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HYDROGEOMORPHIC FACTORS INFLUENCING CLONAL RECRUITMENT
OF COTTONWOODS IN MOUNTAIN VALLEYS

by

Michael D. Roberts

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Watershed Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1999

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ABSTRACT

Hydrogeomorphic Factors Influencing Clonal Recruitment of Cottonwoods
in Mountain Valleys

by

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Utah State University, 1999

Major Professor: Dr. James P. Dobrowolski
Program: Watershed Science

Riparian cottonwoods (*Populus* spp.) are keystone pioneer species that contribute to critical streamside and in-stream habitats, water quality, and aesthetic and recreational value. Land use and river regulation have caused a widespread reduction in the extent and regeneration of this genus. The majority of research on *Populus* species' reproduction has examined seedling recruitment that dominates in wide alluvial valleys. In contrast, I evaluated reproductive strategies of *Populus angustifolia* in mountain valleys. Research was conducted in northern Utah on the Little Bear River, a gravel-bedded stream that flows north out of the Bear River Range onto deposits of Ancient Lake Bonneville. I used allozyme electrophoretic data and vegetation mapping to investigate recruitment mechanisms of cottonwoods at two steep, confined mountain valley sites and two wide, alluvial valley sites. Allozyme electrophoretic analysis on samples from sites one through four revealed 60%, 69%, 86%, and 84% clonal

recruitment, respectively. The size of cottonwood clones may be on the order of 200-300 m in this system. Vegetation mapping supported allozyme data and suggested that clonal recruitment dominates the system.

I also collected data at four sites containing no cottonwoods to compare hydrogeomorphic influences at non-cottonwood (NC) sites and cottonwood recruitment (CR) sites. CR sites possess a distinctive geomorphic template relative to NC sites and this template may facilitate root disturbance resulting in clonal recruitment. A high frequency of woody debris and mid-channel islands characterizes CR sites. Channels at CR sites are less entrenched, more sinuous, and exhibit larger bankfull channel width and width to depth ratios, and finer grain sizes than channels at NC sites. At CR sites, estimates of bankfull average boundary shear stress and unit stream power are less compared to those at NC sites.

Cottonwood recruitment models that typically describe seedling reproduction in alluvial valley environments do not apply in narrow, steep-gradient environments. I found clonal recruitment of cottonwoods to correlate spatially and temporally with channel and root disturbance associated with rain on snow events on the order of the 25-30-yr flood event.

DEDICATION

I would like to dedicate this work to my family. They have made this work possible. They introduced me to the outdoors as a child and the memories of those experiences that we share have shaped my life. They have provided the strength to choose my own path, for which I cannot thank them enough. Dad, you are my hero. I hope to be like you when I grow up. Leigh, you are my best bud. Mom and Kathy, thank you both so much for all of your love and support.

I would also like to dedicate this work to my adopted family, the Flynns. I thank them all for allowing me to grow up as part of their clan.

All of you are always in my thoughts.

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Michael D. Roberts

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CHAPTER 1

INTRODUCTION

Riparian zones encompass sharp environmental gradients and complex ecological processes. Plant communities within these systems provide an intricate linkage between terrestrial and aquatic ecosystems (Gregory et al. 1991) and there is a growing awareness that the health of rivers is critically tied to the surrounding vegetation they sustain (Braatne et al. 1996). Ecological services of riparian zones include filtering nutrients and improving water quality, reducing sediment delivered to streams, ameliorating flood flows by decreasing velocity, and increasing bank strength with root networks (Patten 1998). Aside from societal benefits, riparian ecosystems also are some of the most diverse ecosystems of the arid west (Anderson et al. 1983, Hunter et al. 1987, Finch and Ruggiero 1993). In addition, a high percentage of the animal species in arid regions need riparian habitats for some stage in their life cycles (Brinson et al. 1981, Kondolf et al. 1996).

Many land uses can potentially alter the function of riparian zones such as channelization, road construction, timber harvesting, livestock grazing, mining, and water diversions (National Research Council 1995). These land uses often result in a lack of regeneration of dominant, pioneer, riparian species such as cottonwoods (*Populus* spp.) and lead to a degraded river system (Braatne et al. 1996, Rood and Mahoney 1990, Poff et al. 1997). This reduction in cottonwood regeneration has initiated an effort to understand cottonwood recruitment ecology and develop process-based restoration solutions (Braatne et al. 1996, Poff et al. 1997).

Most management programs and published literature regarding riparian vegetation recruitment ecology have focused on the hydrogeomorphic requirements for seedling establishment and subsequent survival of riparian species (Rood et al. 1994). Scott et al. (1993) describe how seedling germination and establishment of riparian vegetation occur in response to the character and pattern of stream flow within a given year or growing season. Mahoney and Rood (1998) provide an ecological model that describes the relationship between seedling recruitment and alluvial settings.

The fundamental hydrogeomorphic processes that facilitate cottonwood seedling recruitment in wide alluvial valleys typically have been quantified by correlating the flow regime and the time of seedling establishment. Studies typically use dendrochronological, geomorphic, and stream flow data to correlate the timing of stream flow and seedling recruitment (Bradley and Smith 1986, Scott et al. 1993, 1996, Friedman et al. 1996, Rood et al. 1998, Mahoney and Rood 1998). Using these techniques, workers have suggested that channel narrowing, vertical floodplain deposition, and point bar formation are the primary processes that create the bare, moist geomorphic surfaces widely regarded as the appropriate seedbeds for colonization by cottonwoods (Scott et al. 1996). These processes perpetuate the spatial distribution of cottonwoods by forming the appropriate seedling surfaces in unconfined alluvial valleys. This focus on seedling recruitment assumes, at least implicitly, that seedling recruitment is the principal reproductive strategy of cottonwoods (Rood et al. 1994).

Much less attention has been focused on vegetative recruitment mechanisms and few studies have sought to document the relative role of sexual versus asexual

recruitment (Rood et al. 1994, L. A. Gom and S. B. Rood *unpublished manuscript*).

Studies have demonstrated that cottonwoods have the capacity to vegetatively propagate through a number of mechanisms (Everitt 1968, Schier and Campbell 1976, Shaw 1976, Rood et al. 1994, L. A. Gom and S. B. Rood *unpublished manuscript*). These studies often have relied upon excavation and analysis of root systems to determine parentage. An alternative to destructive sampling is to use some form of genetic test, such as cost effective protein electrophoresis (Murphy et al. 1996) to determine genotype in *Populus* spp. (Rajora and Zsuffa 1988, Keim et al. 1989).

Hydrogeomorphic factors in steep, confined mountain valleys also influence riparian vegetation ecology. However, these factors have rarely been linked to processes affecting riparian vegetation recruitment mechanisms in these valleys. River processes differ in confined compared to unconfined valleys. Often cottonwoods of the *Tacamahaca* section, the narrow-leaved cottonwoods, are found in mountain valleys (Eckenwalder 1984, Rood and Mahoney 1990, Mahoney and Rood 1998, L. A. Gom and S. B. Rood *unpublished manuscript*). These cottonwoods display a higher propensity to propagate clonally than cottonwoods of the *Aigeiros* section, the wide-leaved cottonwoods, found in wide alluvial valleys (Rood et al. 1994, Schier and Campbell 1976, Shaw 1976, Kranjcec et al. 1998).

L. A. Gom and S. B. Rood (*unpublished manuscript*) recently mapped the distribution of cottonwood clones on an island, in the Oldman River near Lethbridge. They suggested clones distributed in areas subjected to scour. However, no one has identified the hydrogeomorphic influences on clonal recruitment of cottonwoods or

developed an ecological model for clonal recruitment similar to Mahoney and Rood's (1998) model for seedling recruitment.

Restoration efforts in unconfined alluvial valleys attempting to incorporate natural processes are being formulated with research that has focused on seedling recruitment in wide alluvial valleys (Barinaga 1996, Klotz and Swanson 1997, Rood et al. 1998). It may be similarly appropriate to formulate restoration efforts in confined mountain valleys based on clonal mechanisms where these mechanisms play a large role in the ecology of the system.

Thus, evaluation of clonal recruitment mechanisms in mountain valley settings deserves further investigation. The Little Bear River is a gravel-bedded stream that flows north out of the Bear River Range onto deposits of Ancient Lake Bonneville and provides an opportunity to undertake such an effort.

I have identified three objectives for this research. The first objective, addressed in Chapter 2, is to evaluate the degree of clonal recruitment of *Populus angustifolia* on the Little Bear River. This objective focuses on determining the proportion of clonal recruitment among vegetation samples collected at different cottonwood groves in the watershed. Differences in recruitment mechanisms with respect to valley type are inferred from the results. The second objective, addressed in Chapter 3, is to evaluate geomorphic influences on the distribution of *Populus angustifolia*. Reach and site scale geomorphic controls are evaluated to determine the nature or extent of relationships between geomorphology and the spatial distribution of *Populus angustifolia*. The final objective, also addressed in Chapter 3, is to evaluate hydrologic influences on recruitment

of *Populus angustifolia*. This objective attempts to correlate hydrologic events with the temporal distribution of recruitment of *Populus angustifolia* in the Little Bear River watershed. Information from this study will be useful to formulate process-based restoration of riparian ecosystems where clonal recruitment plays a role in the recruitment ecology of the system.

LITERATURE CITED

- Anderson, B. W., R. D. Ohmart, and J. Rice. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado River Valley. *Condor* **85**:392-405.
- Braatne, J. H., S. B. Rood, and Paul Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods. Pages 57-80 in R. F. Stettler, H. D. Bradshaw, P. E. Heilman, and T. M. Hinckley, editors. *Biology of populus and its implications for management and conservation*. NRC Research Press, Ottawa, Ontario, Canada.
- Barinaga, M. 1996. A recipe for river recovery? *Science* **273**:1648-1650.
- Bradley, C. E., and D. G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany* **64**:1433-1442.
- Brinson, M. M., B. L. Swift, R. C. Plantico, and J. S. Barclay. 1981. Riparian ecosystems: their ecology and status. USFWS Biological Services Program Washington, D.C., USA. **FWS/OBS-81/17**.
- Eckenwalder, J. 1984. Natural intersectional hybridization between North American species of *Populus* (*Salicaceae*) in sections of *Ageiros* and *Tacamahaca*. I. Population studies of *P. Xparryi*. *Canadian Journal of Botany* **62**:317-324.
- Everitt, B. L. 1968. Use of the cottonwood on an investigation of the recent history of a flood plain. *American Journal of Science* **266**:417-439.
- Finch, D. M., and L. R. Ruggiero. 1993. Wildlife and biological diversity in the Rocky Mountains and north Great Plains. *Natural Areas Journal* **13**:191-203.
- Friedman, J. M., W. R. Osterkamp, and W. M. Lewis, Jr. 1996. Channel narrowing and vegetation development following a Great Plains flood. *Ecology* **77**:2176-2181.

- Gregory, S. V., F. J. Swanson, W. A. McKee, and K.W. Cummins. 1991. An ecosystem perspective on riparian zones. *Bioscience* **4**:540-551.
- Hunter, W. C., B. S. Anderson, and R. D. Ohmart. 1987. Avian community structure changes in a mature floodplain forest after extensive flooding. *Journal of Wildlife Management* **51**:495-502.
- Keim, P., K. N. Paige, T. G. Whitham, and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. *Genetics* **123**:557-565.
- Klotz, J. R., and S. Swanson. 1997. Managed instream flows for woody vegetation recruitment, a case study. Pages 483-489 in J. Warwick, editor. Symposium proceedings: water resources education, training, and practices: opportunities for the next century. American Water Resources Association, Universities Council on Water Resources, American Water Works Association, Keystone, Colorado, USA.
- Kondolf, G. M., R. Kattlemann, M. Embury, and D. C. Erman. 1996. Status of riparian habitat. Sierra Nevada ecosystem project: final report to congress. Center for Water and Wildland Research. University of California, Davis, California, USA.
- Kranjcec, J., J. M. Mahoney, and S. B. Rood. 1998. The response of three riparian cottonwood species to water table decline. *Forest Ecology and Management* **110**:77-87.
- Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment--an integrative model. *Wetlands* **18**:634-645.
- Murphy, R. W., J. W. Sites, Jr., D. G. Buth, and C. H. Haufler. 1996. Proteins: isozyme electrophoresis. Pages 51-95 in D. M. Hillis, C. Moritz, and B. K. Mable, editors. *Molecular systematics*, 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- National Research Council (US). 1995. Committee on characterization of wetlands. Wetlands--characteristics and boundaries. National Academy Press, Washington, D.C., USA.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid north America: diversity and human impacts. *Wetlands* **18**:498-512.
- Poff, L. N., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime, a paradigm for conservation and restoration. *Bioscience* **47**:769-784.
- Rajora, O. P., and L. Zsuffa. 1989. Multilocus genetic structure, characterization, and relationships of *Populus x canadensis* cultivars. *Genome* **32**:99-108.

- Rood, S. B., C. Hillman, T. Sanche, and J.M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. *Canadian Journal of Botany* **72**:1766-1774.
- Rood, S. B., A. R. Kalischuk, and J. M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands* **18**:557-570.
- Rood, S. B., and J. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management* **14**:451-464.
- Schier, G. A., and R. B. Campbell. 1976. Differences among *Populus* species in ability to form adventitious shoots and roots. *Canadian Journal of Forestry* **6**:253-261.
- Scott, M. L., J. M. Friedman, and G. T. Auble. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology* **14**:327-339.
- Scott, M. L., M. A. Wondzell, and G. T. Auble. 1993. Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation. Pages 237-246 in H.J. Morel-Seytoux, editor. *Proceedings of the 13th annual American geophysical union hydrology days*. Hydrology Days Pub., Atherton, California, USA.
- Shaw, R. K. 1976. A taxonomic and ecological study of the river-bottom forest on St. Mary, Lee Creek, and Belly River in southwestern Alberta, Canada. *Great Basin Naturalist* **36**:243-271.

CHAPTER 2

AN INVESTIGATION OF COTTONWOOD RECRUITMENT MECHANISMS IN MOUNTAIN VALLEYS, NORTHERN UTAH

INTRODUCTION

Riparian forests are some of the most diverse ecosystems of the arid western United States (Anderson et al. 1983, Hunter et al. 1987, Finch and Ruggiero 1993). Riparian vegetation favorably contributes to critical streamside and in-stream habitat, water quality, bank stability, and aesthetic and recreational values (Patten 1998). Riparian cottonwoods (*Populus* spp.) are a keystone pioneer species that is the foundation of this forest type, but land use and river regulation have caused a widespread reduction in the extent and regeneration of this genus (Braatne et al. 1996, Rood and Mahoney 1990). This reduction has generated an effort to understand cottonwood recruitment ecology to provide a basis for future management to retain the societal benefits of riparian vegetation.

Recruitment of cottonwoods from seedlings has been extensively studied and is a function of many complex interactions. However, some general patterns have emerged from the literature. Seed germination and establishment of riparian vegetation occur in response to the character and pattern of stream flow within a given year or growing season. The appropriate combination of streamflow and sediment-transport characteristics creates sedimentary deposits called seedbeds that are bare, moist, unshaded, and protected from removal by subsequent disturbance (Scott et al. 1993, Auble et al. 1994).

Appropriate seedbeds may be created by lateral floodplain accretion that occurs by channel meandering. Lateral floodplain accretion typically forms point bars in wide alluvial valleys where stream flow and sediment characteristics are conducive to seedling recruitment (Scott et al. 1996, 1997, Bradley and Smith 1986). As channels meander in unconfined alluvial valleys, new seed beds are created and parallel arcuate bands of even-aged trees occur on these point bars (Scott et al. 1996). A certain timing, magnitude, frequency, and rate of stage decline of the hydrograph facilitate seedling recruitment on these point bars by supplying a rate of stage decline that is sufficiently slow such that seedling root elongation maintains contact with available water (McBride and Strahan 1984, Mahoney and Rood 1991, 1992, 1998, Rood et al. 1998). Mahoney and Rood (1998) summarize these ecological relations in their "recruitment box" model.

Vertical floodplain accretion (floodplain deposition) can also produce appropriate seedbeds. Vertical accretion generally results in a linear spatial distribution of appropriate surfaces along channel margins and consequently, linear cottonwood stands (Scott et al. 1996, Auble and Scott 1998). A linear arrangement of cottonwood stems also may result from flood training where stems are buried by flooding and sediment deposition and sprouts emerge from the buried stem (Everitt 1968). The majority of studies where flood training has been noted have been in wide alluvial valleys and the occurrence of flood training may be less common in constricted reaches. Channel margin and previously formed floodplains also may become appropriate seedbeds after large floods scour vegetation from these areas or where channels narrow over time (Friedman et al. 1996).

Particle size on recruitment surfaces also affects seedling recruitment. Mahoney and Rood (1998) found small particle sizes on recruitment surfaces assists in providing soil moisture to developing root systems by increasing the height of the capillary fringe. In addition, other studies have found higher seedling recruitment and survival where geomorphic surfaces were characterized by a high percentage of fines (Merigliano 1998, Virginillo et al. 1991, Johnson 1994).

The observations described above summarize the fundamental ecological relationships that affect seedling recruitment in alluvial settings. Cottonwoods of the section *Aigeiros*, which are broad-leafed species such as *P. deltoides* and *P. fremontii*, generally occur in unconfined alluvial valleys and are adapted to physical conditions of these valleys. The *Aigeiros* cottonwoods are less drought tolerant and more reliant on seedling recruitment mechanisms (Tyree et al. 1994, Mahoney and Rood 1998, L. A. Gom and S. B. Rood *unpublished manuscript*).

The alluvial/seedling recruitment relationships outlined above lead to river management, conservation, and restoration strategies where seedling recruitment is the dominant process (Braatne et al. 1996, Rood et al. 1998). These relationships are typically formulated with *Aigeiros* section cottonwoods. However, these relationships do not account for the reproductive strategy of clonal recruitment in cottonwoods, which may be favored where seedling recruitment is not the dominant mechanism.

The *Tacamahaca* section, or narrow-leafed cottonwoods, includes species such as *P. trichocarpa*, *P. balsimifera*, and *P. angustifolia*, which are commonly found in mountain valleys (Eckenwalder 1984, Rood and Mahoney 1990, Mahoney and Rood

1998, L. A. Gom and S. B. Rood *unpublished manuscript*). Importantly, this section displays a higher propensity to propagate clonally than cottonwoods of the *Aigeiros* section (Rood et al. 1994, Schier and Campbell 1976, Shaw 1976, Kranjcec et al. 1998). Braatne et al. (1996) suggest that crown breakage and tree fall during storms and flooding are the most common sources of clonal recruitment. Root sprouting has received less attention but has been found to occur in response to high water tables (H. Richter pers. com. 1997). Sprouting also has been noted on cutbanks (Webb and Brotherson 1988), scroll bars (Hickin and Nanson 1975), and scoured channel areas (L. A. Gom and S. B. Rood *unpublished manuscript*). Scott et al. (1996) suggest root sprouting may be important in colonizing near channel areas abandoned during channel narrowing. In addition, studies have found that flow regulation can lead to a decrease in fine particle sizes on recruitment surfaces, and a consequent decrease in water-holding capacity of these sediments. This alteration of sediment characteristics may result in a decrease in seedling recruitment survival and a shift towards clonal recruitment (Stromberg and Patten 1989, Rood and Mahoney 1990, 1995).

The *Tacamahaca* section also is more tolerant of rapid groundwater decline (Kranjcec et al. 1998) and drought induced cavitation (Tyree et al. 1994). These life history traits suggest the *Tacamahaca* cottonwoods are adapted to the different conditions of mountain valleys. Whereas fluvial processes facilitate seedling recruitment in unconfined alluvial valleys, processes are different in mountain valleys. Grant and Swanson (1995) point out that the morphology and dynamics of valley floor environments in mountain landscapes differ markedly from their lowland counterparts.

Mountain valley landforms and channel morphology are strongly influenced by processes external to the channel and may be more confined by hillslopes. Typically, particle sizes increase and groundwater fluctuation increase with decreasing drainage basin area (Leopold et al. 1964). In addition, the extent of fluvial geomorphic surfaces decreases upstream (Osterkamp and Hupp 1984, Hupp and Osterkamp 1985). Differences in the hydrologic and geomorphic characteristics of confined and unconfined valleys suggest that proportions of seedling and clonal recruitment may vary between valley types.

Few studies have quantitatively documented the relative role of seedling versus clonal recruitment in cottonwoods (Rood et al. 1994, L. A. Gom and S. B. Rood *unpublished manuscript*). In the Oldman River basin, Rood et al. (1994) excavated root systems and found up to 48% of the cottonwood saplings originated through clonal mechanisms, of which 30% of the total were root sprouts. However, *Populus* are capable of root grafting, which may confound determination of stem origin.

Morphological and phenological characteristics may also be used to assign stems as parts of a clone (Barnes 1969). L. A. Gom and S. B. Rood (*unpublished manuscript*) used traits such stem sex, leaf shape, and floral phenology to discriminate between clones and found that 78% of cottonwood stems on one island on the Oldman River originated from clonal recruitment. In their study, they identified clones linearly extending as much as 50 m. In addition, Merigliano (1996) found up to 805 clonal sprouts per acre on a braided section of the Snake River in Idaho using phenological indicators.

Another alternative to excavation is some form of genetic testing to distinguish between genetic individuals (Rajora and Zsuffa 1989, Cheliak and Pitel 1984, Keim et al.

1989). Stems (ramets) of the same clone (genet) possess identical genotypes and protein electrophoresis is a cost-effective method (Murphy et al. 1996) to determine genotype and identify clones. Once proportions of recruitment mechanisms are known, geomorphic parameters may be evaluated to develop a better understanding of the fundamental ecological relationships facilitating clonal recruitment.

