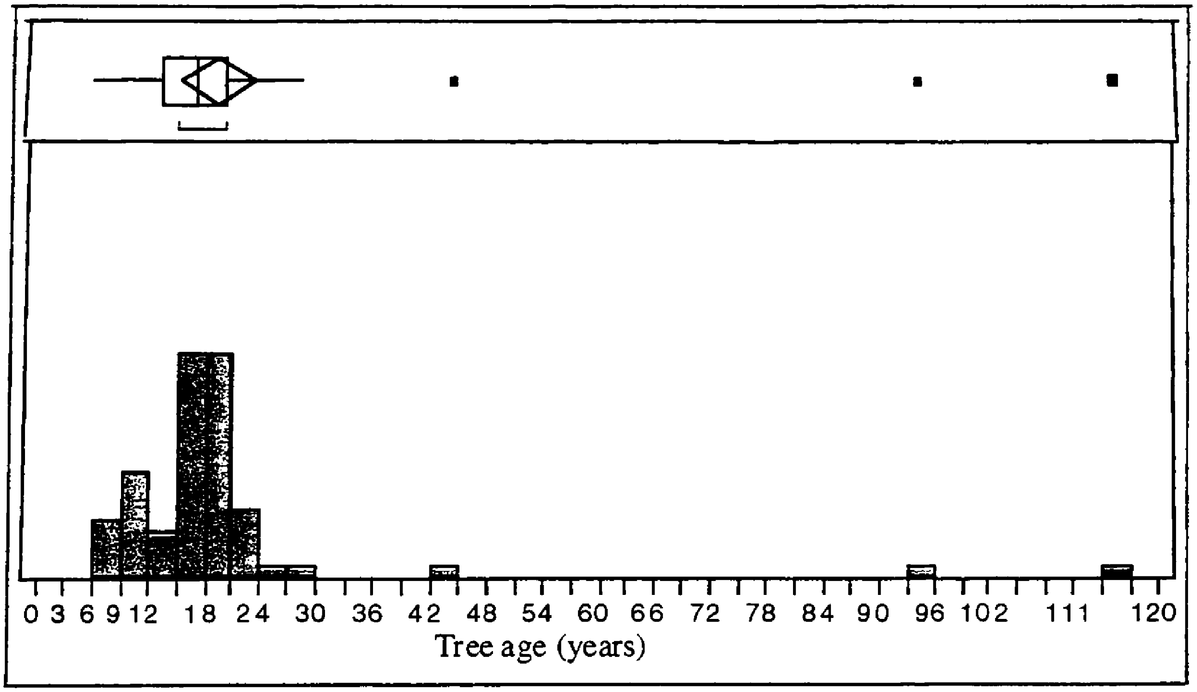


Figure C1. Distribution of tree ages on fourteen islands of the Swan River (n=67).

