CONSTRAINTS ON, AND OPPORTUNITIES FOR, RIPARIAN WILLOW ESTABLISHMENT, ROCKY MOUNTAIN NATIONAL PARK, COLORADO

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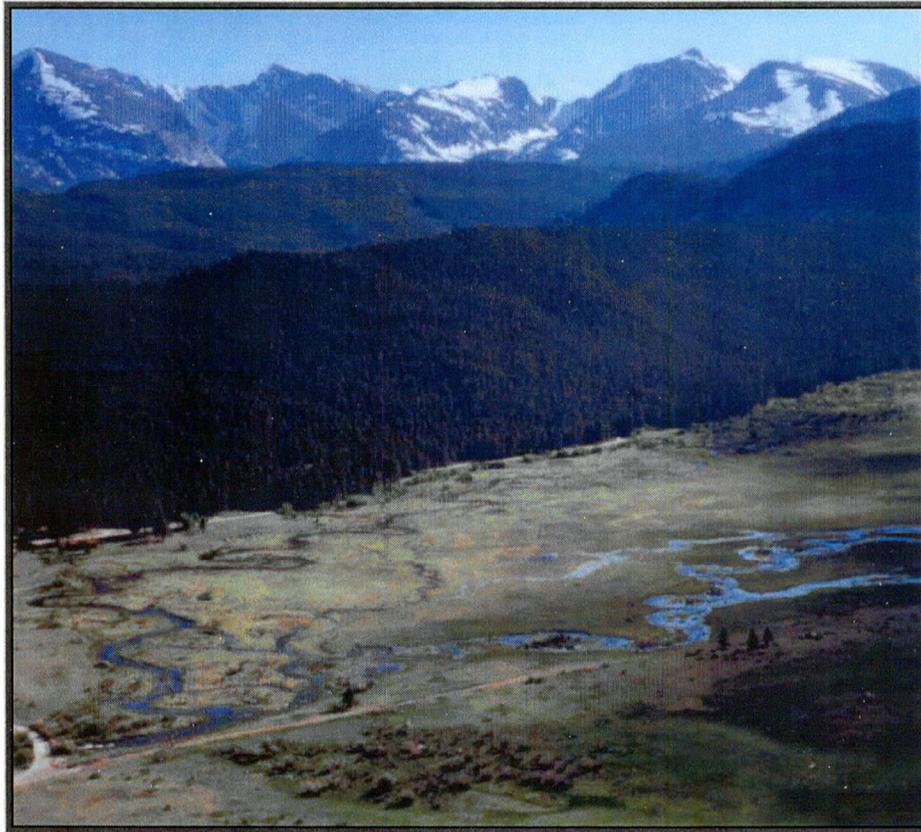
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EXECUTIVE SUMMARY

During 1999 through 2000 we conducted field studies to investigate the factors

constraining willow establishment in Moraine and Horseshoe Parks in Rocky Mountain National

Park, and to conceptualize opportunities for future willow establishment in these areas. These

studies were funded by a grant from the National Park Service Water Resources Division, Rocky

Mountain National Park, and an EPA-STAR grant. We focused our efforts on the processes that

control willow seedling establishment on the time scale of years to decades. While there have

been many studies of mature willows (Cottrell 1995, Singer and Zeigenfuss 2002), willow

seedling establishment has been little studied. The present studies fill gaps in our knowledge on

willow life history, seedling establishment, relationship to geomorphic and hydrologic patterns

and processes, and potential for restoration in the current environment of Moraine and Horseshoe

Parks.

Key findings of our investigations are outlined below.

A. Hydrologic Patterns

1. The ground water flow systems in Moraine and Horseshoe Parks are well connected
   to the stream flowing through each valley. Fall and Big Thompson Rivers recharge
   the shallow aquifers of Horseshoe and Moraine Parks, and the timing of ground water
   level rise and fall, and the height of water level change in most areas is tightly linked
   to stream flow and stream stage.

2. The large bedrock outcrop in the center of Moraine Park acts as a dam forcing ground
   water to the surface where it discharges creating shallow water tables on the west and
   southwestern side of the outcrop, and an area of deep water tables on the eastern side
   of the outcrop. Permanently saturated soils in Moraine Park occur only in this site of

ground water discharge, and in a couple of sites where hillslope ground water enters the parks. One such area is the large peatland located just above Fan Lake in Endo Valley, and at two sites on the north side of Moraine Park.

3. The lack of beavers in the two study sites means that stream stage is near the stream bed level during most of the summer. Thus, ground water recharge is limited and ground water levels throughout the study areas are low. Beaver dams could increase the wetted perimeter of streams in pond areas potentially increasing ground water recharge, and the higher river stage would result in higher ground water levels through much of the study area.

B. Willow Propagule Availability

1. Willows produce an abundance of seed that are adapted for aerial or water dispersal. The seeds have a short period of viability, 1-3 weeks, but typically have high germinability, approaching 100% in many species. The timing of seed dispersal coincides with stage drawdown following the peak flow of the year, thus willow seeds can land on bare and wet mineral soils deposited by floods, which form a suitable seedbed. Willows produce two types of propagules, seeds and asexual stem fragments. Seeds can be wind or water dispersed, and stems are water dispersed. We found all of these characteristics of willows to occur in the study sites.

2. Willow seed rain density decreases rapidly with distance from mature female willows. We found this in both small scale and larger scale analyses in both study areas.

3. Seed availability is a function of the distribution and condition of willow stems that can produce catkins.

4. Few willows in Moraine and Horseshoe Parks produce seed because the condition of willow stems is poor due to heavy ungulate browsing. Many parts of the study areas lack seed-producing willows and receive very low seed rain densities. Much of the eastern portion of Moraine Park receives ~1% of the seed rain density of reference willow stands in the western portions of Moraine and Horseshoe Parks.

5. Little willow seed is dispersed by water (hydrochory), and hydrochory does not compensate for the lack of aerial willow seed rain to the central and eastern portions of Moraine and Horseshoe Parks.

6. Beaver cutting in a few parts of the study area produce willow stem fragments. Willow stem fragments have much greater food reserves than do seeds, therefore they can quickly establish roots, stems and leaves and are an efficient mode of establishment. These fragments can also be transported long distance by streams. However, there are too few beavers to produce large numbers of cuttings for dispersal, and very little stem fragment dispersal occurs in the study areas.

C. Willow Seedling Establishment

1. Willow seeds rapidly germinate on bare wet soil, and seedling establishment is controlled by soil drought and seedling desiccation at higher elevations on landforms, and by erosion during the subsequent years spring flood at lower elevations. Fine-grained soils have higher water holding capacity and can reduce drought stress. Suitable sites for willow seedling establishment occur throughout the study sites.

2. Limited aerial seed dispersal, hydrochory, and low seed entrapment rates leads to few seeds arriving and remaining on the existing sites that are suitable for establishment.

3. Higher willow seedling densities occur in locations closer to seed sources, suggesting that propagule availability limits seedling establishment.

4. Seedling growth is slow, and even after two years plant roots do not reach the late summer water table. The development of roots of sufficient length to reach the water table likely requires 3-4 growing seasons, the length of time we estimate it takes for seedlings to establish. During these years seedlings are highly susceptible to drought desiccation and disturbance, including herbivory.

D. Geomorphic and hydrologic controls on willow establishment.

1. Willows have established on three principal landforms in the study area: point bars, abandoned beaver ponds and abandoned channels or ox-bows. These landforms function differently in their mode of formation, flood frequency, sediment texture, and potential erosion of seedlings.

2. Abandoned beaver ponds and channels are generated by the activities of beavers and their formation has been relatively rare over the past 50 years due to the low populations of beavers present.

3. Landforms change through time and the activities of beaver. A point bar may be flooded by a beaver dam, converting it from bar to pond. After the dam fills with sediment or is abandoned it may erode and a bar may form again.

4. Analysis of willow ages indicates that there has been establishment in recent decades, however willow age and height are not correlated, suggesting that browsing is keeping plants of all ages in a suppressed and shortened stature.

5. Very large floods are not necessary for willow establishment. Most willows have established in years with 2-5 year return interval floods.

6. Global circulation models indicate that climate warming will occur in the future, with longer and drier summers, which could limit willow establishment. However, if beavers were present, their dams and the resultant higher water tables would reduce drought stress on willows and increase survival, thereby counteracting the effects of climate change.

E. Management and Restoration Implications

1. Willow propagule availability is limited by the lack of mature willows in many areas, the lack of mature branches to produce catkins and seeds, and the low number of beavers to produce stem fragments. Therefore, sexual and asexual establishment opportunities are limited.

2. The lack of beaver dams has depressed water tables throughout the study areas and limited the formation of beaver generated landforms, ponds and abandoned channels, which are important sites for willow establishment.

3. Willows can be established by cuttings in sites with a summer water table no deeper than 90 cm below the soil surface. Rooted cuttings have a higher survival rate than unrooted cuttings.

4. Willows can be established using rooted cuttings in areas identified as having suitable water table depths. These areas must then be protected from browsing.

5. New willow populations should be established throughout Moraine and Horseshoe Parks and could serve as new centers of propagule dispersal.

6. New willow populations could increase habitat for beavers, whose dams could raise local and regional water tables increasing the survival of seedlings, and their cuttings could serve as asexual propagules for additional willow propagule dispersal and

establishment. The high water tables created and maintained by beavers could overcome in part the drier, warmer and longer summers predicted to occur in the future by global circulation models.

TABLE OF CONTENTS

CHAPTER 1. INTRODUCTION

Willow (*Salix* spp.) dominated riparian communities are found in montane and boreal regions throughout the Holarctic (Zoltai et al. 1988; Rodwell 1991; Ellenberg 1998). These communities form regional centers of biodiversity (Naiman et al. 1993) and provide a broad array of essential ecosystem functions including habitat and forage for terrestrial wildlife (Schulz and Leininger 1991; Pollack 1998), bank stabilization, and particulate organic inputs to aquatic ecosystems (Gregory et al. 1991; Bisson and Bilby 1998). Riparian communities face a variety of threats throughout their range including hydrologic changes associated with river regulation (Rood and Heinze-Milne 1989; Cooper et al. 1999; Andersson et al. 2000), groundwater extraction (Stromberg et al. 1996; Cooper et al. 2002), exotic species invasions (Busch and Smith 1995; Stromberg 1998; Lesica and Miles 2001), sand, gravel and placer metal mining (Cooper and Van Haveren 1994; Kondolf 1997; Scott et al. 1999), and overgrazing by livestock (Belsky et al. 1999) and native ungulates (Hess 1993; Kay 1997).

Analyses of willow communities within portions of RMNP indicate a ~50% decrease in tall willow cover during the latter half of the twentieth century in the main elk winter range (Peinetti et al. 2002). Several factors may have contributed to this decline, including: (1) herbivory associated with an increase in elk populations since their release from artificial population controls in the late 1960's (Lubow et al. 2002), (2) hydrologic changes resulting from a severe decline in beaver populations (Peinetti et al. 2002), (3) increasingly warm and dry climatic conditions (Singer et al. 1998), and (4) human-induced disturbances resulting from agricultural and recreational development (Peinetti et al. 2002).

While the condition of existing willow stands in the elk winter range has been documented (Singer and Zeigenfuss 2002), there is little information on processes controlling

3

willow recruitment in RMNP or elsewhere in the Rocky Mountain region. Identifying the biotic and abiotic factors that may constrain willow establishment is essential for understanding whether declining mature willow communities will be replaced, for predicting community responses to disturbances such as climate change, and for developing potential management and restoration strategies.

The dispersal of propagules provides a basic template for plant establishment and community succession (Harper 1977). However, there are few data describing dispersal processes in montane willow communities. Research presented in chapter 2 examines aspects of willow propagule dispersal in the elk winter range. We examine the tempora65

1 and spatial patterns of aerial seed dispersal and the role of hydrochory (i.e. dispersal by water) in transporting seeds and asexual propagules. In addition, we examine factors influencing rates of seed entrapment. Lastly, we quantify natural patterns of seedling emergence in relation to the proximity of willow seed sources as a means of assessing whether propagule availability may be limiting willow establishment in portions of the elk winter range.

Within seedling cohorts, multiple factors can influence seedling survivorship. Along western rivers, water is generally considered the primary resource limiting plant establishment (Sacchi and Price 1992; Mahoney and Rood 1998; Cooper et al. 1999), although nutrients may also play a significant role (Adair and Binkley 2002). Mature willows typically have access to perennial groundwater (Alstad et al. 1999; Busch et al. 1992), but it may take several years before seedlings develop root systems deep enough to reach the water table (Cooper et al. 1999). During this stage, seedlings are vulnerable to water stress and desiccation (Sacchi and Price 1992). Flooding is an additional factor limiting seedling establishment along streams. Both erosion and sediment deposition associated with flood events can cause extensive

seedling mortality (McBride and Strahan 1984; Barnes 1985; Johnson 1994). Together, these two factors represent the primary physical controls governing patterns of seedling establishment along riparian areas, although few quantitative studies have examined these processes in montane willow communities.

Studies presented in chapter 3 were designed to identify factors constraining initial willow seedling emergence and survivorship in the elk winter range. In the first study, we experimentally tested the effects of relative elevation and soil texture on patterns of willow seedling establishment. In a second study, we quantified the influence of a range of physical variables on natural seedling emergence and survivorship patterns. Lastly, we characterized above and belowground growth patterns in nursery-grown and field-grown willow seedlings.

Historical patterns of willow establishment during the latter half of the 20th century, defined as willow survival through three growing seasons, were examined, and results are presented in chapter 4. The specific questions we addressed were the following: (1) which fluvial landforms serve as sites suitable for willow establishment? (2) Is willow establishment on these landforms driven by their unique hydrologic regimes? (3) How do, or could, climate driven variations in streamflow influence the establishment of willows?

To examine potential approaches to willow restoration, an experiment was conducted in the study areas to quantify survivorship patterns of willow stem cuttings. The results, found in chapter 5, compare survivorship of rooted and unrooted cuttings in relation to soil texture and depth to water table. In addition, data were used to identify hydrologic thresholds limiting cutting establishment and to delineate areas with suitable conditions for willow planting.

Since willow establishment is strongly controlled by hydrologic factors, we examined ground water and surface water flows across the study areas. Networks of staff gauges and

ground water monitoring wells were installed across both Moraine and Horseshoe Parks and were used to generate cross-sectional water table profiles, well and stream hydrographs, and to help delineate areas with suitable hydrologic regimes for planting willow cuttings. Results are presented in chapter 6.

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CHAPTER 2. PATTERNS AND PROCESSES OF WILLOW PROPAGULE DISPERSAL IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

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ABSTRACT

The documented decline of montane riparian willow communities in portions of Rocky Mountain National Park, Colorado (RMNP) is a significant concern for park managers. This study assessed factors that may constrain willow seedling establishment in Moraine and Horseshoe Parks, the primary winter range for elk in RMNP. We examined the dispersal phenology and seed germinability of the dominant willow species, the temporal and spatial patterns of aerial seed rain, assessed the role of hydrochory (i.e. dispersal by water) in the dispersal of sexual and asexual propagules, quantified the effects of micro-topographic relief, soil texture, and soil moisture on rates of willow seed entrapment, and related natural patterns of seedling establishment on point bars to seed source proximity. Seed rain densities declined exponentially with distance from seed source and many portions of the study areas received seed rain densities < 1 % of those observed in reference areas. Hydrochoric transport of propagules occurred, but at densities too low to compensate for the low levels of aerial seed rain observed in extensive portions of the study area. Rates of seed entrapment varied with soil moisture and surface relief, and were low regardless of treatment, indicating that only a portion

of wind dispersed seeds are entrapped long enough for germination to occur. Observed seedling densities on point bars correlated negatively with distance to seed-producing willows. Small numbers of live willow stem fragments were deposited along study area point bars, but at rates too low to significantly affect willow population dynamics. Collectively, these results indicate that propagule availability may constrain current and future willow establishment in the elk winter range.

INTRODUCTION

In recent years, there has been increasing concern among park managers and members of the scientific community regarding a documented decline in the extent and condition of willow (*Salix* spp.) communities in portions of the elk winter range of Rocky Mountain National Park (RMNP) (Hess 1993, Peinetti 2002; Singer et al. 1998). Extensive areas that historically supported willows now lack them, elk herbivory has suppressed many of the remaining stands, and there is little evidence of current willow regeneration (Peinetti et al. 2002). Identifying the principal factors acting to constrain willow establishment is essential for understanding the long-term future of willow communities and for developing effective management and restoration strategies.

The production and dispersal of propagules are fundamental processes controlling plant establishment (Ridley 1930; Harper 1977). Propagule dispersal can have profound effects on vegetation patterns across a range of temporal and spatial scales, influencing population dynamics of individual species, plant community composition, and community succession (Howe and Smallwood 1982). Inadequate dispersal constrains plant establishment in some community types (Primack and Miao 1992), and restoration efforts frequently involve augmentation of native propagule supplies (Luken 1990).

A wide variety of dispersal mechanisms have been described (Ridley 1930) focusing primarily on the initial movement of propagules from parent plants to the soil surface (primary dispersal *sensu* Chambers and MacMahon 1994). A variety of factors can influence primary dispersal distances in wind-dispersed species such as willows, including seed mass and shape, height of seed release, and morphological adaptations promoting wind dispersal (Augspurger and Franson 1987; Okubu and Levin 1989; Greene and Johnson 1989). The spatial pattern of

aerial seed rain or seed shadow (Janzen 1971) has often been described as leptokurtic (Willson 1992), with seed densities peaking near parent plants and rapidly decreasing outwards. While long distance dispersal may be important for processes such as plant invasions (Cain et al. 2000; Bullock and Clarke 2000), it is probably less important in shaping vegetation patterns at fine and medium scales. The higher propagule densities observed closer to parent plants are more likely to influence processes such as inter and intra-specific competition, and successional change (Walker et al. 1986).

There is evidence that redistribution of propagules (secondary dispersal *sensu* Chambers and MacMahon 1994) can be as important in influencing vegetation patterns as primary dispersal (Fort and Richards 1998), at least at small scales (Chambers et al. 1991; Chambers 2000). While previous research has identified a strong relationship between the fate of locally dispersed seeds and surface characteristics of a soil such as roughness, texture, organic matter content, and the presence or absence of vegetation, (Harper and Williams 1965; Eckert Jr. et al. 1986; Young et al. 1990; Chambers et al. 1991; Chambers 1995; Chambers 2000), little is known about the factors controlling seed entrapment in montane willow communities. Relatively large roughness elements such as cobbles may promote willow seed entrapment when compared with more uniform substrates. Given the small size and mass of willow seeds and their morphological adaptation for wind dispersal, processes of seed entrapment may be critical in influencing where willow seeds ultimately come to rest, thereby influencing patterns of seedling emergence.

Hydrochory (i.e. water-transport of propagules) is an additional mode of propagule dispersal shown to be important in some riparian ecosystems (Ridley 1930; Schneider and Sharitz 1988; Johansson and Nilsson 1993; Cellot et al. 1998; Merritt 1999; Middleton 2000;

13

Merritt and Wohl 2002). While hydrochory may be relatively unimportant in dense willow stands, it may be of greater significance in areas lacking seed-producing plants. Hydrochory may also provide a source of asexual propagules to suitable sites, particularly in low stream energy environments such as beaver ponds, eddys, and oxbows.

The relationship between propagule density and patterns of willow recruitment is unclear. Janzen's "escape hypothesis" (Janzen 1970; Connell 1971) predicts that *per capita* seedling survivorship decreases closer to parent plants due to the cumulative effects of predators and pathogens, with peak recruitment occurring away from parent plants (Nathan et al. 2000). However, it has also been hypothesized that recruitment should be greater near parents, despite density-dependant mortality, because of greater propagule densities (Hubbell 1980). Propagule density can be expected to positively influence seedling recruitment where: (1) essential habitat for establishment is spatially or temporally limited (Howe and Smallwood 1982), (2) seeds rapidly lose viability, and (3) seeds and seedlings are subject to high density-independent mortality rates. These characteristics typify willow-dominated riparian communities, where the fluvial landforms required for establishment comprise a small and dynamic portion of the landscape, and seedlings typically experience high mortality rates due to a range of factors such as desiccation (Sacchi and Price 1992), flood scour (McBride and Strahan 1984), and herbivory.

The patterns of willow seedling emergence observed on fluvial landforms in RMNP vary over short spatial scales suggesting that micro-site characteristics exert strong controls over initial seedling establishment. While mortality due to flood scouring or sediment deposition, and late summer desiccation, may ultimately limit where seedlings survive (McBride and Strahan 1984; Niiyama 1990; Sacchi and Price 1992; Douglass 1995; Cooper et

al. 1999), initial patterns of seedling emergence likely result from the interaction of primary seed dispersal, seed entrapment and seed germination. Documenting the importance of these factors and their relation to the availability of suitable habitat for establishment is critical for understanding current and future vegetation dynamics.

The objectives of this study were the following: (1) to characterize the spatial and temporal patterns of aerial seed dispersal in the elk winter range of RMNP, (2) to identify whether hydrochory is an important mode of willow seed and vegetative propagule transport, (3) to identify factors influencing rates of willow seed entrapment, and (4) to analyze whether low propagule densities may constrain seedling emergence and recruitment in parts of the study areas.

STUDY SITES

This research was conducted in Moraine and Horseshoe Parks, on the east slope of Rocky Mountain National Park, Colorado (Figure 1). Both sites are broad, low-gradient alluvial valleys formed over ancient lakebeds located behind Pleistocene terminal moraines (Elias 1995). Moraine Park (elevation ~ 2,480m) is in the Big Thompson watershed, whereas Horseshoe Park (elevation ~ 2,600m) is located in the Fall River watershed. Vegetation in both sites is a mix of wet and dry meadows and riparian communities dominated by several willow species (primarily *Salix monticola, S. geyeriana* and *S. planifolia*) and river birch (*Betula fontinalis*).

The westernmost portion of Moraine Park is relatively undisturbed, and supports dense tall willow stands. In contrast, the central and eastern portions of Moraine Park have been heavily disturbed. Homesteads were established here in the late 19th century, and many willow stands were cleared to create pasture, and later a golf course. Willows are nearly absent in the

easternmost portion of Moraine Park, and intense levels of elk herbivory suppress the few remaining plants, preventing seed production (Peinetti et al. 2001).

The western portion of Horseshoe Park (near the Endovalley picnic area) also supports tall and high-density willow stands. Density and stature decreases to the east along Fall River, likely the result of past human disturbance, high winter elk density, and the 1982 Lawn Lake flood, which inundated and disturbed many areas (Keigley 1993; Peinetti et al. 2002). The westernmost portions of both sites served as reference areas for this study.

METHODS

Dispersal phenology and seed germination

To better understand the contribution of individual species to observed seed rain patterns, we monitored flowering and fruiting phenology of the dominant willow species found in Moraine and Horseshoe Parks during the summer of 2001. Five female plants each of *Salix monticola, S. planifolia, S. drummondiana, S. geyeriana, S. bebbiana,* and *S. lucida* ssp. *caudata* were identified in the two study areas. Bud-bearing shoots were visually inspected weekly during late May, June, and July for evidence of flowering or seed release.