It is hypothesized here that clonal recruitment dominates in steep, confined mountain valleys due to a lack of geomorphic surfaces and appropriate physical characteristics that are widely regarded as seedbeds for seedling recruitment. It is also hypothesized that appropriate characteristics of these seedbeds are found in lower elevation parts of the drainage network. This study seeks to quantify the degree of clonal recruitment of *Populus angustifolia* in steep, confined mountain valleys and wide alluvial valleys where relative proportions of clonal recruitment may change as a function of geomorphic conditions.

METHODS

Four sites were selected to test the hypothesis that clonal mechanisms should dominate in confined mountain valleys and not unconfined alluvial valleys, due to the lack of the appropriate geomorphic characteristics favoring seedling recruitment. Two cottonwood recruitment sites occur in upstream parts of the basin at 1755 and 1690 m, respectively. These sites occur in steep, confined mountain valleys. These sites have different physical characteristics than those described in the literature that facilitate seedling recruitment (Fig. 2.1). Two cottonwood recruitment sites were located

downstream from the confined sites and at lower elevation in the watershed, at 1495 and 1377 m, respectively. These sites occur in wide, low-gradient alluvial valleys and are located on the delta of the Provo formation. The unconfined sites appear to have characteristics similar to those described in the literature that facilitate seedling recruitment.

Study area

The study area for this research is the Little Bear River watershed (574 km²) located in Cache County in northern Utah (Fig. 2.1). The Little Bear River flows north from the Bear River Range into Cache Valley, a 64 km long and 32 km wide valley. Cache Valley and its surrounding mountains are at the eastern edge of the Basin and Range province. The South Fork descends from an elevation of approximately 2000 m, in a steep confined mountain valley, to 1300 m in the lower most alluvial valley.

The primary lithologies of the surrounding Bear River Range are limestone and dolomite. Williams (1962) summarized the surficial geology of the Little Bear River watershed as exhibiting the influence of Pleistocene Lake Bonneville. He stated deposits of Former Lake Bonneville cover the interior of Cache Valley and deltas were formed at the mouths of canyons as rivers flowed into Lake Bonneville. The Little Bear River formed a delta of the Provo formation at the mouth of its canyon (Williams 1962). Williams described the Provo formation as divided into a gravel and sand member and a silt and clay member. McCalpin (1989) mapped the present channel and valley bottom of the Little Bear River in this formation as clast-supported pebble, cobble, and gravel in a

matrix of sand and minor clay. The channel of the Little Bear River drastically changes character downstream and north from the delta as it flows through clay sediment deposited at the bottom of Pleistocene Lake Bonneville. More cohesive bank material probably contributes to an increase in sinuosity that occurs where the channel encounters clay, and gravel is much less common in this reach.

The hydrology of the Little Bear River is dominated by snowmelt runoff. The spring snowmelt peak typically occurs between April and June. However, examination of U. S. Geological Survey (USGS) flow records reveals that early thaw events, occurring in the winter months, are relatively common. Two of the three largest flood peaks on record for the Little Bear River were events of this type and occurred in 1962 and 1984.

Extensive water development has occurred on the Little Bear River, including the construction of two dams and numerous diversions for irrigation. The U. S. Bureau of Reclamation built Porcupine and Hyrum Dams. Hyrum Dam was constructed in 1935 on the main stem, and Porcupine Dam was constructed in 1962 on the East Fork of the Little Bear River. Floods peaks above approximately a 5-yr return interval appear to be attenuated in magnitude by 10-15% from what would be predicted by regional flood frequency curves (Thomas and Lindskov 1983) for unregulated streams in the region. This suggests that regulation from dams and diversions may attenuate flows.

Padgett et al. (1989) classified the riparian vegetation of the study area as various *Populus angustifolia* (narrow leaf cottonwood) dominated community types. Watershed reconnaissance conducted for our study sites showed that these cottonwoods are present along the channel of the Little Bear River to the northern extension of the Little Bear

River delta (Fig. 2.2). North from the delta, in the valley flat, the exotic *Salix fragilis*, crack willow, is the dominant overstory riparian species. However, isolated stands of the natives *Salix exigua* and *Salix lutea* are intermixed with the crack willow.

Reconnaissance also revealed four distinct patches of cottonwoods where recent recruitment occurs. Other reaches on the river have cottonwood trees present. However, only those with enough individuals of different ages and exhibiting recent recruitment were considered as research sites. Patches containing cottonwood recruitment are separated by reaches dominated by *Salix* spp. (willow) or *Acer negundo* (box elder). Four non-cottonwood sites were located in reaches dominated by vegetation other than cottonwoods and were used in an accompanying study.

Extent of clonal recruitment

I used protein electrophoresis following methods described by Murphy et al. (1996) to determine genotype and the proportion of clonal recruitment at confined and unconfined sites. Dormant vegetative bud sampling was designed to determine whether clonal recruitment among samples collected at each site was occurring over a temporal scale of at least several decades. Because sites were distributed in both confined and unconfined valley types, difference in recruitment mechanisms might be inferred from a comparison of the results with respect to valley type.

In an initial pilot study, I sampled a large population of cottonwoods on the South Fork and main stem of the Little Bear River to estimate allele frequencies. Thirty individual stems were sampled at least 50 m apart along a 5 km reach of the South Fork

and mainstem of the Little Bear River. Montalvo et al. (1997) describe a common problem in genetic studies of clones: allele frequencies are calculated with samples collected from potential clones and these frequencies then are used to verify clonal assignment. To address this problem and obtain an independent estimate of allele frequencies, 30 samples were collected over 50 km throughout Cache Valley and in the same elevation range as the study sites (see Fig. 2.2). Samples for the independent estimate were collected from separate watersheds and were at least 1.5 km apart. The presence and size of cottonwood clones was unknown and 1.5 km was an estimated distance necessary to avoid resampling clones.

All bud samples were sealed in plastic bags and placed in a cooler during transport to the laboratory where they were placed in a refrigerator at 4 °C. One bud per sample was ground with Tris-HCL-PVP solution pH 7.5 grinding buffer (Soltis et al. 1983) with 4% PVP, and 0.1% 2-mercaptoethanol on a cold grinding plate. Four gel systems and 16 enzymes were screened during a pilot study to determine the appropriate combination for resolving loci. The pilot study identified phosphoglucose isomerase (PGI) and phosphoglucomutase (PGM) as appropriate polymorphic enzymes. PGI is run on citric acid monohydrate pH 7.7 (system B from Rajora and Zsuffa 1989). PGM is run on Tris and Citric acid Monohydrate pH 6.2 (system C from Shaw and Prasad 1970) (Fig. 2.3). Gels were run at 18mA for 12 to 13 hrs. Both PGI and PGM were stained with a 1% agarose overlay and were polymorphic for 4 and 5 alleles, respectively. The identified alleles were labeled A through D for PGI, and A through E for PGM. Marker plants,

including all alleles identified throughout the sampling, were run together on the same starch gel as a key to ensure scoring consistency.

Thirty dormant vegetative buds were collected at each of the four cottonwood recruitment sites between September and November 1997 and used to estimate proportions of clonal recruitment. Ten samples were collected along three transects at each of the four sites. Transects were approximately 50 m apart and were perpendicular to the stream encompassing several apparent age cohorts. Cohorts were delineated based on stem height and diameter at breast height. This sampling, addressing recruitment over the past several decades, was termed cohort sampling.

Site 3 was the only site possessing many young stems on point bars. Thousands of young stems, 1-5 cm tall at the time of sampling, were noted on point bars and were thought to have been initiated after high flows in the spring of 1997. Additional sampling, termed point bar sampling, was conducted on two point bars at this site (Fig. 4). Fifteen samples were collected at two different point bars with one transect per bar. Point bar sampling transects were 215 m apart and were parallel to the stream and encompassed only the most recent age cohort.

The probability of a genotype's initial occurrence and probability of multiple occurrences of that same genotype were used to determine clonal origin. Assuming linkage (gametic phase) equilibrium, the probability of a genotype's initial occurrence (P_{gen}) is a multiplicative function of the expected Hardy-Weinberg frequencies of the observed genotype for each locus:

$$P_{gen} = \prod_{i=1}^L g_i \quad (1)$$

where g_i is the expected frequency of the genotype at locus i and L is the number of loci.

Probabilities of multiple occurrences of a genotype follows from Parks and Werth (1993). Equation 2 sums the probabilities of multiple encounters of the same genotype and is calculated from the binomial expression:

$$P_m = \sum_{x=n}^G \frac{G!}{x!(G-x)!} (P_{gen})^x (1-P_{gen})^{G-x} \quad (2)$$

where G is the number of separate genotypes and n is the number of separate fragments with identical genotype to some previously encountered fragment. Equation 2 calculates P_m , the probability of more than two encounters of the same genotype, and accounts for that specific genotype's probability of initial occurrence (P_{gen}) and the number of times that same genotype is encountered. Equation 3 is a simplified version of the binomial expression used in circumstances where I only encountered the same genotype twice (P_i):

$$P_i = 1 - (1 - P_{gen})^G \quad (3)$$

The null hypothesis is that no clonal recruitment occurs. Therefore, P_{gen} , P_m , and P_i values are the probability of encountering a genotype by chance through sexual reproduction and random mating. In the case of a clone, many individual above ground stems called ramets may originate from the same genetic individual, called a genet. Samples from numerous ramets possessing the same genotype potentially indicates that these ramets originated from the same genet. The lower the chance probability of this multiple occurrence the more likely the two ramets are part of a clone. I set $\alpha = 0.05$ to discriminate between genetic individuals.

Following the calculation of P values, the distance between two stems with identical genotypes also was factored into an evaluation of distant stems as ramets of a genet. During the pilot study, gel and buffer systems were tested for appropriateness for resolving loci. At the same time, I encountered five adjacent samples of the same genotype occurring over approximately 200 m. The occurrence of the identical genotype among samples linearly distributed over such a large distance suggested a large clone. Although clone size was previously unknown, I used 200 m as an initial estimate of the potential distance over which stems could be separated and still be evaluated as ramets of a genet.

Phenological indicators also were used to provide an independent estimate of cottonwood clone size. I measured the linear distance along the streambank over which groups of stems were distributed that exhibited similar progression of catkin flushing, because catkin flushing was the spring phenological characteristic that was occurring at the time of observation.

Proportions of clonal and seedling recruitment were calculated for each sample set as:

$$R_s = I/T \quad (4)$$

and

$$R_c = 1 - R_s \quad (5)$$

where I is the number of individual genets meeting the 95% confidence interval, T is the total number of samples at a site, R_s is the proportion of seedling recruitment, and R_c is

the proportion of clonal recruitment. Sampling does not include all of the stems at a site. However, an estimate of the proportion of clonal recruitment at a site can be inferred from sample results.

Geomorphic and vegetation mapping

I used geomorphic and vegetation mapping, in addition to allozyme electrophoretic data, to compare the likelihood of seedling or clonal recruitment mechanisms between confined and unconfined sites. Geomorphic maps were created at each site by adding locations of geomorphic features such as main and side channels, cutbanks, floodplain, and terrace locations to a base map of surveyed topographic data. Age classes, based on estimated height and diameter, of cottonwood stems were coded and also located on geomorphic maps. Estimated age classes of cottonwoods were young stems (.01-0.3 m), small saplings (0.3-0.7 m), large saplings (1.2-2.1 m), poles (4.5-9 m), trees (10.5-12 m), and large trees (greater than 12 m).

I quantified the relative percentage of the young stem size class on different types of geomorphic features as a comparison to the types of geomorphic features that are described in the literature that host seedling recruitment. As described above, the young stems on point bars at site 3 appeared anomalous, as their spatial distribution was similar to the even-aged banded strips of seedling recruitment that are typically found on point bars. Young stems were excavated on a point bar to determine their recruitment mechanism because this was the only site where such associations were found.

I used vegetation mapping to characterize the spatial distribution of stems at confined and unconfined sites. I visually compared stem patterns at confined and unconfined sites to arcuate banding or linear patterns resulting from meandering or over bank deposition respectively, and seedling recruitment.

Geomorphic characterization

Geomorphic data were collected to characterize confined and unconfined sites potential for seedling recruitment, using methods of Harrelson et al. (1994). I evaluated the similarity of confined and unconfined sites in relation to descriptions of alluvial meandering sites described in the literature that facilitate seedling recruitment. Measured geomorphic characteristics and methods of data collection are summarized in Table 2.1. Topographic data were collected with a geodetic total station or measured with a tape. Point bar and lateral bar area was quantified as total bar area measured at low flow (mid-September). However, many geomorphic parameters co-vary with drainage basin area in a predictable fashion and bar area typically increases in the downstream direction (Leopold and Maddock 1953). Therefore, I also calculated the relative proportion of bar area at a site by dividing the total bar area at a site by channel area at a site. Channel area at a site was calculated as the product of mean bankfull width and the surveyed thalweg length. Particle size distributions, in the channel and on point and lateral bar surfaces, were determined using the method of Wolman (1954). A minimum of 150 and 100 particles was measured in the channel bed and on bars, respectively. Pebble counts were

located throughout the surveyed reach to reflect all bar surfaces and channel units at a site.

RESULTS AND DISCUSSION

Extent of clonal recruitment

Estimates of Hardy-Weinberg allele frequencies for the Little Bear River sample set and the Cache Valley-wide sample set were very similar for the identified alleles listed in Table 2.2. However, Cache Valley-wide sampling revealed a rare allele not identified in the Little Bear River sample set. This rare allele was added to the Little Bear River sample set for calculation of allele frequencies. I used the Little Bear River sample set frequencies because they provided a more conservative estimate of clonal origin than the valley wide sample set.

Pilot study data from the Little Bear River sample set indicated the possibility of a large clone. Hence, allele frequencies were calculated first assuming clonal recruitment and then assuming no clonal recruitment. The number of samples considered as genetic individuals can alter estimates of allele frequencies, because the total number of alleles (two per genetic individual, one per parent) would change. However, allele frequencies were almost identical for each assumption and an average of the assumed cloning and assumed no-cloning frequencies was used for subsequent calculations (Table 2.3).

I assumed that samples within a site were in sufficient proximity to be ramets of the same genet based on phenological indicators. I observed and measured the extent of 13 large clusters of trees distributed along approximately 4 km of the South Fork of the

Little Bear River between 1670 m and 1580 m in elevation. Phenological indicators complimented initial estimates from allozyme data that clones on the Little Bear River may extend linearly along the streambank for 200-300 m. The five largest groups measured 322 m, 242 m, 227 m, and two groups of 174 m each. The variation in catkin development varied distinctly between groups of stems and ranged from no catkins present to emerging flowers. Variations in phenology did not follow any temperature gradients that may have resulted from the almost 100 m elevation change occurring over the length of the measured reach.

The size of cottonwood clones estimated in this study differs from previous published work. In contrast to the large estimated size of cottonwood clones on the Little Bear, L. A. Gom and S. B. Rood (*unpublished manuscript*) estimated that 50 m as the approximate length of clone size on an island on the Oldman River in Alberta. Merigiano (1996) found areas with high densities of sprouts, but he reported that long-term survival appeared limited and the areal extent of mature sprouts was small. However, the potential for clones on the order of hundreds of meters is not limited to the Little Bear River. Clone size has been estimated as extending along the streambank of the nearby Weber River for upwards of 200 m based on the same type of phenological indicators described above (T. Whitham *pers. com.* 1999). In addition, clone size in *Populus tremuloides*, which is a related species, has been reported as large as 200 ac² (Kemperman and Barnes 1976).

Cohort sampling for sites 1-4 indicated 60%, 69%, 86%, and 84% clonal recruitment of cottonwoods, respectively, from the collected samples (Table 2.4). The

average of these percentages of clonal recruitment of cottonwoods is 72%. This average is in close agreement with L. A. Gom and S. B. Rood's (*unpublished manuscript*) findings that 78% of the cottonwood stems on an island in the Oldman River originated through clonal mechanisms. In contrast, Rood et al. (1994) found 48% clonal recruitment of cottonwoods on the Oldman River using excavation to assign clonal origin. The high degree of clonal recruitment found in L. A. Gom and S. B. Rood's (*unpublished manuscript*) study and my study suggests that using excavation to determine clonal origin may underestimate the extent and importance of this recruitment mechanism.

The extent of clonal recruitment mechanisms may also have been overlooked in other studies that investigated point bars as recruitment sites and assumed that recruitment in these locations was from seedling. Significantly, point bar sampling at site 3 revealed 73% clonal recruitment for young stems found on point bars that visually appeared similar to banding patterns described to result from seedling recruitment. Table 2.5 summarizes the multilocus heterozygous genotypes at each site, the number of respective encounters within each site, their P_{gen} , P_m , and P_i values and the number of individual genets identified.

Geomorphic and vegetation mapping

Mapping supported findings of the allozyme analysis and suggested significant clonal recruitment. The largest relative proportion of the young stem age class occurred on cutbanks and steeply sloping channel margins (Fig. 2.5). These erosional features are fundamentally different from the depositional surfaces where seedling recruitment is

typically found and is further geomorphic evidence that recruitment is clonal. On the Little Bear River, root material is often exposed on cutbanks and steeply sloping channel margins where stream flow has removed surrounding particles. The bases of many individual stems, young and old, can be seen originating from the exposed streamside root material. Other studies also have found that cutbanks and areas of scour near the channel host root sprouts (Webb and Brotherson 1988, L. A. Gom and S. B. Rood (*unpublished manuscript*). Root sprouting appears to be the dominant form of clonal recruitment on the Little Bear and clonal recruitment from branch material appears less important than has been cited elsewhere (Braatne et al. 1996, Kranjcec et al. 1998).

Mapping and photo evidence also revealed different spatial patterns of stems than the typical arcuate banding produced by meandering. Cottonwood stands in this system often produce a clumped or aggregated appearance (Fig. 2.6). These aggregates often consist of younger trees radiating out from the center of the aggregate with one or two older trees in the center. This is a spatial configuration common in clonal plants (Eriksson 1993) and noted elsewhere for *P. angustifolia* (Merigliano 1996).

A second spatial pattern of cottonwood stems on the Little Bear was the linear arrangement of stems of similar stem height and diameter on the streamward edges of steeply sloping channel margins, cutbanks, and old scarp faces (Fig. 2.7). This linear alignment is similar to the linear spatial distribution of stems described to result from seedling recruitment and channel narrowing or flood plain deposition (Friedman et al. 1996, Scott et al. 1996, Auble and Scott 1998). However, as mentioned above, the fundamental difference in this study is that clonal recruitment was found linearly

distributed on erosional features not depositional seedbeds. Cutbanks and active channel shelves also are relatively linear and this linear distribution results in clonal spatial distribution similar to seedlings.

Similar to young stems found on cutbanks and sloping channel margins, young stems on point bars at site 3 originated from shallow roots. Roots giving rise to sprouts were approximately 0.5 cm in diameter and buried under 5-20 cm of gravel size particles (Fig. 2.8). Clonal recruitment on these point bars appeared similar to banded seedling recruitment typically found on these types of surfaces and has only been documented by Hickin and Nanson (1975), who found clonal recruitment occurring on scroll bars. As the scroll bars grew laterally, new stems were added on the streamward side. The banded spatial configuration of stems at site 3, which can be seen in Fig. 2.4, may occur through a similar process.

Geomorphic characterization

Geomorphic differences are apparent between confined and unconfined sites. Geomorphic characteristics of confined and unconfined sites are listed in Table 2.6. Characterization suggests that confined sites lack some of the characteristics that favor seedling recruitment. Confined sites have lower sinuosity and higher entrenchment values than unconfined sites. This suggests that confined sites have less potential to laterally migrate and form bar area that could serve as potential seedbeds. In support of this inference, the proportion of point and lateral bar area was less in confined sites relative to unconfined sites by almost an order of magnitude. Furthermore, streamside

geomorphic surfaces at confined sites were similar to active channel shelves described by Osterkamp and Hupp (1984) to occur in upstream reaches of high gradient streams.

Most geomorphic characteristics of unconfined sites also indicate variations in channel and valley parameters varying as a function of their location within the channel network. Unconfined sites possess aspects of channel morphology, such as cutbanks opposite point bars, more typically caused by meandering processes. This channel morphology is common in alluvial valleys where processes typically facilitate seedling recruitment.

However, some geomorphic parameters important to seedling recruitment are more similar between confined and unconfined sites than fundamental downstream variation patterns, developed over larger scales, would predict. Although bar area is greater at unconfined sites, presence of bar area does not solely indicate a capacity for seedling recruitment. Particle size distribution on these surfaces also is important for seedling survival, where small particle sizes provide soil moisture to developing seedlings. Median particle size is very similar among the unconfined and confined sites both in channels and on bar surfaces (Fig. 2.9). This pattern is in contrast to a decrease in particle size downstream where sites are typically distributed over large distances (Leopold et al. 1964).

As described above, the features where roots sprouts are found in confined sites are similar to active channel shelves described by Osterkamp and Hupp (1984). Active channel shelves have larger particle sizes because of hydrologic sorting processes closer to the channel. These geomorphic features may not possess the water-holding capacity to

support seedling root systems. Sprouts (ramets) emerging from mature established root networks may have an advantage over new seedlings in confined sites because the transfer of water and nutrients from neighboring ramets can support ramets that are severely shaded or water stressed (Marshall 1990).