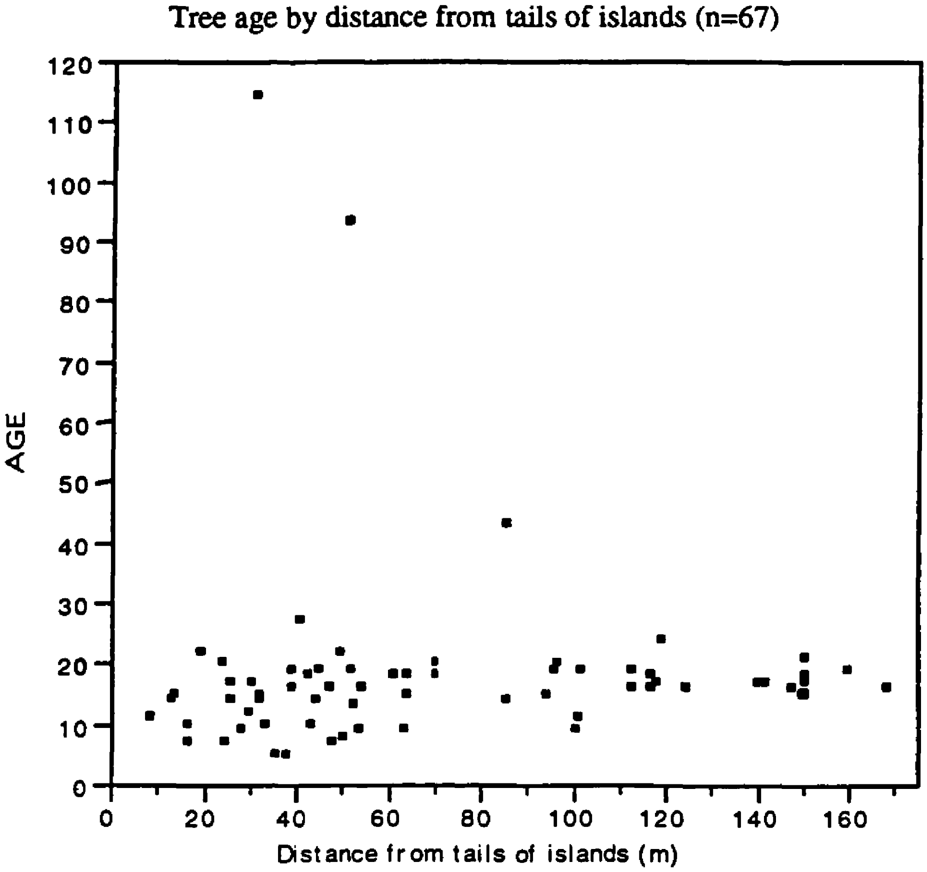
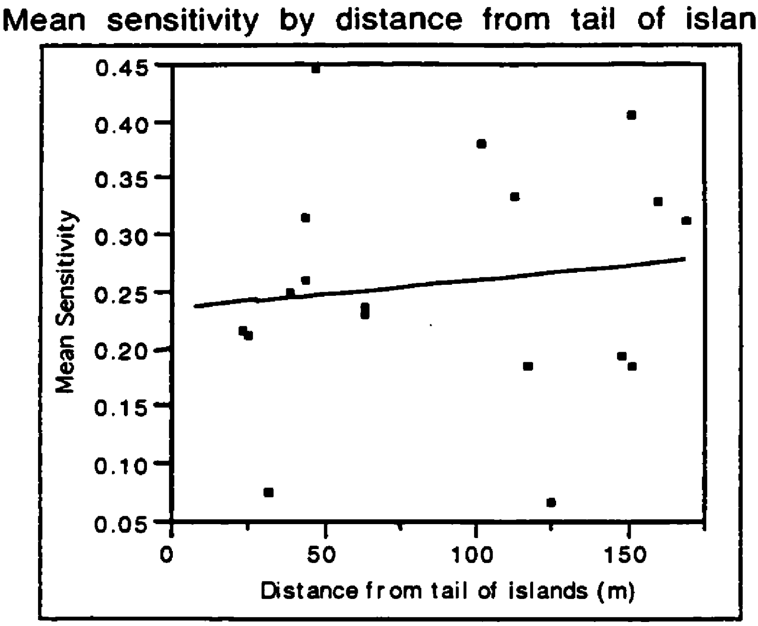


Figure C2. Tree ages by distance from tails of islands



```
          Summary   of   Fit
        RSquare                          0.018282
        RSquare Adj                     -0.04308
        Root Mean Square Error           0.104059
        Mean of Response                 0.259222
        Observations (or Sum Wgts)             18

        Parameter   Estimates
Term                    Estimate   Std  Error  t  Ratio   Prob>|t|
Intercept              0.2355919   0.049756      4.73    0.0002
Location (from tail)   0.0002636   0.000483      0.55    0.5927
```

Figure C3. Mean sensitivity values by distance from tails of islands.