Percent seed germination was examined for *Salix monticola, S. geyeriana, S. planifolia, S. gracilis, S. bebbiana,* and *S. lucida* ssp. *caudata.* Mature catkins from each species were placed in paper bags and stored for 48h at room temperature to promote capsule dehiscence and seed release. For each species, four replicates of 25 seeds each, were randomly selected and placed on moistened Whatman© type 3 filter paper and placed under continuous fluorescent light. Germination was assessed over 10d and recorded as positive if the hypocotyl and cotyledons developed normally. Differences in germination rates among species were

examined using a one-way ANOVA following a Tukey-Kramer multiple comparisons adjustment (Proc GLM; SAS Inc. 2000).

Aerial dispersal of willow seeds

The timing and spatial pattern of willow seed rain was examined using a network of seed rain traps installed across the study areas. Traps were constructed from 900 cm^2 plywood squares mounted horizontally on fence posts ~1.25 m above the ground surface. A coating of Tanglefoot® adhesive was applied to the upper surface of each trap to capture passing seeds. Traps were installed in north-south transects systematically located across the study sites. Forty traps were installed in Moraine Park (Figure 2) and 20 in the smaller Horseshoe Park study site. Seven additional traps were installed off transect lines in high-density tall-morphotype willow stands to serve as reference sites. Captured seeds were tallied and seed traps recoated with Tanglefoot® weekly from the first week in June through the second week in July, when seed rain was complete, in both 2000 and 2001. In 2001, only seed rain traps in Moraine Park and reference traps in Horseshoe Park were monitored, and all but the reference traps were lowered to a height of ~20cm above the ground surface to better characterize seed rain at ground level.

In 2001, additional seed rain traps were installed at regular distances from willow patches to quantify seed rain attenuation with distance from seed sources. Two isolated seed-producing willow patches termed the island and peninsula sites were selected in Moraine Park (Figure 2). At the peninsula site, traps were placed at distances of 0, 7, 14, 21, 28, 35, 42, 49, 56, 63, 77, 91, 112, 140, 168, and 203m from the base of individual seed-bearing plants along two east trending transects. A smaller number of traps were also placed at 7m intervals along N, S, NE, and SE trending transects and in the interior of the patch. At the island site, traps were installed at 7m intervals along four transects oriented in the four cardinal directions.

17

Since the prevailing winds are from the west, the east trending transects were most intensively studied at both sites. Traps were prepared and maintained in a similar fashion to other seed rain traps, with seeds tallied and removed weekly. Seed rain vs. distance to seed source was examined using nonlinear regression (SigmaPlot; SPSS Inc. 2002). Two phenomenological models were fit to the data: a negative exponential and an inverse power function (Willson 1992; Nathan et al. 2000). Curves were compared using the slope and intercept parameters estimates for each fitted function.

The inverse distance weighted method in the ArcView Spatial Analyst extension (ESRI Inc. 1999) was used to interpolate values between traps and generate contour maps of seed rain density. The distances from traps to seed sources were calculated within ArcView. Cumulative seed rain values were then plotted against distance from seed source and a nonlinear regression curve fit using SigmaPlot (SPSS Inc. 2002). Temporal patterns of seed rain were examined using trap data from the reference stands.

Hydrochoric transport of willow propagules

During the 2001 period of seed rain, aquatic seed traps were used to sample the main stem of the Big Thompson River in Moraine Park for water dispersed seeds at four sites: two upstream sites within willow communities, and two downstream sites where seed-producing willow are absent (Figure 2). Traps were constructed of polyester mesh fabric sown to a skeleton of brass rings, terminating in a removable PVC collection container. Traps were installed at the thalweg in river reaches with minimal turbulence. Initial samples were collected after 15 minutes; however, the sampling interval was increased to approximately 3 hours due to low levels of material collected in the traps. All sites were sampled for an identical time period on each sampling date.

Following sampling, trap contents were sorted to remove coarse debris. The remaining material was spread onto 10x15x5 cm trays of loamy sand that were kept moist, in a well-lighted environment to promote seed germination. The number of willow germinants was analyzed by sampling location and date using a two-way ANOVA following (log+1) transformation to stabilize variances (Proc GLM; SAS 2000).

The role of hydrochory in transporting willow stem fragments was examined at the same locations as the hydrochory seed analysis (Figure 2). 52x52 cm metal grids, with a 3.5 x 3.5 cm cell size, were mounted on fence posts with grids oriented perpendicular to the direction of flow. The grid was submerged leaving approximately 5 cm of the grid above the stream surface. The initial sampling interval of three hours was increased to 24 hours due to the small amount of collected material. The volume of flow sampled was estimated by multiplying the sampling interval by the estimated surface velocity and trap area. Following sampling, trap contents were sorted, and willow stem fragments removed and their viability assessed by partially submerging fragments in water under continuous light. Fragments were considered viable if either adventitious roots or shoots formed within a period of two weeks.

Willow seed entrapment

A replicated 2x2x3 factorial experiment was used to analyze willow seed entrapment relative to surface relief, soil texture and degree of soil wetness. Five replicates of each treatment were randomly located in a homogenous area of meadow vegetation adjacent to the Big Thompson River in Moraine Park. Vegetation surrounding each block of plots was clipped and a section of burlap was stapled to the ground surface. In each replicate, six vinyl trays 18cm in diameter and 5cm in depth were buried flush with the ground surface in holes cut into the burlap. Trays were randomly assigned soil texture and surface relief treatments. Two soil textures were used: coarse sand collected from point bars and loamy fine sand collected from a

nearby abandoned beaver pond. Surface relief treatments were created by placing 2.6 cm tall wood cubes on the surface of each tray. Relief levels tested were low (no blocks, 0% of soil surface area), medium (5 blocks, 30% of surface area), and high (10 blocks, 60% of surface area). The effect of soil wetness was examined by running the experiment under two different soil moisture conditions. In the "dry" experiment, trays equipped with drainage holes were saturated and allowed to drain to field capacity before seed addition. In the "wet" experiment, designed to simulate the presence of a high water table, trays without drainage holes were saturated to a depth of 1cm below the soil surface to maintain consistently moist soils over the length of the trial.

Ten *S. monticola* seeds were dropped individually into a cylinder placed flush with the tray margins. Seeds were allowed to settle on the soil surface before careful removal of the cylinder. After three hours, seeds remaining on the tray surface were tallied and an additional 10 seeds were added. Entrapped seeds were tallied again after a period of 6 hours and 30 hours. For the "wet" experiment, the number of seeds added in each addition was increased from 10 to 15. The entrapment rate was calculated for each factor-level combination by dividing the number of seeds observed in each count by the original number of seeds added. An ANOVA analysis was conducted on the 30-hour entrapment data (Proc GLM; SAS 2000) for the combined dry and wet trials, and pairwise comparisons were made following a Tukey-Kramer multiple comparison adjustment.

Natural patterns of willow seedling establishment

Natural willow seedling emergence was examined along the Big Thompson River in Moraine Park during September 2001. All point bars were identified and mapped using a GPS unit and aerial photographs. The main stem was divided into 4 sections and seven bars in each section were randomly selected for sampling (Figure 2). On each bar, the area available for

20

seedling establishment was estimated using the high and low stage recorded by local staff gauges during the period of seed rain. Current-year seedlings were sampled using a series of continuous 0.25 m^2 quadrats placed along lines oriented perpendicular to the main axis of the point bar. Transect lines ran from the edge of perennial vegetation to the edge of the bar estimated to be available for colonization during the seed rain period, and were spaced at 2m increments along the main axis of the bar. The distance from sampled bars to the nearest seed-producing willow patch was calculated in ArcView (ESRI Inc.1999). Non-linear regression analysis was used to relate mean seedling density for each bar to distance from seed-producing willows.

The deposition of willow stem fragments > 5 cm in length was quantified on all point bars along the main stem of the river. Only live stems were counted, assessed by abrading the outer bark with a fingernail and noting the presence or absence of live cambium. Tallied stem fragments were assigned to one of four classes corresponding to different depositional environments on bars: upstream 1/3, middle 1/3, downstream 1/3, and backwater/eddy. In addition, the origin of stem fragments (beaver cut or not) was recorded.

RESULTS

Dispersal phenology and seed germination

Reproductive phenology varied among willow species, with *S. planifolia* initiating and completing seed dispersal first, and *S. lucida* ssp. *caudata* last. The two most prevalent willow species in both study areas, *S. monticola* and *S. geyeriana*, had dispersal periods that overlapped considerably. Measurable seed rain occurred for approximately a 4-week period in both years, from early June through early July, and was commensurate with a decline in river stage (Figure 3).

21

Nearly all seeds initiated germination within 72h of placement onto the moistened filter paper, and seed germination rates were high for all species. *Salix planifolia* had the lowest germination rate (85%), significantly lower than *S. monticola* (99%), *S. gracilis* (99%), or *S. bebbiana* (96%) (Figure 4).

Aerial dispersal of willow seeds

Seed rain densities varied widely both within and among the two study sites, with the highest cumulative seed rain occurring in the western portions of Moraine and Horseshoe Parks. Although reference area seed rain densities were similar between study sites, Horseshoe Park exhibited greater spatial heterogeneity in seed rain densities due to a wider distribution of seed-producing willow stands. In contrast, seed rain densities were more than two orders of magnitude lower in the central and eastern portions of Moraine Park than in the west (Figure 5), and a large area of Moraine Park received $\leq$25 seeds/m^2 during the 2000 and 2001 seasons. Only one trap captured zero seeds during the two study years, and non-linear regression analysis of total annual seed rain and distance to seed-producing willows [log(y) = -0.078 + $1.52^{(-0.0026\,x)}$; R^2=0.74] suggests that a measurable base level of seed rain of ~25 seeds/m^2/yr occurs in all portions of Moraine Park (Figure 6).

Results from small-scale trap transects indicate that seed rain densities rapidly decrease with distance from a seed source. The negative exponential models fit to the three east trending transects exhibited a leptokurtic form, with peak densities occurring a short distance from the transect origin (Figure 7). Parameter estimates for these dispersal curves were highly variable, likely the result of variation in willow fecundity, seed release height, and local wind conditions. However, each model displayed a strong fit to the data, with R^2 values of 0.92, 0.82, and 0.84 for the island and the two peninsula transects, respectively. More than 50% of the cumulative seed rain along these transects occurred within 30m of the willow patch edge.

22

In contrast, there were only weak trends in the N and NE transects, probably the result of seed rain inputs from nearby willow patches.

Hydrochoric transport of willow propagules

Total numbers of willow seeds recovered and successfully germinated from the four sampling locations was low. The maximum total number of germinants from the four sampling locations was 12 from a location within seed producing willows, and the minimum was 1 at the easternmost sampling location. Neither site location (ANOVA; F = 2.37; P = 0.122) nor sampling date (F = 0.65; P = 0.64) was significant in the analysis. However, a general trend was observed, with higher numbers of seeds recovered from the western portion of the study area. Direct additions of *S. monticola* seeds to hydrochory traps and subsequent attempts at seed recovery using the methods followed for earlier samples resulted in a ~40% recovery rate, significantly lower than expected based on the high germinability of seeds observed in the germination trials. Thus, seeds were either killed during water transport, or were unable to germinate following removal from traps. Only a single viable beaver-cut willow stem fragment was found in all samples recovered from the metal grids. The bulk of the material recovered from these traps consisted of partially decomposed organic matter, leaves, and algae.

Willow seed entrapment

Mean entrapment rates varied from ~2% to 30% over the 30-hour sample period (Figure 8). In general, high relief treatments exhibited higher entrapment rates than low or intermediate relief treatments. The percentage of retained seeds declined over the 30hr sampling period in both the dry and wet trials. Higher overall entrapment rates were observed in the wet treatment. Both relief (ANOVA; F = 14.74; P < 0.0001) and soil moisture (F = 27.71; P < 0.0001) treatments were significant, as was the interaction of roughness and soil

moisture (F = 4.74; P = 0.013) (Table 1). Several factor-level contrasts were also significant (Figure 8; Table 2).

Natural patterns of willow establishment

The highest seedling densities were observed in western Moraine Park. Seedling densities on point bars decreased greatly with increasing distance from seed-producing willow stands (Figure 9). The negative exponential model best fit the data, although the proportion of variability of explained by the model was relatively low (R^2 = 0.47).

Eight (9.8%) of 82 bars and backwaters examined contained live willow stem fragments. The majority of these were found in western Moraine Park, near active beaver colonies and 93% of the 14 fragments found originated as beaver cuttings. Fragments were preferentially deposited along the lower 1/3 (50% of total fragments) of the bars and in backwaters (43%).

DISCUSSION

Dispersal phenology and seed germination

General requirements for seed germination in the *Salicaceae* are well known (Moss 1938; Krasny et al. 1988). Willow seeds are small and light, contain little endosperm, and with few exceptions (see Densmore and Zasada 1982) exhibit high initial germinability. Seeds tested in this study also had high germinability, consistent with previously published results (Junttila 1976; Krasny et al. 1988; Vansplunder et al. 1995). Because willow seeds cannot attain overwinter dormancy to form a soil seed bank, seeds must land on a suitable substrate for establishment soon after dispersal. In fluvial environments the bare mineral substrates suitable for seed germination are exposed as river stage declines. The rate and magnitude of stage change varies annually with differences in streamflow, resulting in high temporal and spatial variability in the availability of suitable substrates. As a consequence, the degree of

synchrony between seed dispersal and stage decline strongly influences the probability of initial seedling establishment. Differences in reproductive phenology may help explain the coexistence of the numerous congeneric willow species observed in the study area. Niiyama (1990) examined reproductive traits among coexisting willow species on a floodplain in Japan and found evidence that dispersal phenology provides a means of "regeneration niche" separation (Grubb 1977).

Willow propagule dispersal

Although willows produce large numbers of wind dispersed seeds, data collected in the study areas indicate that high seed rain densities are only found in and adjacent to mature unsuppressed willow stands, which comprise only a small portion of the elk winter range. Willow seed production in much of the study area appears to be prevented by intense levels of elk herbivory (Peinetti et al. 2001), a phenomenon demonstrated in other areas with high ungulate densities (Kay and Chadde 1992; Case and Kauffman 1997). Analyses indicate that seed rain densities decline rapidly with distance from a seed source, asymptotically leveling at distances of < 200m from parent plants in the larger Moraine Park analysis, and at distances as short as 50 m along small-scale seed rain transects.

These results are surprising considering the potential distance that willow seeds can travel. However, while distance from a parent plant increases as a linear function, the area a seed can land in increases as the square of that distance. The abandoned channels, point bars and beaver ponds providing the bare and wet substrates required for colonization remain a small and fixed portion of the landscape. Thus, the probability of a seed reaching a suitable site declines exponentially with distance from seed-producing willows. The low seed rain densities observed in extensive portions of the study areas, particularly in eastern Moraine Park, suggest

that seed rain is too low to support significant levels of seedling establishment, especially given the high rates of seedling mortality observed.

Hydrochory provided few viable seeds to the downstream portions of Moraine Park, indicating that hydrochory was relatively unimportant for willow establishment during the study period. In addition, we observed no evidence of hydrochoric seed deposition such as drift lines of seeds or seedlings on backwaters. Thus, it appears unlikely that hydrochory can compensate for the low aerial seed rain densities that occur in the eastern portion of the study area.

Some researchers have suggested that beavers play a significant role in the vegetative establishment of willows (Cottrell 1995). However, we found little evidence that vegetative propagules are dispersing downstream with sufficient frequency to play a major role in willow establishment in the study areas. With declining beaver populations, fewer stem fragments are being generated and transported downstream. In addition, fewer opportunities exist for live willow stems, incorporated into dams, to root and grow. However, the higher beaver populations found in the study areas in the early and mid 20th century (Packard 1947; Mitchell et al. 2000) may have resulted in higher historical rates of asexual establishment.

Willow seed entrapment

Both soil wetness and microtopographic relief strongly influenced willow seed entrapment suggesting that seed entrapment rates differ among fluvial landforms. Along gravel bedded alluvial rivers, pronounced patterns of sediment sorting occur, from downstream fining longitudinally, to sorting at the scale of individual clasts (Powell 1998). In the study areas, willow establishment primarily occurs on abandoned beaver ponds, oxbow channels, and point bars (Dickens *unpublished data*) each differing in the degree of surface relief present. Point bars are located adjacent to the active stream channel, are regularly flooded, and are typically

composed of large gravel and cobbles providing a high degree of surface relief. Beaver ponds have very low-velocity flow, fine-grained substrates, and low surface relief. Microtopographic relief in oxbow channels is generally intermediate, with fine textured materials deposited within a matrix of cobbles.

High soil moisture levels promote entrapment by allowing seed plumes to adhere to wet soil surfaces. Beaver dams, with their fine-textured soils, high water-holding capacity and large capillary fringe, create moist conditions more favorable to seed adhesion than other fluvial features. Newly formed oxbows may present an ideal compromise between factors affecting soil moisture and seed entrapment because they contain a matrix of cobbles and large gravel in a low stream energy environment where fine textured materials can be deposited. Similar combinations of coarse clasts with drapes of fine textured sediment also occur on the downstream portions of well-vegetated bars and islands. In general, landforms with low physical relief may be expected to trap relatively few seeds. However, this effect may be ameliorated if the soils are constantly moist. This is consistent with results from the wet trial, where higher overall rates of seed entrapment were observed and the effect of surface relief was diminished in importance relative to the dry trial.

For establishment to occur, seeds must remain in contact with a suitable substrate long enough for germination and root penetration. The relatively low entrapment rates observed across all treatments suggests that measures of seed rain alone overestimate the number of seeds likely to germinate in any location. The seed rain densities observed in the study area indicates the maximum number of potential germinants. However, the number of seed retained in favorable microsites is likely significantly lower.

Natural patterns of willow establishment

The trend of decreasing willow seedling densities with increasing distance from seed-producing willow patches suggests that propagule availability is limiting willow establishment in the central and eastern portions of Moraine Park. However, other factors may contribute to this pattern as well, including spatial variation in elk and human trampling and systematic differences in geomorphology along the length of the river. For instance, recreational fishing activity is more concentrated in the eastern portions of the study area due to road access. Although there was no evidence of a systematic change in the character (e.g. grain size distribution and channel geometry) of point bars along the sampled reach, point bars in the far western portion of Moraine Park were slightly larger than those downstream.

Counter to the predictions of the "escape hypothesis" (Janzen 1970; Connell 1971), seedling densities are highest near parent plants. This is likely due in great part to the large gradient in propagule density observed across the study area (Hubbell 1980). It is also possible that density-dependant mortality factors may be of less importance relative to ecosystems where supporting evidence for the "escape hypothesis" have been found (Clark and Clark 1984; Nathan et al. 2000). In the study area, density-independent abiotic factors, specifically desiccation and flood scour, appear to most strongly influence initial seedling survivorship.

CONCLUSION

Propagule availability can determine the potential population of any species in any given habitat (Harper 1977). For the willow communities examined in this study, multiple factors appear to constrain seedling establishment. Assessment of the relative importance of these factors is scale-dependant. At landscape scales, primary dispersal patterns are of critical importance. These are determined principally by the distribution of seed-producing willow

28

stands and the orientation of prevailing wind patterns. However, it is also clear that small-scale processes such as seed entrapment must also be examined.

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Table 1. Results from ANOVA analysis of 30h entrapment data from combined wet and dry trials. Treatments indicated in bold text are statistically significant (α=0.05).

Treatment	DF	Type III SS	F statistic	Pr > F
Texture	1	0.0013	0.16	0.689
Relief	2	0.2376	14.74	**<0.0001**
Texture*Relief	2	0.0380	2.36	0.105
Moisture	1	0.2233	27.71	**<0.0001**
Relief*Moisture	2	0.0764	4.74	**0.013**
Texture*Moisture	1	0.0029	0.36	0.549

Table 2. Factor-level contrasts from ANOVA analysis of 30h entrapment data from combined wet and dry trials. Means followed by the same letter are not significantly different (α=0.05) following Tukey-Kramer adjustment.