The similarity in median particle size between confined and unconfined sites may indicate that surfaces at unconfined sites may also lack the appropriate sediment sizes to facilitate seedling recruitment. This also would explain the discrepancy between some unconfined site characteristics suggesting that seedling recruitment should be the dominant mechanism and the actual findings that clonal recruitment dominates these sites. Rood et al. (1998) described recruitment surfaces in areas of cottonwood establishment on the Oldman River as both fines dominated (matrix-supported) and other areas of establishment consisting of cobbles and gravels with fines in between (clast-supported). Success of seedling establishment varied in the two conditions as a function of water availability. Seedling survival decreased in the clast-supported area where there was decreased water availability. Potential recruitment surfaces on the Little Bear River appear to be much coarser than the pictures of establishment surfaces in the Oldman River.

Median particle size and particle distribution is different at site 2, than elsewhere, and this is the only site which includes a tributary confluence. Different sediment size distribution at site 2 may be the result of tributary deposition.

Flood-prone widths were also similar among all four sites, which typically increase downstream where broader valleys are typically found. Similar geomorphic

form, commonly used as a surrogate for process between confined and unconfined sites may indicate similar processes functioning at the two site types. Greater flood-prone width is more typical of broad alluvial valleys where floodwaters spread over the floodplain and recharge groundwater, decreasing groundwater fluctuations, and providing riparian water tables favorable to seedling recruitment. Processes responsible for the formation of flood-prone width may be altered at unconfined sites resulting in unconfined site parameters similar to confined sites. The dominance of clonal recruitment found at all four sites may be partially explained by this similarity.

Geomorphic similarities between confined and unconfined sites may be a function of large-scale, relictual hydrologic or geomorphic influences, because the current macro-scale structure of the mountain landscapes may bear a strong historical imprint (Baker 1989). In addition, the legacy of past events, stored in such relictual landscape elements, imposes constraints on the degree of fluvial adjustments to current processes (Graf 1982). A possible explanation for geomorphic similarities between unconfined and confined sites is that unconfined sites occur on the delta of the Provo formation. Both Williams (1962) and McCalpin (1989) described this formation primarily consisting of larger particle sizes with less sand and clay. McCalpin specified clast-supported as opposed to matrix-supported, which may indicate fewer fine particles for seedling establishment. The sediment characteristics of the delta may favor the dominance of clonal mechanisms. New seedlings may attempt to establish on the bar area present at unconfined sites but may be out-competed over time by ramets supported by mature root systems.

A second observation supports the inference that characteristics of the delta exert an influence over cottonwood recruitment. Interestingly, the distribution of cottonwoods on the Little Bear River extends to approximately the southern most end of the primarily gravel delta. Site 4, the northern most cottonwood stand on the Little Bear, is situated at the northern end of the end of the delta (Fig. 2.2). Downstream and north from the delta, the bed and banks of the Little Bear River drastically change from a mixture of sand, cobble, and gravel, to clay sediment deposited at the bottom of Pleistocene Lake Bonneville. At this point exotic and native willows dominate the overstory and this is probably due to the drastic change to clay particle sizes creating too wet of an environment for cottonwoods. Baker (1989) also noted similar large-scale relictual geomorphic influences on site sedimentology. He suggested characteristics developed during the Pleistocene were controlling present day riparian vegetation distribution and delineating between areas with fine grained deposits possessing willows and areas of larger particles possessing other trees.

Vegetation types themselves may be relicts of a landscape, which has been suggested for *Populus tremuloides* (aspens) (Moss 1938, Kemperman and Barnes 1976, McDonough 1985, Jelinsky and Cheliak 1992). Aspens may have been more adapted to cooler and wetter glacial climatic conditions, which may have provided more "windows of opportunity" for seedling recruitment. Seedling requirements for aspens are described as moderate temperatures, moist but well drained seed beds, a high light environment, and freedom from competitors (Moss 1938, McDonough 1985). However, seedling recruitment in aspens is rare and they sprout prolifically. Interestingly, these recruitment

characteristics are similar to cottonwoods found in mountain valleys, which are often in close proximity to aspen distribution. The identification of large cottonwood clones in this study and the identification of large aspen clones in other studies (Kemperman and Barnes 1976) also suggests the two are similar. Cottonwoods in mountain valleys may be likened to a stand of aspens occurring in the stream bottom as opposed to the hillslope. These cottonwoods may have relied more heavily on seedling recruitment in the Pleistocene when climate and geology combined to produce glacial rivers with very different hydrologic regimes than those same drainages today.

However, similarities among confined and unconfined sites may not only be the result of sediment characteristics of the Provo formation but may also indicate altered conditions. Studies have suggested clonal recruitment may become increasingly important in altered environments (Stromberg and Patten 1989, Rood and Mahoney 1995). Studies have prioritized flow regulation and cattle grazing as negative impacts to seedling establishment (Rood and Mahoney 1990, Braatne et al. 1996).

Dams impact riparian establishment in many ways (Poff et al. 1997, Friedman et al. 1998). Especially important to riparian seedling survival, growth, and abundance is the decrease in fine sediment supply. Cumulative frequency distributions of sediment sizes for both unconfined sites do in fact show less fine sediment in the channel than the two sites above the dams. This effect has been termed a silt shadow and the creation of these conditions may favor clonal recruitment (Rood and Mahoney 1990, Rood and Bradley 1993) by decreasing the potential for fine sediment to provide water to seedling root systems.

Alterations to sediment supply also affect many aspects of channel morphology (Andrews 1986, Collier et al. 1996), which may explain similar flood-prone widths between confined and unconfined sites. Channels below dams often increase gradient and become entrenched. Degrading channels exhibit a sequence of characteristic channel metamorphosis in response to increased gradient that has been found to affect riparian vegetation (Hupp and Osterkamp 1996, Simon 1989). Channels downcut, widen, then rebuild floodplains. This sequence may limit the potential for seedling recruitment until floodplain reconstruction has built appropriate seedbeds. Decreased flood-prone width at unconfined sites may indicate channels at these sites are in some phase of this response sequence.

More extensive geomorphic data collected over time would be necessary to evaluate the effects of dams on the Little Bear. However, anecdotal evidence indicates that the channel is degrading. USGS flow records reveal that large floods occurred in the area in 1984 and 1986. The landowner of site 4 noted approximately 2.5 m of degradation in parts of the channel after the flood of 1986. In addition, repeat longitudinal profiles have been surveyed by the Utah Department of Environmental Quality at this site. Surveys reveal a scour hole approximately 6 m deep at the site after the floods.

In summary, river regulation has been changed to benefit many species (Poff et al. 1997) where society deems this appropriate (Schmidt et al. 1998). The growing body of literature on the fundamental relationships between stream flow and riparian vegetation has been used to alter dam operation. A number of cases where flow has been naturalized

have demonstrated that successful regeneration of riparian forest is possible (Barinaga 1996, Klotz and Swanson 1997, Rood et al. 1998). The case studies in the past have mimicked conditions favoring seedling recruitment where this is the dominant recruitment mechanism. Perhaps similar process-based solutions could be formulated for clonal recruitment with further understanding of the processes facilitating this mechanism.

CONCLUSIONS

In contrast to findings of many previous studies examining cottonwood recruitment mechanisms, I found clonal recruitment is the dominant recruitment mechanism of cottonwoods on the Little Bear River. The average proportion of clonal recruitment among four sites was 72% and the potential size of cottonwood clones on the Little Bear River is on the order of 200-300 m. Significantly, clonal recruitment not only dominates confined mountain valleys where geomorphic characteristics suggest this should be the case, but also in wide alluvial valleys on the Little Bear River. Clonal recruitment was also documented on point bars, which other studies typically describe as hosting seedling recruitment. Geomorphic parameters such as sediment size distribution and flood-prone widths of these alluvial valleys were found to be more similar to confined mountain valleys, which is likely the result of geomorphic influences enhanced by flow regulation.

Cottonwood species found in environments where seedling recruitment conditions are less likely, such as confined mountain valleys, are more dependent on clonal

recruitment. Quantification of the hydrogeomorphic processes responsible for clonal recruitment of cottonwoods in these valley types would facilitate the formation of flow recommendations where clonal recruitment is the dominant process.

LITERATURE CITED

- Anderson, B. W., R. D. Ohmart, and J. Rice. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado River Valley. *Condor* **85**: 392-405.
- Andrews, E. 1986. Downstream effects of flaming gorge reservoir on the Green River. *Geological Society of America Bulletin* **97**:1012-1023.
- Auble, G. T., J. M. Friedman, and M. L. Scott. 1994. Relating riparian vegetation to present and future streamflows. *Ecological Applications* **4**:544-554.
- Auble, T., and M. L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. *Wetlands* **18**:546-556.
- 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.
- Barinaga, M. 1996. A recipe for river recovery? *Science* **273**:1648-1650.
- Barnes, B. V. 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. gradidentata* in northern lower Michigan. *Silvae Genetica* **18**:130-142.
- . 1976. The clonal growth habit of American aspens. *Ecology* **47**:439-447.
- Braatne, J. H., S. B. Rood, and P. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods. Pages 57-80 in R. F. Stettler, H. D. Bradshaw, P. E. Heilman, and T. M. Hinckley, editors. *Biology of populus and its implications for management and conservation*. NRC Research Press, Ottawa, Ontario, Canada.
- Bradley, C. E., and D. G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany* **64**:1433-1442.
- Cheliak, W. M., and J. A. Pitel. 1984. Electrophoretic identification of clones in trembling aspen. *Canadian Journal of Forest Resources* **14**:740-743.

- Collier, M., R. H. Webb, and J. C. Schmidt. 1996. Dams and rivers: a primer on the downstream effects of dams. U. S. Geological Survey Circular 1126.
- Eckenwalder, J. 1984. Natural intersectional hybridization between North American species of *Populus* (*Salicaceae*) in sections of *Aigeiros* and *Tacamahaca*. I. Population studies of *P. X parryi*. Canadian Journal of Botany **62**:317-324.
- Eriksson, O. 1993. Dynamics of genets in clonal plants. *Tree* **8**:313-317.
- Everitt, B. L. 1968. Use of the cottonwood on an investigation of the recent history of a flood plain. *American Journal of Science* **266**:417-439.
- Finch, D. M., and L. R. Ruggiero. 1993. Wildlife and biological diversity in the Rocky Mountains and north Great Plains. *Natural Areas Journal* **13**:191-203.
- Friedman, J. M., W. R. Osterkamp, and W. M. Lewis Jr. 1996. Channel narrowing and vegetation development following a Great Plains flood. *Ecology* **77**:2176-2181.
- Friedman, J. M., W. R. Osterkamp, M. L. Scott, and G. T. Auble. 1998. Downstream effects of dams on channel geometry and bottomland vegetation: regional patterns in the Great Plains. *Wetlands* **18**:619-633.
- Graf, W. L. 1982. Spatial variation of fluvial processes in semi-arid lands. Pages 193-217 in C. E. Thorne, editor. *Space and time in geomorphology*. George Allen and Unwin, New York, New York, USA.
- Grant G. E., and F. J. Swanson. 1995. Morphology and processes of valley floors in mountain streams, western Cascades, Oregon. Pages 83-101 in J. E. Costa, A. J. Miller, K. W. Potter, and P. R. Wilcock, editors. *Natural and anthropomorphic influences in fluvial geomorphology*. American Geophysical Union Geophysical Monograph **89**.
- Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. Stream channel reference sites: an illustrated guide to field technique. USDA Forest Service General Technical Report **RM-245**.
- Hickin, E. J., and G. C. Nanson. 1975. The character of channel migration on the Beaton River, northeast British Columbia, Canada. *Geological Society of America Bulletin* **86**:487-494.
- Hunter, W. C., B. S. Anderson, and R. D. Ohmart. 1987. Avian community structure changes in a mature floodplain forest after extensive flooding. *Journal of Wildlife Management* **51**:495-502.
- Hupp, C. R. and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology* **66**:670-681.

- . 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology* **14**:277-295.
- Jelinski, D. E., and W. M. Cheliak. 1992. Genetic diversity and spatial subdivision of *Populus tremuloides* (*Salicaceae*) in a heterogeneous landscape. *American Journal of Botany* **79**:728-736.
- Johnson, W. C. 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. *Ecological Monographs* **64**:45-84.
- Keim, P., K. N. Page, T. G. Whitham, and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *populus*: occurrence of unidirectional introgression. *Genetics* **123**:557-565.
- Kemperman, J. A., and B. V. Barnes. 1976. Clone size in American aspens. *Canadian Journal of Botany* **54**:2603-2607.
- Klotz, J. R., and S. Swanson. 1997. Managed instream flows for woody vegetation recruitment, a case study. Pages 483-489 in J. Warwick, editor. Symposium proceedings: water resources education, training, and practices: opportunities for the next century. American Water Resources Association, Universities Council on Water Resources, American Water Works Association, Keystone, Colorado, USA.
- Kranjcec, J., J. M. Mahoney, and S. B. Rood. 1998. The response of three riparian cottonwood species to water table decline. *Forest Ecology and Management* **110**:77-87.
- Leopold, L. B., and T. Maddock Jr. 1953. The hydraulic geometry of stream channels and some physiographic implications. U.S. Geological Survey Prof. Paper **252**.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Dover Publications, Inc., New York, New York, USA.
- Mahoney, J. M., and S. B. Rood. 1991. A device for studying the influence of declining water table on poplar growth and survival. *Tree Physiology* **8**:305-314.
- . 1992. Response of a hybrid poplar to water table decline in different substrates. *Forest Ecology and Management* **54**:141-156.
- . 1998. Streamflow requirements for cottonwood seedling recruitment-an integrative model. *Wetlands* **18**:634-645.
- Marshall, C. 1990. Source-sink relations of interconnected ramets. Pages 52-86 in J. van Groenendaal and H. de Kroon, editors. Clonal growth in plants: regulation and function. SPB Academic Publishing, The Hague, The Netherlands.

- McCalpin, J. P. 1989. Surficial geology map of the East Cache fault zone. USGS Miscellaneous Field Studies Map. MF-2107, 1:50,000.
- 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.
- McDonough, W. T. 1985. Sexual reproduction, seeds, and seedlings. Pages 25-33 in N. V. DeByle and R. P. Winokur, editors. *Aspens: ecology and management in the Western U.S.* USDA Forest Service General Technical Report RM-119.
- Merigiano, M. F. 1996. Flood plain and vegetation dynamics of along a gravel bedded river in the Northern Rocky Mountains. Dissertation. University of Montana, Missoula, Montana, USA.
- . 1998. Cottonwood and willow demography on a young island, Salmon River, Idaho. *Wetlands* **18**:571-576.
- Moss, E. H. 1938. Longevity of seed and establishment of seedlings in species *populus*. *Botanical Gazette* **49**:529-542.
- Montalvo, A. M., S. G. Conard, M. T. Conkle, and P. D. Hodgskiss. 1997. Population structure, genetic diversity, and clone formation in *Quercus chrysolepis* (*Fagaceae*). *American Journal of Botany* **84**:1553-1564.
- Murphy, R. W., J. W. Sites, Jr., D. G. Buth, and C. H. Haufler. 1996. Proteins: isozyme electrophoresis. Pages 51-95 in D. M. Hillis, C. Moritz, and B. K. Mable, editors. *Molecular systematics*, 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- 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.
- Padgett, W. G., A. P. Youngblood, and A. H. Winward. 1989. Riparian community type classification of Utah and southeastern Idaho. USDA Forest Service General Technical Report **R4-Ecol-89-01**.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* **18**:498-512.
- Parks, J. C., and C. R. Werth. 1993. A study of spatial features of clones in a population of bracken fern, *Pteridium aquilinum* (*Dennstaedtiaceae*). *American Journal of Botany* **80**:537-544.

- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime, a paradigm for conservation and restoration. *Bioscience* **47**:769-784.
- Rajora, O. P., and L. Zsuffa. 1989. Multilocus genetic structure, characterization, and relationships of *Populus x canadensis* cultivars. *Genome* **32**:99-108.
- Rood, S. B., and C. Bradley. 1993. Assessment of riparian cottonwoods along the Bow River downstream from Calgary, Alberta. The University of Lethbridge, Lethbridge, Canada.
- Rood, S. B., C. Hillman, T. Sanche, and J. M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. *Canadian Journal of Botany* **72**:1766-1774.
- Rood, S. B., A. R. Kalischuk, and J. M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands* **18**:557-570.
- Rood, S. B., and J. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management* **14**:451-464.
- . 1995. River damming and riparian cottonwoods along the Marias River, Montana. *Rivers* **5**:195-207.
- Rosgen, D. L. 1994. A classification of natural rivers. *Catena* **22**:196-199.
- Schier, G. A., and R. B. Campbell. 1976. Differences among *populus* species in ability to form adventitious shoots and roots. *Canadian Journal of Forestry* **6**:253-261.
- Schmidt, J. C., R. H. Webb, R. A. Valdez, R. Marzolf, and L. E. Stevens. 1998. Science and values in river restoration in the Grand Canyon. *Bioscience* **48**:735-747.
- Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* **7**:677-690.
- Scott, M. L., J. M. Friedman, and G. T. Auble. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology* **14**:327-339.
- Scott, M. L., M. A. Wondzell, and G. T. Auble. 1993. Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation. Pages 237-246 in H.J. Morel-Seytoux, editor. *Proceedings of the 13th annual American geophysical union hydrology days*. Hydrology Days Pub., Atherton, California, USA.

- Shaw, D. V., and R. P. Prasad. 1970. Starch gel electrophoresis of enzymes--a compilation of recipes. *Biochemistry of Genetics* **4**:297-320.
- Shaw, R. K. 1976. A taxonomic and ecological study of the river-bottom forest on St. Mary, Lee Creek, and Belly River in southwestern Alberta, Canada. *Great Basin Naturalist* **36**:243-271.
- Simon, A. 1989. A model of channel response in disturbed alluvial channels. *Earth Surface Processes and Landforms* **14**:11-26.
- Soltis, D. E., C. H. Haufler, D. C. Darrow, and G. J. Gastony. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. *American Fern Journal* **73**:9-27.
- Stromberg, J. C., and D. T. Patten. 1989. Early recovery of an eastern sierra riparian system following forty years of stream diversions. Pages 399-404 in D. L. Abell, editor. *Proceedings of the California riparian systems conference*. U. S. Forest Service General Technical Report **PSW-10**.
- Thomas, B. E., and K. L. Lindskov. 1983. Methods for estimating peak discharge and flood boundaries of streams in Utah. *USGS Water Resources Investigation Report* **#83-4129**.
- Tyree, M. T., K. J. Kolb, S. B. Rood, and S. Patino. 1994. Vulnerability to drought induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem. *Tree Physiology* **14**:455-466.
- Virginillo, M. J., J. M. Mahoney, and S. B. Rood. 1991. Establishment and survival of poplar seedlings along the Oldman River, southern Alberta. Pages 55-61 in S. B. Rood and J. M. Mahoney, editors. *The biology and management of southern Alberta's cottonwoods*. University of Lethbridge, Lethbridge, Alberta, Canada.
- Webb, M. G., and J. D. Brotherson. 1988. Elevational changes in woody vegetation along three streams in Washington county, Utah. *Great Basin Naturalist* **48**:512-529.
- Williams, J. S. 1962. *Geology of the southern Cache Valley Utah*. USGS Professional Paper **257-C**.
- Wolman, G. M. 1954. A method of sampling coarse river bed material. *Transactions, American Geophysical Union* **35**:951-956.

TABLE 2.1. Geomorphic data used to characterize study sites and sources of this data.

Data	Source
Valley width	Field measurement
Valley slope	USGS topographic map
Drainage basin area	Geographic information system
Flood-prone width*	Site survey
Entrenchment**	Site survey
Bankfull channel width	Site survey
Bankfull channel depth	Site survey
Bankfull channel slope	Site survey
Channel sinuosity	Site survey
Particle size distribution	Wolman pebble count
Bar area***	Field measurement

* Width at twice bankfull depth, which is an estimate of the area inundated during the 50-year flood (Rosgen 1994).

** Width at twice bankfull depth divided by bankfull width.

*** Total area of point bars as a percentage of the area calculated as bankfull width times surveyed thalweg length.

TABLE 2.2. Comparison between Little Bear River estimated allele frequencies and an independent estimate.

Loci and alleles	Estimated allele frequencies	
	Cache Valley samples	Little Bear River
PGI		
A	0.066	0.087
B	0.033	0.046
C	0.866	0.862
D	0.033	0.023
PGM		
A	0.450	0.430
B	0.033	0.050
C	0.016	0.035
D	0.480	0.460
E	0.016	0.025

TABLE 2.3. Averaged allele frequencies used to calculate P_{gen} and probabilities of clonal origin between ramets.

Loci and alleles	Assumption		Averaged frequency
	Cloning	No cloning	
PGI			
A	0.088	0.086	0.087
B	0.058	0.034	0.046
C	0.820	0.860	0.840
D	0.029	0.017	0.023
PGM			
A	0.410	0.450	0.430
B	0.060	0.040	0.050
C	0.030	0.040	0.035
D	0.470	0.450	0.460
E	0.030	0.020	0.025

TABLE 2.4. Proportion of clonal recruitment at study sites.

Location	Sample size (T)	Individuals (I)	Clonal proportion (R_c)
Site 1	30	12	60%
Site 2	29*	9	69%
Site 3	30	9	86%
Site 4	30	5	83%
Point bars	30	8	73%

*One bud sample determined dead after processing for electrophoresis.