APPENDIX D

SOIL PROFILES AND PHOTOGRAPHS

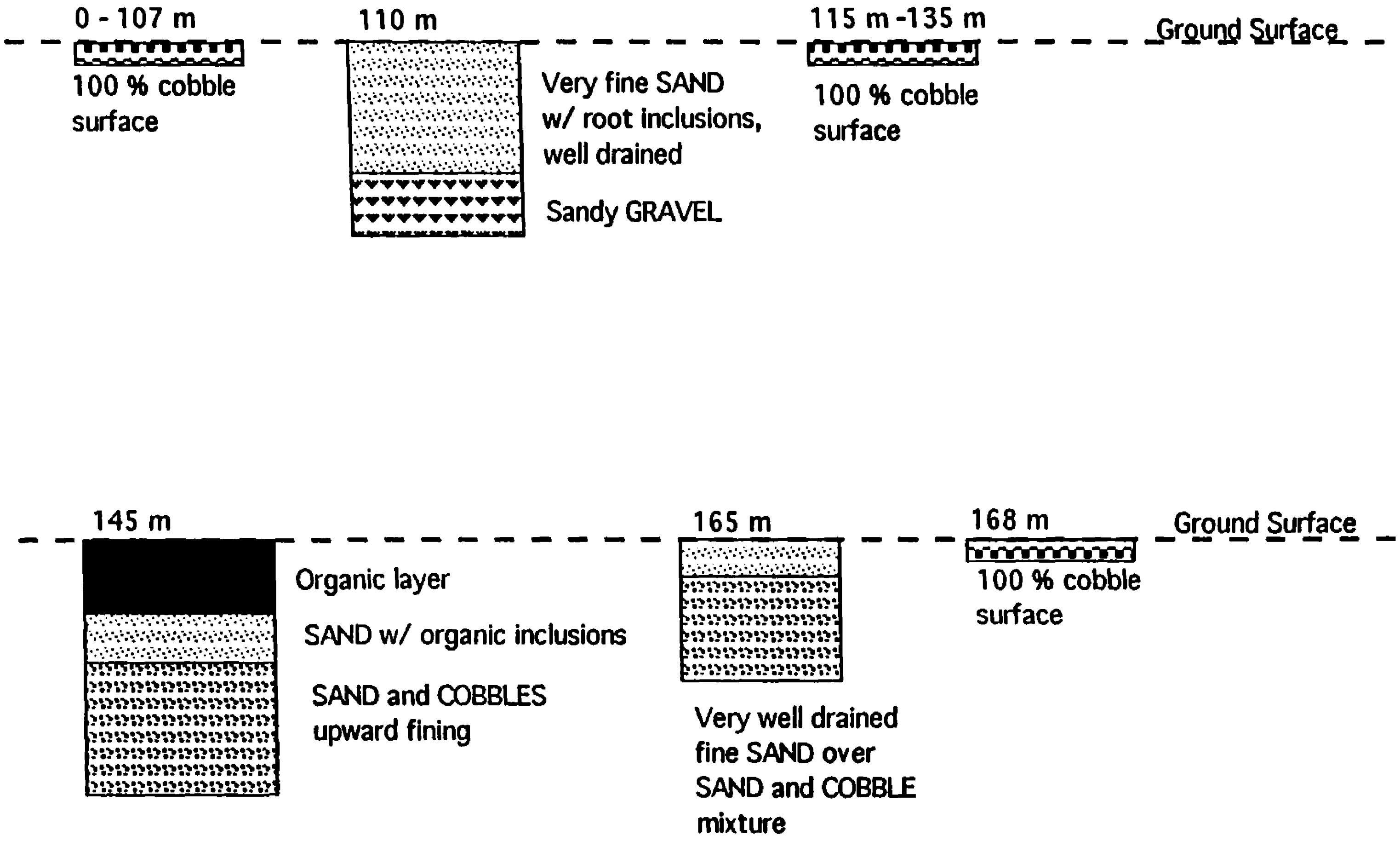


Figure D1. Soil profile of island PO 4 (Locations referenced from tail of island).
Depth scale: 1 cm = 5 cm