Texture	Surface relief	Moisture	Mean % entrapment	
Fine	High	Dry	30.0	a
Fine	High	Wet	32.0	a
Fine	Low	Dry	10.0	bc
Fine	Low	Wet	27.4	ac
Fine	None	Dry	3.0	bd
Fine	None	Wet	16.0	acde
Coarse	High	Dry	22.0	acde
Coarse	High	Wet	25.4	ace
Coarse	Low	Dry	7.0	be
Coarse	Low	Wet	29.4	ac
Coarse	None	Dry	7.0	be
Coarse	None	Wet	22.0	acde
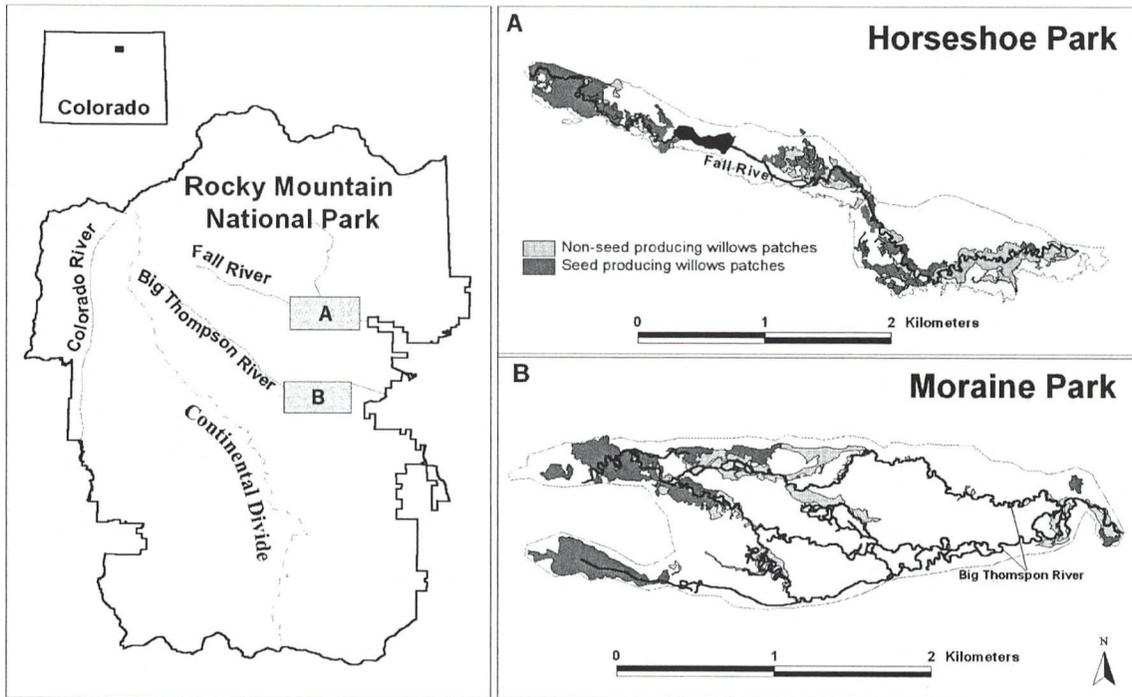
Figure 1. Location of the study areas (inset maps A and B) within Rocky Mountain National Park.
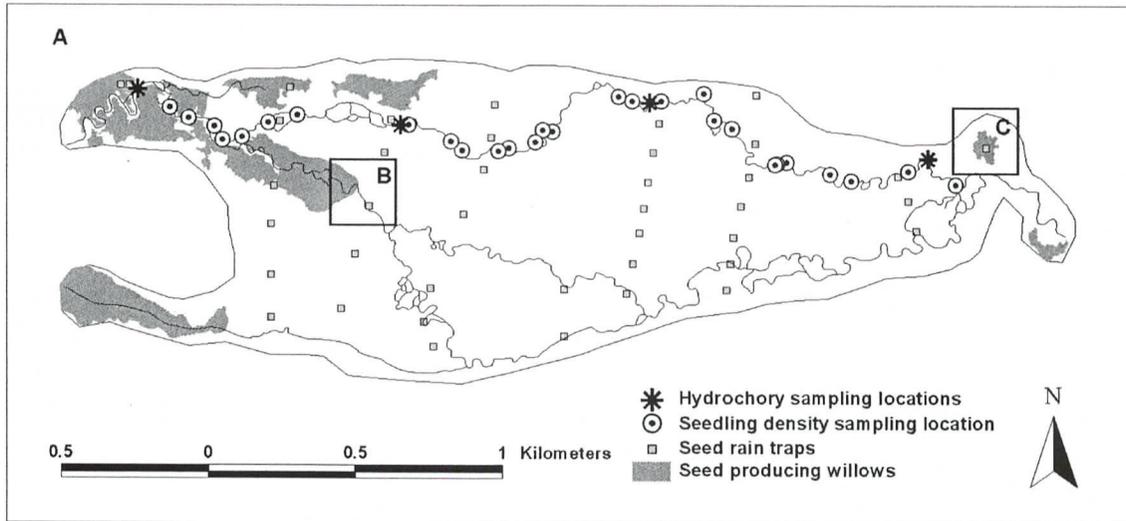
Figure 2. Locations of dispersal studies within Moraine Park (A). Inset boxes B (peninsula) and C (island) denote locations of small-scale seed trap networks.
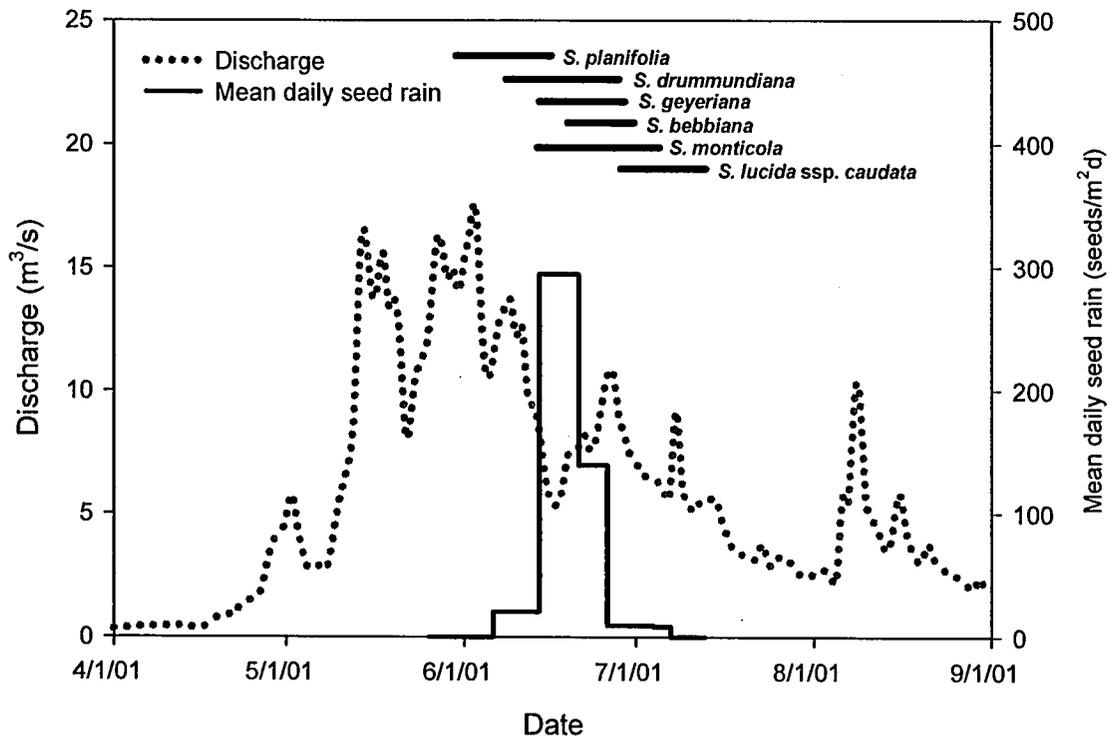
Figure 3. Mean daily seed rain (solid black line) for all reference seed rain traps plotted against mean daily flow for the Big Thompson River as measured at USGS Gauge # 06733000 (dotted gray line) during the 2001 field season. Bars above stream hydrograph correspond to approximate period of seed release for the dominant willow species found in study area.
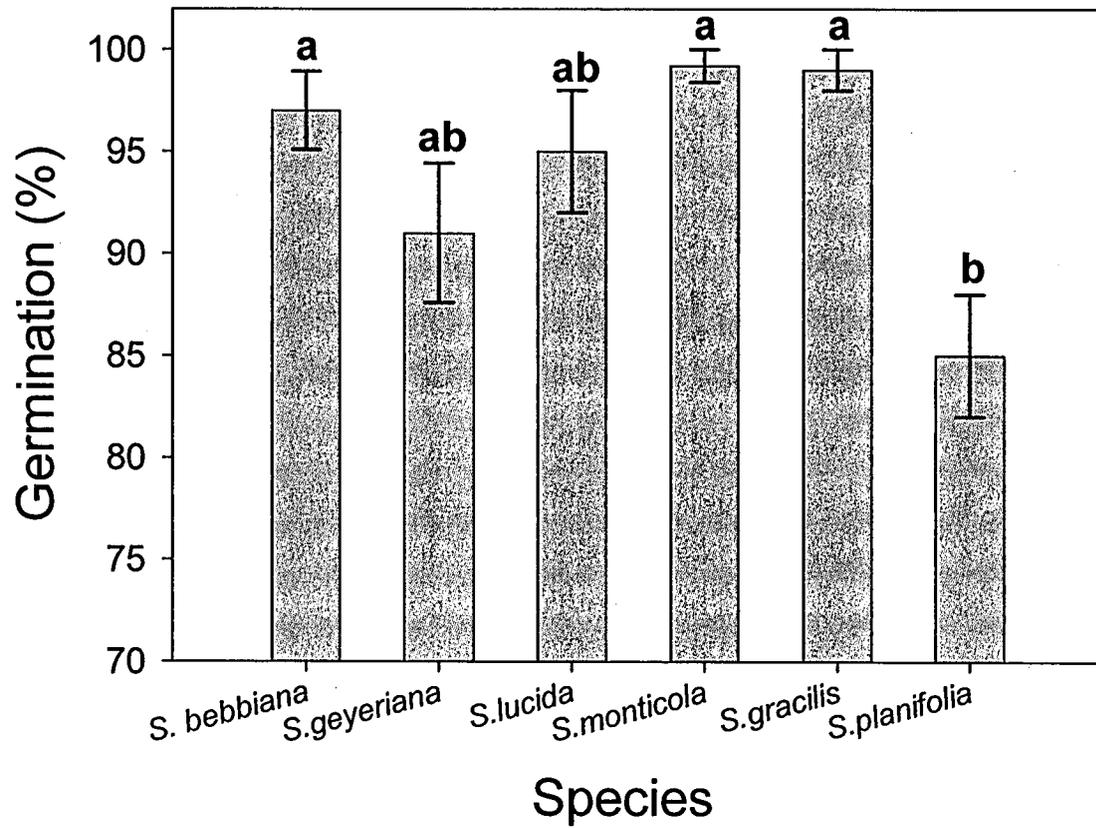
Figure 4. Mean percent germination (+/- 1 std. error) for the dominant willow species in study area. Means sharing the same letter were not significantly different (α=0.05) in a one-way ANOVA analysis.
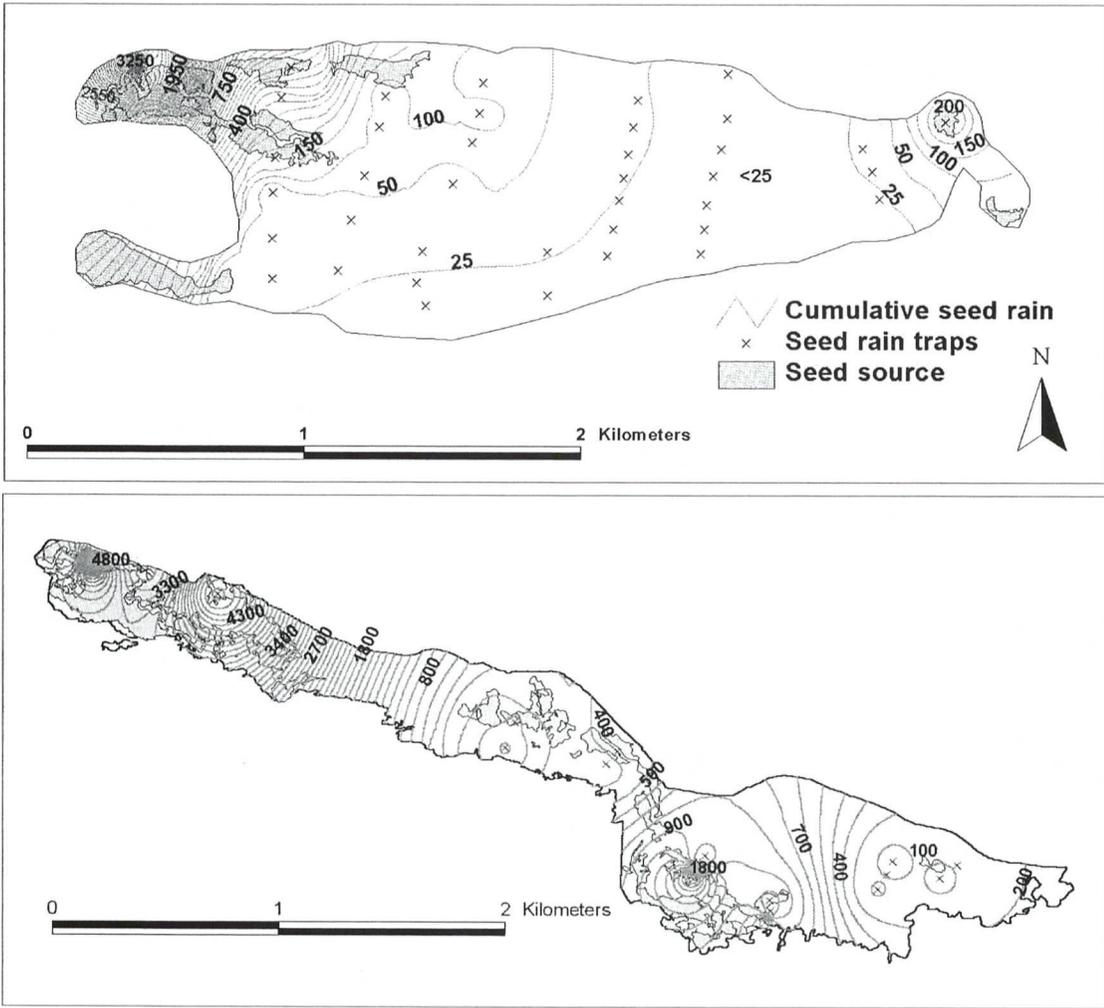
Figure 5. Cumulative annual seed rain for the 2000 season in Horseshoe Park (above) and the 2001 season in Moraine Park (below). Contour lines are at intervals of 50 seeds/m^2, with the exception of the central portion of Moraine Park, where lines represent 25 seeds/m^2.

41
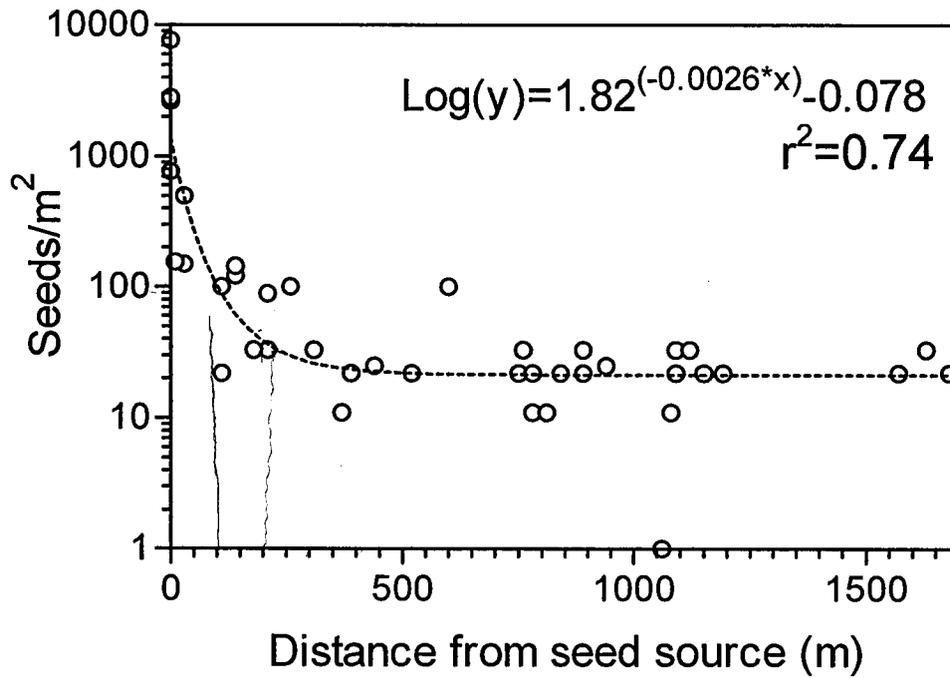
Figure 6. Cumulative annual seed rain plotted against distance from the nearest seed-producing willow patch in Moraine Park for the 2000 field season. Dotted line represents best-fit nonlinear regression line.
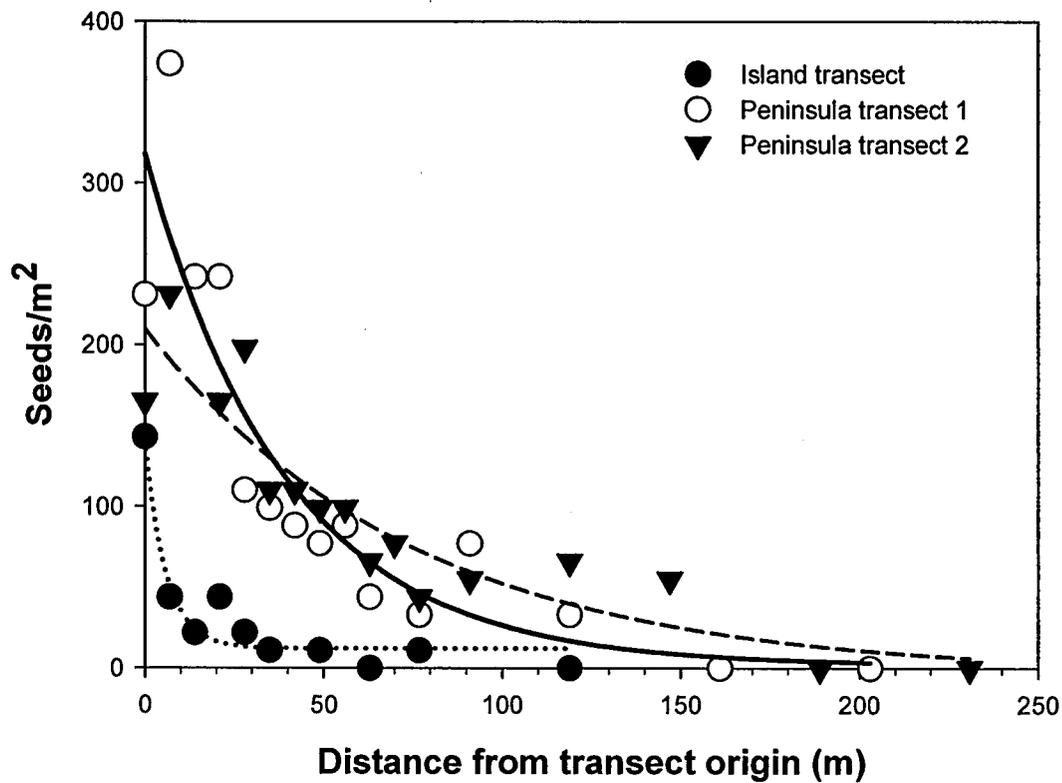
Figure 7. Attenuation rates for the three east-trending trap transects in Moraine Park. Plotted points represent cumulative seed rain densities for traps.
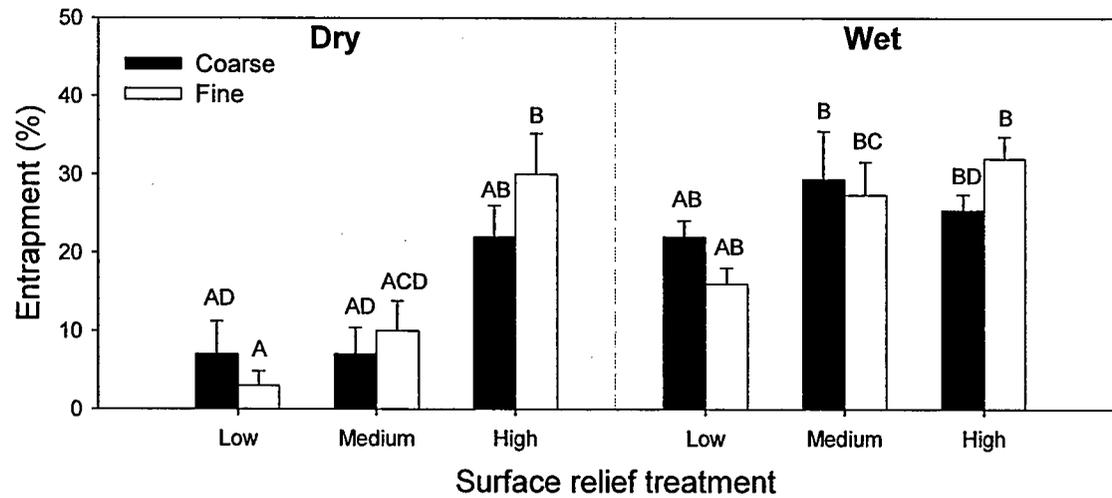
Figure 8. Percent entrapment (+/- 1 std. error) from seed entrapment experiment. Treatment means with the same superscript are not significantly different (α=0.05).
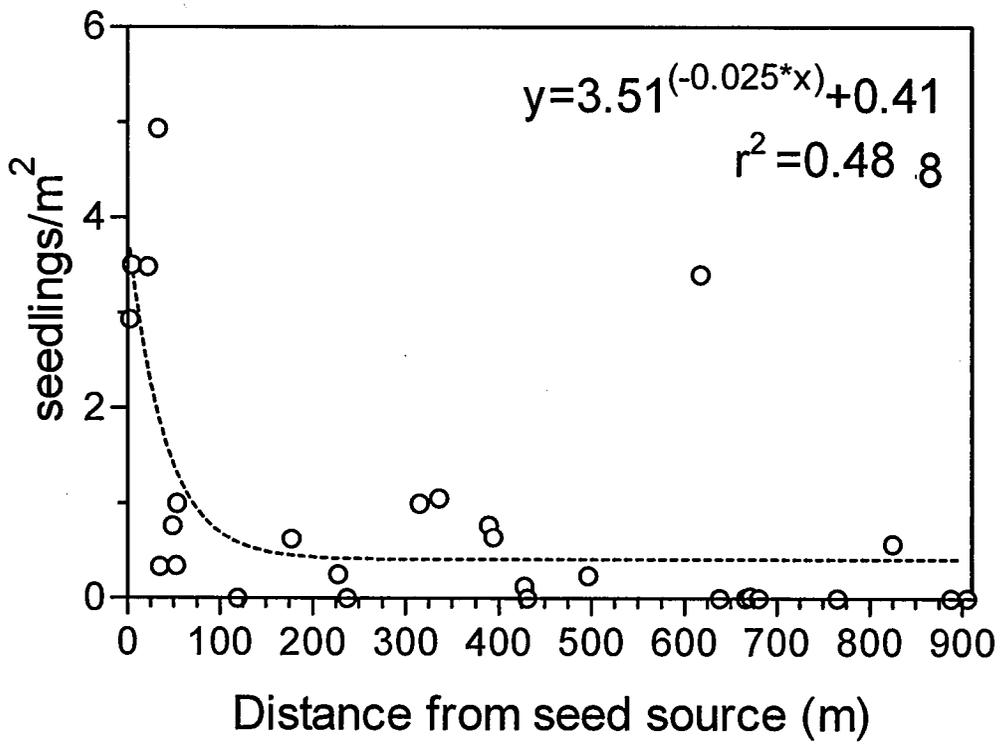
Figure 9. Seedling density (seedlings/m^2) plotted against distance from nearest seed-producing willow patch. Dotted line represents best-fit nonlinear regression line.

CHAPTER 3. CONSTRAINTS ON WILLOW SEEDLING ESTABLISHMENT IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

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ABSTRACT

A variety of factors may constrain willow establishment from seed in montane riparian willow communities in Rocky Mountain National Park. We investigated the following: (1) the growth characteristics of greenhouse and field grown willow seedlings, (2) the effects of soil texture and elevation above river stage on willow seedling survival, and (3) natural patterns of seedling emergence and survivorship on two different landform types. Biomass allocation patterns for seedlings grown in controlled settings changed over the 2 year study period, with aboveground structures providing 55-65% of total biomass in the first months of growth, but contributing <20% of total biomass by the end of the study period. Seedlings grown in field plots exhibited a similar pattern of biomass allocation to greenhouse grown seedlings after two summers of growth. Seedling survival on point bars was highest in fine-textured plots and those occurring at high and mid-elevations, indicating that both soil-water availability and scour by spring floods limit the portions of point bars that are suitable for establishment. Relative elevation, landform type, vegetation cover, and percent cover of coarse woody debris and bare ground were all significant variables in a logistic regression analysis of seedling survivorship. These results suggest that multiple factors influence the spatial and temporal

availability of safe sites for seedling establishment and may constrain rates of willow establishment in the elk winter range.

INTRODUCTION

Riparian ecosystems comprise a small portion of the landscape, yet provide a wide array of essential ecological functions (Gregory et al. 1991; Naiman et al. 1993). In montane areas of the Rocky Mountains, willows (*Salix* spp.) are the dominant woody riparian plant species. In recent years, there has been increasing concern regarding declines in the extent and condition of willow communities in the elk winter range of Rocky Mountain National Park (RMNP) (Hess 1993; Berry et al. 1997), and other national parks in the Rocky Mountain region (Singer et al. 1994; Kay 1997; Singer et al. 1998; Shafer 2000; Keigley 2000). Although previous studies have analyzed several aspects of RMNP willow communities (Alstad et al. 1999; Peinetti et al. 2001; Peinetti et al. 2002), there have been no investigations specifically evaluating willow establishment. Also, while several studies have examined seedling establishment requirements in riparian species of the *Salicaceae* (Scott et al. 1997; Cooper et al. 1999), none have focused on montane willow communities. Identifying the factors that constrain willow establishment is essential for developing effective vegetation management and restoration strategies for the elk winter range in RMNP.