TABLE 2.5. Summary of allozyme data and clonal probability calculations

Location	PGI	PGM	P_{gen}	P_t	P_m	Encounters (n)	Individuals
Site 1	CC	AD	0.27	----	0.07	8	8
	CC	AA	0.12	0.87	----	2	2
	CD	AD	0.01	----	1.75E-21	13	1
	CD	AA	0.005	----	1.21E-10	7	1
Site 2	CC	AD	0.27	----	0.13	7	7
	CC	DD	0.14	----	8.32E-7	12	1
	CD	DD	0.006	----	1.11E-16	10	1
Site 3	CC	AD	0.27	----	2.83E-9	18	1
	CC	AA	0.12	----	5.54E-2	7	7
	CD	DD	0.006	----	----	1	1
	CD	AD	0.01	----	8.16E-4	4	1
Site 4	CC	AC	0.02	----	.036	3	1
	AC	BC	0.0004	0.00	----	2	1
	CC	CC	7×10^{-4}	----	2.25E-28	11	1
	BB	CD	7×10^{-5}	----	2.52E-47	13	1
	BB	DE	5×10^{-5}	----	----	1	1
Point Bars	CC	AD	0.27	----	1.65E-2	11	1
	CC	DD	0.14	----	1.54E+0	4	4
	CC	AA	0.12	----	4.09E-3	8	1
	CD	AA	0.005	----	7.00E-5	4	1
	CD	AD	0.01	----	1.2E-2	3	1

* P_t and P_m values provided where applicable. $G = 16$.

TABLE 2.6. Summary of geomorphic characteristics at study sites.

Category	Site #	Drainage basin area (km ²)	Valley width (m)	Valley slope	Channel Entrenchment	Flood-prone width (m)	Bf* Channel width (m)	Bf Channel depth (m)	Bf Channel W:D	Bf Channel slope	Channel sinuosity	Channel D50 (mm)	Point bar D50 (mm)	Point bar area (m ²)**
Confined	1	26.9	62.7	0.037	4.2	27.6	6.6	0.33	19.9	0.03	1.3	52	32	45/3%
	2	45.8	66.7	0.024	7.2	49.6	7.5	0.34	26.2	0.02	1.2	19	12	100.5/9%
Unconfined	3	411.2	390	0.01	2.4	42.4	18.1	0.59	30.9	0.008	1.5	50	30	1510/20%
	4	537.3	600	0.008	2.8	33.7	13.2	0.54	25.2	0.007	2.0	45	31	965/22%

*Bf = bankfull

**Point bar surface area as a total and a percentage of bankfull area.

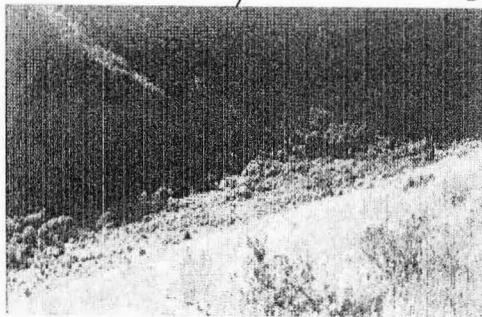
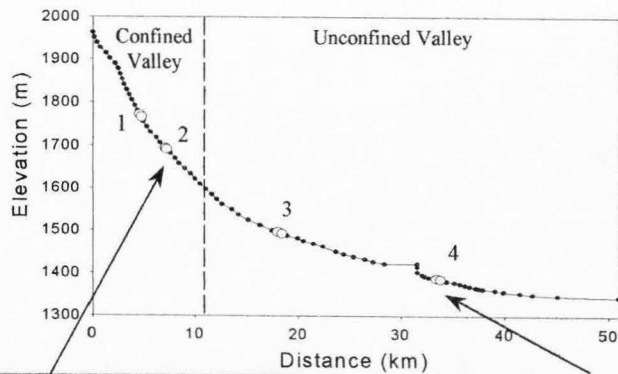


FIG. 2.1. Valley types and study site locations found on the longitudinal profile of the Little Bear River. Notice the Hyrum Dam spillway in the right photo and reflected as a distinct feature in the longitudinal profile.

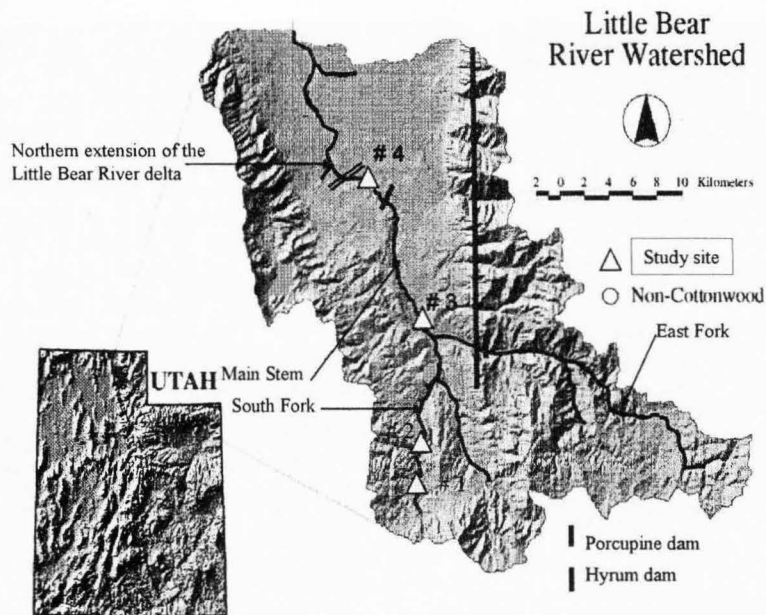
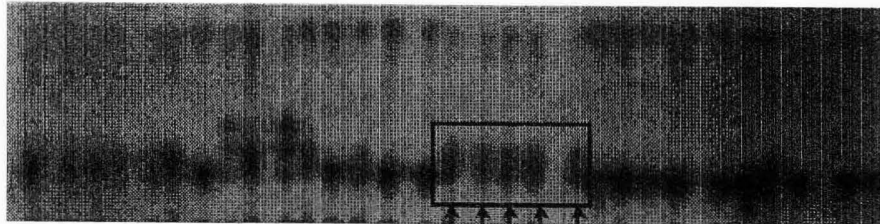


FIG. 2.2. Shaded relief of the Little Bear River watershed depicting study site locations. The black line represents the location of Cache Valley-wide vegetative bud sampling determining independent estimated allele frequencies.

PGI



PGM

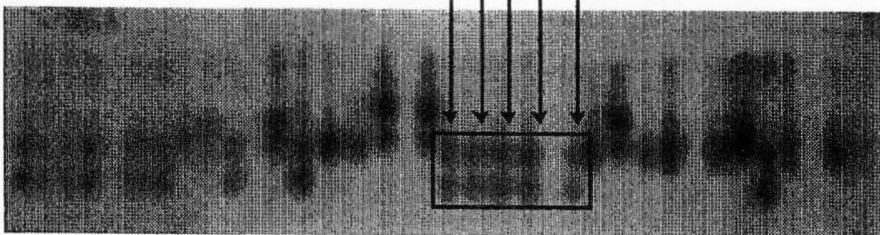


FIG. 2.3. Examples of starch gels containing stained allozyme data for 30 stems sampled at site 4. Data from 5 different stems (boxes) show identical allozyme patterns stained in the starch gel. This indicates that these five stems possess the same heterozygous, multi-locus genotype (PGI: BB, PGM: CD; $P_{gen} = 7 \times 10^{-5}$) and are potentially parts of the same clone, based on calculations using equation 2.

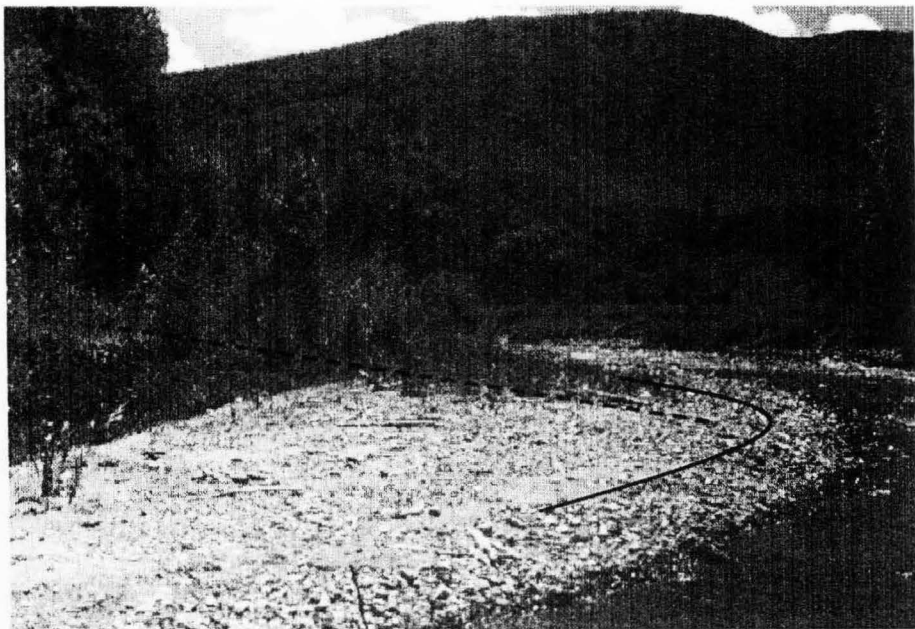


FIG. 2.4. Example of point bars found at site 3. Cohort sampling, depicted by the dashed line, included numerous aged cohorts and represents recruitment over several decades. Point bar sampling, depicted by the curved solid line, sampled young stems that were assumed to have developed recently.

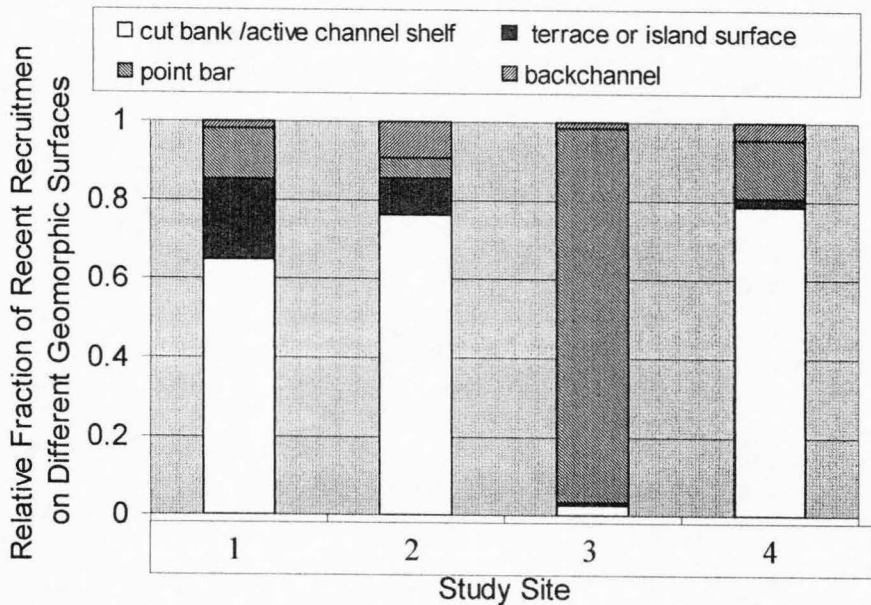


FIG. 2.5. Bar chart showing the relative fraction of recent recruitment on different geomorphic surfaces. The majority of the young stem age class (stem height < 0.3 m) occurs on geomorphic features very different than those described to provide the appropriate conditions for recruitment from seed.

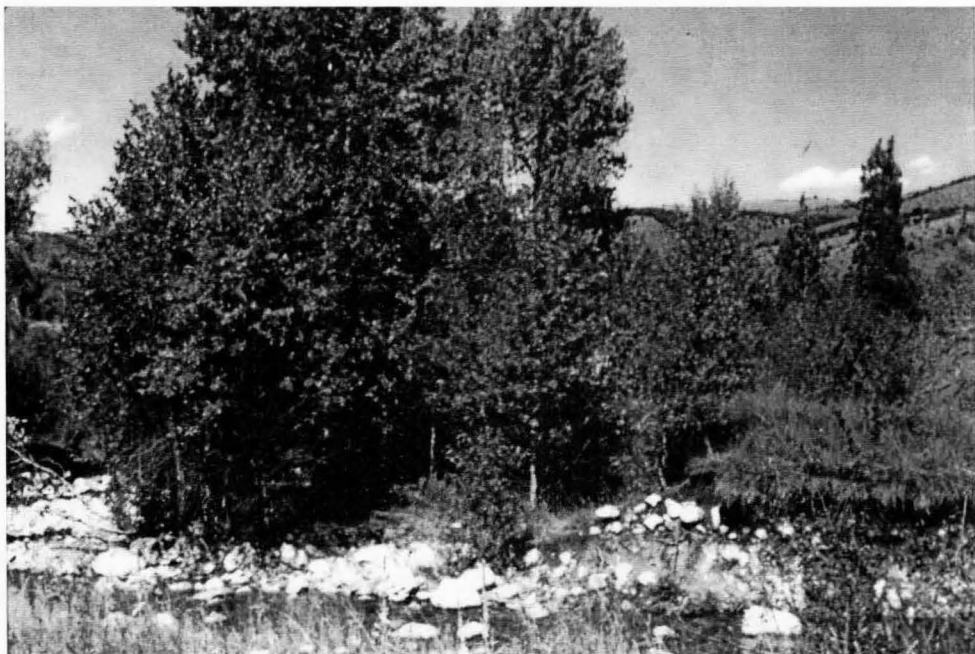


FIG. 2.6. Photo from site 2 depicting the type of clumped spatial distribution of cottonwood stems found on the Little Bear River. Also note the large particle size found on streamside surfaces at confined sites.

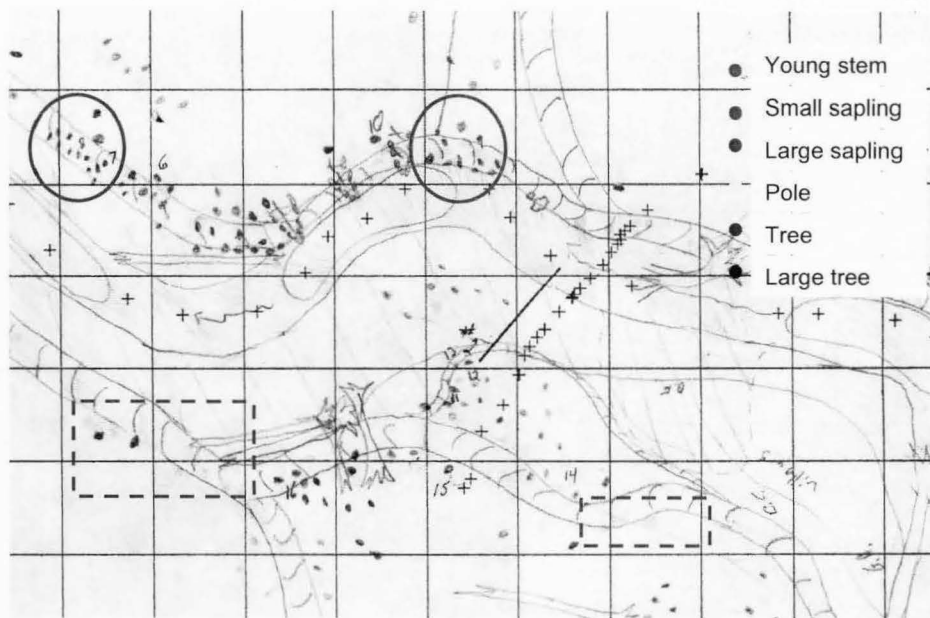


FIG. 2.7. Planview field map (grids are 10 m X 10 m) showing the clumped spatial distribution of cottonwood stems (in circles) or a linear arrangement (in dashed boxes) on terrace edges. The youngest age class (red dots) is seen recruiting on cutbanks where exposed roots are prevalent. Note a surveyed channel cross section and an allozyme sampling transect can be seen in the center of the figure.

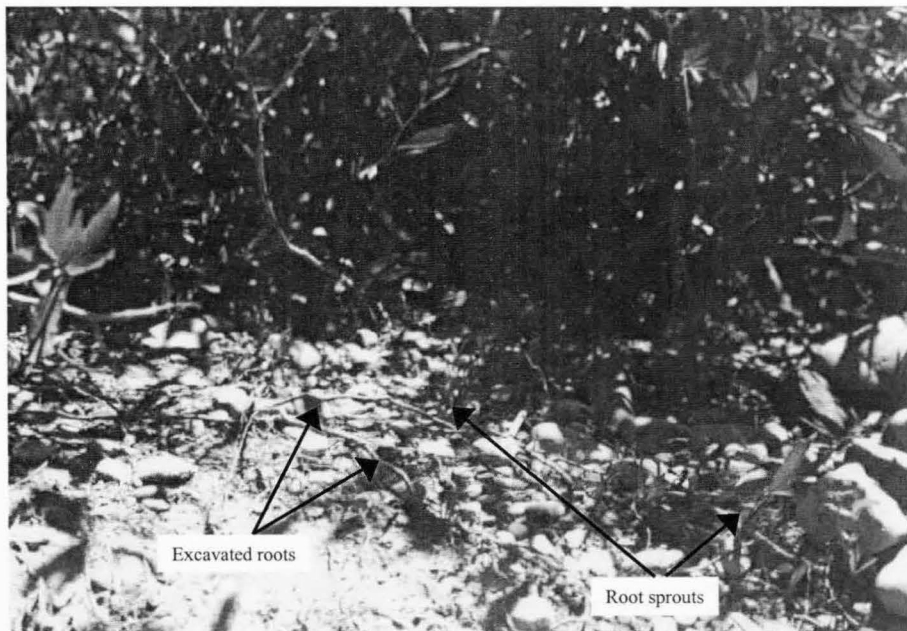


FIG. 2.8. Photograph of excavated point bar deposits revealing clonal recruitment originating from the excavated roots. A band of young stems is seen here streamward of a band of older vegetation and immediately below bankfull elevation.

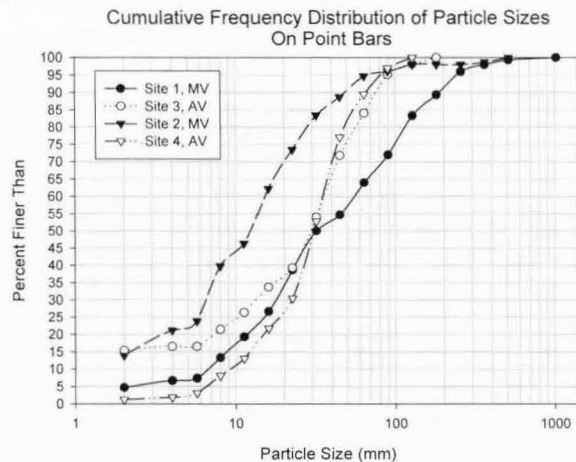
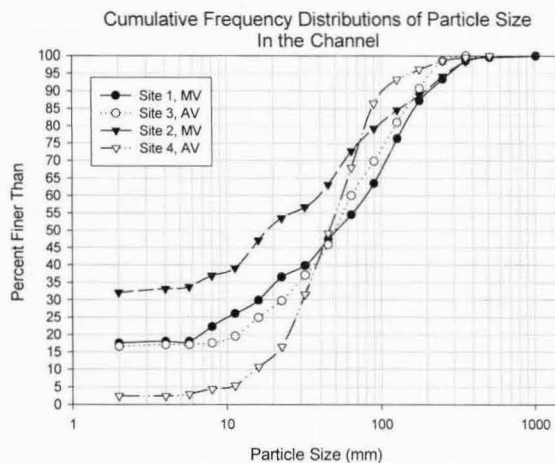


FIG. 2.9. Confined site data shown in dark symbols. Un-confined site data is shown in light symbols. These plots suggest that the dams may be decreasing the percentage of fine sediment at un-confined sites. Site 2 is the only site that includes a tributary confluence. Deposition from the tributary may explain differences in particle size distribution at this site.

CHAPTER 3

HYDROGEOMORPHIC INFLUENCES ON CLONAL RECRUITMENT OF
COTTONWOODS IN MOUNTAIN VALLEYS, NORTHERN UTAH

INTRODUCTION

Riparian forests are some of the most diverse ecosystems of the arid western United States (Anderson et al. 1983, Hunter et al. 1987). Riparian vegetation favorably contributes to critical streamside and in-stream habitat, water quality, and aesthetic and recreational values. Riparian cottonwoods (*Populus* spp.) are a keystone pioneer species that are the foundation of this forest type (Patten 1998), but land use and river regulation have caused a widespread reduction in the extent and regeneration of this genus (Braatne et al. 1996, Rood and Mahoney 1990). This reduction has generated an effort to understand riparian recruitment ecology and the processes that affect these environments. Where society has deemed it appropriate, this understanding has been applied to restoration strategies and identification of restoration sites that incorporate natural processes (Schmidt et al. 1998, Barinaga 1996, Klotz and Swanson 1997, O'Neill et al. 1997, Rood et al. 1998).

Most management programs and published literature regarding cottonwood recruitment have focused on the hydrogeomorphic requirements for seedling establishment and subsequent survival (Rood et al. 1994). In addition, many studies have focused on cottonwoods found in wide alluvial valleys. The fundamental hydrogeomorphic processes that facilitate cottonwood seedling recruitment in wide alluvial valleys are quantified by correlating the flow regime and the time of seedling

establishment. Studies typically use dendrochronological, geomorphic, and stream flow data to evaluate correlated with stream flow and seedling recruitment data (Bradley and Smith 1986, Scott et al. 1993, 1996, Friedman et al. 1996, Rood et al. 1998, Mahoney and Rood 1998).