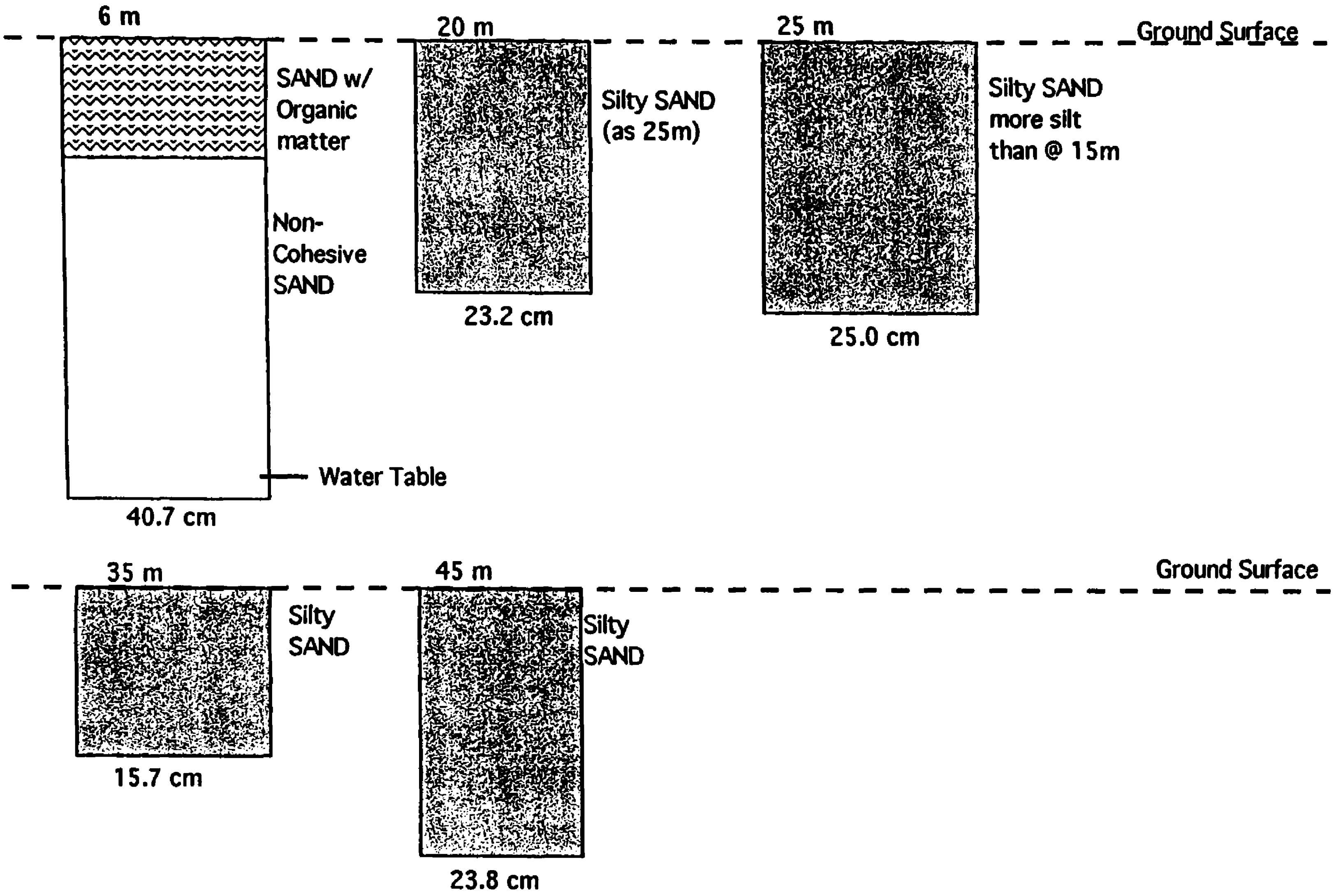


Figure D2. Soil profile of Island PO 2 (locations referenced from tail of island). Depth scale: 1 cm = 5 cm