General requirements for willow establishment, defined here as when seedlings become phreatophytic, are well described in the literature (Moss 1938; Ware and Penfound 1949). Willows produce large numbers of light, wind-dispersed seeds that readily germinate on bare and moist soils. Seeds lack significant endosperm reserves and seed viability declines rapidly following seed maturation with no soil seed bank being formed (Ware and Penfound 1949; Brinkman 1974; Douglass 1995). In riparian systems, willow establishment is dependent upon fluvial processes. Sediment mobilization and deposition creates the bare sites required for seedling establishment. In addition, depth to groundwater under fluvial landforms is strongly

correlated with changes in river stage (Mahoney and Rood 1998; Woods 2000; Amlin and Rood 2002).

The term "safe site" has been used to describe sites free from hazards and possessing the necessary conditions and resources required for seed germination and seedling recruitment (Harper 1977). The principal resource constraining riparian plant establishment in arid and semi-arid regions is generally considered to be water (Sacchi and Price 1992; Mahoney and Rood 1998; Cooper et al. 1999), although nutrients may also play a significant role (Adair and Binkley 2002). Mature willows are typically phreatophytes (Alstad et al. 1999; Busch et al. 1992). However, seedlings may not develop taproots of sufficient length to gain access to perennial groundwater for several years (Cooper et al. 1999). Until an adequate root system is developed, seedlings are prone to water stress and death due to desiccation (Sacchi and Price 1992). Suitable sites for establishment are also limited by erosion and deposition associated with flood events (McBride and Strahan 1984; Barnes 1985). These two factors, in tandem, broadly determine the spatial and temporal distribution of safe sites. However, there are few quantitative data available describing these processes for willows in montane environments.

The objectives of this study were the following: (1) to identify how relative elevation and soil texture affect willow seedling emergence and survivorship, (2) to assess above and belowground growth patterns in nursery-grown and field-grown willow seedlings, and (3) to quantify factors influencing natural patterns of seedling emergence and survivorship on different fluvial landforms.

STUDY SITES

Research was conducted in Horseshoe (elevation ~ 2,600m) and Moraine Parks (elevation ~ 2,480m), two low-gradient alluvial valleys located on the east slope of Rocky

Mountain National Park, Colorado. The sites occupy former lakebeds located behind Pleistocene terminal moraines (Elias 1995). Fall River flows eastward through Horseshoe Park, and is characterized by a strongly meandering, pool-riffle morphology. The Big Thompson River splits into a series of distributaries at the head of Moraine Park, converging again in the far eastern end of the site. Streamflow is snowmelt dominated, with ~37% of the annual streamflow occurring during June (USGS gauge #06733000; 1948-1998). Peak flow typically occurs in early June, with discharge rapidly declining over the remainder of the summer. The area receives a mean annual precipitation of ~35 cm, a significant portion of which comes during the late-summer monsoon season (Western Regional Climate Center; Estes Park station #052759; 1948-2001).

Riparian shrub communities dominated by willows (primarily *Salix monticola, S. geyeriana*, and *S. planifolia*) occur along with wet and dry meadows dominated by a range of herbaceous plant species. The westernmost portions of both sites are relatively undisturbed, and support dense tall willow communities. The density and stature of willows decreases to the east, probably the result of intense historical disturbance, high winter elk density, and in Horseshoe Park, the effects of the 1982 Lawn Lake flood (Keigley 1993; Peinetti et al. 2002).

METHODS

Growth characteristics of greenhouse and field-grown willow seedlings
In June of 2000, mature catkins were collected from six *S. monticola* plants, and air-dried for approximately 2 days to allow full capsule dehiscence. Plant nomenclature for species follows Weber and Wittmann (2001). Catkins from each willow were pooled and approximately 50 seeds from each individual were randomly selected and placed onto the surface of propagation trays filled with a 50:50 (v:v) mix of topsoil and horticultural sand and

placed under misting benches in the RMNP greenhouse. After three weeks, emerging seedlings were transferred to plastic-lined trays filled with water maintained to a depth of 4 cm below the soil surface. Approximately every three weeks during the summer of 2000, 10 to 12 seedlings were randomly selected and harvested. Soil was removed from roots by gently immersing seedlings in water, taking care to avoid root breakage, and the lengths of both the shoot and the taproot were measured. Harvested seedlings were oven-dried to a constant mass and the above and belowground portions separated and weighed to assess biomass. In September of 2000, all remaining seedlings were transplanted into 30cm deep Zipset® plant containers (Monarch Manufacturing Inc.) and moved outside to the RMNP nursery to overwinter. Seedlings were watered three times a week during the spring and summer of 2001, and were harvested during the second week of September. Above and belowground mass and plant height and root length were analyzed using linear regression methods (Sigmaplot; SPSS Inc. 2002).

Seedlings 15 months in age from the experimental plots (described below) were carefully excavated in late September of 2001. Rooting depth and shoot height were measured in the field, and excavated seedlings collected for analysis. Seedlings were oven-dried at 105° C for 24 hours and the above and belowground portions separated and weighed. A significant numbers of seedlings showed evidence of small mammal herbivory and were excluded from analyses. The remaining seedlings were pooled for analysis.

Experimental analysis of willow seedling emergence and survivorship

In early June 2000, a replicated 2x3 factorial experiment was established on point bars in Horseshoe Park to test the effects of soil texture and relative elevation on seedling emergence and survivorship. Six replicate sets of paired 0.25 m² plots were established at 30, 55 and 80 cm above the mid-July stream stage. Soil in one of each pair consisted of native coarse sand and gravel, whereas the soil in the other plot was removed to a depth of

approximately 30cm and replaced with a loamy-sand excavated from nearby cut banks and backwater areas. Due to concerns regarding low levels of natural seed rain in the study sites, willow seeds were broadcast at a density of ~300 seeds/m^2. In addition, plots were misted daily with approximately 500 ml of water for one week following seeding to encourage seed germination. Small exclosures were constructed around each pair of plots to reduce elk herbivory and prevent human trampling. Willow seedlings were tallied in the second week of July and the first week of September of 2000, and the second week of June and the second week of September 2001.

Repeated measures ANOVA using the MIXED procedure in SAS was used to analyze seedling count data. Seedling counts were square-root-transformed to meet the assumption of equal variance for ANOVA. Differences between individual treatment means were compared after the Tukey-Kramer multiple comparisons adjustment.

Analysis of natural seedling emergence and survivorship

The importance of soil surface characteristics, vegetation cover, relative elevation, and soil texture to patterns of natural seedling emergence and survivorship was investigated on one point bar and one recently abandoned channel in Moraine Park. In July of 2000, three randomly selected bands of 0.25 m^2 cells running perpendicular to the stream margin were established along an elevation gradient from the late summer water line to the margin of continuous vegetation cover. Elevation was measured in each cell using a laser level, and live seedlings tallied in July and September of 2000 and September 2001. At the time of the first count, ocular cover measurements of vegetation, coarse fragments (clasts >3cm in diameter along the intermediate axis), coarse woody debris (>3cm in diameter), litter, and bare ground were made in each cell. Soil samples were collected to a 10cm depth immediately adjacent to

each cell and the percentage sand and fines (silt+clay) was determined using the hydrometer method (Gee and Bauder 1986).

Stepwise logistic regression was used to model seedling survivorship over the study period in relation to elevation, landform type, percent fines, and ocular cover measurements. Percent litter was not analyzed due to concern regarding collinearity with other ocular variables. Factors were eliminated from consideration until only those with ≥ 0.05 significance remained. Model fit was assessed using the likelihood ratio statistic and McFadden's ρ^2, an analogue to the coefficient of determination in linear regression.

RESULTS

Growth characteristics of greenhouse and field-grown willow seedlings

The ratio of above versus belowground biomass in nursery-grown seedlings changed over two summers of growth. During the first year of growth, leaves and stems accounted for 55-65% of biomass. However, root length increased at a faster rate than shoot height, exceeding shoot height by a factor of five by the end of the first summer (Figure 1). After ~75 days of growth, above and belowground biomass were approximately equal (Figure 1), but by the end of 2001, root growth accounted for nearly 80% of total plant biomass. A similar allocation pattern was observed in seedlings of the same age excavated from field plots (Figure 2).

Experimental analysis of willow seedling emergence and survivorship

Initial seedling densities varied among treatments and replicates, ranging from 0 to over 230 seedlings/m^2. Despite the initial watering treatment, no seeds successfully germinated in any high elevation coarse textured plots. Significant mortality occurred across all treatments over the two-year study period. In the spring of 2001, low elevation plots were inundated by

spring floods, resulting in a 96% mean mortality rate between 2000 and 2001. In contrast, the high elevation fine textured plots had the highest mean survivorship rate of 29.3% over the study period. Although seedlings in the fine and coarse textured plots at intermediate elevations experienced higher overall mortality rates (81.9% and 83.9%, respectively) than the high elevation fine-textured plots, they had higher mean seedling densities (Figure 3). Type III fixed effect tests for the three main factors (date, texture, and elevation), as well as all two-way interactions, were statistically significant at α=0.05 (Table 3-1).

Natural seedling emergence and survivorship

The density of first year seedlings was highly variable, ranging from 0 to >250 seedlings/m^2. The highest seedling densities in both 2000 and 2001 were found at low and intermediate elevations in the abandoned channel (Figure 4 a & c). Seedlings occurred in sites with a range of vegetation cover values in the abandoned channel, but were limited to areas with low and intermediate plant cover on the point bar (Figure 4 b & d). Second year survivorship showed a much weaker correlation to vegetation cover on both landforms. A greater percentage of fines were found on the abandoned channel (t-test; t= -4.93; P < 0.0001), perhaps contributing to the higher initial seedling densities observed there. However, the range of soil textures present on both landforms was relatively low (Figure 5), and percent fines was not a statistically significant predictor of seedling survivorship. In the logistic model fit to September 2000-September 2001 survivorship data, elevation, landform, vegetation cover, bare ground, and coarse woody debris were significant variables [Logit (probability of survival) = -5.78 + 1.29(landform) + 0.188(elevation) – 0.004(elevation)^2 + 0.046(%vegetation cover) + 0.063(coarse woody debris)]. The likelihood ratio indicated adequate model fit (χ^2 = 130.8; d.f. = 6; P < 0.001), however, the McFadden's ρ^2 value of 0.20 was relatively low.

DISCUSSION

Two mechanisms appear to be important in determining initial seedling emergence and survivorship on point bars in the study areas. First, the failure of willow seeds to germinate in the high elevation coarse textured plots despite watering indicates that these sites may be prohibitively dry for seedling establishment except during years with high peak flows or significant precipitation. The relative success of seedlings in the fine-textured high elevation plots, which have a higher soil water holding capacity, suggests that soil moisture is the principal factor influencing initial willow seedling establishment at high elevations on point bars.

The importance of soil texture to willow seedling survivorship, through its influence on soil water holding capacity, is consistent with other published studies of riparian plant establishment. In a study of cottonwood establishment in western Colorado, Cooper et al. (1999) found that the presence of loam-textured soils controlled the locations where seedlings could survive. Although germinants appeared at a wide range of elevations and soil textures, they survived only in sites well above baseflow stage where fine-textured sediments had been deposited. In a series of experiments in Arizona, Sacchi and Price (1992) demonstrated that a lack of soil moisture was the predominant cause of mortality among willow seedling cohorts. Woods (2001) directly linked willow seedling survivorship with soil moisture in his study of a subalpine willow community in Rocky Mountain National Park, in which seedling survivorship was significantly correlated with soil texture and relative elevation above the groundwater table.

Shear forces created by flood events are another major factor influencing willow establishment patterns. For example, Johnson (1994) found that June flows above a certain

threshold value effectively prevented willow and cottonwood seedling establishment on the Platte River, Nebraska. Levine and Stromberg (2001) demonstrated that willow seedlings were particularly vulnerable to flood scour when they were less than 3 to 4 cm in height, greater than the mean height of 2.8 cm observed after one summer of growth in greenhouse-grown seedlings in this study.

Our results suggest that only a small portion of any point bar is likely to meet a seedling's requirements for both sufficient soil moisture during dry and hot summer months, and adequate protection from flood erosion and sediment deposition during subsequent spring floods. The extent and distribution of sites suitable for establishment is variable spatially and temporally and is controlled by the magnitude and frequency of flood events and the general shape of the discharge hydrograph (Mahoney and Rood 1998; Levine and Stromberg 2001; Amlin and Rood 2002).

Results from these studies suggest that fluvial landform types differ in the opportunities they provide for willow establishment. In the study areas, willow establishment occurs primarily on abandoned beaver ponds, oxbow channels, and point bars, each differing in several important characteristics. Point bar soils primarily consist of large gravel and cobbles, providing a high degree of surface relief favorable to willow seed entrapment, but with low water-holding capacity and annual exposure to high-energy flood events. In contrast, sediments deposited behind beaver ponds are more fine-textured with higher water-holding capacity. Beaver dams may continue to impound water long after abandonment (Butler and Malanson 1995; Gurnell 1998; Meentemeyer and Butler 1999), providing stable high water tables. In addition, beaver dams may cause channel avulsions, diverting the stream and reducing the risk of flood erosion. Point bars and beaver ponds represent distinct endpoints of a stream energy

gradient. Abandoned channels may be intermediate between these two landforms with regard to soil moisture and stream energy. These sites typically experience low current velocities resulting in low shear stress and the deposition of more fine-textured sediments than typically found on point bars.

Higher seedling densities on the abandoned channel compared with the point bar suggests that landform type can affect initial rates of seedling emergence and survivorship. The landforms were located close spatially, and likely had identical willow seed rain inputs. The logistic regression model explained only a small portion of the overall variation in seedling establishment, suggesting that additional, unmeasured variables or stochastic processes are contributing to the observed establishment patterns.

The distinctive growth and allocation patterns exhibited by both the nursery and field-grown seedlings highlight the challenges faced by seedlings in obtaining critical resources. The high initial investment in leaves and shoots observed in the weeks following germination reflects a need to develop adequate photosynthetic area. The shift in biomass allocation towards root growth observed in the middle of the first season suggests that water, and possibly nutrient acquisition, become more important. Although mature willows are generally considered phreatophytic (Alstad et al. 1999), observed rooting depths of field grown seedlings indicates that several years of growth is required before access to groundwater is achieved.

CONCLUSIONS

This study suggests that multiple factors influence willow seedling establishment in the study area. The availability of water, controlled largely by soil water-holding capacity and height above the declining summer water table, is critical for both seed germination and initial seedling survivorship. However, mortality from flood erosion and sediment deposition also

limits survival at low elevations on fluvial landforms. Thus, the spatial distribution of safe sites is bounded by these two factors. The spatial and temporal distribution of suitable sites is dynamic, driven by high variability in intra and inter-annual streamflow and mediated by factors including channel geometry, landform type, soil texture, and summer rainfall. The relative importance of these physical factors on establishment patterns is also influenced by the growth and allocation patterns of individual plants. Access to resources such as light, water, and nutrients, as well as resistance to flood erosion or sedimentation, are influenced by above and belowground growth patterns.

In the study area, geomorphic processes, historically influenced by the activities of beaver, are ultimately responsible for the creation of the landforms required for willow establishment. Even absent other potential limitations such as lack of seed rain or strong herbivory pressure, changes in geomorphic drivers, whether the result of declining beaver populations or climate change, may threaten future willow recruitment in the elk winter range.

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Table 3-1. Results of repeated measures ANOVA from experimental seedling survivorship plots. Main treatment effects are texture (fine, coarse); elevation (low, intermediate, high); and date (September 2000, June 2001, September 2001).