A common source of error in determining an age of a stem from cores arises from burial of stems by flooding and sediment deposition, or flood-training (Everitt 1968). Tree cores collected above the ground may not account for additional rings (years) that only exist below the ground surface, thereby underestimating the age of the original buried stem. In wide alluvial reaches on the Missouri River, Scott et al. (1997) found cores collected above the ground underestimated true tree age by an average of 5.1 years compared to cores collected from excavated root crowns. However, they state that error arising from flood-training is probably more common in geomorphic settings similar to their study site and the occurrence of stem burial is probably less common in mountain valleys.

Seedling recruitment of cottonwoods is a function of many complex interactions however, some general patterns have emerged from the literature. Channel narrowing, floodplain deposition, and channel meandering are suggested as the primary processes that create the bare, moist geomorphic surfaces widely regarded as the appropriate seedbeds for colonization by cottonwoods (Scott et al. 1996). Consequently, the spatial distribution of cottonwoods is perpetuated by the spatial distribution of processes facilitating seedling recruitment in wide alluvial valleys.

Hydrogeomorphic factors also influence riparian vegetation ecology in steep confined mountain valleys. These include effects of flooding (Hack and Goodlet 1960, Hupp and Osterkamp 1985, Harris 1987), valley morphology (Baker 1989), stream power (Bendix 1994a), in-stream flow needs (Stromberg and Patten 1991), elevational gradient (Webb and Brotherson 1988), lithology (Bendix 1994b), channel gradient (Hupp and Osterkamp 1996), and characteristics of geomorphic surfaces (Osterkamp and Hupp 1984). However, these factors are rarely linked to processes affecting riparian vegetation recruitment mechanisms in these valleys. Meandering may not be a dominant process in mountain valleys, whereas channel narrowing, including abandonment of side channels, and overbank deposition may be processes responsible for creating appropriate seedbeds for colonization in constricted reaches (Scott et al. 1996). Merigliano (1996) found overbank deposition important in forming appropriate surfaces on islands for cottonwood seedling recruitment on a braided reach of the Snake River in Idaho. Although Scott et al. (1996) suggest that clonal recruitment may occur in cases of channel narrowing, all of the above processes focus on seedling recruitment. This assumes, at least implicitly, that seedling recruitment is the principal reproductive strategy of cottonwoods (Rood et al. 1994).

In contrast, I have demonstrated with allozyme electrophoretic data, geomorphic and vegetation mapping, photographic documentation, and phenological indicators that clonal mechanisms dominate cottonwood recruitment in the steep, confined mountain valleys of the Little Bear River, in northern Utah (see Chapter 2). A recent study on the Oldman River in Alberta also has found a surprisingly high degree of clonal recruitment

where 78% of the evaluated cottonwood stems originated from clonal mechanisms (L. A. Gom and S. B. Rood *unpublished manuscript*). They described the setting as a foothill river, more confined and with a higher gradient than what they call a prairie river.

Cottonwood recruitment through root sprouting may be induced by environmental conditions different from those needed for seedling establishment (Stromberg and Patten 1989). Tiffney and Niklas (1986) identified trauma to lateral meristem as a primary ecological stimulus resulting in clonal recruitment from root sprouting, and this recruitment mechanism is recognized as a response to stream disturbance in riparian species (Gecy and Wilson 1990, Sigafos 1964).

In steep confined rivers, cottonwoods are more likely to root sprout than species found in wide alluvial rivers (Schier and Campbell 1976, Rood and Mahoney 1990, Rood et al. 1994, L. A. Gom and S. B. Rood *unpublished manuscript*, Kranjcec et al. 1998). Schier and Campbell (1976) noted root sprouts originating from damaged root cambium and the cut end of roots. Other studies have found root sprouts (Webb and Brotherson 1988, Shaw 1976) and older clones (L. A. Gom and S. B. Rood *unpublished manuscript*) spatially distributed in channel areas subject to high scour. This ability may be a life history adaptation to hydrogeomorphic disturbance processes common to steep, confined mountain valleys that could result in root trauma and consequent clonal recruitment.

Multiple channels are often found in montane and piedmont valleys (Grant and Swanson 1995, Stanford et al. 1996, Osterkamp 1998), and channel avulsion, the scouring of new channels into the floodplain and reoccupation of old channels, is a process that forms multiple channels in these valleys (Knighton and Nanson 1993,

Nanson and Knighton 1996). Avulsion and multiple channels tend to occur in aggradational environments, which occur where local transport capacity is exceeded by sediment supply (Fahnestock 1963, Leopold et al. 1964, Kellerhals et al. 1972, Bull 1979, Nanson and Knighton 1996). Aggradational environments may result from a decrease in slope in mountain valleys (Knighton 1976, Miller 1991). Other conditions facilitating channel avulsion in mountain valleys include high bed-load, and some mechanism for displacing stream flow to overbank flow.

Mechanisms responsible for displacing stream flow include interactions with vegetation and debris dams (Hickin 1984, Harwood and Brown 1993, Thompson 1995), channel sedimentation (Church 1983, Germanosky and Schumm 1993, Ashworth 1996), and the spatial distribution of channel bends and valley width variations (Miller 1990, Miller and Parkinson 1993, Osterkamp 1998).

All of the above-mentioned geomorphic conditions must interact with a geomorphically effective flood, capable of creating a new landform or changing an existing one (Wolman and Gerson 1978) for channel avulsion to occur. Avulsion and other geomorphic changes can result from highly variable flow regimes (Nanson and Knighton 1996) and high discharges (Baker and Costa 1987, Miller 1990, Magilligan 1992). The duration of a high discharge may greatly influence the degree of its geomorphic effectiveness. Abrupt high discharges may not produce significant geomorphic change in humid environments (Costa and O'Conner 1995), whereas a similar type of flood can cause extensive geomorphic change in arid environments (Baker 1977).

Studies have correlated recruitment of *Populus angustifolia* with stand-destructive events (Baker 1988, 1990, Baker and Walford 1995); however, seedling versus clonal recruitment mechanisms were not investigated. Clonal recruitment of cottonwoods from root sprouting may be a dominant recruitment response to the hydrogeomorphic disturbance processes common in steep, confined mountain valleys. This study seeks to identify a process-based recruitment model for clonal recruitment similar to those identified for seedling recruitment. I hypothesize that the spatial distribution of clonal recruitment of cottonwoods correlates with a geomorphic template that facilitates channel and consequent root disturbance. A decrease in channel slope in a wider valley is hypothesized to result in a lower energy channel reach susceptible to lateral instability and avulsion (Fig. 3.1). Large variations in discharge can result in channel disturbance and clonal recruitment may temporally correlate to peak discharges in the hydrograph that are different from those that correlate to seedling recruitment.

METHODS

Eight sites were selected to investigate clonal recruitment of cottonwoods by comparing hydrogeomorphic processes at sites containing clonal recruitment (CR sites) to sites where cottonwoods do not exist (NC sites). Four pairs of sites, one CR site and one NC site per pair, were located along the South Fork and main stem of the Little Bear River (Fig. 3.2). Sites were paired along the longitudinal profile to avoid comparing characteristics between CR and NC sites that vary as a function of scale and progression downstream. NC sites were located in the reach closest to their respective paired CR sites

where site access was allowed. One NC site was located an additional 3 km upstream to take advantage of data collected at an abandoned United States Geological Survey (USGS) gage. Sites are numbered 1-8 as they occur in the downstream direction. Sites 1-4 are referred to as upper sites occurring above the canyon mouth, and sites 5-8 are referred to as lower sites occurring below the canyon mouth.

I collected geomorphic data to evaluate differences between CR and NC sites. I estimated bankfull hydraulic conditions and used average boundary shear stress and unit stream power as surrogates of disturbance potential at CR and NC sites. A non-parametric Mann-Whitney test was used to evaluate differences between site averages of geomorphic and hydraulic parameters at CR sites and NC sites. Site averages were calculated as the mean value of all cross section values for each geomorphic and hydraulic parameter. I used dendrochronological and hydrologic data to evaluate temporal correlation between streamflow and clonal recruitment events. I used aerial photos and geomorphic and vegetation field maps to evaluate spatial correlation between areas of channel disturbance and clonal recruitment.

Study area

The study area for this research is the Little Bear River watershed (574 km²) located in Cache County in northern Utah (Fig. 3.2). The Little Bear River flows north from the Bear River Range into Cache Valley, a 64 km long and 32 km wide valley. Cache Valley and its surrounding mountains are at the eastern edge of the Basin and

Range province. The South Fork descends from an elevation of approximately 2000 m in a steep, confined mountain valley, to 1300 m in the lower most alluvial valley.

The primary lithologies of the surrounding Bear River Range are limestone and dolomite. Williams (1962) summarized the surficial geology of the Little Bear River watershed as exhibiting the influence of Pleistocene Lake Bonneville. He stated deposits of Former Lake Bonneville cover the interior of Cache Valley and deltas were formed at the mouths of canyons as rivers flowed into Lake Bonneville. The Little Bear River formed a delta of the Provo formation at the mouth of its canyon (Williams 1962). Williams described the Provo formation as divided into a gravel and sand member and a silt and clay member. McCalpin (1989) mapped the present channel and valley bottom of the Little Bear River in this formation as clast-supported pebble, cobble, and gravel in a matrix of sand and minor clay. The channel of the Little Bear River drastically changes character downstream and north from the delta as it flows through clay sediment deposited at the bottom of Pleistocene Lake Bonneville. More cohesive bank material probably contributes to an increase in sinuosity that occurs where the channel encounters clay, and gravel is much less common in this reach.

The hydrology of the Little Bear River is dominated by snowmelt runoff. The spring snowmelt peak typically occurs between April and June. However, examination of U. S. Geological Survey (USGS) flow records reveals that early thaw events, occurring in the winter months, are relatively common (Fig. 3.3). Two of the three largest flood peaks on record for the Little Bear River were events of this type and occurred in 1962 and 1984.

Extensive water development has occurred on the Little Bear River including the construction of two dams and numerous diversions for irrigation. The U. S. Bureau of Reclamation built Porcupine and Hyrum Dams. Hyrum Dam was constructed in 1935 on the main stem, and Porcupine Dam was constructed in 1962 on the East Fork of the Little Bear River. Floods peaks above approximately a five-year return interval appear to be attenuated in magnitude by 10-15% from what would be predicted by regional flood frequency curves (Thomas and Lindskov 1983) for unregulated streams in the region. This suggests that regulation from dams and diversions may attenuate flows.

Padgett et al. (1989) classified the riparian vegetation of the study area as various *Populus angustifolia* (narrow leaf cottonwood) dominated community types. Watershed reconnaissance conducted for our study sites showed that these cottonwoods are present along the channel of the Little Bear River to the northern extension of the Little Bear River delta. North from the delta, in the valley flat, the exotic *Salix fragilis*, crack willow, is the dominant overstory riparian species. However, isolated stands of the natives *Salix exigua* and *Salix lutea* are intermixed with the crack willow.

Reconnaissance also revealed four distinct patches of cottonwoods with recently recruited saplings. Other reaches on the river have mature and decadent cottonwood trees present. However, only those with enough individuals of different ages and exhibiting recent recruitment were considered as research sites. Patches containing cottonwood recruitment are separated by reaches dominated by *Salix* spp. (willow) or *Acer negundo* (box elder).

Geomorphic characterization

Geomorphic data were collected at CR and NC sites, following methods described by Harrelson et al. (1994). These data were used to evaluate the likelihood of channel and consequent root disturbance at CR sites and NC sites. Geomorphic parameters that I measured and their respective methods are presented in Table 3.1. A longitudinal profile of the South Fork and main stem of the Little Bear River was created from 1:24,000 scale topographic maps to investigate spatial correlation between locations of CR and NC sites and breaks in slope at the reach scale. A decrease in slope was used as a surrogate of a decrease in the energy slope hypothesized to result in a lower energy environment susceptible to avulsion and disturbance to root material.

At the site scale, channel morphology parameters were collected using a geodetic total station or measured with a tape. I determined particle size distributions by Wolman (1954) pebble counts. Counts were distributed throughout the surveyed reach to reflect different channel units and contained a minimum of 150 particles. Detailed maps were created at each site to describe geomorphic features such as channel, floodplain, and terrace locations.

Aerial photos (1937, 1953, 1959, 1966, 1974, 1981, 1987, 1988, and 1993) were matched using a reflecting projector for two CR and two NC sites to evaluate lateral channel stability over time. Lateral movement was used as a surrogate for increased channel and root disturbance potential. The four sites used for this analysis were the only sites where vegetation did not obscure the channel location.

Hydraulic characterization

I used power functions from regional flood frequency curves (RFFC) to estimate discharge for the 2-yr, 5-yr, 10-yr, 15-yr, and 25-yr flood at CR and NC sites. For unregulated sites (1-4), I used power functions developed by Thomas and Linskov (1983). Their power functions were developed for un-regulated streams in similar physiographic regions and weighted for elevation. I used 23 concurrent years (1964-1986) of USGS flow records at three gages and extended records at two gages (Table 3.2) to develop RFFC's and power functions for regulated sites (5-8) (Fig. 3.4). I used annual maximum (mean daily) data, transformed to fit a Log Pearson Type III distribution, to generate curves at individual gages. I only used spring runoff peaks to ensure a homogeneous population of hydrologic events. I used a regional skew value, and the mean and standard deviation values from the 23 years of concurrent log transformed discharge data.

Gage records at two sites were extended with ordinary least squares regressions of annual mean daily peaks from the closest gage possessing the strongest regression relation (see Table 3.2). The Hyrum (# 10107500) and Paradise (# 10106000) gages included 31 concurrent years of data and the Hyrum record was extended 13 years ($r^2 = 0.91$). The Avon (# 10406000) and Davenport (# 10104700) gages included eight concurrent years of data and the Avon record was extended 12 years ($r^2 = 0.7$).

I used the software program WINXSPRO (version 2.1A, Grant et al. 1992) to develop stage-discharge relations at all surveyed cross sections. WINXSPRO offers a

number of resistance equations to express channel roughness. The empirical relation from Hey (1979):

$$\frac{1}{\sqrt{f}} = 2.03 \log \left(\frac{aR}{3.5D_{84}} \right) \quad (1)$$

where f is the dimensionally correct Darcy-Weisbach friction factor, a is an expression of bed and bank roughness as a function of channel shape, and R is the hydraulic radius, is appropriate for our data set. After estimating f using surveyed channel morphology, it is inserted into the Darcy-Weisbach equation:

$$f = \frac{8gRS}{V^2} \quad (2)$$

where g is acceleration due to gravity, S is channel slope, and V is average cross section velocity. The Darcy-Weisbach equation provides an estimate for V that is subsequently inserted into the continuity equation:

$$Q = AV \quad (3)$$

where Q is discharge and A is cross-sectional area of flow at stage (h).

I solved the continuity equation for Q , where Q was the estimated flood discharge from the flood frequency calculations, and estimated average boundary shear stress (τ_o) from:

$$\tau_o = \rho gRS \quad (4)$$

where ρ is density of water, g is the acceleration of gravity, R is hydraulic radius, and S is water slope. Unit stream power (ω) was estimated in the same way from:

$$\omega = \tau_o V \quad (5)$$

where V is the average cross section velocity.

Prior to analysis, the same technique was applied to a surveyed cross section located at a USGS gage site (# 10104600) to determine the nature and magnitude of potential errors in the technique. Flood frequency analysis for the gage estimated the bankfull Q (2-yr return interval) as $4.12 \text{ m}^3/\text{s}$. WINXSPRO estimated $4.18 \text{ m}^3/\text{s}$ at a bankfull stage that was based on field indicators. WINXSPRO requires a low and high slope value and a D_{84} value when using Hey's (1979) empirical relation. The closest match between bankfull Q from flood frequency estimates and Hey's relation was obtained by using only the slope data of the channel unit containing the cross section. A local D_{84} , determined from pebble count data collected closest to the cross section also improved the match. More error in the stage-discharge relation was introduced if reach averages of these values were used.

Temporal and spatial correlation and clonal recruitment

Dendrochronological data were collected to determine the dates of clonal recruitment events. Based on estimated height and stem diameter, six age classes of cottonwoods were present at all four CR sites. Age classes were young stems (.01-0.3m), small saplings (0.3-0.7 m), large saplings (1.2-2.1 m), poles (4.5-9 m), trees (10.5-12 m), and large trees (greater than 12 m). Thirty stems, five stems from each estimated age category, were sampled per site. Stem cross sections typically yield more accurate age estimates than cores (Fritts and Sweetnam 1989). However, cores were collected from stems with diameters larger than 4 cm. Slabs from stems with diameters greater than 4 cm could not be collected at study sites located on private property where riparian habitat

is limited. Where possible, stems were cored completely to allow two ring count totals, one from each side of the stem. Both slabs and cores were collected approximately 30 cm above the present ground surface except in the seedling and sapling sizes where size necessitated collection from lower on the stem. The first three stems sampled at each site were excavated to determine whether they originated from buried stems. Slab and cores were taken to the laboratory facilities and air-dried, mounted onto grooved boards, and sanded with a graded series of sandpaper to 600 grit, buffed to remove fine dust from the vessels, wetted, and viewed with a dissecting scope to count annual rings. Cores were cross-dated with skeleton plots to decrease error resulting from intra-annual rings (Fritts and Sweetnam 1989).

USGS flow records from two gage locations were plotted as a time series to evaluate temporal correlation between flow characteristics and cottonwood establishment events. Spring runoff and early thaw annual peaks from the Davenport and Paradise gages were used to characterize flow conditions at the upper and lower CR sites, respectively. The Davenport gage is the farthest upstream and it is located above the confluence with the East Fork of the Little Bear River (see Fig. 3.2). It is assumed that discharge data from the Davenport gage better represents flow conditions at the study sites than the Paradise gage, which is located below the confluence with the East Fork. The Paradise gage is located between the two lower CR sites (6 and 7) and records from this gage are representative of flow conditions at these sites.

Cottonwood stems were coded by estimated age classes and located on geomorphic maps to quantify the relative percentage of recent recruitment on geomorphic

features. I defined stems less than 0.3 m as recent recruitment because most other cottonwood stems were at least twice this size, which suggested that stems below 0.3 were recruited much more recently than other stems. I also mapped the spatial distribution of cottonwood stands and used field maps and aerial photographs to evaluate spatial correlation between recruitment locations and areas of channel disturbance.

RESULTS AND DISCUSSION

Geomorphic characterization

CR and NC sites differ in their geomorphic characteristics (Table 3.3) and characteristics at CR sites are similar to characteristics of the geomorphic "template" hypothesized to facilitate clonal recruitment (see Fig. 3.1). The most noticeable difference was the multiple channel planform found at all CR sites, which is a planform other studies have found to coincide with wider valleys that have lower gradient (Miller 1990, Miller and Parkinson 1993, Grant and Swanson 1995, Stanford et al. 1996, Osterkamp 1998). Except for the lowest pair of sites, CR sites had wider valleys and lower slopes than paired NC sites. However, valley width and gradient differences between CR and NC sites were not statistically significant. Furthermore, channels immediately upstream from CR sites occurred adjacent to constraining features such as valley walls or abandoned terraces. Where channels abruptly turn away from these constraining features, the channel alters from a single-thread to a multiple channel planform. Below valley constrictions, avulsion may be common where flow is no longer constricted between valley walls, especially where the channel bends below the

constriction (Miller 1990, Miller and Parkinson 1993). Where channels were adjacent to constraining features at NC sites, the channels continued to follow these features with no abrupt bends.

Geomorphic parameters were also different between CR and NC sites at the reach scale; however, parameters did not always fit the hypothesized template. In support of the hypothesized template, the upper CR sites occurred in reaches with lower channel slopes relative to their respective paired NC sites (Fig. 3.5). The transition to a lower gradient, typically where the valley widened, was assumed to represent a decrease in the energy slope and a decrease in velocity. This decrease in velocity may cause sediment deposition and multiple channel formation (Knighton 1976, Miller 1991, Nanson and Knighton 1996). This interaction suggests an explanation for the existence of multiple channels at upper CR sites. However, it does not account for the presence of multiple channels at lower CR sites.

In contrast, the lower two CR sites grade into reaches with higher slopes relative to their respective paired NC sites, which follows a long established relationship. Leopold and Wolman's (1957) plot of channel slope versus bankfull discharge may provide an explanation for slope differences found between CR and NC sites lower in the basin network. The contributing area of these lower sites is more similar to the contributing areas of the sites used to develop Leopold and Wolman's relationship. The data included in their plot empirically indicate a braided planform where channel gradient increases for a given basin area. The farthest downstream NC site (#8), which has a single-thread planform, plots where their relationship predicts a single-thread meandering

channel. Both of the lower CR sites, 6 and 7, plot where other data predicts multiple or braided channels. Thus far, it appears that the farthest downstream sites respond with somewhat predictable channel patterns. However, the rest of the sites farther upstream plot at contributing areas smaller than that at sites used to develop their plot. Leopold and Wolman's (1957) plot may be applicable to sites with the similar contributing areas to those used in the plot. However, processes are likely different in steep, confined mountain valleys that cause multiple channel planform. Debris dams may complicate a relationship that only relies on contributing area as a predictor.

Hydraulic damming upstream from wood loading and sediment input from tributaries also can alter local sediment supply and transport relationships. Debris dams may cause stream flow velocity to decrease, resulting in sediment deposition and a loss of channel competence. Lower channel competence may contribute to changes in planform if flow is forced overbank, which can erode floodplain deposits and form new channels. Debris dams may also redirect stream flow against the banks, resulting in erosion. No debris dams were found at NC sites, whereas all CR sites were characterized by a high frequency of debris dams. These dams occur at the upstream end of many side channels at CR sites, which suggests that debris dams were facilitating avulsion either through hydraulic damming or through redirecting channel flow against stream banks. In addition, debris dams and the beginning of side channels were often situated where the channels turned away from constraining features.