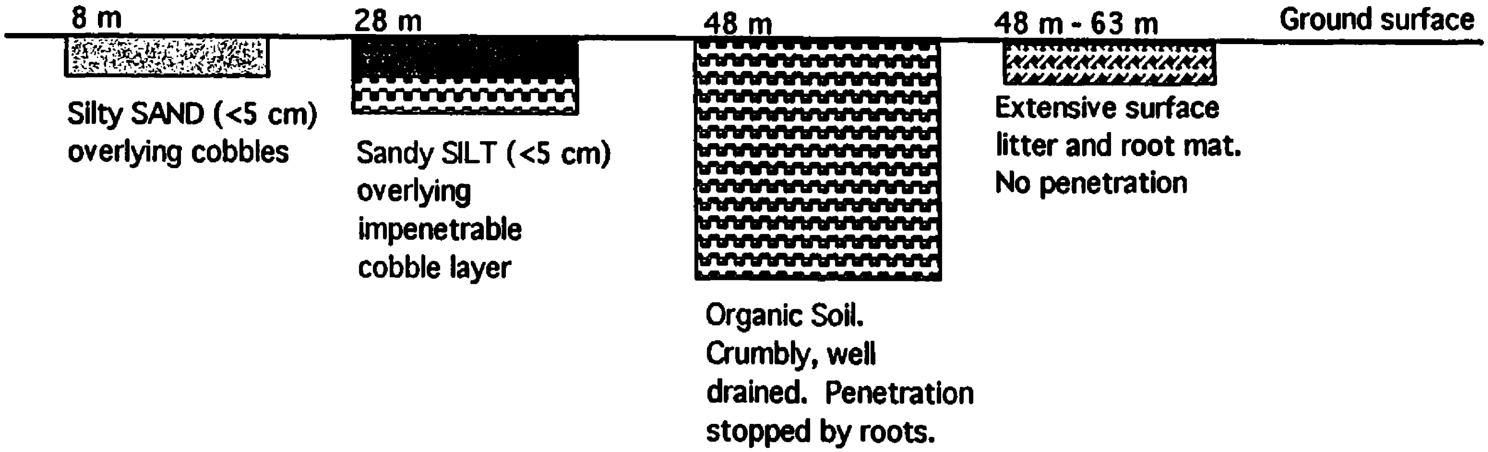


Figure D3. Soil profile of island PO 1 (locations referenced from tail of island).
Depth scale: 1 cm = 5 cm