Effect	DF	F statistic	P value
Texture	1	22.95	<0.001
Elevation	2	5.81	0.013
Texture*Date	2	14.66	0.009
Date	2	47.71	<0.001
Texture*Date	2	6.53	0.004
Elevation*Date	4	10.11	<0.001
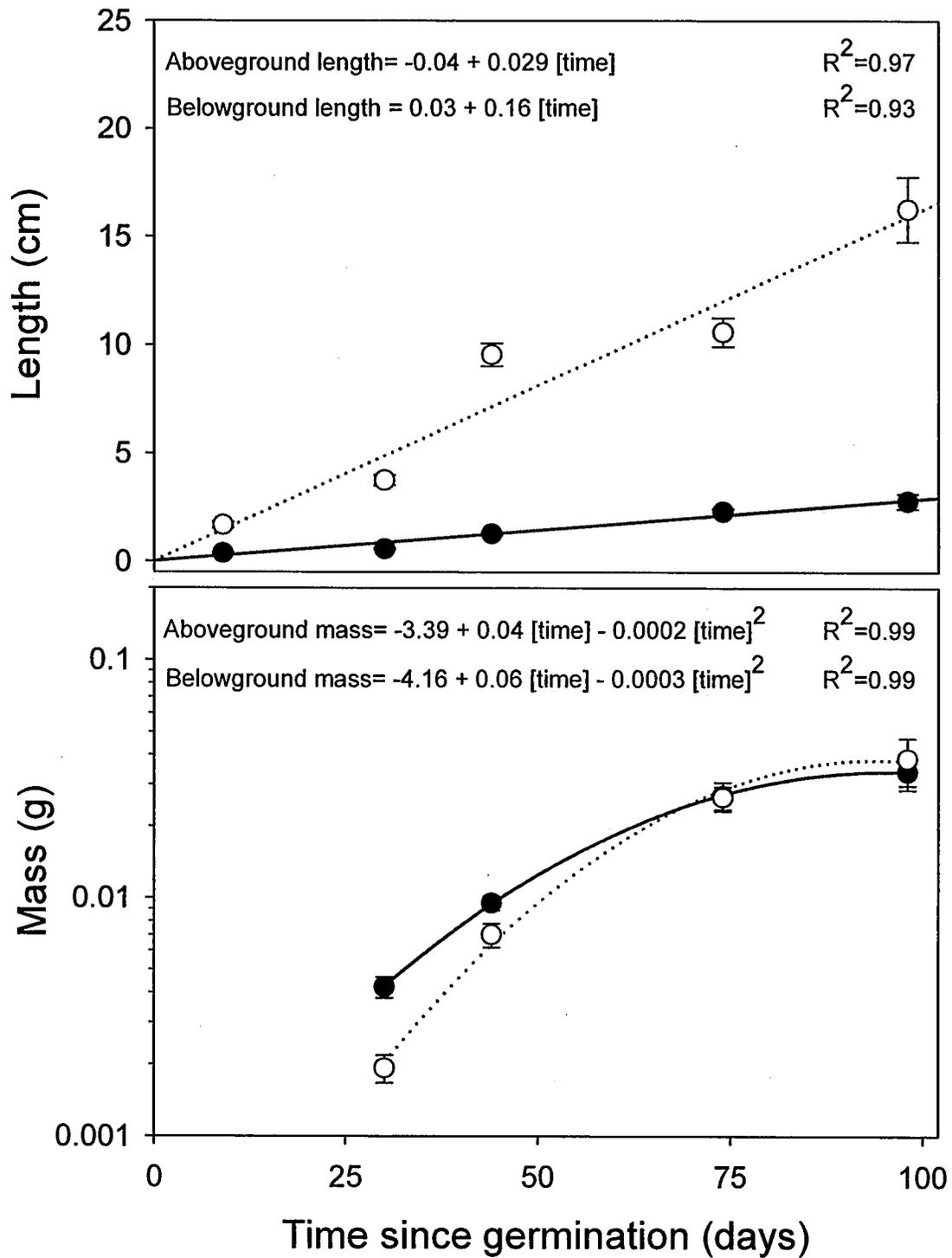
Figure 1. Mean length (top) and biomass (bottom), +/- 1 s.e., for above (●) and belowground (○) portions of greenhouse-grown seedlings. Plotted lines represent least squares regression lines.
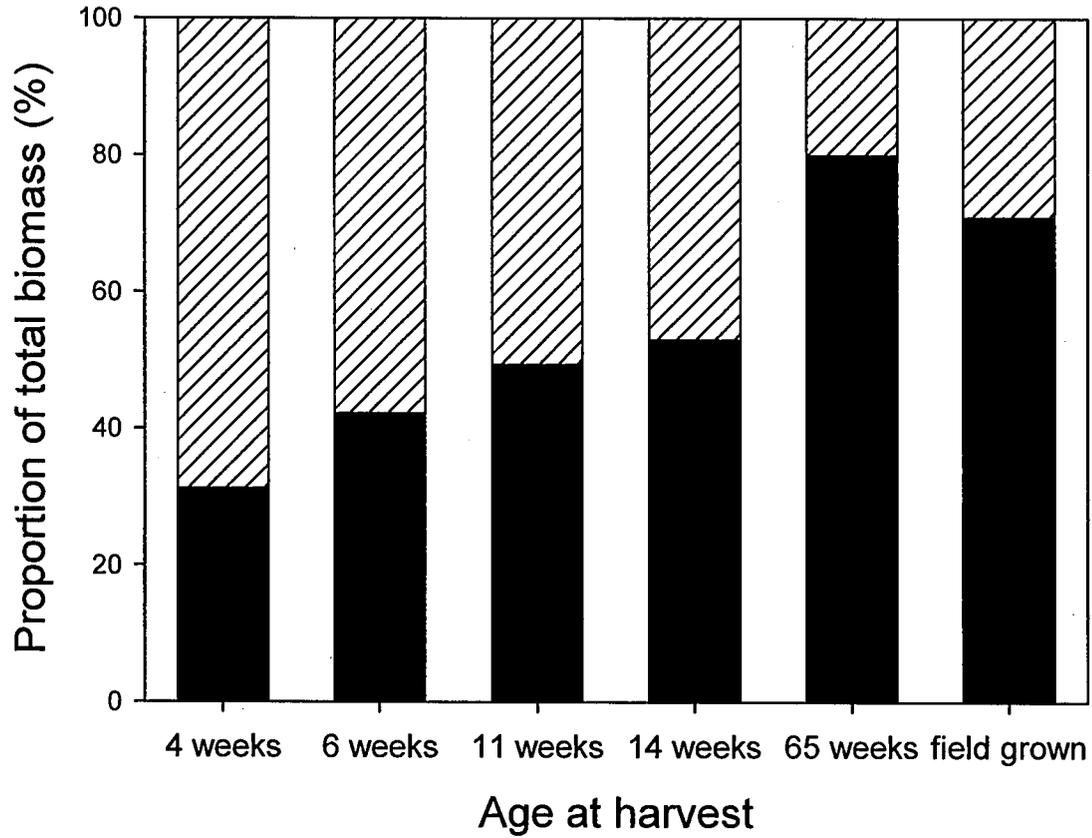
Figure 2. Proportion of above (hatched area) and belowground (solid area) biomass in *Salix monticola* seedlings grown in a controlled setting and excavated from field plots. Field-grown seedlings were approximately 65 weeks old.
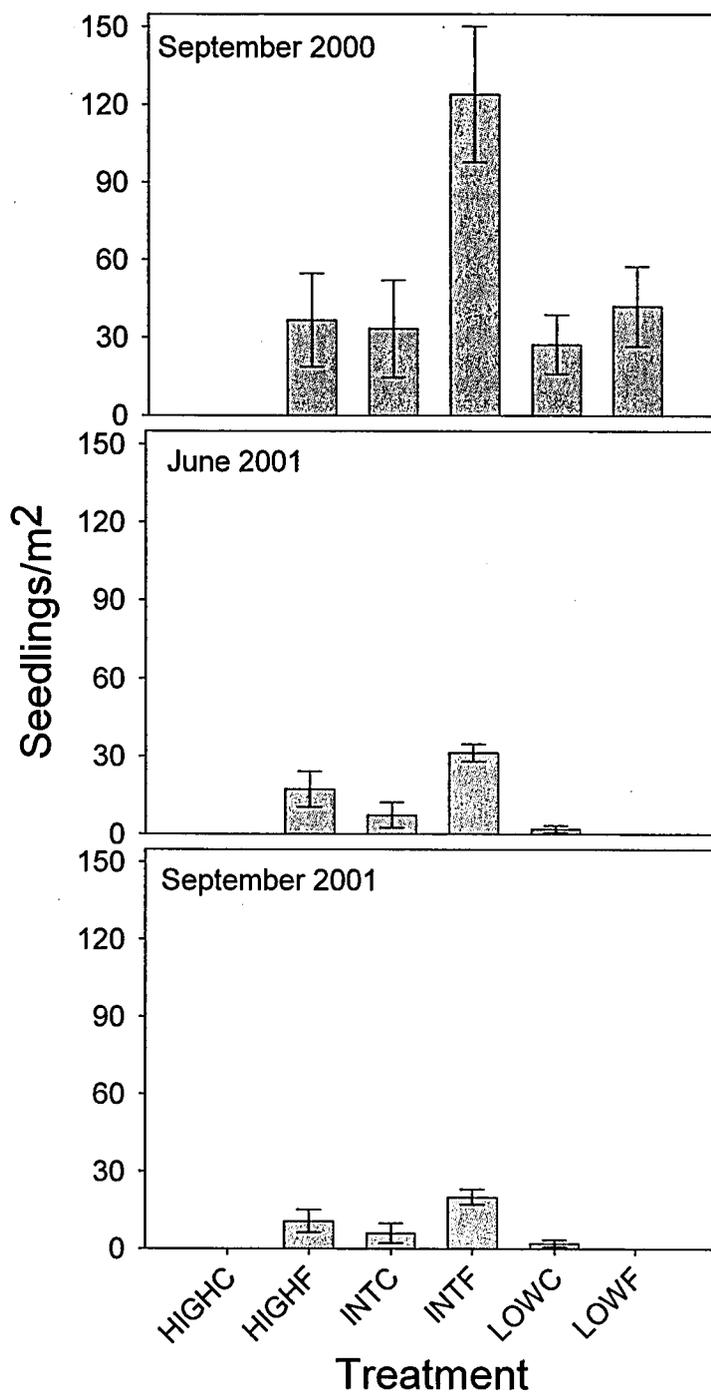
Figure 3. Mean seedling density (+/- 1 std. error) in study plots in September 2000; June 2001; and September 2001. Treatment abbreviations are: highc=high elevation, coarse texture; highf=high elevation, fine texture; intc=intermediate elevation, coarse texture; intf=intermediate elevation, fine texture; lowc=low elevation, coarse texture, and lowf=low elevation, fine texture.
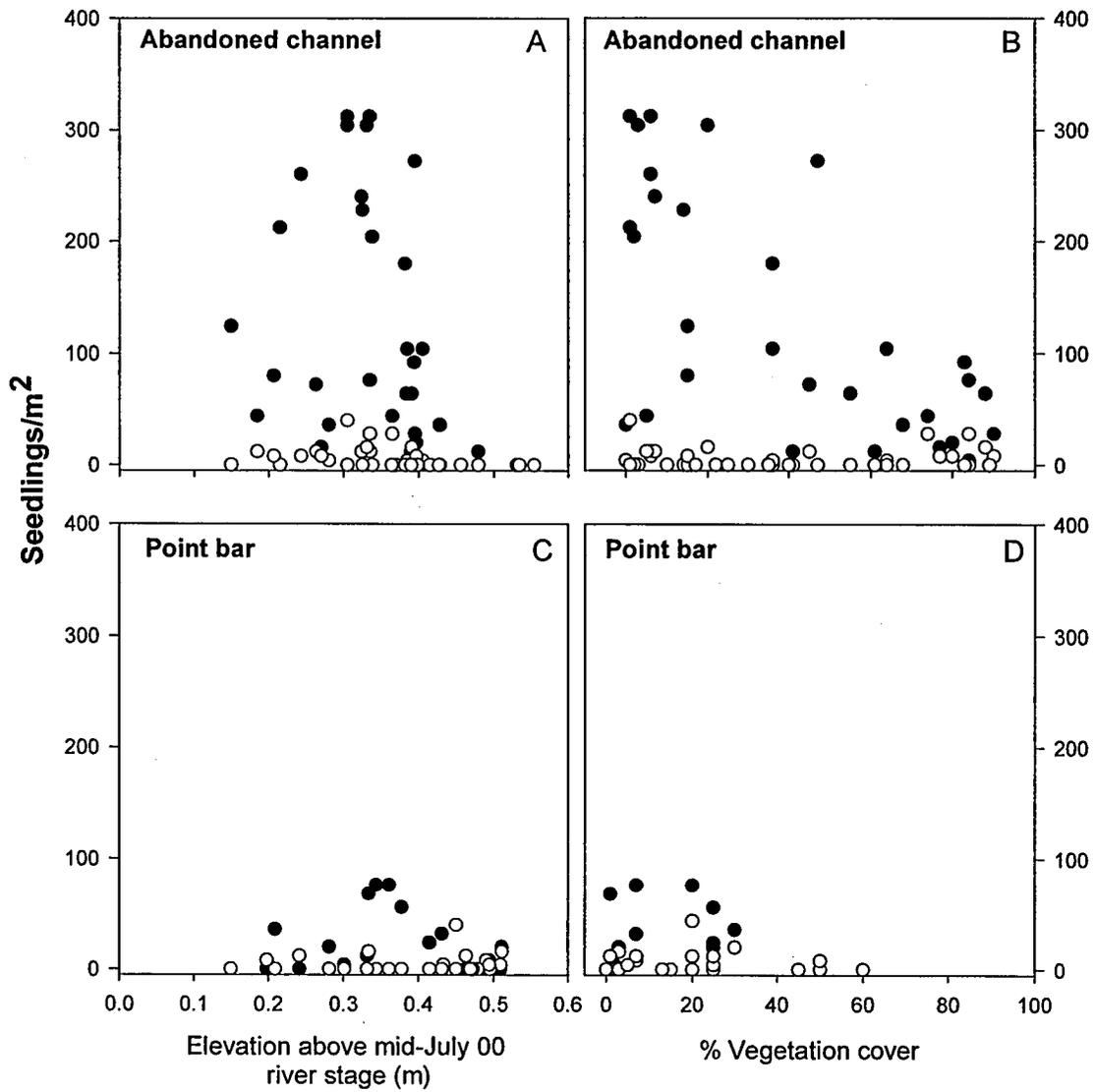
Figure 4. Seedling density in September 2000 (●) and September 2001 (○) plotted against elevation (A and C) and vegetation cover (B and D) for abandoned channel and point bar landforms.
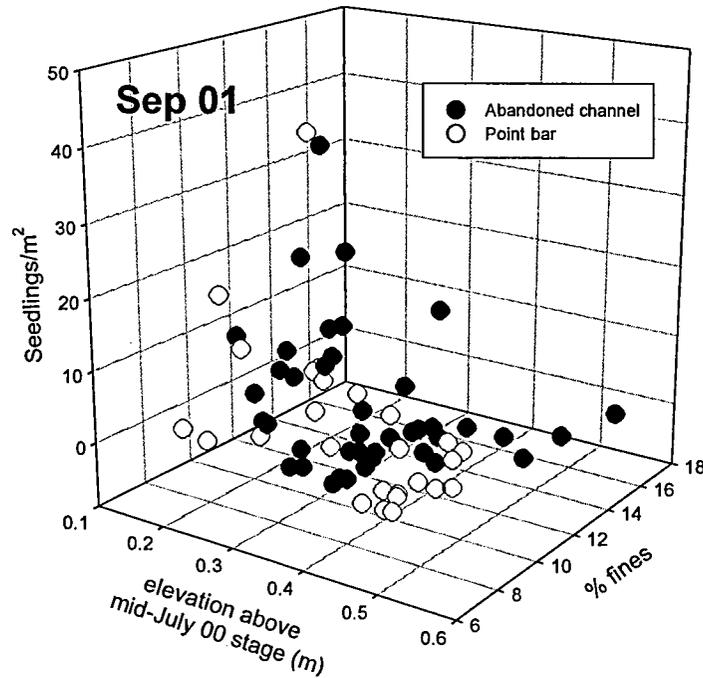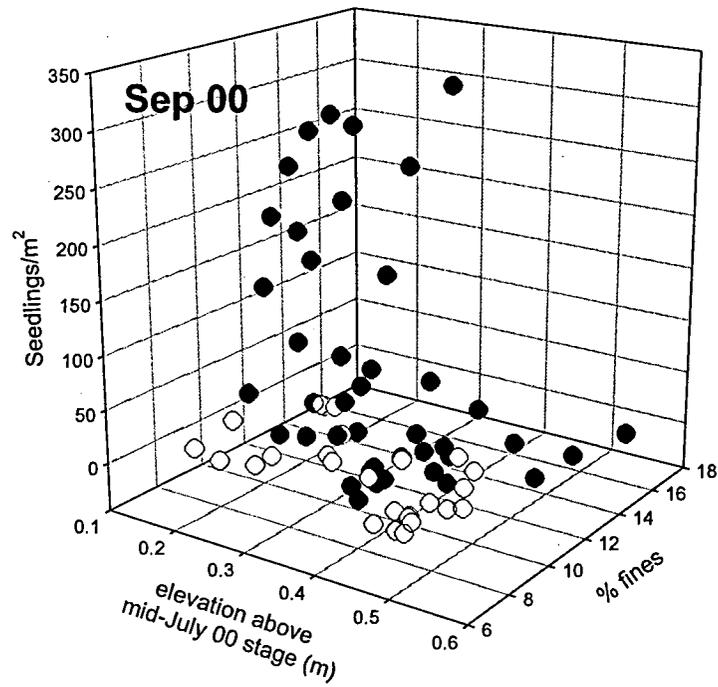
Figure 5. Seedling density (z axis) in September 2000 (above) and September 2001 (below) plotted against relative elevation (x axis) and the combined percentage of silt and clay (y axis) on an abandoned channel and point bar. Each point represents the seedling density in one 0.25 m² plot.

CHAPTER 4. HYDROLOGIC, GEOMORPHIC AND CLIMATIC PROCESSES CONTROLLING WILLOW ESTABLISHMENT IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

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ABSTRACT

Although willow communities dominate mid-elevation riparian complexes in Rocky Mountain National Park, the stands are rapidly declining in aerial cover and condition. Our research is an effort to understand the processes that have facilitated or limited willow establishment, defined as survival through three growing seasons, over the last half of the 20th century. The questions addressed here are: (1) which fluvial landforms serve as sites suitable for willow establishment? (2) Is willow establishment on these landforms driven by their unique hydrologic regimes? (3) How do, or could, climate driven variations in streamflow influence the establishment of willows?

At sites in Moraine and Horseshoe Parks, three fluvial landforms provide the bare, moist mineral substrate necessary for willow establishment: (1) point bars along stream channels, (2) draining beaver ponds, and (3) abandoned channels that function as ox-bows. Excavation and precise aging of willows from each landform type was used to determine the historical spatial and temporal patterns of willow establishment.

70

Point bars had willow recruitment nearly every year. Former beaver complexes generally experienced a single episode of establishment following dam-breach, while abandoned channels showed continuous recruitment over a limited period of time following abandonment.

Using records of stream flow available from USGS gauges in the vicinity of the study areas, we analyzed relationships between instantaneous peak flow magnitude and years that willows did and did not establish on each landform. Analysis of relationships between peak flow and the periodicity of willow establishment reveals that the critical peak flow for establishment varies, depending on the site's dominant geomorphic process. Establishment on point bars and abandoned channels is driven by peak flows between the 2 and 5-year return interval flow levels, while abandoned beaver ponds experience most establishment in the year of and following dam breach, which is associated with flow events >5-year return interval flow.

Global climate change models predict that temperatures will increase and precipitation seasonality will shift over the next decade in the Rocky Mountains. The Regional Hydro-Ecological Simulation Systems model (RHESSys) predicts these changes will result in earlier spring runoff, lower flows from late-spring to fall, decreased snowpack and decreased soil moisture in the Colorado Front Range. This means a longer, drier summer in the riparian corridor, resulting in higher seedling mortality due to water stress. The reduction in snowpack predicted is likely to result in a significant decrease in moderate and high peak flows, decreasing the opportunities for willow establishment and causing significant changes in the rate of landform creation. However, the return of beaver to the system may be able to mitigate

water table and soil moisture declines and create increased opportunities for willow

establishment through the creation of abandoned beaver complex and abandoned channel sites.

INTRODUCTION

Willows (Salix spp.) are the dominant woody plants of riparian corridors in boreal and montane regions throughout the Holarctic, including mid-elevation regions (2,800 - 3,500 m) throughout the southern and central Rocky Mountains (Bliss 1957, Ellenberg 1988, Zoltai et al. 1988, Rodwell 1991). Willows enhance stream bank stability, provide the majority of riparian primary production, shade streams and provide organic matter input that drives aquatic food chains (Naiman and Decamps 1997). In addition, willow stands provide habitat for passerine birds, beavers and ungulates (Knopf 1986, Baker and Cade 1995).

Most willows are obligate riparian shrubs, tied in all life history stages to the hydrologic and geomorphic environments of river margins and riparian corridors. Riparian corridors are defined here as the landscape extending from the low flow stream channel margin to the edge of upland vegetation, including all areas influenced by stream-controlled hydrologic, geomorphic and ecological processes. Salicaceae species establishment is tied to riparian corridors because of seedling needs for high soil water content, and relatively shallow water table depths (Krasny et al. 1988, Sacchi and Price 1992, Mahoney and Rood 1998, Cooper et al. 1999), as well as stream flow characteristics, such as annual peak flow and seasonal flow variability that provide the bare mineral soil where plants can establish (Everitt 1968, Bradley and Smith 1986, Baker 1990). Most previous research on Salicaceae seedling establishment has been on Populus species, little research has been performed on Salix species.

Throughout the central and southern Rocky Mountains, willow communities are declining in size and condition and little willow reproduction occurs. Thus, the future of montane willow-dominated ecosystems is uncertain (Singer et al. 1998; Stromberg et al. 1996, Peinetti et al. 2000). The decline may be attributable to a number of factors, including a

73

warmer 20th century climate (Singer et al. 1998), overgrazing by native or introduced ungulates (Kay 1997, Keigley 2000), flow regulation (Bradley and Smith 1986, Auble et al. 1997, Merritt and Cooper 2000), or declining beaver populations (Singer et al. 1998, Mitchell et al. 1999). Elk and beaver both use willows for food, and beavers use willows for dam and lodge building materials. Attempts to identify the cause of willow decline are hampered by a lack of information on the hydrologic and geomorphic requirements of willow establishment.

Willows produce a large quantity of small, wind and water dispersed seeds, which remain viable for 3 days to at most several weeks (Densmore and Zasada 1983). The seeds typically germinate within 24 hours of arrival on bare, moist substrates (Fenner et al. 1984), therefore it is important that the timing of willow seed rain aligns with the formation of suitable bare and moist sites (Walker et al. 1986, Johnson 1994). However, little is known about the fluvial landforms and hydrologic regimes that provide suitable habitat for willow establishment and survival past the seedling stage. Seedling mortality rates are very high during the first growing season (Walker et al. 1986, Sacchi and Price 1992, Johnson 1994). After 3 years, the likelihood of a willow's survival is increased by the development of a well-established root system (Sacchi and Price 1992, Cooper et al. 1999). Survival over the initial 3 years depends largely on soil moisture and protection from disturbance.

Seedlings established in low landscape positions near an active stream channel are subject to scour and burial by subsequent high flows (Nanson and Beach 1977, Friedman and Scott 1995). When buried by sediment, willow stems may adventitiously root and replace stems by sprouting (Densmore and Zasada 1978, Krasny et al. 1988). Germinants on higher riparian landforms are subject to increased risk of desiccation as water tables decline during the growing season and soils dry out. The likelihood of seedling establishment and survival is highest where

desiccation and disturbance risks are balanced by elevation, rates of stream flow recession and water table decline, and soil water-holding capacity (Krasny et al. 1988, Sacchi and Price 1992, Cooper et al. 1999). Mahoney and Rood (1998) refer to this zone as the "recruitment box".

Riparian corridors are dynamic, and fluvial processes are constantly creating and destroying sites suitable for willow establishment (Hupp and Osterkamp 1996, Scott et al. 1996). The rate of suitable landform creation can be altered by changes in the timing, magnitude, frequency or duration of flows and by the resultant changes in stream power and sediment load. These changes can occur due to abiotic controls such as flow regulation or climate change, and biotic factors such as beavers, which dam streams. Developing an understanding of the geomorphic and hydrologic processes that facilitate or limit willow establishment is essential for determining effective conservation and restoration strategies.

Models of global climate predict that temperatures and possibly precipitation will increase over the next decade in the Rocky Mountains (Kittell et al. 1997, Kittell et al. 2000, Hadley Centre (HADCM2) and Canadian Climate Center (CGCM1) climate change experiments, (<http://ipcc-ddc.cru.uea.ac.uk/cru_data/datadownload/ download_index.html>). The Regional Hydro-Ecological Simulation Systems model (RHESSys) has been used to determine how these climate changes may affect hydrologic regimes of streams. Earlier spring runoff and lower peak flows are predicted for the Colorado Front Range streams (Landrum, pers comm). By determining the hydrologic conditions critical to willow establishment, it will be possible to predict willow response to climate change scenarios.

The present research focuses on the following questions: (1) which fluvial landforms serve as sites suitable for willow establishment? (2) Is willow establishment on these landforms driven

by their unique hydrologic regimes? (3) How do, or could, climate driven variations in streamflow influence the establishment of willows?

STUDY SITES

We studied two montane riparian areas, Moraine and Horseshoe Park, located on the eastern side of Rocky Mountain National Park, Colorado (Figure 1). Moraine Park (2.51 km^2) is in the Big Thompson watershed at an elevation of 2481 m. Horseshoe Park (1.95 km^2) is located in the Fall River watershed at 2598 m. Both the Big Thompson and the Fall River are free flowing without either upstream dams or water diversions, and large riparian communities dominated by willows occur along both rivers. Six willow species are most abundant, *Salix bebbiana, S. geyeriana, S. monticola, S. planifolia, S. lucida* ssp. *lasiandra* and *S. gracilis*. Plant species nomenclature follows Weber and Whittmann (2001).

During the summer of 2000, we identified three major landforms that can provide the bare, moist substrate necessary for willow establishment: (1) point bars along active stream channel margins, (2) abandoned and drained beaver pond complexes, and (3) abandoned river channels/ox-bows. The suitability of these sites for willow establishment was determined by the presence of bare moist substrate and confirmed by an abundance of willow seedlings.

Point bars form on meandering streams where erosion of outside meander banks and deposition on inside banks occurs. Sediment deposition occurs largely in years with flows of less than 5-year recurrence (Wolman and Miller 1960). Because point bars are continually aggrading and being reworked by moderate flows, we anticipated that willows would establish in years of moderate flows, when sufficient sediment is deposited and disturbance is moderate. Point bars in this study were defined by position on the inside of meander bends, a cobble/gravel substrate and a gradual slope to waters edge rather than a steep bank (Figure 2).

76

Beaver dams form ponds which inundate and drown existing vegetation and cause the deposition of fine-grained sediments. When a dam and pond is abandoned it may leave bare, moist soil in the former pond bed and may drain slowly, temporarily maintaining a high water table (Figure 3). This may provide establishment sites at higher elevations relative to the channel height than point bar establishment sites. We anticipated that establishment would occur in the years following abandonment because as the dam was breached and the pond drained water tables would fall causing the substrate to dry, limiting establishment opportunities. If the active stream channel resumes flow through the pond, the site may switch from a pond to a stream environment leading to point bar formation. An abandoned beaver complex in this study was identified by remnants of a dam and/or lodge.

Channel abandonment may occur when beavers divert water from the stream onto the floodplain leading to the formation of new channels (Woo and Waddington 1990). Under these conditions, when the dam is breached the former stream channel may be abandoned and function as an ox-bow. In addition to channel abandonment due to beaver activity, avulsion may occur in meandering stream reaches where erosion causes channel cut offs (Figure 4). The majority of flow bypasses the cutoff portion of the channel, which forms a low-energy channel reach. Bare, moist sediment may accumulate in the ox-bow until water can no longer flow through the former channel. Abandoned channels may have greater soil texture variability than other fluvial landforms due to their transitory nature. Varying flow velocity, both within the site and through time, would cause coarse deposition early in the cutoff process and on the upstream end of the oxbow, while fine deposition would occur in the later stages and towards the downstream end of the oxbow. Once the channel cutoff is complete, bare moist soil is no longer available and willow establishment opportunities are limited. In this study, an

abandoned channel was defined as having no flow or flow only during peak flow periods and aerial photo evidence that the site historically was the active stream channel.

METHODS

In the first year of this study, one of each landform type was chosen for analysis. One to three 0.5 m wide transects were established on each site across an elevation gradient from stream edge to the point at which perennial vegetation and increased steepness indicated the boundary of the active portion of the landform. All willows within these transects were excavated for aging. Willow seedlings and saplings of known age were also analyzed to perfect our analytical technique, particularly concentrating on the diameter of the first year's annual growth ring. The age structure at each site was used to determine a sampling method for subsequent sampling. Data from multiple grids at a single site were pooled.

Site Selection

In the second year of the study replicate study sites were selected. All point bars, former beaver ponds and ox-bows in the two study areas were identified using aerial photos from 1937, 1946, 1969, 1987, 1990, 1996, 1999 and 2001 and verified by walking the length of all major channels. 1937 photographs were not available for Horseshoe Park. Air photo scales ranged from 1:24000 to 1:3600. 1990 and 2001 photos were digital orthoquads and were used to rectify other photos for mapping and data presentation. Three examples of each geomorphic type were then randomly selected for study, for a total of 9 additional study sites.

Willow Age Determination

In dynamic riparian corridors willows may be buried with layers of sediment during floods (Figure 5) and herbivores often cut willow stems. Because willows are shrubs with

relatively short-lived stems, no stem may be as old as the plant. Therefore, it is necessary to excavate plants to collect root crowns for precise age analysis.