Tributary confluences also may complicate simple channel planform and contributing area versus slope relationships. Tributary confluences were in close

proximity to the upper CR sites, whereas no tributaries entered the main stem in close proximity upstream to NC sites. Additional sediment input from tributaries steeper than the main stem may exceed the main stem capacity to move the sediment (Osterkamp 1998) and contribute to avulsion by reducing channel competence. At a constant discharge and slope, larger particles added to the channel may result in aggradation and an alteration in planform (Germanosky and Schumm 1993).

Geomorphic parameters also were different between CR and NC sites at the channel scale (Table 3.3). Channels at CR sites have greater bankfull width and width depth ratios, are less entrenched with wider flood-prone width, higher sinuosity and total sinuosity. Wider more shallow channels in gravel bedded rivers are commonly associated with reaches where the local transport capacity has been exceeded by sediment input (Germanosky and Schumm 1993, Nanson and Knighton 1996, Ashworth 1996). These conditions suggest that channels are more likely to be laterally active than channels at NC sites that are more entrenched with lower sinuosity and lower width-to-depth ratios.

Inspection of historic aerial photos showed channel planform at CR sites is less stable relative to NC sites (Fig. 3.6). Thalweg location at CR sites has varied greatly through time, whereas thalweg locations at NC sites are less sinuous and appear to be stable. Stable thalwegs over a period of at least 56 years at NC sites suggest a lower potential for a spatially dynamic disturbance mechanism likely to provide disturbance to cottonwood roots. The lack of such a mechanism facilitating clonal recruitment may explain why cottonwoods are absent from these reaches.

Hydraulic characterization

Thus far, the discussion has focused on geomorphic form differences between CR and NC sites, which are often used as a surrogate for geomorphic process. In addition, I used τ_o and ω as surrogates of the energy available for channel and consequent root disturbance between CR and NC sites. Estimated values of τ_o and ω were lower in CR sites relative to NC sites (Table 3.3), which suggests that CR sites are lower energy reaches more likely to avulse and disturb root material. Grant and Swanson (1995) also found multiple channels at sites with lower shear stress in wider mountain valleys. Smaller mean particle sizes at CR sites also suggest reduced transport capacity relative to NC sites.

The relationship between lower energy reaches and an increased likelihood of channel disturbance is counter-intuitive. Although the process of overbank floods creating new channels in floodplain sediment is an erosional process, it is depositional processes that may set the stage for an interaction between streamflow and channel banks that creates multiple channels (Nanson and Knighton 1996). NC sites, possessing higher τ_o and ω , would seem more likely to provide disturbance to root material. However, it is likely that lower τ_o and ω , debris dams, or other causes facilitate temporary storage of sediment at CR sites. Sediment deposition may lead to channel sedimentation or bar formation that redirects flow against the stream bank and facilitates lateral channel activity or the formation of new channels (Kellerhals et al. 1972, Germanosky and Schumm 1993, Ashworth 1996). The aggradational environments facilitating multiple

channel formation would likely occur during lower flow, whereas the actual erosional event would likely occur at higher flows (Leopold et al. 1964).

A high discharge would have to be geomorphically effective, where resisting forces are overcome by driving forces, to disturb channel morphology and streamside roots. Geomorphic effectiveness is a function of many factors that vary among sites and driving forces can be calculated. However, the resisting forces at a site are often unknown until geomorphic change is documented (Baker 1977).

Spatial and temporal correlation and clonal recruitment

The hypothesis that a geomorphically effective flood results in channel and root disturbance and consequent clonal recruitment of cottonwoods is supported by the spatial correlation of disturbed channel areas and the occurrence of clonal recruitment. This was investigated with geomorphic mapping and historic aerial photographs.

Mapping revealed that older stems at CR sites were typically aligned on the leading edges of steeply sloping channel margins, cutbanks, and old scarp faces. These channel areas have high scour potential and studies have found clonal recruitment of cottonwoods in similar channel position (Shaw 1976, Webb and Brotherson 1988, L. A. Gom and S. B. Rood *unpublished manuscript*). In fact, many stems occurring on cutbanks could be seen originating from exposed root material (Fig. 3.7).

Examination of channel positions from historic aerial photos, overlaid onto geomorphic field maps for this same cutbank, documented a change in channel position some time between 1981 and 1987 (Fig. 3.8). Because of this change, flow was

redirected against cutbanks and altered the shape of previous cutbanks on both sides of the channel. Young stems of approximately the same stem diameter and height as the clonal stems in Fig. 3.7 also occur on the opposite cutbanks, where flow collided with the bank, and originate from exposed root material (Fig. 3.9). An older stem also is in close proximity to younger stems and large roots that younger stems originate from may be roots of this older stem. Similar spatial arrangement suggests the stems on both cutbanks were recruited through similar mechanisms at or near the same time. In addition, the spatial arrangement of clonal stems at lower CR sites suggests that younger stems may be initiated with successive root disturbance events and is a configuration different from that produced by meandering, channel narrowing, or flood deposition.

The same technique of overlaying historic channel position onto geomorphic maps at upper CR sites is not possible because overstory vegetation covers the channel position. However, large stems also are found aligned along cutbanks and the majority of recent clonal recruitment at upper CR sites occurs on cutbanks and areas of high scour potential (Fig. 3.10). Overbank deposits of large gravels and cobbles can be seen in the Fig. 3.10 in proximity to recent clonal recruitment and suggest that sediment scoured root material during a large flood. In addition, a debris dam is present in Fig. 3.10 at the upstream end of an old channel and probably redirected flow at some time to cause the formation of the present channel. These observations suggest that similar disturbance mechanisms, documented with aerial photographs and mapping at the lower CR sites, are perpetuating cottonwood recruitment at upper CR sites. Flows responsible for forming cutbanks and placing overbank deposits of large gravels and cobbles might provide the

scour to damage root material and initiate the physiological response of sprouting (Sigafoos 1964, Tiffney and Niklas 1986, Kranjcec et al. 1998).

Dendrochronological analysis was used to evaluate temporal correlation between flow events and clonal recruitment. Clonal recruitment of cottonwoods temporally correlates with early thaw events and not the spring runoff event as studies investigating seedling recruitment have shown. For example, the same period which encompassed the channel change documented in Fig. 3.8 also encompassed the largest early thaw event ($Q = 38.79 \text{ m}^3/\text{s}$) and spring runoff event ($Q = 42.75 \text{ m}^3/\text{s}$) recorded at the nearby Paradise gage. The spring runoff event occurred in 1984 and the early thaw event occurred in 1986 (Fig. 3.3). The young stems shown in Figs. 3.7 and 3.9 occurring on cutbanks were cored and these stems were recruited in 1987 and 1988, coinciding with the early thaw event.

Other stems at other sites also temporally correlated to early thaw events and suggest that early thaw events are a formative geomorphic event and the disturbance mechanism that causes recruitment. Age was determined for 98 of the 120 samples collected that included pith material, which facilitated accurate aging by including all annual rings. Nineteen cored stems did not include the pith but were estimated to be within five annual rings of the pith. Ages of samples with pith material were plotted in relation to a time series of spring runoff and early thaw events (Fig. 3.11). Cores with estimated ages also were included but displayed independently of samples that included pith.

Different temporal patterns of recruitment events were evident between upper and lower CR sites, which may be explained by differences in peak flows reflected at two different gage sites. Annual peak data from the Paradise gage, which is located between the lower CR sites generally reflected flow conditions affecting these sites (Fig. 3.2). Recruitment at lower CR sites primarily correlated with early thaw events occurring in 1962, 1963, and 1986 that were reflected in peak discharge data at the Paradise gage (Fig. 3.11). A distinct gap in recruitment occurred at lower sites in the 1970's. Importantly, this same recruitment gap did not include early thaw events reflected in peak discharge data at this gage. However, different temporal patterns of recruitment were evident at upper two CR sites and peak flow data from the Paradise gage may not reflect all disturbance events that may affect these upper sites.

Recruitment at the upper CR sites correlates with 1945, 1962, and 1986 early thaw events. However, recruitment at the upper sites also occurred throughout the 1970's and early 1980's, a period when there were no early thaw events at the Paradise gage. However, early thaw events did occur at the Davenport gage in 1969, 1976, 1978, 1980, and 1989 and recruitment at the upper CR sites correlates with these events (Fig. 3.11). Early thaw events, detectable at the Davenport gage, may not be detectable at the Paradise gage due to the addition of East Fork discharge. East Fork flows probably mask peaks that originate on the South Fork that correlate to clonal recruitment at upstream sites.

There is error involved in any study using dendrochronological data. This study has a number of advantages that may decrease the error in stem dating, however. The

root crowns of all 12 excavated stems occurred very near the present ground surface. Although the sample size of excavated stems is small, results suggest flood-training is not a serious source of stem dating error in this type of system. Flood training may be more of a problem in larger alluvial rivers with extensive lateral accretion of floodplains (Scott et al. 1997). Moreover, as opposed to many studies investigating seedling recruitment, I did not necessarily have to find the original root crown of the entire organism because I was not looking for a recruitment surface. I was only looking for the most recent occurrence of clonal recruitment, which usually was visible as a sprout originating from exposed root material. However, clonal recruitment events occurred as a lagged response during or in the years following early thaw events (Fig. 3.12). The first few rings of stems may have been missed because stems were cored at 0.3 m above the ground surface. These early rings could be missed by coring at this elevation on the stem because the tree may not have attained a height of 0.3 m in the first 1 or 2 years.

Many studies investigating seedling recruitment have grouped trees aged 3-5 yr after a high spring runoff event that correlates with the majority of the recruitment events determined with dendrochronological data. Grouping often was done in other studies. Because dendrochronological methods are imperfect, tree ages are grouped as a compensation for errors involved in methods. A 2-5 yr error in the accuracy of the recruitment year has often been estimated, therefore any recruitment events within this 2-5 yr range are grouped into one year. This grouping demonstrates a more precise temporal correlation with flow events and distinct difference between age classes. I

chose to illustrate stem ages without grouping the ages because this is the first study to focus specifically on temporal correlation of flow events and clonal recruitment.

However, the less distinct differences between age classes in my study may not only be a function of not having grouped stem ages. Studies have suggested that clonal recruitment dilutes the typical age class structure found with seedlings (Rood et al. 1994, Scott et al. 1996). Displaying actual tree ages for clonal recruitment is appropriate until future studies can support or dispute the findings presented here. Jones and Raynal (1986) noted unexpanded adventitious buds in American beech as old as two years from the time trauma had initiated their formation. Some similar physiological process may explain the lag in clonal recruitment at the Little Bear River sites.

The lack of distinct age classes is even more prevalent at upper CR sites than lower CR sites, which may be a result of the higher frequency of early thaw events at the upper sites. Examination of climate data from two nearby weather stations, Hardware Ranch (# 42367105) and the Upper Little Bear (# 4211H25S) (Fig. 3.2), indicated that early thaw events occurred the day of or after the annual maximum 24-hr rainfall. Although rainfall runoff relations are complex, this temporal correlation suggests that these large abrupt discharge events are rain-on-snow floods. Storms often cover a greater proportion of the smaller basins found higher in the drainage network. These smaller basins are less able to ameliorate flood flows resulting from precipitation events, which may occur and disturb root material more frequently.

The fact that the peaks that temporally correlate to clonal recruitment occur in winter raises the interesting question of what influence ice may play in recruitment of

riparian vegetation. Although there is little evidence of ice as a major factor in riparian recruitment (Patten 1998), it could conceivably play a part in the scour interactions described above. Early thaw events may break up channel ice that could scour roots at or near bankfull elevation without the need to transport sediment to that elevation to accomplish the root disturbance.

The rain on snow recruitment mechanism described above was quantified in a number of ways as a comparison to spring runoff events responsible for seedling recruitment. To reiterate, rain-on-snow events are channel and root scouring events, not seedbed building events for seedling recruitment. Return intervals of spring runoff events resulting in seedling recruitment often are in the range of 2-10-yr events (Mahoney and Rood 1998). Rain on snow events correlating to clonal recruitment in this system are on the order of 25-30-yr events.

Other studies have also shown recruitment of *Populus angustifolia* to occur following events with similar return intervals (Baker 1988, 1990, Baker and Walford 1995); however, recruitment mechanisms were not discussed. Baker described an event occurring in 1927 ($T_r = 25$ yr) on the Animas River in Colorado as a stand-disturbing event resulting in widespread recruitment. Baker described cottonwood recruitment occurring on deposits that would only be mobilized by exceptional velocities, which suggests that a scour-based model for recruitment may have been involved.

Although return intervals are similar between my study and Baker's, magnitudes of discharges that resulted in recruitment were very different. Thresholds of disturbance resulting in geomorphic change and root disturbance will vary among sites as a function

of site-specific resisting forces. However, other studies have suggested minimum values of 100 N/m² and 300 W/m² to cause geomorphic change in low-gradient alluvial channels in humid environments (Baker and Costa 1987, Miller 1990, Magilligan 1992).

I estimated τ_o and ω in the channel area that was changed in Fig. 3.8 by passing the 1986 peak discharge through a surveyed cross section in that same area. Estimated τ_o and ω values were 55 N/m² and 115 W/m², respectively. Perhaps these values are lower because channel morphology or conditions affecting the channel since 1986 have changed. Remnants of a large tree extend into the channel off the right bank. This tree is positioned to redirect the current at the scoured left bank. The channel constriction resulting from the fallen tree may have caused a nozzle effect that is not apparent now that the tree canopy has decomposed. Obstruction by vegetation could increase stage, which may increase the depth term and estimate a higher value of shear stress.

In summary, managers of riparian ecosystems are increasingly incorporating hydrogeomorphic processes as the basis for restoration strategies or identification of restoration sites (Carothers et al. 1990, O'Neill et al. 1997, Rood et al. 1998). Thus far, these strategies have used seedling recruitment and alluvial valley relationships. However, the findings of this study suggest that similar considerations may now be possible to facilitate clonal recruitment where this is the management goal. Identification of a geomorphic template facilitating clonal recruitment may provide practitioners with geomorphic aspects to include in restoration planning. In addition, rain-on-snow events may be mimicked to produce clonal recruitment similar to those mimicked for seedling recruitment.

General management of multiple channel areas should consider preserving the processes that create and maintain this planform. In addition to relations between multiple channel areas and cottonwood recruitment in this study, other studies have recognized multiple channels as areas of high biodiversity (Gregory et al. 1991, Sedell et al. 1991, Stanford et al. 1996). Activities that alter processes resulting in the formation and maintenance of multiple channels in steep, confined mountain valleys, such as removal of large woody debris, should be avoided. Dams may also result in channel simplification and the abandonment of multiple channels (Ligon et al. 1995), which results in a long term loss of riparian recruitment from seedling (Friedman et al. 1998). The same loss of processes that create multiple channels will likely also result in a loss of clonal recruitment from the scour-based relationships described by this study.

CONCLUSIONS

Characteristics of a geomorphic template were identified that facilitate channel and root material disturbance at sites containing cottonwood recruitment. Cottonwoods were recruiting at multiple channel sites, and characteristics common to recruitment sites may facilitate the formation of multiple channels. Characteristics common to recruitment sites included lower average boundary shear stress and unit stream power, debris dams, and proximity to tributary confluences. Sites containing cottonwood recruitment generally occurred in wider valleys with lower gradient and had channels with low entrenchment, high sinuosity, high width-to-depth ratios, and smaller median particle sizes compared to sites without cottonwoods.

In contrast to previous studies that correlate seedling recruitment to spring runoff events that build appropriate seed beds, I found clonal recruitment of cottonwoods to spatially and temporally correlate with channel and root disturbance associated with rain-on-snow events. These events are different because they do not occur during the timing of seed throw and provide a highly variable flow regime that may facilitate channel avulsion. Rain-on-snow events were on the order of 25-30-yr events, which is in contrast to lower return intervals generally associated with seedling recruitment. A threshold of disturbance resulting in clonal recruitment at one location was estimated as 55 N/m^2 and 115 W/m^2 for average boundary shear stress and unit stream power, respectively.

Clonal recruitment may dominate steep, confined mountain valleys due to the hydrologic and geomorphic processes occurring in these valleys, which are different than those in wide alluvial valleys. This study represents the first attempt at developing a process-based ecological model facilitating clonal recruitment in these mountain valleys. The findings of this study may provide the basis for developing flow recommendations to facilitate clonal recruitment of cottonwoods if this is the desired management goal.

LITERATURE CITED

- Anderson, B. W., R. D. Ohmart, and J. Rice. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado River Valley. *Condor* **85**: 392-405.
- Ashworth, P. J. 1996. Mid channel bar growth and its relationship to local flow strength and direction. *Earth Surface Processes and Landforms* **21**:103-123.
- Baker V. R. 1977. Stream-channel response to floods, with examples from central Texas. *Geological Society of America Bulletin* **88**:1057-1071.

- Baker V. R., and J. E. Costa. 1987. Flood power. Pages 1-21 in L. Mayer and D. Nash, editors. Catastrophic flooding. Allen and Unwin, Boston, Massachusetts, USA.
- Baker, W. L. 1988. Size class structure of contiguous riparian woodlands along a rocky mountain river. *Physical Geography* 9:1-14.
- . 1989. Macro- and micro-scale influences on riparian vegetation in western Colorado. *Annals of the Association of American Geographers* 79:65-78.
- . 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *Journal of Biogeography* 17:59-73.
- Baker, W. L., and G. M. Walford. 1995. Multiple stable states and models of riparian vegetation succession on the Animas River, Colorado. *Annals of the Association of American Geographers* 85:320-338.
- Barinaga, M. 1996. A recipe for river recovery? *Science* 273:1648-1650.
- Bendix, J. 1994a. Among site variation in riparian vegetation of the southern California transverse ranges. *American Midland Naturalist* 132:136-151.
- . 1994b. Scale direction and pattern in riparian vegetation-environment relationships. *Annals of the Association of American Geographers* 84:652-665.
- Braatne, J. H., S. B. Rood, and P. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods. Pages 57-80 in R. F. Stettler, H. D. Bradshaw, P. E. Heilman, and T. M. Hinckley, editors. *Biology of populus and its implications for management and conservation*. NRC Research Press, Ottawa, Ontario, Canada.
- Bradley, C. E., and D. G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany* 64:1433-1442.
- Bull, W. B. 1979. Threshold of critical power in streams. *Geological Society of America Bulletin* 90:453-464.
- Carothers, S. W., G. S. Mills, and R. R. Johnson. 1990. The creation and restoration of riparian habitat in southwestern arid and semi-arid regions. Pages 351-366 in J. Kulser and M. E. Kentula, editors. *Wetland creation and restoration: the status of the science*. Island Press, Washington D. C., USA.
- Church, M. 1983. Patterns of instability in a wandering gravel bed channel. *Special Publication of the International Association of Sedimentologists* 6:169-180.

- Costa, J. E. and J. E. O'Conner. 1995. Geomorphically effective floods. Pages 45-56 in J. E. Costa, A. J. Miller, K. W. Potter, and P. R. Wilcock, editors. *Natural and anthropomorphic influences in fluvial geomorphology*. American Geophysical Union, Geophysical Monograph **89**.
- Everitt, B. L. 1968. Use of the cottonwood on an investigation of the recent history of a flood plain. *American Journal of Science* **266**:417-439.
- Fahnestock, R., K. 1963. Morphology and hydrology of a glacial stream--White River, Mount Rainier, Washington. USGS Professional Paper **422-A**.
- Friedman, J. M., W. R. Osterkamp, and W. M. Lewis Jr. 1996. Channel narrowing and vegetation development following a Great Plains flood. *Ecology* **77**:2176-2181.
- Friedman, J. M., W. R. Osterkamp, M. L. Scott, and G. T. Auble. 1998. Downstream effects of dams on channel geometry and bottomland vegetation: regional patterns in the Great Plains. *Wetlands* **18**:619-633.
- Fritts, H. C., and T.W. Swetnam. 1989. Dendrochronology: a tool for evaluating variations in past and present forest environments. *Advances In Ecological Research* **19**:111-176.
- Gecy, J. L., and M. V. Wilson. 1990. Initial establishment of riparian vegetation after disturbance by debris flows in Oregon. *American Midland Naturalist* **123**:282-291.
- Germanosky, D., and S. A. Schumm. 1993. Changes in braided river morphology resulting from aggradation and degradation. *Journal of Geology* **101**:451-466.
- Grant, G. E., J. E. Duval, G. J. Koerper, G. J. Fogg, and L. James. 1992. XSPRO: a channel cross-section analyzer. U.S. Dept. of the Interior, Bureau of Land Management and U. S. Dept. of Agriculture, Forest Service. Tech. Note **387**.
- Grant G. E., and F. J. Swanson. 1995. Morphology and processes of valley floors in mountain streams, western Cascades, Oregon. Pages 83-101 in J. E. Costa, A. J. Miller, K. W. Potter, and P. R. Wilcock, editors. *Natural and anthropomorphic influences in fluvial geomorphology*. American Geophysical Union Geophysical Monograph **89**.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones: focus on links between land and water. *Bioscience* **41**:540-551.
- Hack, J. T., and J. C. Goodlet. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. USGS Professional Paper **347**.