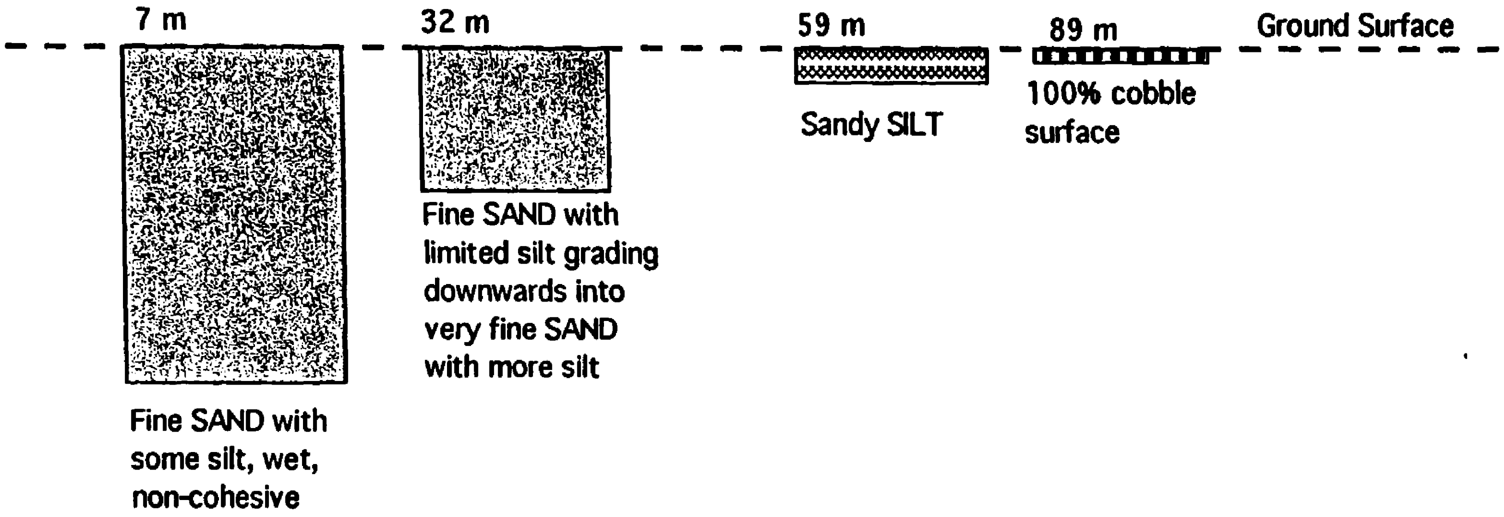


Figure D4. Soil porfile of island PP 3 (locations referenced from tail of island). Depth scale: 1 cm = 5 cm.