To determine the age structure of willow populations on the three landform types, we excavated and aged willows from each site. Previous aging of willows collected early in the growing season showed that current year growth rings were difficult to detect until significant leaf development occurred in mid to late June. Excavation of willows took place between late-July and early October to ensure a distinct current-year growth ring. At each site, 9-25 plants, each more than 3 years old were analyzed. Plants were selected to reflect the full range of plant sizes, elevation above the stream, and species present. Plants were carefully excavated, and sketched to identify their major roots, position in the soil stratigraphy and depth below current ground surface. Within study sites only *S. monticola, S. bebbiana, S. geyeriana* and *S. gracilis* were present.

Once plants were excavated, they were dried, cut into cross-sections at locations believed to be above, at and below the root crown based on morphologic characteristics such as branching patterns and bark texture, and then mounted on thin planks. Cross sections were then sanded using a handheld random orbit palm sander with progressively finer sandpapers, finishing with a median particle size of 30 μ to allow annual growth rings to be visible for counting under a high power binocular microscope. Willow ages were determined by counting rings at the root crown. Two criteria were used to select the appropriate section: (1) the lowest cross section containing pith, and (2) the section containing the greatest number of annual growth rings. It is common for willows to have partial growth rings, producing a lobate root crown. Where there were differing numbers of rings within a single sample, age was determined from the lobe containing the greatest number of rings.

79

Willow Growth Characteristics

The height of each willow was measured prior to sectioning. Average stem height was used to group willows into seven 10 cm classes from 1-10 cm to 60-70 cm. Root crown diameter was measured by taking the average of two perpendicular measurements. We analyzed willow age versus both average stem height and root crown diameter using linear regression.

Soils

The soil stratigraphy at each excavated willow was sketched to assist in determining site history and identifying the landform on which germination occurred. Soil samples were taken from each horizon for particle size analysis. Five replicate surface soil samples were collected at each of 10 reference sites located within the study area, including 5 point bars, 4 beaver complexes and 1 abandoned channel, to characterize the near-surface soils in each environment. Point bar reference sites had been functioning as bars for at least 20 years based on historic aerial photograph analysis. Beaver complex reference sites were current or recently abandoned ponds. Abandoned channel reference sites had been cutoff from the main channel since 1969. Abandoned channel reference sites were limited because few are unaffected by other factors such as beaver activity. Only one adequate reference site was identified and variation within that site was high.

Soil particle size analysis (hydrometer method modified from Gee and Bauder 1986) was used to quantify the sand, silt and clay content of soil samples collected after samples were run through a 2 mm sieve. Organic matter content appeared low and was not removed prior to particle size analysis. One-way ANOVA was used to determine if the particle size distribution was significantly different between reference landforms. Particle size distributions of soil samples from willow excavation sites were compared to those from reference sites to help identify the landform present when each willow germinated.

Germination Elevation

A one-way ANOVA was used to determine whether elevation of the root crown above the low flow channel differed for the three fluvial landforms analyzed. Three sites could not be included in this analysis because they were not adjacent to an active stream channel. Thickness of sediment deposition over each cross-section location was recorded before cutting. The burial depth of the root crown was subtracted from ground surface elevation to determine germination elevation for each plant.

At one abandoned beaver complex site willows were established on a steep channel bank over a three-year period, a scenario typical of draining beaver pond sites. Willows at this site were excavated from $8 - 0.5 \text{ m}^2$ grid cells located across a gradient from top to bottom of the former channel. Willows excavated from these grid cells were grouped into 4 classes, each consisting of two adjacent grid cells. Class 1 included elevations from 0.71 m to 0.57 m above the channel bottom, Class 2 from 0.57 m to 0.38 m , Class 3 from 0.38 m to 0.29 m to and Class 4 from 0.29 m to 0.16 m. A X^2 test for homogeneity of proportions was used to test the null hypothesis that willows of similar ages were represented at all elevations. The purpose of this test was to determine if willows established at progressively lower elevations each year following dam breach.

Stream Flow

Willow establishment was related to annual instantaneous peak flow using flow records available from USGS gauges. Flow records were obtained from the Big Thompson River at Estes Park (USGS gauge #06733000), which has the longest, most complete period of record, 1946-1998, in the region. The Fall River at Estes Park gauge (USGS gauge #06732500) has a period of record from 1945-1994 and was used for sites in Horseshoe Park. The Big Thompson River at Moraine Park gauge (USGS gauge #402114105350101) has only a two year period of

record, from 1996-1997. The proportion of stream flow at the Estes Park gauge contributed by each of the Big Thompson and Fall Rivers was estimated by subtracting the flow of the Big Thompson River at Moraine Park for the two years when these data are available, from the flow at the Big Thompson River at Estes Park gauge. These percentages were averaged over monthly periods from May thru August and used to calculate the Big Thompson flow in Moraine Park for other years and Fall River flow since 1994.

We analyzed the relationship between instantaneous annual peak flow and the number of willows established per year because of the known importance of peak flow to woody riparian plant establishment (Bradley and Smith 1986, Baker 1990, Johnson 1994). Return intervals for stream flows are presented in Appendix 1, and the 2-year return interval flow was used to classify each year's peak flow as either high or low. High flow years had instantaneous peak flows greater than the 2-year return interval flow at the Big Thompson at Estes Park gauge (29.0 m^3/s), while low peak flow years had peak flow less than or equal to the 2-year return interval flow. The proportion of established individuals germinating in high versus low flow years was calculated and compared to that expected if flow had no effect on likelihood of establishment using a X^2 homogeneity of proportions test.

To determine whether high but frequent flows or infrequent large flood events were more important in willow establishment at these sites, a second X^2 homogeneity of proportions test was conducted. Years with large flood events were years in which the instantaneous peak flow was equal to or greater than the 5-year return interval flow (38.2 m^3/s). This test compared the likelihood of establishment during large flood events with that expected if flow had no significant effect on the likelihood of willow establishment. In all instantaneous peak flow analyses, the secondary peak flow value was used for 1982 because a flood of unnatural

82

magnitude occurred when the Lawn Lake Dam failed flooding the Fall River with a catastrophic flow greater than 155 m³/s. This flood only affected areas downstream of my study sites.

Predicted Climate Change

The potential effects of climate change on stream flow in Rocky Mountain National Park have been modeled using the Regional Hydro-Ecological Simulator System (RHESSys) (Baron et al. 2000). Two global climate models, one from the Hadley Centre for Climate Prediction and Research (Johns et al. 1997) and the other from the Canadian Center for Climate Modeling and Analysis Project (CCC) (Flato et al. 2000) were used to make climate change predictions for the 2031 to 2050 period. This time period was chosen as representative of future climate and because previous modeling and studies associated with this study have been based on the same time period. The Hadley and CCC models were chosen because they are used by the U.S. National Assessment of Potential Consequences of Climate Variability and Change (<www.usgcrp.gov/usgcrp/nacc>). The Hadley model predicts a 2.0 to 2.5 °C increase in temperature and an 8% increase in precipitation in the Rocky Mountain region. The CCC model predicts a 3.0 to 4.0 °C temperature increase and no net precipitation change although it predicts changes in the seasonality of precipitation. Temperature increase estimates are based on average monthly differences from baseline maxima and minima. RHESSys output was combined with the knowledge of flows critical to willow establishment determined in this study to predict the impact of likely changes in climate on willow establishment.

The relationship of snow water equivalent (SWE) on May 1, (Bear Lake Snotel site - site:322 station id: 05j39s USDA Natural Resources Conservation Service; <http://www.wcc.nrcs.usda.gov/water.w_data.html>) to annual instantaneous peak flow at the Big Thompson River at Estes Park gauge was analyzed using linear regression. The Bear Lake

83

site is the only Snotel site located in the Big Thompson watershed. Precipitation and temperature data from a Bureau of Reclamation weather station at Estes Park (station 05-2759-4) were used to further examine years with higher runoff than predicted by the SWE vs. peak flow relationship. The increase in temperature prior to peak flow was determined by subtraction of the "previous average temperature" from the highest temperature occurring during the 7 days preceding peak flow. The "previous average temperature" was defined as the average temperature during the 14 days prior to the week preceding peak flow.

RESULTS

Stream Flow Characteristics

On average, ~47% of flow in the Big Thompson River at Estes Park gauge is derived from the Big Thompson River, which flows through Moraine Park. The remaining ~53% is from Fall River, which flows through Horseshoe Park. Both streams have a snowmelt-driven early summer peak flow followed by declining flows through late summer and autumn. For the period of record, the annual instantaneous peak flow has ranged from 11.5 to 53.0 m^3/s (Figure 6), with minimum and maximum values occurring in 1954 and 1995, respectively. The mean instantaneous peak flow for the period of record is 29.8 m^3/s. A peak flow of 155.8 m^3/s was reached when the Lawn Lake dam broke in 1982 sending its water down Fall River. Peak flows have occurred from May 21 to July 15, with 75% of the annual peaks occurring between June 1 and 21. This period coincides closely with the willow seed dispersal period, which during 2000 and 2001 occurred from early June through the second week of July, and peaked in the third week of June (Gage, unpublished ms.) (Figure 7).

Soil Analysis

Surface soil texture was significantly different between reference landform types (F = 32.48, P < 0.001). Point bar soils had the highest mean sand content, 91.49%, while beaver pond

and abandoned channel soils had mean sand contents of 63.49 and 80.57 %, respectively (Figure 8). Mean clay content was highest in beaver ponds (23.4%), moderate in abandoned channels (11.8%) and low in point bars (3.5%).

In pits excavated for willow collection, stratigraphic analyses suggest that for some sites, sediment accreted under more than one geomorphic regime. For example, a coarse sand and gravel horizon deposited on a point bar may be overlain by a sandy loam horizon deposited in the slack water environment of a beaver pond, indicating that many sites change from one landform type to another due to changes in the position of beaver dams, and the pattern of channel avulsion. Of the 10 sites chosen in this study, 4 showed evidence of a recent shift in landform type.

Germination Elevation

Willows germinated at significantly different elevations among landform types (F = 10.80, P < 0.001), with germination in abandoned beaver complexes at significantly higher elevations than willows in point bar and abandoned channel sites (Figure 9). In the gridded elevation analysis of an abandoned beaver complex, most willows germinated the year following dam breach, however germination continued to occur in subsequent years at significantly lower elevations each year (X^2 = 18.46 P = 0.072) (Figure 10).

Willow Growth Characteristics

Willow root crowns ranged from 0.3 to 6.9 cm in diameter, with minimum and maximum values from 3 and 40 year-old plants, respectively. A log transformed linear regression indicates that root crown diameter was positively related to willow age (R^2 = 0.519, P < 0.001). With a single exception, all willows were less than 50 cm in height and most were 10 – 20 cm tall (Figure 11). No significant relationship existed between willow height and age (R^2 = 0.014, P =

0.311). Evidence of heavy browsing was obvious on all willows (Figure 12), with the majority of stems being browsed.

Willow Establishment Patterns and Relationship to Stream Flow

A total of 189 willows were excavated and aged (57 from point bars, 58 from abandoned beaver complexes and 74 from abandoned channels). Sampled willows ranged in age from 5 to 52 years, representing germination dates between 1950 and 1997. The majority of willows germinated after 1970.

When all landforms were combined in an analysis, peak flows with a return interval of >2 years were significantly related to an increased likelihood of willow establishment (X^2 = 17.86, P < 0.001). Peak flows with a return interval of >5 years did not significantly increase the likelihood of willow establishment (X^2 = 0.00, P = 1.000) indicating that flows between the 2 and 5 year return interval flow were most critical. However, when landforms were analyzed separately, these patterns did not apply to all landforms. Table 2 summarizes the results of X^2 tests.

On point bars, recruitment was continuous throughout the life of each bar with establishment occurring in the majority of years (Figure 13a). Table 1 shows the period when each landform developed as well as the period when establishment occurred.

There is a positive influence of peak flows with return intervals >2 years on willow establishment on point bars (X^2 = 10.13, P = 0.015). Of 57 point bar willows analyzed, 39 (68%) germinated in years with flows > 2-year return interval flows. Alternatively, establishment in years with peak flows >5 year return interval flow was significantly less likely (X^2 = 3.03, P = 0.082), and only 5 willows (9%) from my sample were established in the largest flow years.

Beaver pond sites had a fairly even-age stand structure with willows significantly more likely to establish in the year of or following dam failure (X^2 = 249.8, P < 0.001) with 78% of willows sampled germinating in these years (Figure 13b). There is no evidence of ongoing establishment at these sites, with the exception of seedlings established on newly formed point bars that develop along the newly active stream channel following dam breach.

Flows with return intervals of >5 years and <2 years were important for willow establishment in abandoned beaver complexes. Both beaver complexes studied were abandoned in ~1995, and willows that established prior to 1995 were significantly more likely to be established in years with peak flows less than the 2-year return interval flow (X^2 = 5.87, P = 0.015). In and after 1995, there was a strong positive relationship of establishment with flows greater than the 5-year return interval flow (X^2 = 23.68, P < 0.001).

Abandoned channels showed continuous recruitment for a period of 3 to 36 years after the time of avulsion (Figure 13c). Flows with a return interval of >2 years significantly increased the likelihood of willow establishment in abandoned channels (X^2 = 15.67, P < 0.001). Of 74 abandoned channel willows analyzed, 70% germinated in years with flows > 2-year return interval. A significant number of willows were established in the year of or following a year with flow >2-year return interval flow (X^2 = 25.23, P < 0.001). Years with flows >5-year return interval flow did not produce significantly more willows than expected (X^2 = 0.37, P = 0.540) and willows were less likely to have established in years following flood years (X^2 = 4.66, P = 0.031).

Climate and Stream Flow Relationships

In ~75% of years, peak flow can be predicted by May 1 SWE. However, in other years a much steeper linear relationship occurs (Figure 14), which corresponds with dramatic increases

in temperature or significant precipitation events immediately preceding the recorded peak flow. Either a temperature increase of more than 6.7 °C from the "previous average temperature" or a precipitation event exceeding 1.5" occurred in 4 of the 5 years with rapid meltout. A temperature increase or precipitation event of this magnitude did not occur in any of the normal meltout years.

DISCUSSION

Key Fluvial Landforms for Willow Establishment

Few previous studies have identified the range of fluvial landforms that provide suitable sites for riparian plant establishment (Everitt 1968, Bradley and Smith 1986, Baker 1990, Scott et al. 1997, Mahoney and Rood 1998). We identified three fluvial landforms of primary importance to willow establishment: point bars, draining beaver ponds and abandoned channels. These three landforms function differently in sediment retention and hydrologic regime, and provide distinctly different opportunities for, and limitations on, willow seedling establishment.

Point bars have been widely recognized as key landforms for woody riparian plant establishment (Bradley and Smith 1986, Baker 1990, Johnson 1994). They are prevalent along meandering streams (over 50 were identified in the study areas) and require only moderate, variable flows for formation and reworking (Wolman and Miller 1960). Point bars can be inundated by ponds formed behind beaver dams, which may temporarily eliminate meandering, and allow fine-grained sediment deposition over the very coarse grained sediment of point bars. Willows that established on a point bar may drown in a pond environment. Since 1937, beavers have occupied fewer and fewer areas in either study area. It follows that ponding has been of limited extent and point bar formation has increased in importance for creating suitable sites for willow recruitment.

The process of channel narrowing following a large flood event or due to climate change (Friedman et al. 1996a, Allred and Schmidt 1999) has received considerably more attention for providing sites for woody plant establishment than has the abandonment of entire channel segments (Scott et al. 1996). Avulsed channels form when upstream erosion of a meander bend cuts off a section of channel, or when an obstruction in the channel, such as a beaver dam, causes the creation of a new downstream path, leaving the original channel inactive.

During the period of photographic record, channel abandonment in Moraine and Horseshoe Parks is linked in most cases to beaver dams. The concentrated flow caused by spillover at dams can result in new channel formation (Woo and Waddington 1990, Gurnell 1998), and aerial photo analysis indicated that beaver activity led to the formation of 5 of 7 abandoned channels identified in the study areas. From the limited aerial photo history it was not possible to determine definitively that beaver activity significantly impacted the channel at the remaining two sites during the period of abandonment . One oxbow was formed in an area of Moraine Park where no evidence of beaver activity can be found, but a tight meander occurred. The second is in an area where relict dams and lodges are present but air photographs indicate that beaver activity did not occur in the 20 years prior to cutoff. Opportunities for willow establishment occur in the years following abandonment as the abandoned channel aggrades, a window that varies greatly between sites. Eventually the decreasing availability of moisture due to increased distance from the channel and water table causes the site to become unsuitable for establishment.

During this study we observed considerable variation in the density of willows in abandoned channel sites. Although some sites supported dense willow stands, others had few

to no willows. This suggests that additional factors, such as water table depth and soil water-holding capacity may also influence the suitability of an abandoned channel for willow establishment.

Previous studies have not addressed the indirect impacts of beavers on woody riparian plant establishment (Everitt 1968, Bradley and Smith 1986, Baker 1990, Friedman et al. 1996b, Scott et al. 1996, Scott et al. 1997), however in my study areas the small stream width allows beavers to form ponds across the entire stream channel. When abandoned, these sites can create large areas suitable for willow establishment. Hammerson (1994) found that beaver ponds can cause a several hundred-fold increase in the wetted surface area of the channel and increase the elevation of the water table over an extensive area. Johnson and Naiman (1990) found an average area of 4 ha was inundated by each beaver colony in a boreal forest. Successful establishment of woody riparian species has been linked to depth of water table and soil water availability (Krasny et al. 1988, Sacchi and Price 1992, Mahoney and Rood 1998, Cooper et al. 1999) suggesting that beaver ponds could dramatically increase the area suitable for establishment. While dams are in place ponded water and anaerobic soils make conditions unfavorable for willow establishment (Merritt and Cooper 2000). However, the large-scale establishment that occurs following dam breach suggests that a period of favorable conditions, including suitable water table depths and soil water availability, occurs during and immediately following pond drainage. This period of site availability lasts from dam failure through the following 2 years or longer if drainage occurs slowly.

Beaver ponds are still being created in the study areas although at relatively low rates and the photographic record indicates a significant decrease in beaver activity over the past 65 years. This decrease in the rate of beaver pond formation can be linked to dramatic declines in the

population of beavers in Rocky Mountain National Park during the 20th century, discussed later in this thesis.

Patterns of Stream Flow and Willow Establishment

In previous studies there are conflicting views on the primary importance of infrequent large flood events (Everitt 1968, Friedman et al. 1996a, Scott et al. 1997, Friedman and Lee 2002) versus sustained moderate flows (2 to 5 year return interval) in woody riparian plant establishment (Bradley and Smith 1986, Baker 1990). Our results suggest that both moderate high flows and large flood events are important, but function in different ways and on different landforms. Because the hydrologic characteristics of a site combine with its geologic and geomorphic characteristics to create the physical template for riparian plant establishment (*sensu* Cooper et al. unpublished ms.), an identical flow would not be expected to provide the same opportunities for plant establishment in all types of sites.

Most previous studies of woody riparian plant establishment have either focused on the process of river meandering (Everitt 1968, Bradley and Smith 1986, Mahoney and Rood 1998) or have not distinguished between landforms (Baker 1990, Scott et al. 1997). Scott et al. (1996) has suggested that much of the variation found in the relationship of riparian vegetation to stream flow can be explained by placing results in a geomorphic context. This suggestion is supported by the present study in which we found that low, moderate and high flows are all important, depending on the site's dominant geomorphic process (Table 3).

The likelihood of willow establishment is significantly related to peak stream flow in all three landform types addressed here. On point bar landforms, annual peak flows between the 2 and 5-year return interval flow levels have led to the establishment of most willows that are present. These critical flows fall below those identified by Mahoney and Rood (1998) as the recruitment box for cottonwoods, and the establishment elevation identified here is also lower.

Mahoney and Rood (1998) reported a band of successful recruitment 0.6 – 2 m above the late summer stream stage, while we found establishment occurring only below 0.5 m, which is reasonable considering that their work was conducted on a river considerably larger than the Big Thompson. This difference in elevations may also be due to differing physical requirements of *Populus* and *Salix* species. There are some indications that willows may be more susceptible to drought stress than Populus species (McBride and Strahan 1984, Friedman and Scott 1995, Shafroth et al. 1998).

Willow establishment in abandoned channels is linked to peak flows with return intervals between the 2 and 5-year flows. Both the year of and the year following flows with a return interval of 2 –5 years were important for establishment. The elevation of abandoned channels is initially low and sites are frequently inundated. The majority of establishment occurs at low elevation in these sites (Friedman et al. 1996a, Scott et al. 1996) and flows of high magnitude are likely to inundate the landform during the entire period of seed rain, preventing germination. Although high flow events (>5-year return interval flow) are not linked directly to increased likelihood of willow establishment in abandoned channels, they are likely instrumental in causing the cutoff and initiating aggradation that will allow willow colonization in subsequent years.

For both point bars and abandoned channels there appears to be a threshold in peak flow above which flows are not beneficial to establishment and may even be harmful. Johnson (2000) found similar evidence of a threshold for *Populus deltoides* establishment on the Platte River, Nebraska, and suggested that high June flow limited recruitment by inundating suitable landforms during the period of seed dispersal and removing young plants. Such a threshold

appears to occur at approximately the 5-year return interval flow for point bar and abandoned channel landforms in these study areas.

A different situation occurs in draining beaver ponds in the study areas. The majority of establishment at these sites occurred in or after 1995 and in years with or following a flow >5-year return interval flow. Because aerial photographs were available for 1990 and 1996 it was possible to establish that the dams at both beaver pond study sites were breached during this period, and most willows established in 1995 and 1996 indicating the availability of the largest amount of bare and wet sediment. The likelihood of dam failure increases with larger floods due to increased stream power and sheer stress associated with the transport of larger debris and sediment. The instantaneous peak flow in 1995 was the highest on record for the Big Thompson at Estes Park gauge suggesting that dam breach likely occurred that year. These data indicate that the association of flood events and willow seedling establishment at beaver dam sites is due to an increased likelihood of dam failure in large flood years. However, once a dam is abandoned, the absence of flood events is unlikely to prevent establishment, but drainage would occur more slowly as moderate flows cause the deterioration and ultimate failure of the dam.

Although the majority of willow establishment in Moraine and Horseshoe Park beaver ponds occurred as seedling establishment following dam failure and pond drainage, Cottrell (1995) suggested that willows may establish asexually from stems that beavers incorporated into their dams. During my investigations we found little direct evidence of asexual reproduction. All but one sampled individual had a distinct root crown located within a continuous woody segment, rather than a stem and root growing from a buried willow stem section. We observed sprouting stem fragments in several study sites, but none survived. It is likely that a small number of willows establish asexually in the study areas, but there is so little

beaver activity in the study areas that asexual establishment appears to be relatively unimportant at present.

Establishment prior to 1995 occurred only in years with peak flow <2-year return interval flow. Because this pattern is distinctly opposite to the conditions under which willows established post-1995, it suggests a shift in site conditions. Establishment during years with relatively low-flows suggests that pond levels were lowered leaving a ring of bare, moist sediment suitable for establishment.

The age distribution of willows that established in beaver ponds appear to be controlled by the rate of pond drainage, with slower drainage allowing several willow cohorts to establish, with the oldest plants at higher elevations than younger plants. When the beaver dam completely erodes, the oldest plants are left high above the post-dam channel and water table. A gradual pond drainage likely leads to a longer period of willow establishment because water availability remains high for several years.