- Harris, R. R. 1987. Occurrence of vegetation on geomorphic surfaces in the active floodplain of a California alluvial stream. *American Midland Naturalist* **118**:393-405.
- Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. Stream channel reference sites: an illustrated guide to field technique. USDA Forest Service General Technical Report **RM-245**.
- Harwood, K., and A. G. Brown. 1993. Fluvial processes in a forested anastomosing river: flood partitioning and changing flow patterns. *Earth Surface Processes and Landforms* **18**:741-748.
- Hey, R. D. 1979. Flow resistance in gravel bed rivers. *Journal of the Hydraulics Division, Proceedings of the ASCE* **105**:365-379.
- Hickin, E. J. 1984. Vegetation and river channel dynamics. *Canadian Geographer* **18**:111-126.
- Hunter, W. C., B. S. Anderson, and R. D. Ohmart. 1987. Avian community structure changes in a mature floodplain forest after extensive flooding. *Journal of Wildlife Management* **51**:495-502.
- Hupp, C. R., and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology* **66**:670-681.
- . 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology* **14**:277-295.
- Jones, R., and D. J. Raynal. 1986. Spatial distribution and development of root spouts in *Fagus grandifolia* (Fagaceae). *American Journal of Botany* **73**:1723-1731.
- Kellerhals, R., C. R. Neill, and D. I. Bray. 1972. Hydraulic and geomorphic characteristics of rivers in Alberta. Research Council of Alberta, River Engineering and Surface Hydrology Report **72-1**.
- Klotz, J. R., and S. Swanson. 1997. Managed instream flows for woody vegetation recruitment, a case study. Pages 483-489 in J. Warwick, editor. Symposium proceedings: water resources education, training, and practices: opportunities for the next century. American Water Resources Association, Universities Council on Water Resources, American Water Works Association, Keystone, Colorado, USA.
- Knighton, A. D. 1976. Stream adjustment in a small Rocky Mountain basin. *Arctic and Alpine Research* **8**:197-212.
- Knighton, A. D., and G. C. Nanson. 1993. Anastomosis and the continuum of channel pattern. *Earth Surface Processes and Landforms* **18**:613-625.

- Kranjcec, J., J. M. Mahoney, and S. B. Rood. 1998. The response of three riparian cottonwood species to water table decline. *Forest Ecology and Management* **110**:77-87.
- Leopold, L. B., and M. G. Wolman. 1957. River channel patterns: braided, meandering, and straight. USGS Professional Paper **282-B**.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Dover Publications, Inc., New York, New York, USA.
- Ligon F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams, a geomorphic perspective. *Bioscience* **45**:183-192.
- Magilligan, F. J. 1992. Thresholds and the spatial variability of flood power during extreme floods. *Geomorphology* **5**:373-390.
- Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment-an integrative model. *Wetlands* **18**:634-645.
- McCalpin, J. P. 1989. Surficial geology map of the East Cache fault zone. USGS Miscellaneous Field Studies Map. MF-2107, 1:50,000.
- Merigliano, M. F. 1996. Flood-plain and vegetation dynamics along a gravel-bed, braided river in the northern Rockies. Ph.D. Dissertation. The University of Montana, Missoula, Montana, USA.
- Miller, A. J. 1990. Flood hydrology and geomorphic effectiveness in the central Appalachians. *Earth Surface Processes and Landforms* **15**:119-134.
- Miller, A. J., and D. J. Parkinson. 1993. Flood hydrology and geomorphic effects on river channels and flood plains: the flood of November 4-5, 1985, in the South Branch Potomac River basin of west Virginia. U.S. Geological Survey Bulletin **1981-E**.
- Miller, J. R. 1991. Development of anastomosing channels in south central Indiana. *Geomorphology* **4**:221-229.
- Nanson, G. C., and A. D. Knighton. 1996. Anabranching rivers: their cause, character, and classification. *Earth Surface Processes and Landforms* **21**:217-239.
- O'Neill, M. P., J. C. Schmidt, J. P. Dobrowolski, C. P. Hawkins, and C. M. U. Neale. 1997. Identifying sites for riparian wetland restoration: application to the upper Arkansas River basin. *Restoration Ecology* **5**:85-102.
- Osterkamp, W. R. 1998. Processes of fluvial-island formation with examples from Plum Creek, Colorado, and Snake River, Idaho. *Wetlands* **8**:530-545.

- 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.
- Padgett, W. G., A. P. Youngblood, and A. H. Winward. 1989. Riparian community type classification of Utah and southeastern Idaho. USDA Forest Service General Technical Report **R4-Ecol-89-01**.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* **18**:498-512.
- Rood, S. B., and J. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management* **14**:451-464.
- Rood, S. B., C. Hillman, T. Sanche, and J. M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. *Canadian Journal of Botany* **72**:1766-1774.
- Rood, S. B., A. R. Kalischuk, and J. M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands* **18**:557-570.
- Rosgen, D. L. 1994. A classification of natural rivers. *Catena* **22**:196-199.
- Schier, G. A., and R. B. Campbell. 1976. Differences among *populus* species in ability to form adventitious shoots and roots. *Canadian Journal of Forestry* **6**:253-261.
- Schmidt, J. C., R. H. Webb, R. A. Valdez, R. Marzolf, and L. E. Stevens. 1998. Science and values in river restoration in the Grand Canyon. *Bioscience* **48**:735-747.
- Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* **7**:677-690.
- Scott, M. L., J. M. Friedman, and G. T. Auble. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology* **14**:327-339.
- Scott, M. L., M. A. Wondzell, and G. T. Auble. 1993. Hydrograph characteristics relevant to the establishment and growth of western riparian vegetation. Pages 237-246 in H.J. Morel- Seytoux, editor. *Proceedings of the 13th annual American geophysical union hydrology days*. Hydrology Days Pub., Atherton, California, USA.
- Sedell J. R., R. J. Steedman, H. A. Regier, and S. V Gregory. 1991. Restoration of human impacted land water ecotones. Pages 110-129 in P. G. Risser, R. J. Naiman, editors. *Ecotones: the role of landscape boundaries in the management and*

- restoration of changing environments. Chapman and Hall, New York, New York, USA.
- Sigafoos, R. 1964. Botanical evidence of floods and floodplain deposition. Geological Survey Professional Paper **485-A**.
- Shaw, R. K. 1976. A taxonomic and ecological study of the river-bottom forest on St. Mary, Lee Creek, and Belly River in southwestern Alberta, Canada. Great Basin Naturalist **36**:243-271.
- Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissel, 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**:392-413.
- Stromberg, J. C., and D. T. Patten. 1989. Early recovery of an eastern sierra riparian system following forty years of stream diversions. Pages 399-404 in D. L. Abell, editor. Proceedings of the California riparian systems conference. U. S. Forest Service General Technical Report **PSW-10**.
- . 1991. Instream flow requirements for cottonwoods at Bishop Creek, Inyo county, California. Rivers **2**:1-11.
- Thomas, B. E., and K. L. Lindskov. 1983. Methods for estimating peak discharge and flood boundaries of streams in Utah. USGS Water Resources Investigation Report **83-4129**.
- Thompson, D. M. 1995. The effects of large organic debris on sediment processes and stream geomorphology in Vermont. Geomorphology **11**:235-244.
- Tiffney, B. H., and K. J. Niklas. 1986. Clonal growth in land plants. Pages 110-135 in J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.
- Webb, M. G., and J. D. Brotherson. 1988. Elevational changes in woody vegetation along three streams in Washington County, Utah. Great Basin Naturalist **48**:512-529.
- Williams, J.S. 1962 Geology of the southern Cache Valley, Utah. USGS Professional Paper, **257-C**.
- Wolman, G. M. 1954. A method of sampling coarse riverbed material. Transactions, American Geophysical Union **35**:951-956.
- Wolman, G. M., and R. Gerson. 1978. Relative scales of time and effectiveness of climate in watershed geomorphology. Earth Surface Processes and Landforms **3**:189-208.

TABLE 3.1. Geomorphic parameters measured at study sites.

Data	Method
Valley width	Tape measure
Valley slope	USGS topographic map
Drainage basin area	Geographic Information System
Flood-prone width*	Topographic survey
Entrenchment**	Topographic survey
Bankfull channel width	Topographic survey
Bankfull channel depth	Topographic survey
Bankfull channel slope	Topographic survey
Channel sinuosity	Topographic survey
Channel planform	Field mapping
Multiple channel length	Tape measure
Total sinuosity***	Tape measure
Particle size distribution	Wolman pebble count
Bankfull average boundary shear stress	RFFC's/WINXSPRO
Bf unit stream power	RFFC's/WINXSPRO

* Width at twice bankfull depth and is an estimate of the area inundated during the 50-year flood (Rosgen 1994).

** Width at twice bankfull depth divided by bankfull width.

*** Includes side channel lengths.

TABLE 3.2. USGS gages used to create regional flood-frequency curves.

Name	USGS Gage #	Area above gage (km. ²)	Period of record	Gage used to extend record	Period of extended record	Concurrent record (yr)	r ²
Avon	10104600	67	1966-1974	Davenport	1975-1986	8	0.70
Davenport	10104700	159	1960-1992	none			
Paradise	10106000	513	1942-1986	none			
Hyrum	10107500	564	1942-1974	Paradise	1974-1986	31	0.91
Blacksmith	10113500	681	1918- present	none			

TABLE 3.3. Geomorphic and hydraulic parameters.

Site #	Type	Basin Area	Q bf	Entrenchment	Flood prone width	Valley slope	Valley width	Bankfull w/d	Bankfull width
Units		km ²	m ³	*	m	*	m	*	m
#2	CR	26.87	2.07	4.16	27.56	0.0370	62.67	19.93	6.62
#3	CR	45.85	3.10	7.18	49.60	0.0240	66.67	26.21	7.52
#6	CR	411.20	10.73	2.42	42.37	0.0100	390.00	30.91	18.13
#7	CR	537.35	13.44	2.81	33.67	0.0080	600.00	25.20	13.16
#1	NC	17.17	1.46	2.43	9.46	0.0510	29.25	16.67	3.97
#4	NC	46.44	3.13	3.61	27.28	0.0240	50.00	23.94	7.80
#5	NC	69.19	4.14	2.70	25.20	0.0130	170.00	19.21	7.59
#8	NC	555.75	12.71	2.64	21.50	0.0009	1750.00	13.91	8.13
CR average				4.14	38.30	0.0198	279.84	25.56	11.36
NC average				2.84	20.86	0.0222	499.81	18.43	6.87
Significant**				No	Yes	No	No	Yes	No

TABLE 3.3. Cont'd.

Site #	Type	BF depth	BF slope	Channel slope	Sinuosity	Total sinuosity	Median particle size	Bankfull τ_o	Bankfull ω
Units		m	*	*	*	*	mm	N/m ²	W/m ²
#2	CR	0.33	0.030	0.028	1.30	1.56	52.00	73.37	90.06
#3	CR	0.34	0.019	0.019	1.18	1.37	19.00	65.73	99.45
#6	CR	0.59	0.008	0.008	1.47	1.91	50.00	38.80	47.49
#7	CR	0.54	0.007	0.007	1.96	2.71	45.00	37.68	58.17
#1	NC	0.25	0.037	0.036	1.20	1.20	68.00	66.09	112.58
#4	NC	0.36	0.022	0.021	1.16	1.16	25.00	66.66	86.95
#5	NC	0.43	0.014	0.015	1.11	1.25	37.00	70.23	106.68
#8	NC	0.63	0.004	0.000	1.10	1.10	N/A (clay)	44.18	123.86
CR average		0.45	0.016	0.015	1.48	1.89	41.50	53.89	73.79
NC average		0.42	0.019	0.018	1.14	1.18	43.33	61.79	107.52
Significant**		No	No	No	No	Yes	No	No	Yes

* Dimensionless

** I used non-parametric Mann-Whitney tests to test for significant differences between site type mean values for each parameter. (P = 0.05).

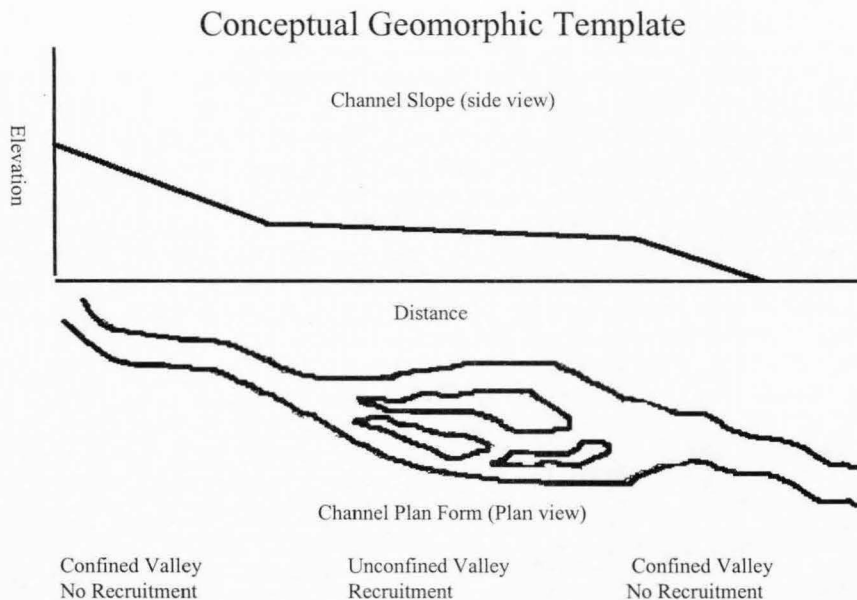


FIG. 3.1. Possible correlation of multiple channel planform to a geomorphic template that includes a decrease in channel slope in a wider valley, which facilitates channel avulsion and consequent root disturbance. The resulting trauma to root material may correlate with clonal recruitment of cottonwoods.

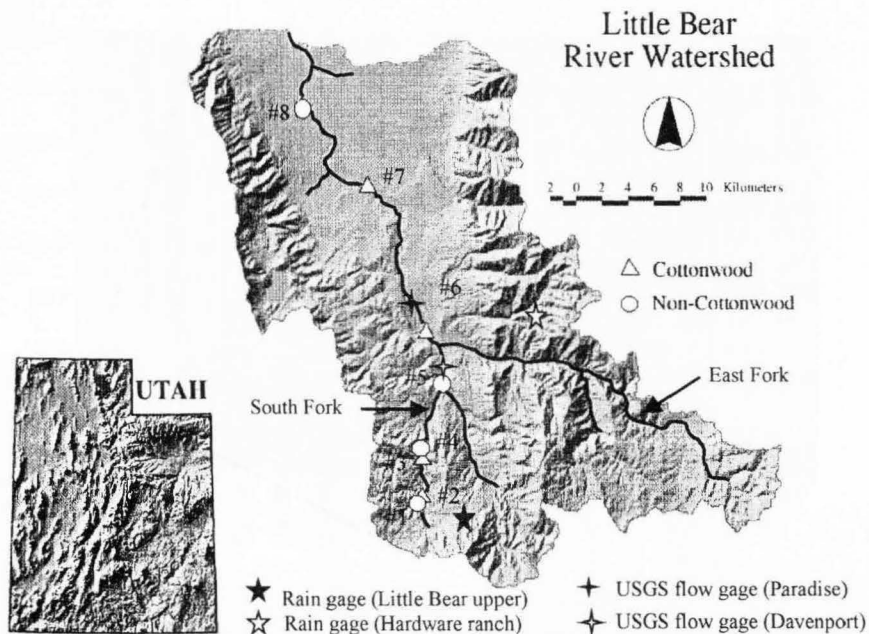


FIG. 3.2. Shaded relief of the Little Bear River watershed depicting cottonwood (CR) and non-cottonwood (NC) sites, 1 through 8 in the downstream direction. Locations of stream flow and rain gauges used in the study also are shown.

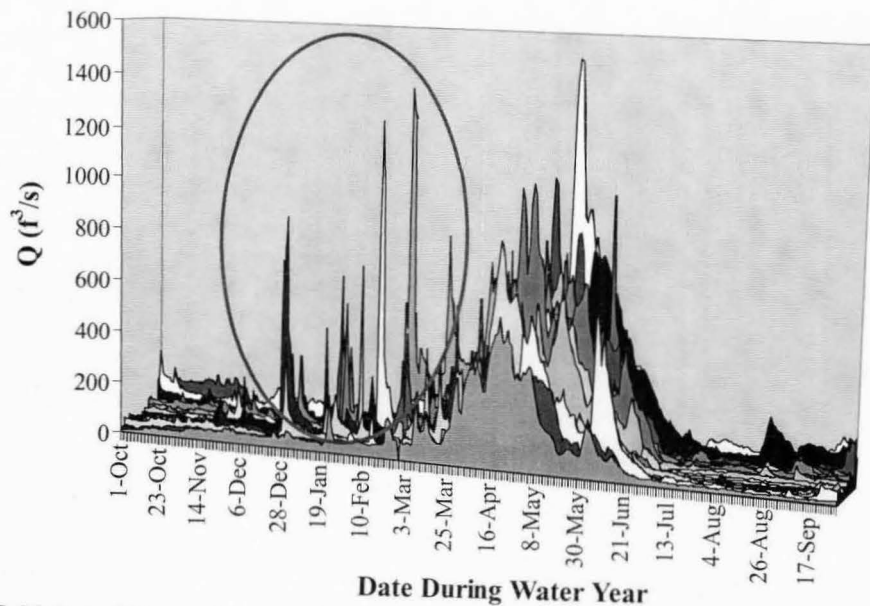


FIG. 3.3. Forty eight years (shown in different colors) of hydrographs from the Paradise Gage demonstrating that the hydrology of the Little Bear is dominated by spring runoff from snowmelt. However, a high frequency of early thaw events (in circle) are a significant characteristic of the system.

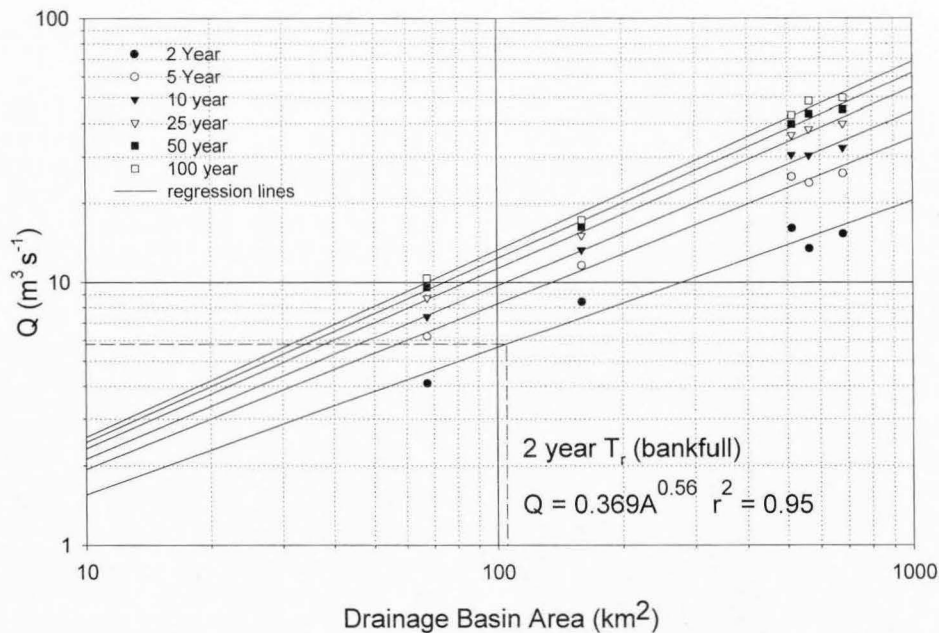


FIG. 3.4. An example of a power function of regional discharge per unit area where basin area at an un-gaged site is used to estimate the two year return interval (approximate bankfull flood) at the site. Vertical groups of symbols are the results of Log Pearson Type III Flood frequency analyses at 5 gage sites used to create regional flood frequency curves.

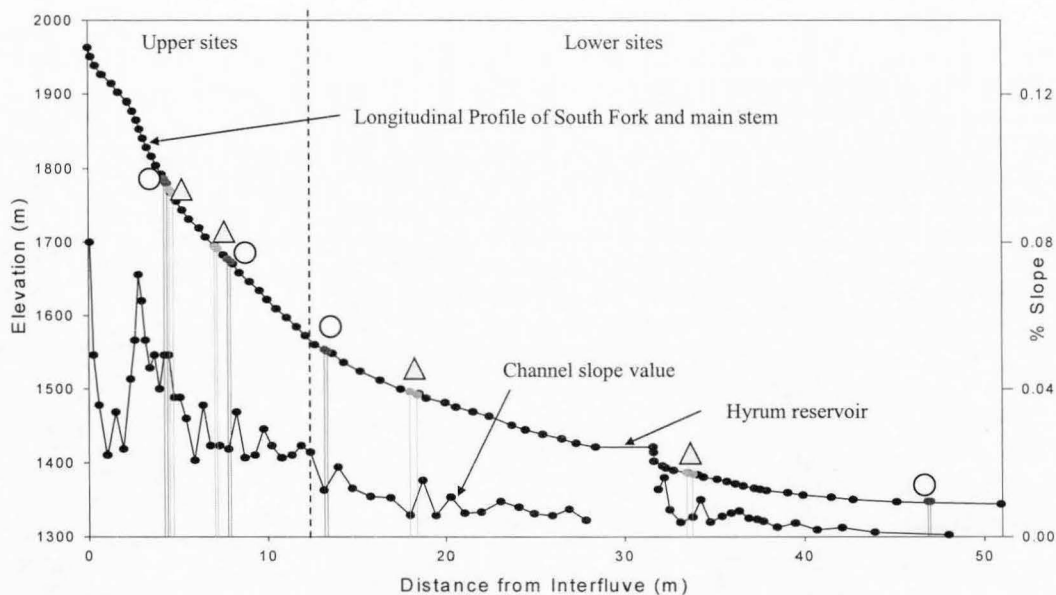


FIG. 3.5. CR (triangles) and NC (circles) study site locations along the longitudinal profile of the South Fork and main stem of the Little Bear River showing upper CR sites located in reaches with lower slopes than paired NC sites. The pattern is reversed in lower study sites where CR sites have higher slopes than paired NC sites. The canyon mouth (dashed line) is the distinction between upper and lower sites.