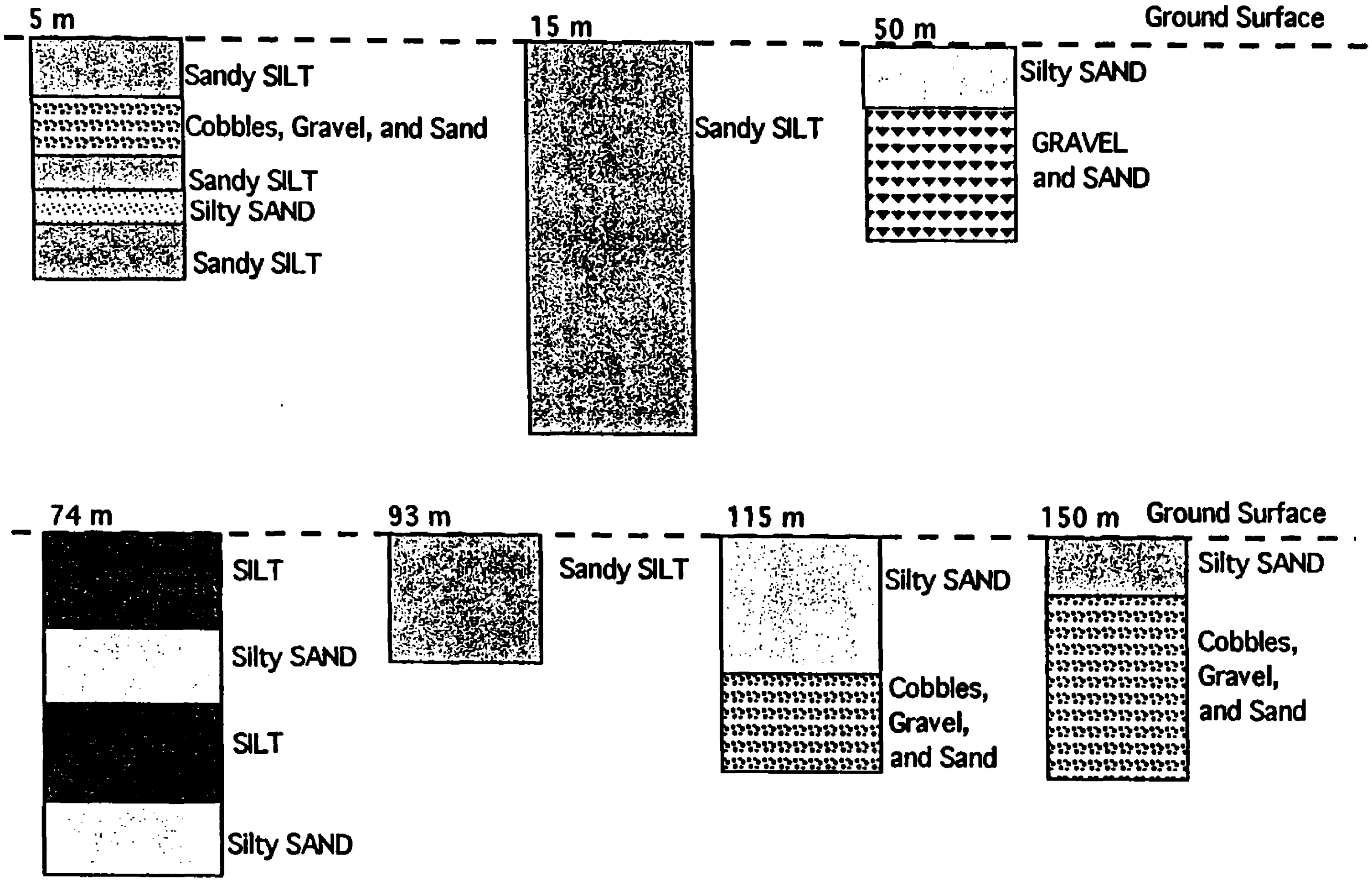


Figure D 5. Soil profile of island PP 1 (Locations referenced from tail of island).
Depth scale: 1 cm = 5 cm.

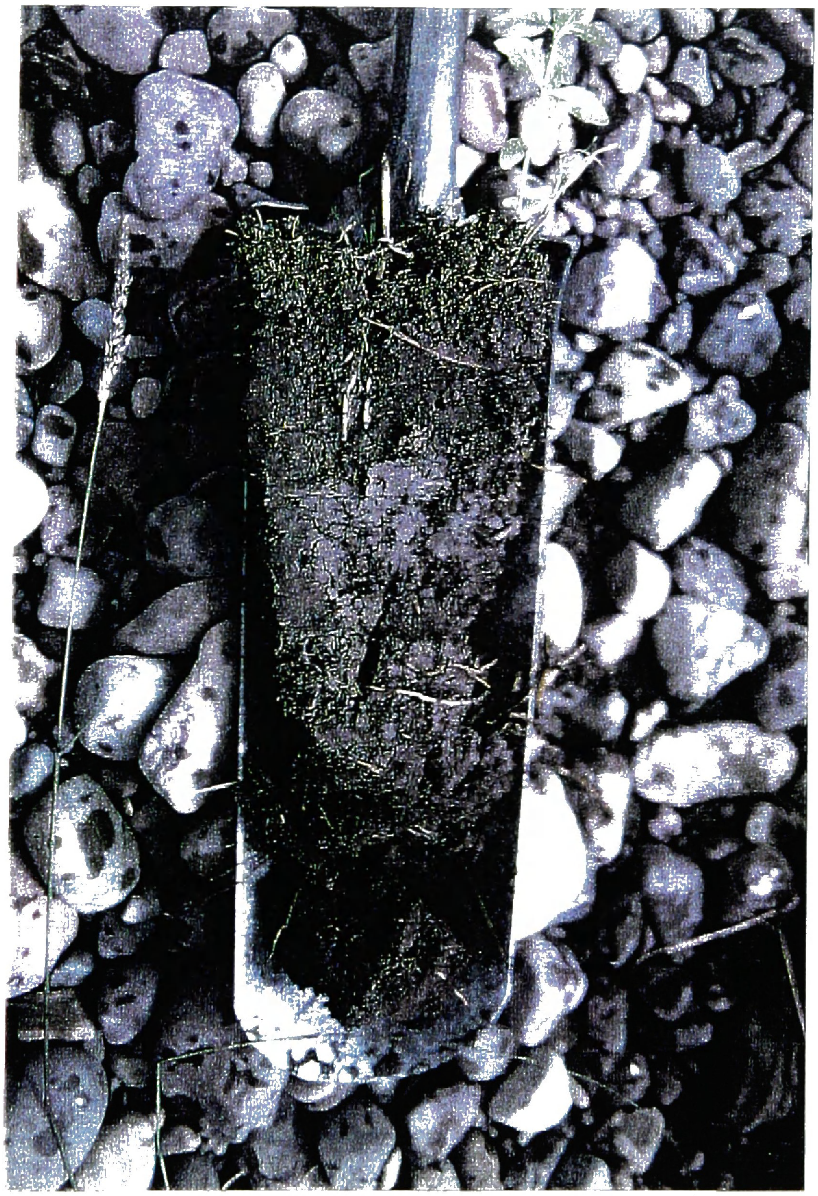


Figure D6. Soil column from a study island. The bottom and top of the profile are sandy deposits. The middle is a combination of clay and silt.

Figure D7. Soil profile of a river island exposed at a cut-bank.