Necessity of Excavation

Previous studies of woody riparian plant establishment have focused primarily on *Populus* and many have relied on cores collected from near the soil surface (Bradley and Smith 1986, Baker 1990). However, Scott et al. (1997) and Gutsell and Johnson (2002) have showed this approach is inaccurate for studies attempting to determine the precise year and hydrologic conditions under which the plants established. Willows in my study areas showed little relationship between age and stem height and a stronger relationship between root crown diameter and age that can only be established by excavation. The poor relationship between plant height and age is likely due to heavy ungulate browsing pressure and all plants > 5 years old are approximately the same height.

We also found that the belowground form of plants was impossible to determine from their aboveground characteristics. Willow clumps appearing to be separate plants were often connected by buried stems as shown in Figure 5, while in other instances what appeared to be a single clump was comprised of several individuals, often more than one species of willow. Without excavation, the size, shape, and age of willows may be misrepresented.

Predicted Impact of Climate Change on Willow Establishment

Although the Hadley model did not predict a significant change in the timing of snowmelt and spring runoff, the CCC model predicts that snowmelt and spring runoff will occur 4 to 8 weeks earlier than in the present climate (Landrum, pers com.). The snowmelt driven hydrograph is predicted to retain its current magnitude and shape yet drawdown will occur 4 to 8 weeks earlier than at present. This shift in timing of hydrologic events may influence the timing and success of willow flowering, seed production and seed dispersal. Therefore, it is likely that climate warming may alter the timing of willow life history characteristics.

The recession of flows in late-April through May will create a significantly longer growing season and willows may be subject to a longer summer. Under the CCC scenario for 2011-2020, maximum August and September temperatures will increase ~1.1 °C, and July and September have ~7 % more precipitation. However, August precipitation is expected to decline by 20 %. Under the Hadley scenario conditions are more extreme, with maximum temperatures in both August and September increasing ~1.8 °C and precipitation decreasing ~2 – 4 % in July and September, and ~17 % in August.

RHESSys predicts that under both climate scenarios soil moisture will decline, particularly in the late summer when the greatest water stress occurs. Past RHESSys model runs indicated that under similar scenarios upland soils would dry to a greater extent than at

present during the late summer due to increased evapotranspiration and earlier snowmelt; they also indicated that soil water deficit is controlled more by increases in temperature than precipitation (Baron et al. 2000). RHESSys also predicted that stream flow would be lower than at present from late-spring through fall, resulting in lower water tables during the summer. Because willow seedling roots do not reach the summer water table during at least their first two growing seasons (Gage pers comm.) they are dependent on soil water for survival. Thus, reduced soil water content and a longer summer could reduce seedling survival.

The proportion of years in which normal vs. rapid meltout of the snowpack occurs may change as the likelihood of spring precipitation and rapid warming during the snowmelt runoff period changes. A disproportionate increase in May temperatures or an increase in May precipitation, resulting in more rain-on-snow events, would likely increase the frequency of years with rapid snowmelt leading to higher stream peak flows.

Under the CCC scenario, maximum April temperatures will increase < 0.5 °C, while maximum May temperatures will increase ~2.0 °C. These changes are likely to increase the rate of snowmelt, leading to a higher incidence of rapid meltout. Precipitation in April and May is also projected to increase, particularly in, May when peak flows would occur, with a 15% increase. Under the CCC scenario, warmer winter temperatures and a decrease in winter precipitation would result in reduced snowpack, and lower peak stream flows. Based on the strong linear relationship between 1 May SWE and the instantaneous peak flows in normal meltout years, a decrease in SWE of 19% could significantly reduce the frequency of years having peak flows of 2-5-yr return interval flow, which are critical for willow establishment. However, an increase in the frequency of years with rapid snow meltout may offset the overall decrease in stream peak flows and maintain opportunities for willow seedling establishment.

Even if 1 May SWE were decreased by 50%, rapid meltout would still result in moderate peak flows in 35% of years.

Under the Hadley scenario, snowpack is reduced despite an increase in winter precipitation, due to elevated winter temperatures. This reduction is likely to lead to a reduction in the frequency of peak flows between the 2 and 5 year return intervals. The Hadley model also predicts an ~2.0 °C increase in maximum April temperatures, while May temperature maxima increase slightly (0.4 °C) effectively broadening the snowmelt period. The Hadley model also predicts a very slight (~3%) increase in May precipitation not likely to influence the likelihood of rapid snowpack melt. Because all peak flows with return intervals >5 years occurring between 1982 and 1998 occurred in rapid meltout years, it is likely that a reduction in the incidence of rapid meltout would decrease the frequency of larger floods.

Under both the Hadley and CCC models stream flows critical to willow establishment (>2-year return interval) will occur with reduced frequency, decreasing the opportunities for willow establishment. Because large floods likely have considerable importance in point bar formation, channel avulsion, and beaver dam breaching, geomorphic processes could change significantly. In addition, increased summer water stress would likely cause a significant decrease in willow seedling survival.

Importance of Beaver

Beavers control the hydrologic regime of many riparian sites through dam construction and water routing and in so doing can alter the location and form of stream channels. Beavers commonly expand their travel pathways across floodplains by constructing canals for travel. The ability of beavers to modify the landscape prompted Gurney and Lawton (1996) to call them "ecosystem engineers". Water storage in beaver pond complexes can prolong the rising of the flood hydrograph, dampen the magnitude of flood peaks and provide a higher water table

(Hammerson 1994). Gradual seepage of water to the floodplain can help sustain stream low flows (Hammerson 1994, Gurnell 1998). Beaver activity also increases wetted surface area, soil moisture content and in general provides more favorable conditions for willow growth (Hammerson 1994).

Over the past century beaver populations in the study areas have dramatically declined, as have the landforms that they create. Beaver population surveys in the Big Thompson River watershed were conducted in 1939 (Packard 1947), 1964 (Hickman 1964), 1980 (Stevens and Christianson 1980) and 1999 (Mitchell et al. 1999) with estimates of 315, 102, 18 and 12 animals, respectively with most beaver occurring in Moraine Park. Surveys in the Fall River drainage, including Horseshoe Park, were conducted in the same years, except 1964, with population estimates of 96, 24 and 6 animals, respectively.

The decline of beaver in the study areas has limited the formation of dams, ponds, and abandoned channels, reducing the area suitable for willow seedling establishment and growth (Peinetti et al. 2002). Between 1937 and 1996 dramatic reductions in the complexity of the river pattern occurred. The length of the main stream channel in Moraine Park decreased by 56%, in Horseshoe Park by 44% and the area of ponds decreased 69% and 47%, respectively. There has been a decrease in willow cover of ~20% in both areas as well (Peinetti et al. 2002).

At the same time, the elk population has risen dramatically. Although hunted to extinction by 1900, elk were reintroduced in 1913 and 1914 and by 1942 their population had risen to ~1500 animals. Hunting kept the numbers at ~500 animals until 1967 when hunting was outlawed and the population grew rapidly, reaching >3000 animals in 2001 (Lubow et al. 2002). Approximately 1000 animals winter in Rocky Mountain National Park, and the rest in the Estes Park valley.

Abundent elk provide extreme competition with beaver for willows. Elk browsing is very heavy in the study areas and many areas lack willow stems with sufficient diameter and length for beaver dam construction. Willows are an important food source for beaver (Busher 1996) and food availability is one of three primary characteristics determining suitability of a site for beavers (Gurnell 1996). Although beaver eat grass, herbaceous dicots and aquatic vegetation in summer, they rely on woody food sources during the winter in areas with snow cover (Gurnell 1998). The distance from water that they will forage also limits beavers. Most foraging occurs within 10 m of water, and the maximum distance traveled for food is ~100 m (Howard and Larson 1985, Nolet et al. 1994).

Spring runoff in both the Hadley and CCC climate models is predicted to occur significantly earlier than today, producing a longer and drier summer. Beaver activity is likely to be even more critical in maintaining floodplain ground water levels high enough to support willow seedling establishment. Already a key landform providing establishment opportunities over a large area, beaver ponds are likely to become even more important as continued changes in climate occur in the coming decades.

CONCLUSIONS

Willows have established on three primary landforms over the past 60 years: point bars, abandoned beaver complexes and abandoned channels. The pattern of willow establishment among these landforms varies due to differing dominant fluvial processes. Establishment on point bars occurs continuously throughout the life of the bar. In abandoned beaver complexes establishment occurs in brief episodes following dam breach and abandoned channels experience a limited period of continuous establishment sometime after the channel is cutoff.

Years with moderate peak flows are critical to willow establishment on point bars and abandoned channels, while high flows are most important in abandoned beaver complexes. However, episodes of establishment in abandoned beaver complexes are the result of dam failure and it is likely that once a dam is abandoned, the absence of high flows is unlikely to prevent its deterioration and ultimate failure.

Predicted climate changes are likely to have three main results. First, seedling mortality will increase due to a longer, drier growing season caused by earlier snowmelt and reduced soil moisture. Second, the frequency of establishment on point bar and abandoned channel landforms will decrease due to a reduction in frequency of moderate peak flows caused by a reduced snowpack. Third, significant changes will occur in the rate of landform creation due to a decrease in the frequency of high flows, also the result of a reduction in snowpack. However, the return of beaver to the ecosystem could mitigate some of the negative effects of climate change on willow establishment by increasing both soil water availability and the frequency of formation of abandoned beaver complex and abandoned channel landforms.

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Table 1. Year of formation of each study site as determined from aerial photographs, first year represents last photo available prior to landform formation, second year represents the earliest photo showing the landform. Range of Establishment indicates years represented by establishment dates of samples.

Site	Time Formed	Range of Establishment Years
P1	1990 to 1996	1996 - 1998
P2	1969 to 1987	1984 - 1998
P3	1946 to 1969	1961 - 1998
B1	1990 to 1996	1992 - 1997
B2	1990 to 1996	1993 - 1998
C1	1969 to 1987	1985 - 1987
C2	1946 to 1969	1963 - 1985
C3	1969 to 1987	1982 - 1997
C4	1990 to 1996	1992 - 1998
C5	Prior to 1937	1950 - 1986

Table 2. Results of X^2 test for a relationship between instantaneous peak flow and willow age distribution. Observed willow frequency refers to the number of sampled willows that were established in years with peak flows of a particular return interval. Expected willow frequency refers to the number of willows which would be expected to have established in years with peak flows of a given return interval if there were no significant relationship between peak flow and willow establishment likelihood. Two year return interval flow = 29.0 m³/s; Five year return interval flow = 38.2 m³/s. Significant P values are bolded.

Site Type	Return Interval (years)	Observed Willow Frequency	Expected Willow Frequency	X^2	P
Point Bar	0-2	18	30	10.13	**0.015**
	>2	39	27		
	0-5	52	47	3.03	0.082
	>5	5	10		
Beaver Complex	0-2	31	31	0	1
	>2	27	27		
	0-5	34	48	23.68	**<0.001**
	>5	24	10		
Abandoned Channel	0-2	22	39	15.67	**<0.001**
	>2	52	35		
	0-5	59	61	0.37	0.543
	>5	15	13		
All Willows	0-2	71	100	17.86	**<0.001**
	>2	118	89		
	0-5	150	150	0	1
	>5	39	39		

Table 3. Patterns of willow establishment produced by key fluvial processes.

Fluvial Process	Critical Flow	Landform	Community Patterns
Meandering	Moderate to high flows (2-5-yr. return interval flow)	Point bar	- Continuous establishment - Establishment at intermediate elevations above channel
Beaver Pond Drainage	Flood event (>5-yr return interval flow)	Abandoned beaver pond	- Periodic establishment prior to dam breach - Brief episodes of widespread establishment following abandonment - Establishment at high elevations relative to active channel
Channel avulsion	Moderate to high flows (2-5-yr return interval flow)	Abandoned channel	- continuous establishment over limited period of time (as oxbow fills) - establishment at low to moderate elevations relative to active channel
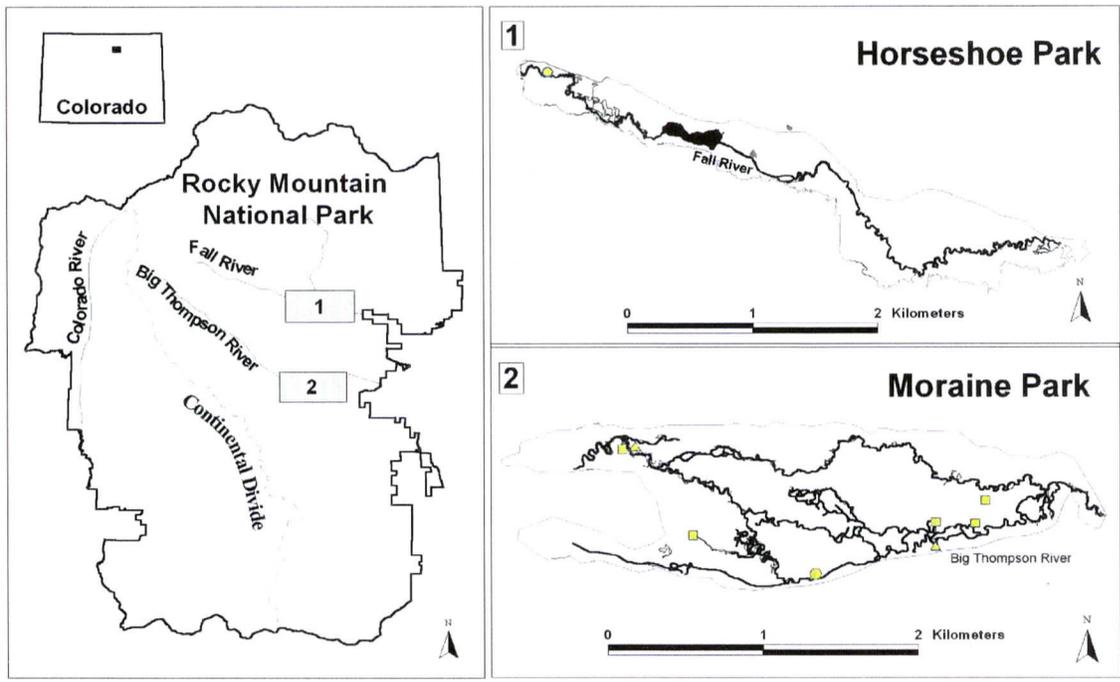
Figure 1. Location of study areas within Rocky Mountain National Park are represented by numbered rectangles. Within each study area, point bar sites are marked by a triangle, abandoned beaver ponds by a circle and abandoned channels by a square.

Figure 2. Example of a relatively new point bar site showing position on inside of a meander bend, cobble substrate and gradual slope to waters edge.

Figure 3. Example of a beaver pond in the process of draining. Notice bare moist soil exposed in the background and the relatively high water table.

Figure 4. Example of a channel in the process of abandonment due to erosion. Cutoff occurred ~5 years prior to photograph. When this picture was taken water still flowed through the oxbow until late summer. The abandoned channel is seen at the front, while the main active channel can be seen in the backround directly below the arrow. The arrow indicates direction of flow.
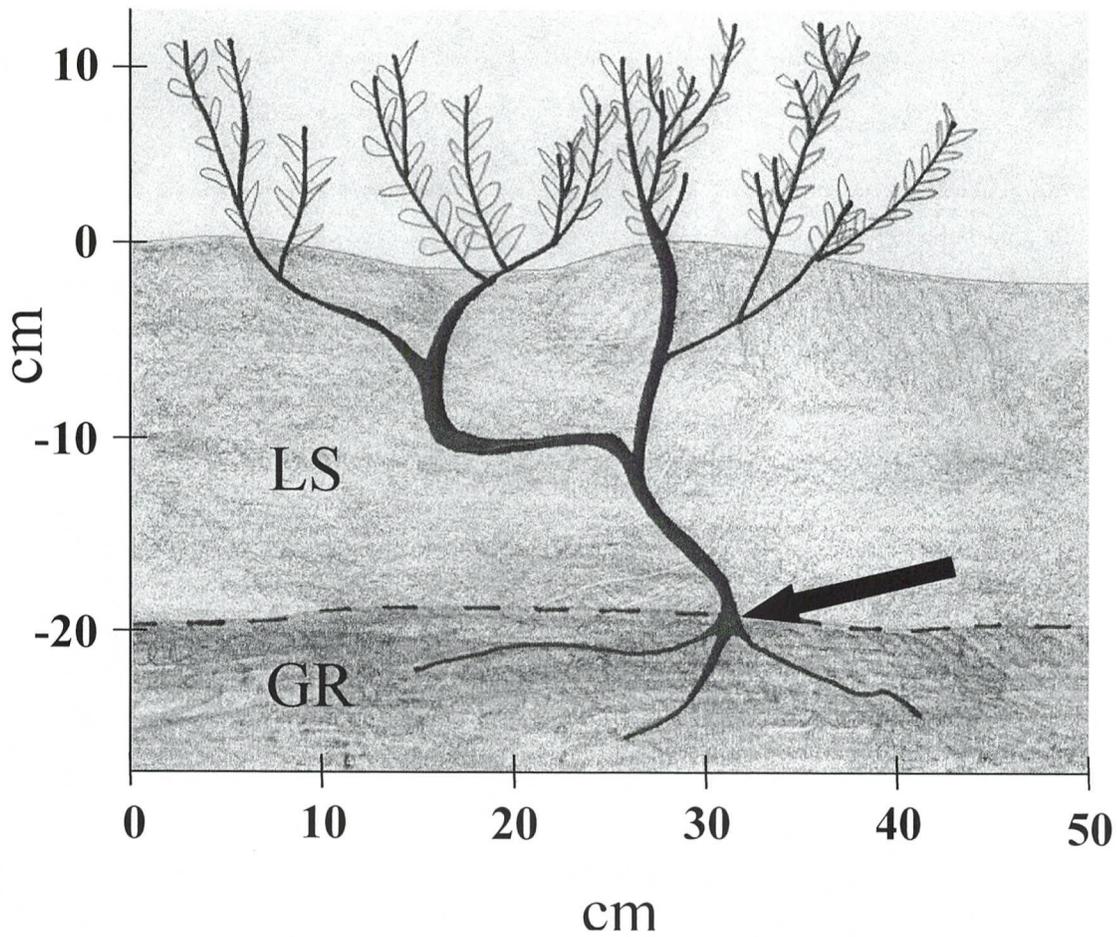
Figure 5. Sketch of a buried willow sapling that has given rise to several clumps of young stems. This example is typical of the morphology of willows in the sample area. The root crown is identified with an arrow. All portions of the plant between the root crown and ground surface are buried stems. This particular willow germinated on gravel substrate (GR) when a channel was abandoned, the channel subsequently filled in with finer textured substrate (LS-loamy sand).
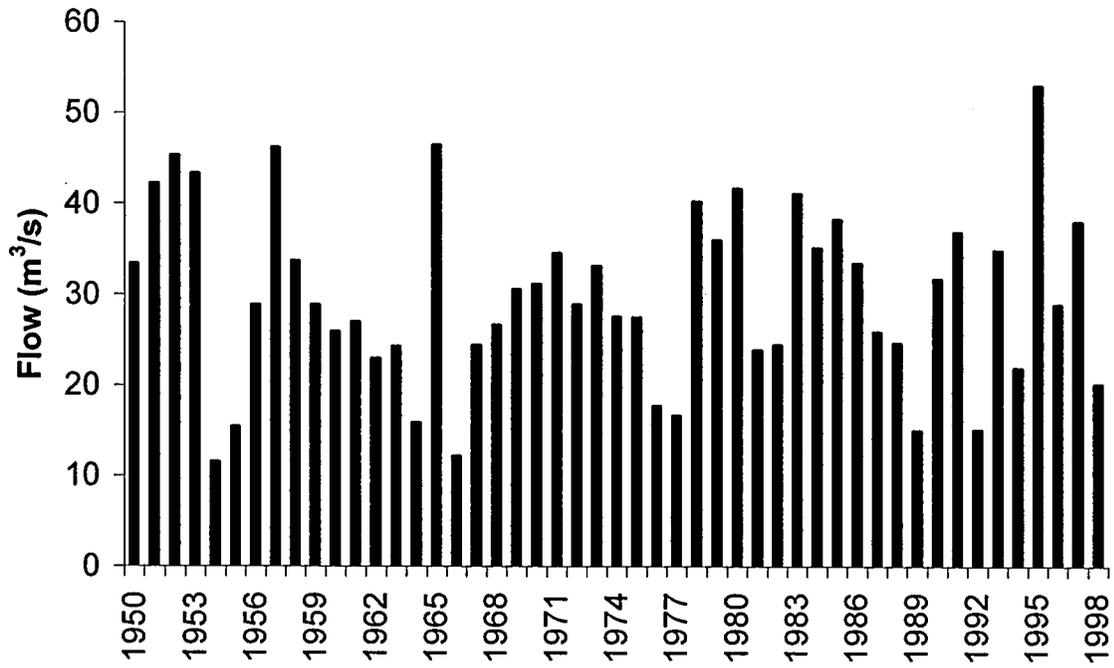
Figure 6. Instantaneous annual peak flows from the Big Thompson at Estes Park (USGS gauge #06733000) for the period 1950-1998.
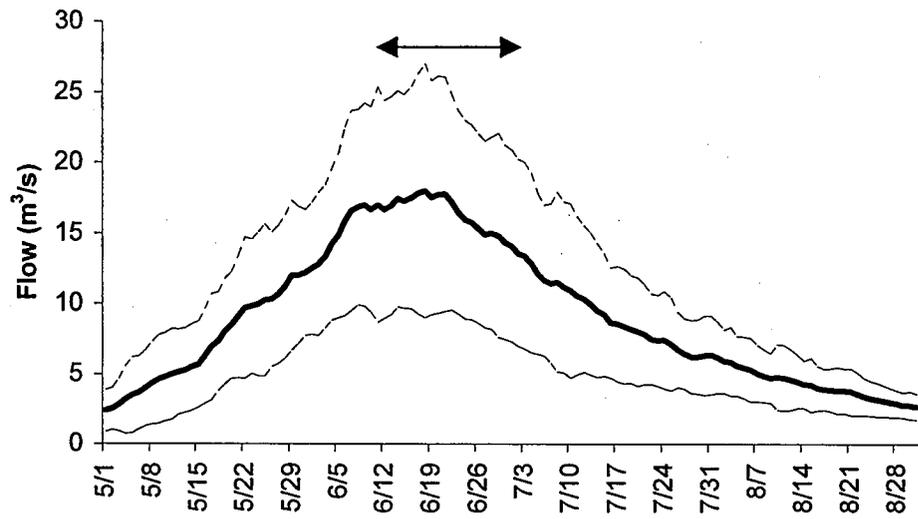
Figure 7. Mean daily flow at Big Thompson at Estes Park gauge for the period 1947-1998. Dotted lines are plus and minus one standard deviation from the mean. Peak period of seed rain period is represented by the double-headed arrow.
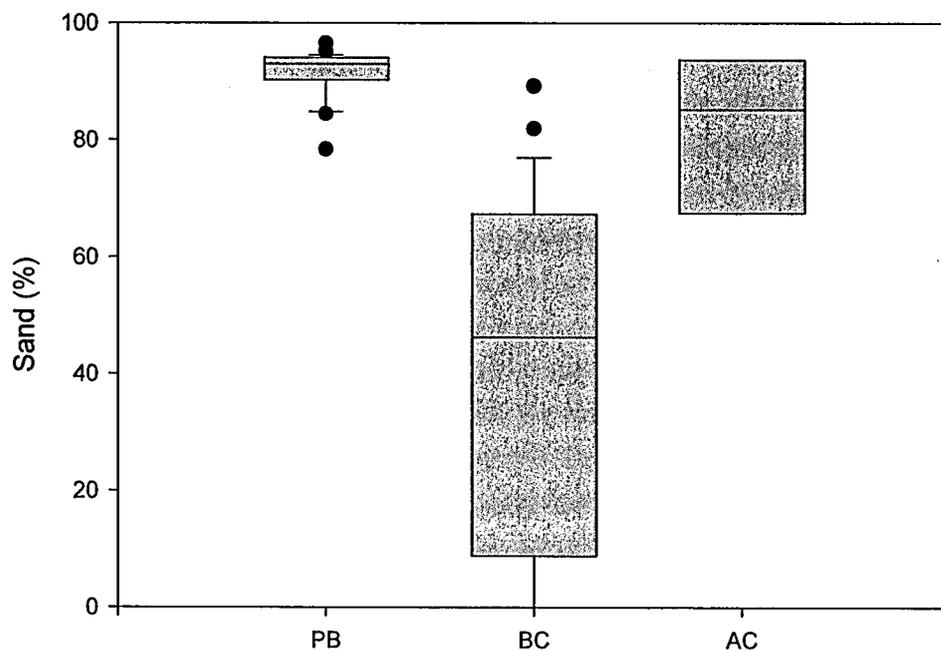
Figure 8. Boxplots showing % sand-size particles in reference soils from each of the three landform types (PB = Point Bars, BC = Beaver Complexes and AC = Abandoned Channels). Mean is represented by the solid line. Box indicates one standard deviation, flat-ended lines indicate two standard deviations, and solid circles represent outliers. Sand content in beaver ponds was significantly lower than on point bars (P < 0.001) and abandoned channels (P = 0.006). Point bar and abandoned channel soils were nearly significantly different (P = 0.053). Abandoned channel samples were limited to 4 samples from a single site. Mean sand content on point bars was 91.5%, while beaver complexes and abandoned channels had means of 63.5% and 80.6%, respectively.
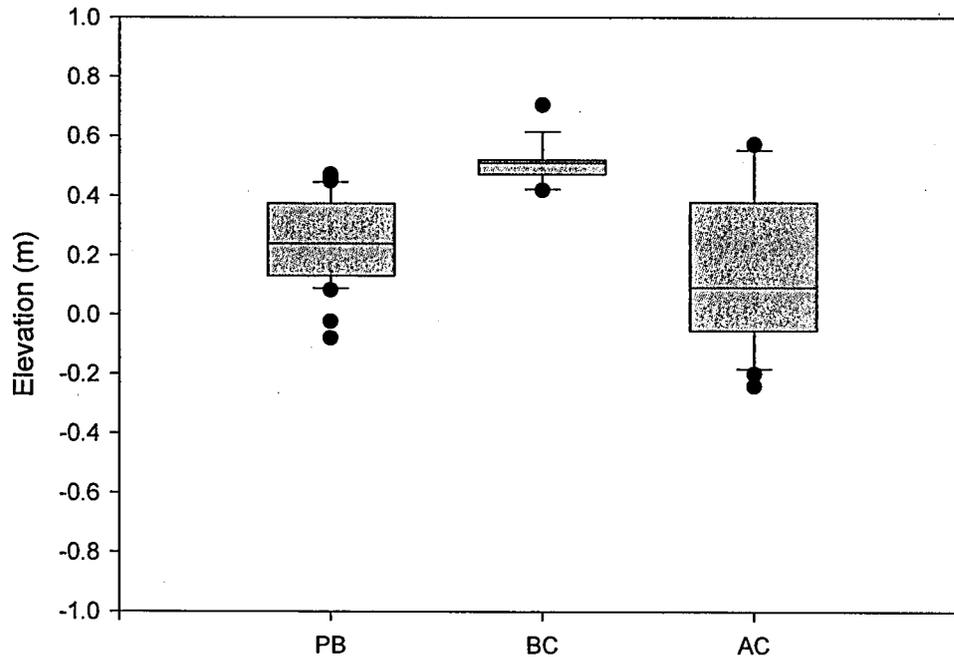
Figure 9. Boxplots showing elevation of germination for sampled willows on the three landform types (PB = Point Bars, BC = Beaver Complexes and AC = Abandoned Channels). All elevations are relative to channel height on 5 January 2002, which had a recorded flow of $0.31 m^3/s \pm 0.03$ (hand measurement at USGS gauge #0673300). The mean elevation for each landform is represented by a line, while the shaded box represents +/- one standard deviation. Flatheaded lines represent two standard deviations and solid circles are outliers. Samples from beaver complexes germinated at significantly higher elevations than on point bars (P < 0.001) and abandoned channels (P < 0.001). Elevations at point bars and abandoned channels were not significantly different (P = 0.108). Mean elevation of germination was 0.51m above low flow channel height for beaver ponds, 0.26m for point bars and 0.17m for abandoned channels. Germination occurring below the low flow channel occurred only on landforms removed from the active channel.