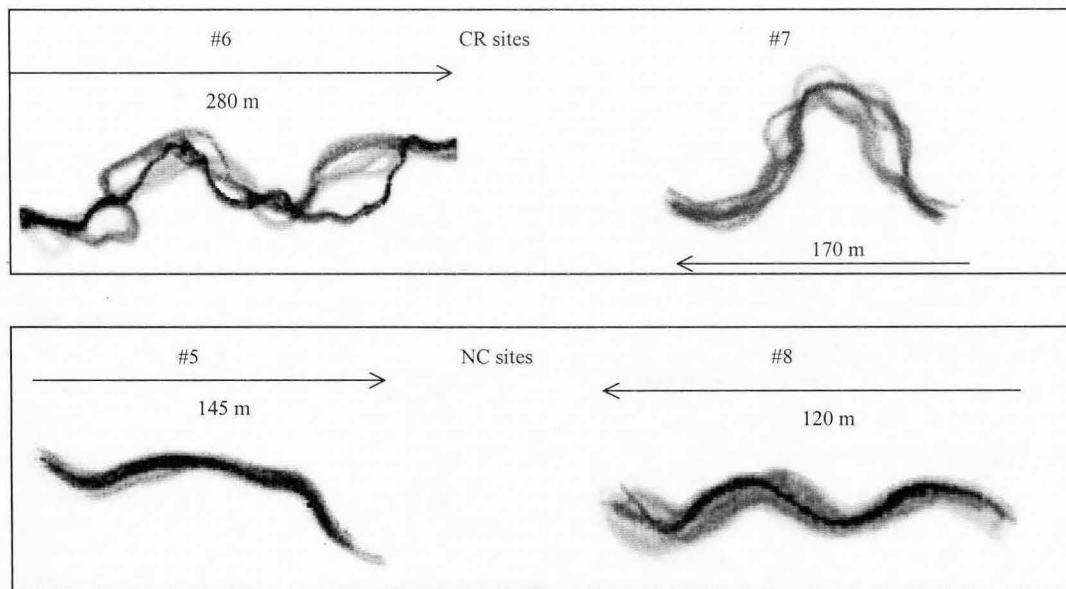


FIG. 3.6. Colored lines depicting channel location during different years (1937-1993) in historic aerial photos. CR sites are much more laterally active than at NC sites. Channels at NC sites also are less sinuous than channels at CR sites. Arrows depict the direction of flow and reach length.

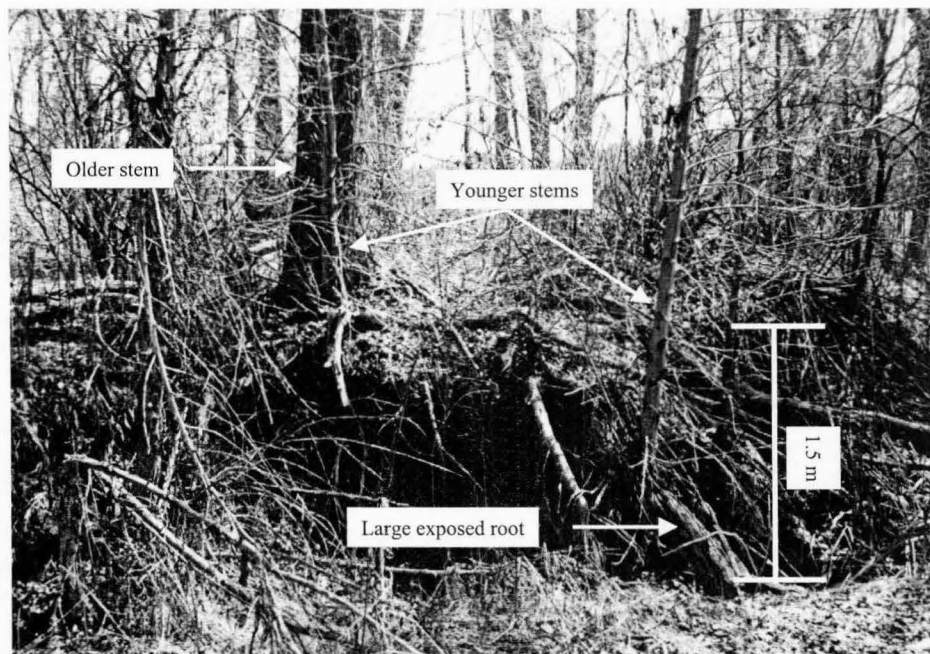


FIG. 3.7. Photograph from site 7 depicting a typical relationship between the distribution of cottonwood stems and cutbanks. Notice the large older stem aligned on the edge of a 1.5 m high cutbank. Younger stems of similar age occur near the older stem and originate from exposed root material.

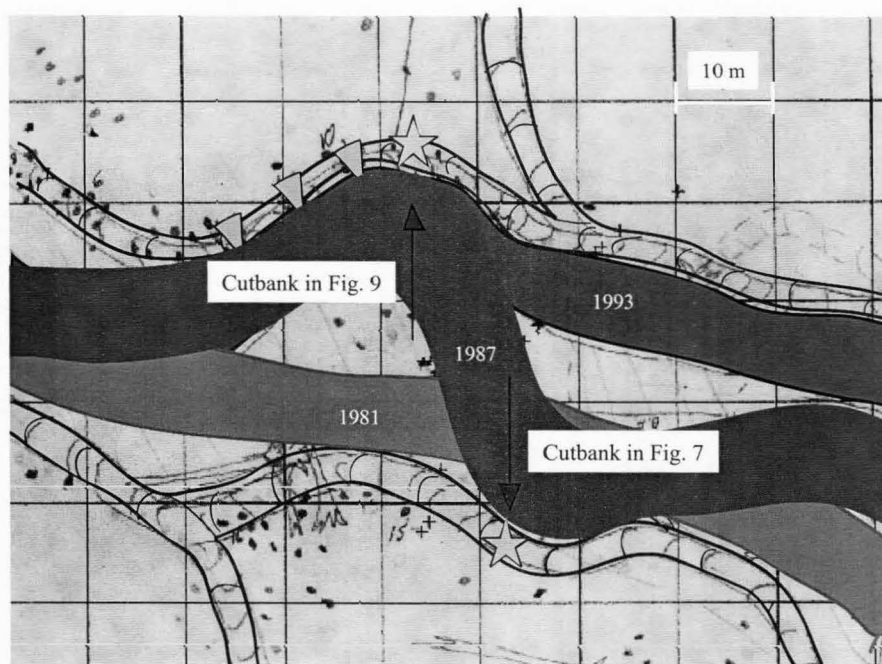


FIG. 3.8. Past channel locations showing the change in channel position that occurred between 1981 and 1987. The 1981, 1987, and 1993 channels are labeled and arrows show the location of similar sized stems originating from root material on the cutbanks in Figs 7 and 9.



FIG. 3.9. Young stems of similar stem diameter and height originating from exposed root material on the opposite bank shown in Fig. 7. Similar spatial arrangement and stem size suggests the stems on both cutbanks were recruited through similar mechanisms at or near the same time.

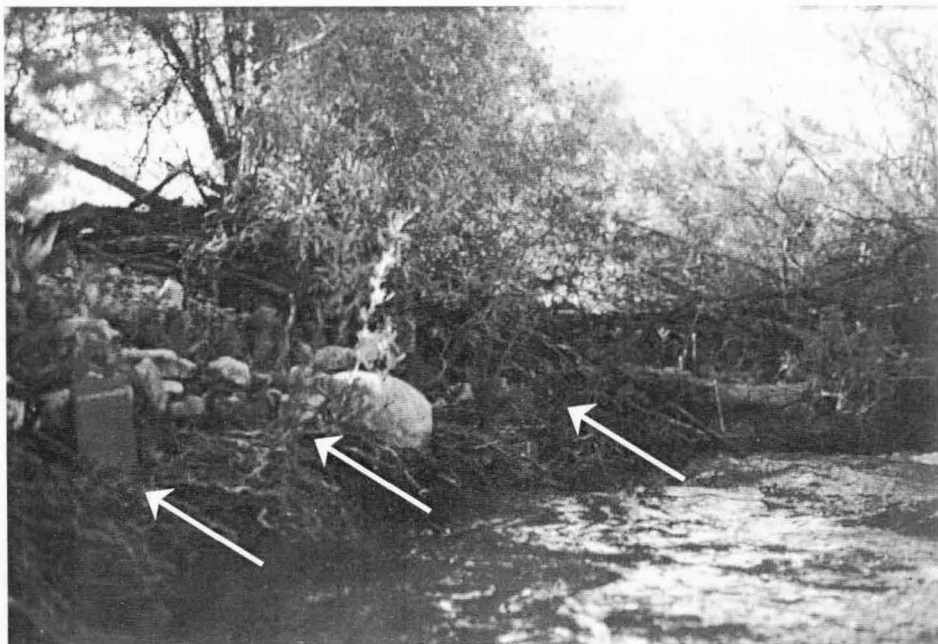


FIG. 3.10. Recent clonal recruitment (arrows) seen originating from root material exposed at an upper CR site. A debris dam in the background and large particles from overbank deposition suggest potential root trauma. Streamflow is away and to the right in the photo and discharge is approximately bankfull.

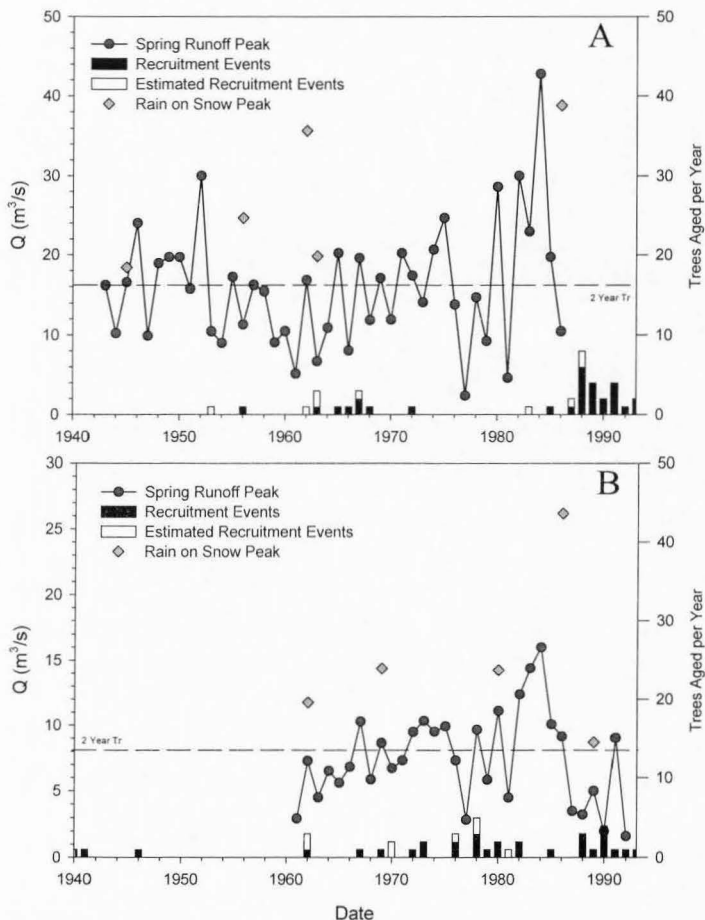


FIG. 3.11. Clonal recruitment events temporally correlated with early thaw events, not the spring runoff events that other studies correlate with seedling recruitment. Plot A demonstrates temporal correlation between recruitment at lower CR sites and early thaw events reflected at the Paradise gage. Plot B demonstrates temporal correlation between recruitment at upper CR sites and early thaw events reflected at the Davenport gage, some of which are absent from the Paradise records.

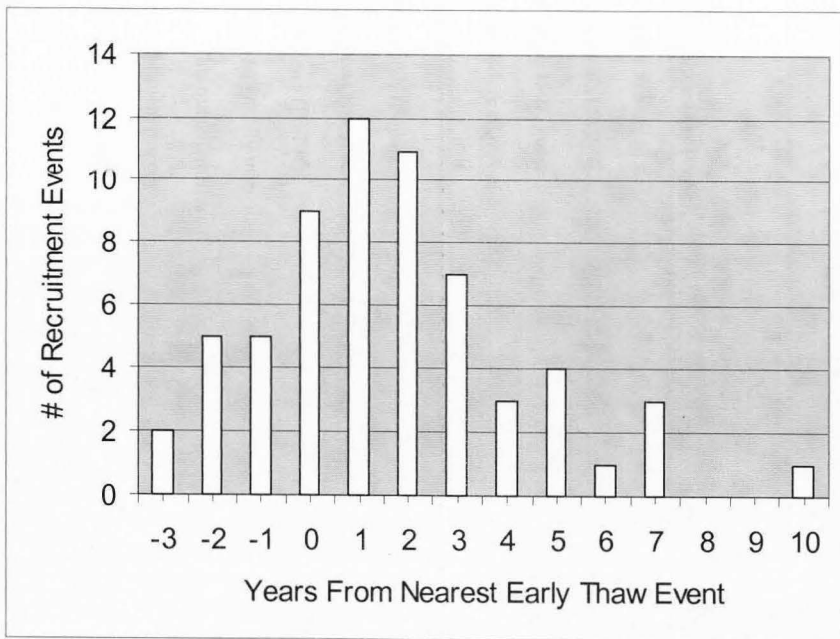


FIG. 3.12. Bar chart showing that stem ages most often lag a few years from when rain-on-snow events occur, which is represented as year 0.

CHAPTER 4

CONCLUSIONS

BACKGROUND

Riparian ecosystems are a highly valued resource both for the ecological services they have to offer to society and to wildlife (Brinson et al. 1981, Anderson et al. 1983, Hunter et al. 1987, Finch and Ruggiero 1993, Braatne et al. 1996, Kondolf et al. 1996, Poff et al. 1997, Patten 1998). Many land uses can degrade these systems and result in a general failure of natural regeneration (Rood and Mahoney 1990, National Research Council 1995, Braatne et al. 1996, Poff et al. 1997). This is the case for riparian cottonwoods (*Populus* spp.), which are a keystone pioneer species that is the foundation of this forest type (Patten 1998). Because cottonwoods are intricately linked to natural flow regimes (Poff et al. 1997), they serve as effective indicators of altered conditions and may potentially indicate land uses affecting the natural flow regime.

This reduction in cottonwood regeneration has generated an effort to understand their recruitment ecology. This research has resulted in ecological models (i.e., Mahoney and Rood 1998) that describe the fundamental ecological relationships between seedling recruitment and hydrogeomorphic processes facilitating this recruitment mechanism in wide alluvial valleys.

Seedling and alluvial valley relationships have been used to develop process-based restoration solutions (Braatne et al. 1996, Poff et al. 1997). Where society deems it appropriate (Schmidt et al. 1998), dam operation and river regulation have been altered to

benefit many species (Poff et al. 1997) and a number of cases have demonstrated that successful regeneration of riparian forest is possible (Barinaga 1996, Klotz and Swanson 1997, Rood et al. 1998).

In contrast, much of the past research had not addressed clonal recruitment in cottonwoods, which may play a large role in the ecology of cottonwoods in confined mountain valleys (Schier and Campbell 1976, Rood and Mahoney 1990, Rood et al. 1994, L. A. Gom and S. B. Rood *unpublished manuscript*, Kranjcek et al. 1998, Mahoney and Rood 1998). In order to address several of the gaps in our knowledge of clonal recruitment mechanisms in mountain valleys, my study focused on three objectives.

FINDINGS

My first objective for this study was to evaluate the degree of clonal recruitment of *Populus angustifolia* on the Little Bear River. I used allozyme electrophoresis, and vegetation and geomorphic mapping to address the objective. In contrast to findings of many previous studies examining cottonwood recruitment mechanisms, I found clonal recruitment is the dominant recruitment mechanism of cottonwoods on the Little Bear River. The average proportion of clonal recruitment among four sites was 72% and the potential size of cottonwood clones on the Little Bear River was on the order of 200-300 m.

Significantly, clonal recruitment not only dominated confined mountain valleys where geomorphic characteristics suggest this should be the case, but also in wide alluvial valleys on the Little Bear River. I also found, in contrast to other studies, that clonal

recruitment was occurring on point bars typically described as hosting seedling recruitment. Geomorphic parameters such as sediment size distribution and flood-prone widths of alluvial valley sites were found to be more similar to confined mountain valley sites, which is likely the result of geomorphic influences enhanced by flow regulation.

My second objective was to evaluate geomorphic influences on the distribution of *Populus angustifolia*. I used topographic surveying, dendrochronological data, USGS stream flow records, historic aerial photographs, and vegetation and geomorphic mapping to address the objective. Characteristics of a geomorphic template were identified that facilitate channel and root material disturbance at sites containing cottonwood recruitment. Cottonwoods were recruiting at multiple channel sites and characteristics common to recruitment sites may facilitate the formation of multiple channels.

Characteristics common to recruitment sites included lower average boundary shear stress and unit stream power, debris dams, and proximity to tributary confluences. Sites containing cottonwood recruitment generally occurred in wider valleys with lower gradient and had channels with low entrenchment, high sinuosity, high width-to-depth ratios, and smaller median particle sizes compared to sites without cottonwoods.

My third objective was to evaluate hydrologic influences on recruitment of *Populus angustifolia*. I used topographic surveying, dendrochronological data, stream flow records, historic aerial photographs, and vegetation and geomorphic mapping to address the objective. In contrast to previous studies that correlate seedling recruitment to spring runoff events that build appropriate seedbeds, I found clonal recruitment of cottonwoods to spatially and temporally correlate with channel and root disturbance

associated with rain-on-snow events that occur at a different timing than when seed throw occurs. These events provide a highly variable flow regime that may facilitate channel avulsion and were on the order of 25-30-yr events, which is in contrast to lower return intervals generally associated with seedling recruitment. A threshold of disturbance resulting in clonal recruitment at one location was estimated as 55 N/m² and 115 W/m² for average boundary shear stress and unit stream power, respectively.

Clonal recruitment may dominate steep, confined mountain valleys due to the hydrologic and geomorphic processes occurring in these valleys, which are different than those in wide alluvial valleys. This study represents the first attempt at developing a process-based ecological model facilitating clonal recruitment in these mountain valleys. The findings of this study may provide the basis for identifying restoration sites or developing flow recommendations and other management applications to facilitate clonal recruitment of cottonwoods where this is the desired management goal.

LITERATURE CITED

- Anderson, B. W., R. D. Ohmart, and J. Rice. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado River valley. *Condor* **85**: 392-405.
- Barinaga, M. 1996. A recipe for river recovery? *Science* **273**:1648-1650.
- Braatne, J. H., S. B. Rood, and P. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods. Pages 57-80 in R. F. Stettler, H. D. Bradshaw, P. E. Heilman, and T. M. Hinckley, editors. *Biology of *populus* and its implications for management and conservation*. NRC Research Press, Ottawa, Ontario, Canada.

- Brinson, M. M., B. L. Swift, R. C. Plantico, and J. S. Barclay. 1981. Riparian ecosystems: their ecology and status. USFWS Biological Services Program **FWS/OBS-81/17**.
- Klotz, J. R., and S. Swanson. 1997. Managed instream flows for woody vegetation recruitment, a case study. Pages 483-489 in Warwick J., editor. Symposium proceedings: water resources education, training, and practices: opportunities for the next century. American Water Resources Association, Universities Council on Water Resources, American Water Works Association, Keystone, Colorado, USA.
- Kondolf, G. M., R. Kattlemann, M. Embury, and D. C. Erman. 1996. Status of riparian habitat. Sierra Nevada ecosystem project: final report to Congress. Center for Water and Wildland Research. University of California, Davis, California, USA.
- Kranjcec, J., J. M. Mahoney, and S. B. Rood. 1998. The response of three riparian cottonwood species to water table decline. *Forest Ecology and Management* **110**:77-87.
- Finch, D. M., and L. R. Ruggiero. 1993. Wildlife and biological diversity in the Rocky Mountains and north Great Plains. *Natural Areas Journal* **13**:191-203.
- Hunter, W. C., B. S. Anderson, and R. D. Ohmart. 1987. Avian community structure changes in a mature floodplain forest after extensive flooding. *Journal of Wildlife Management* **51**:495-502.
- Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment-an integrative model. *Wetlands* **18**:634-645.
- National Research Council (US). 1995. Committee on characterization of wetlands. Wetlands-characteristics and boundaries. National Academy Press, Washington, D.C., USA.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* **18**:498-512.
- Poff, L. N., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime, a paradigm for conservation and restoration. *Bioscience* **47**:769-784.
- Rood, S. B., C. Hillman, T. Sanche, and J.M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. *Canadian Journal of Botany* **72**:1766-1774.
- Rood, S. B., and J. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management* **14**:451-464.

- Rood, S. B., A. R. Kalischuk, and J. M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands* **18**:557-570.
- Schier, G. A., and R. B. Campbell. 1976. Differences among *Populus* species in ability to form adventitious shoots and roots. *Canadian Journal of Forestry* **6**:253-261.
- Schmidt, J. C., R. H. Webb, R. A. Valdez, R. Marzolf, and L. E. Stevens. 1998. Science and values in river restoration in the Grand Canyon. *Bioscience* **48**:735-747.