118
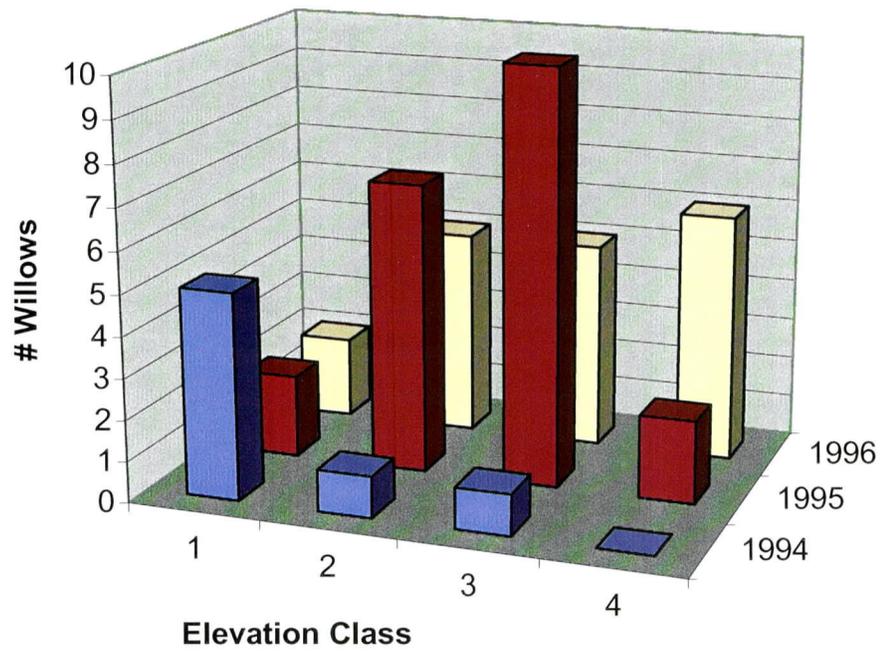
Figure 10. Number of willows sampled in each elevation class germinating in 1994 through 1996. See text for explanation of elevation classes.
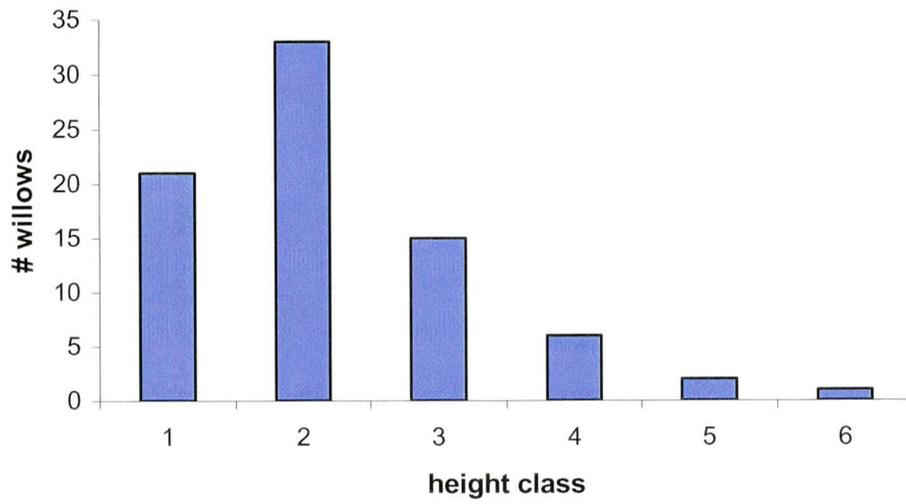
Figure 11. Number of sampled willows in 10 cm height classes. Class1 = 0-10 cm, Class 2 = 11-20 cm, Class 3 = 21-30 cm, Class 4 = 31-40 cm, Class 5 = 41-50 cm and Class 6 >50 cm.

Figure 12. Heavily browsed stems common at study sites. Willow pictured is 50 years old. Each line on the scale to the left of the willow denotes 2cm. Dashed line shows position of the soil surface at excavation. Three white lines indicate locations where cross-sections will be cut, the root crown is located at the uppermost cross section location. The toe of my boot used to stabilize the willow for photographing is visible bottom center.
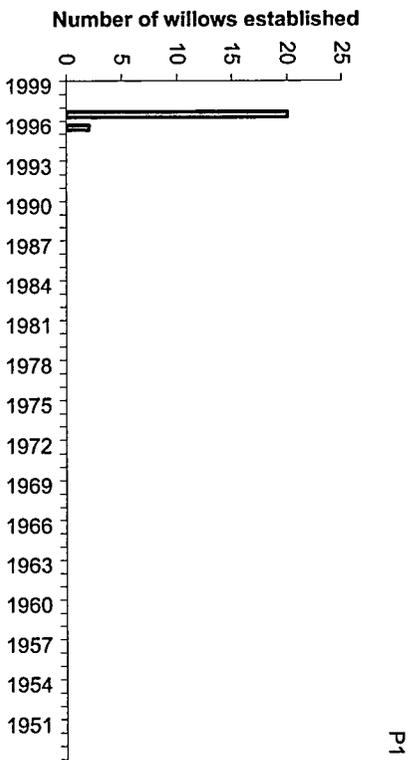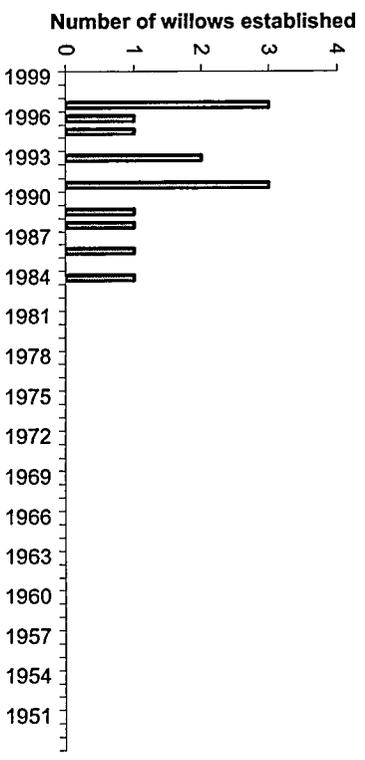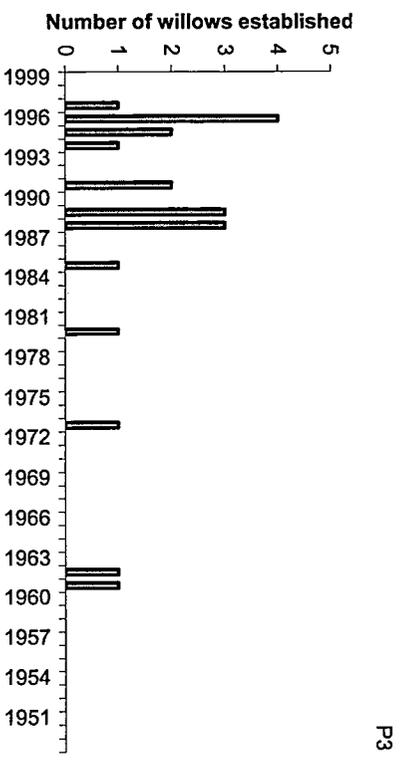
Figure 13a. Years of establishment for sampled willows at point bar study sites, P1-P3.
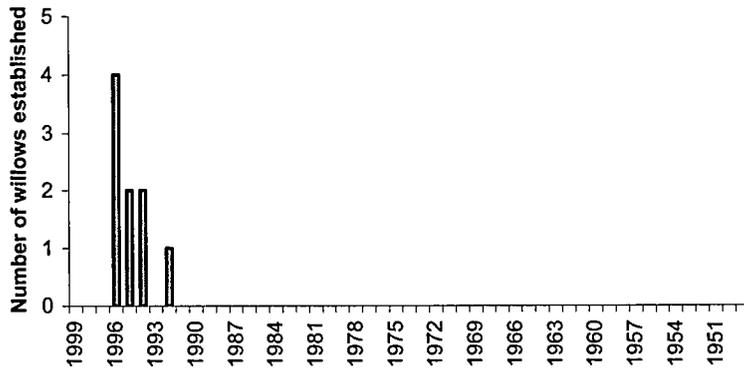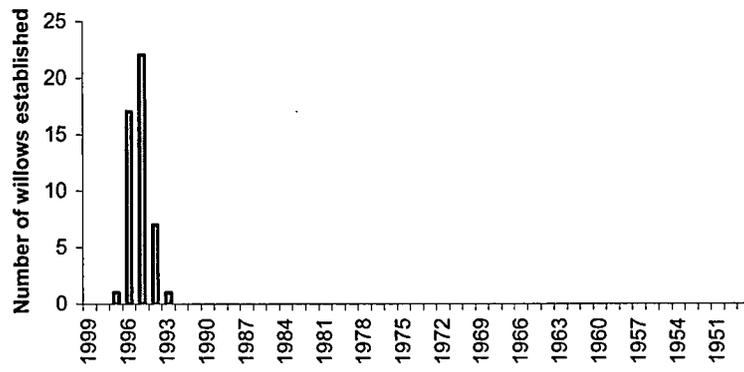
Figure 13b. Year of establishment for sampled willows from abandoned beaver pond sites, B1 and B2. Estimated year of dam breach for both sites was 1995.
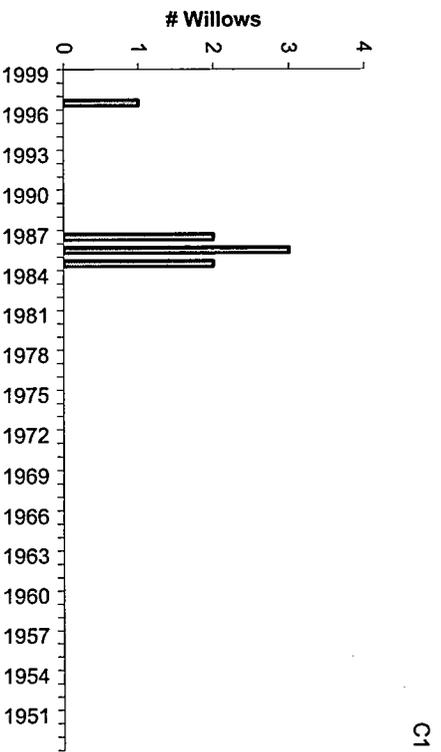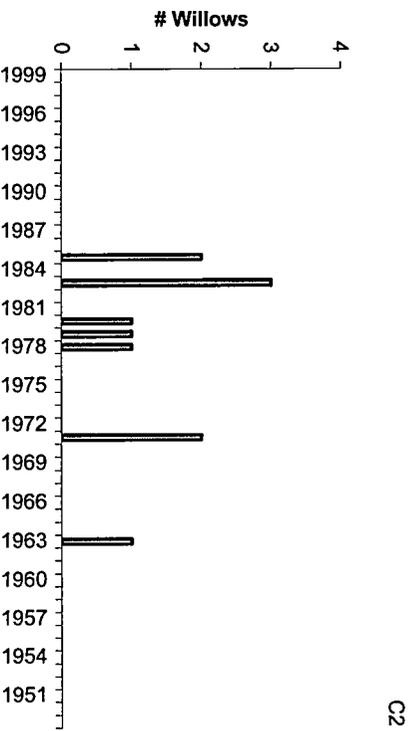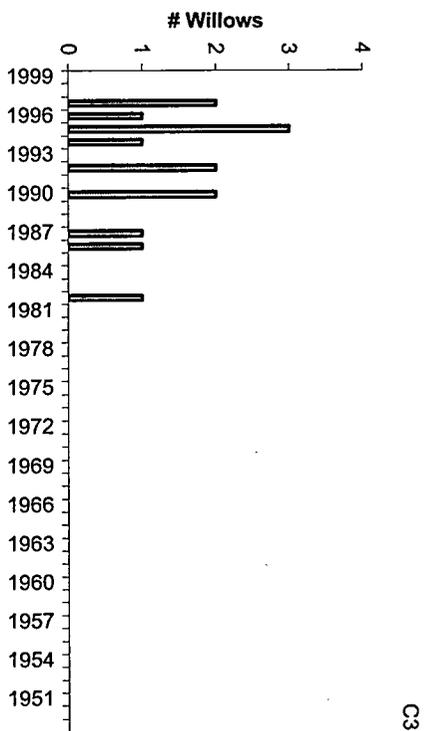
Figure 13c. Year of establishment for sampled willows from abandoned channel sites, C1-C5.

124
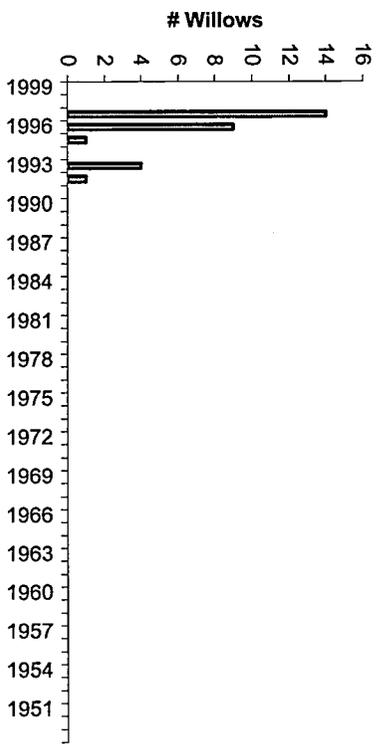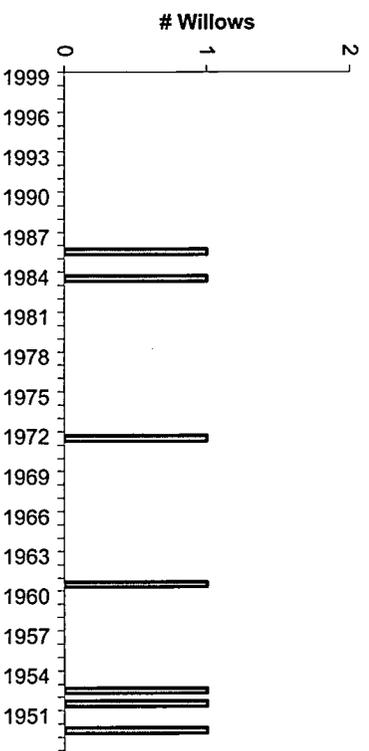
Figure 13c. Year of establishment for sampled willows from abandoned channel sites, C1-C5.

125

Figure 10. Interpolated water table surface (m asl) for Moraine Park generated using ground water monitoring well data from June 28, 2001

153
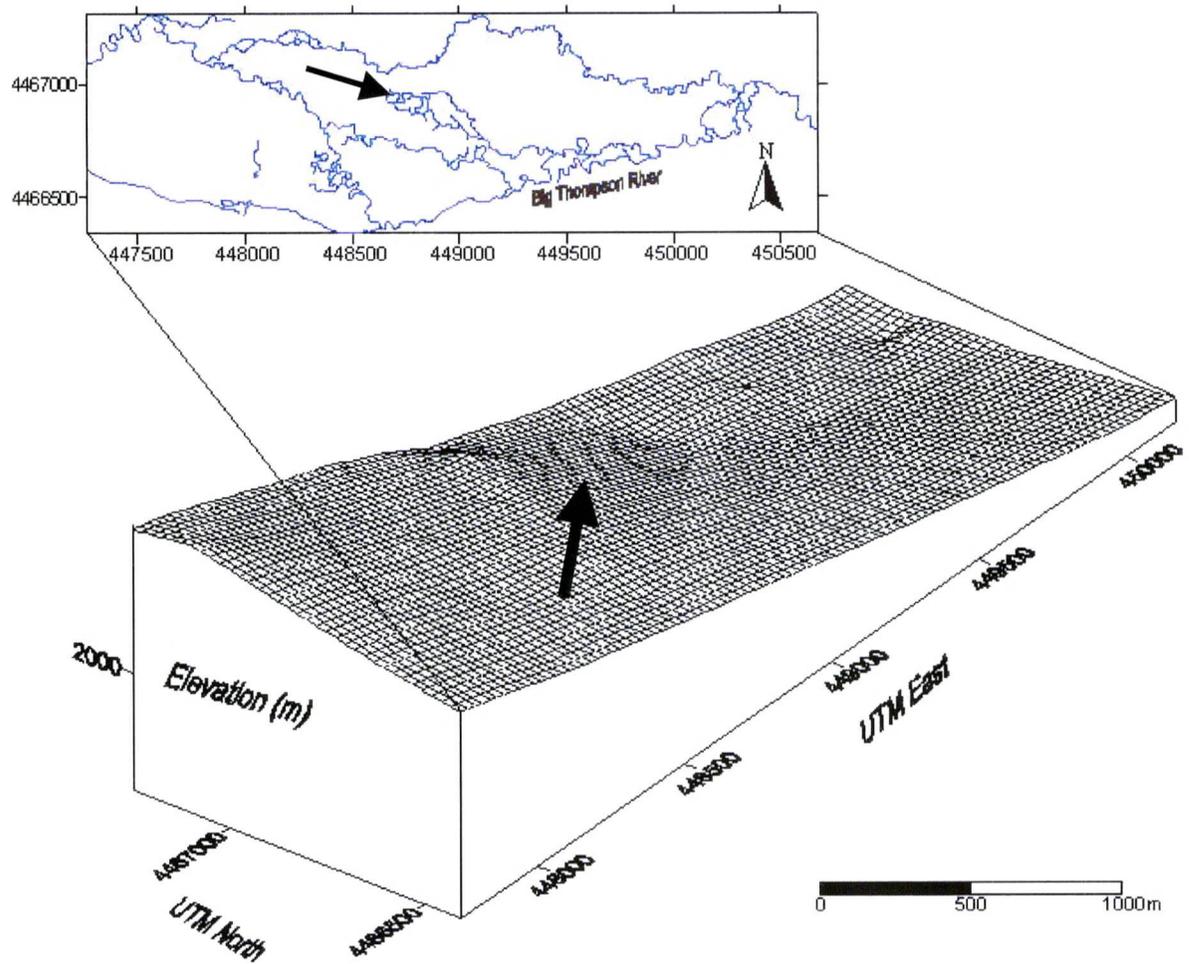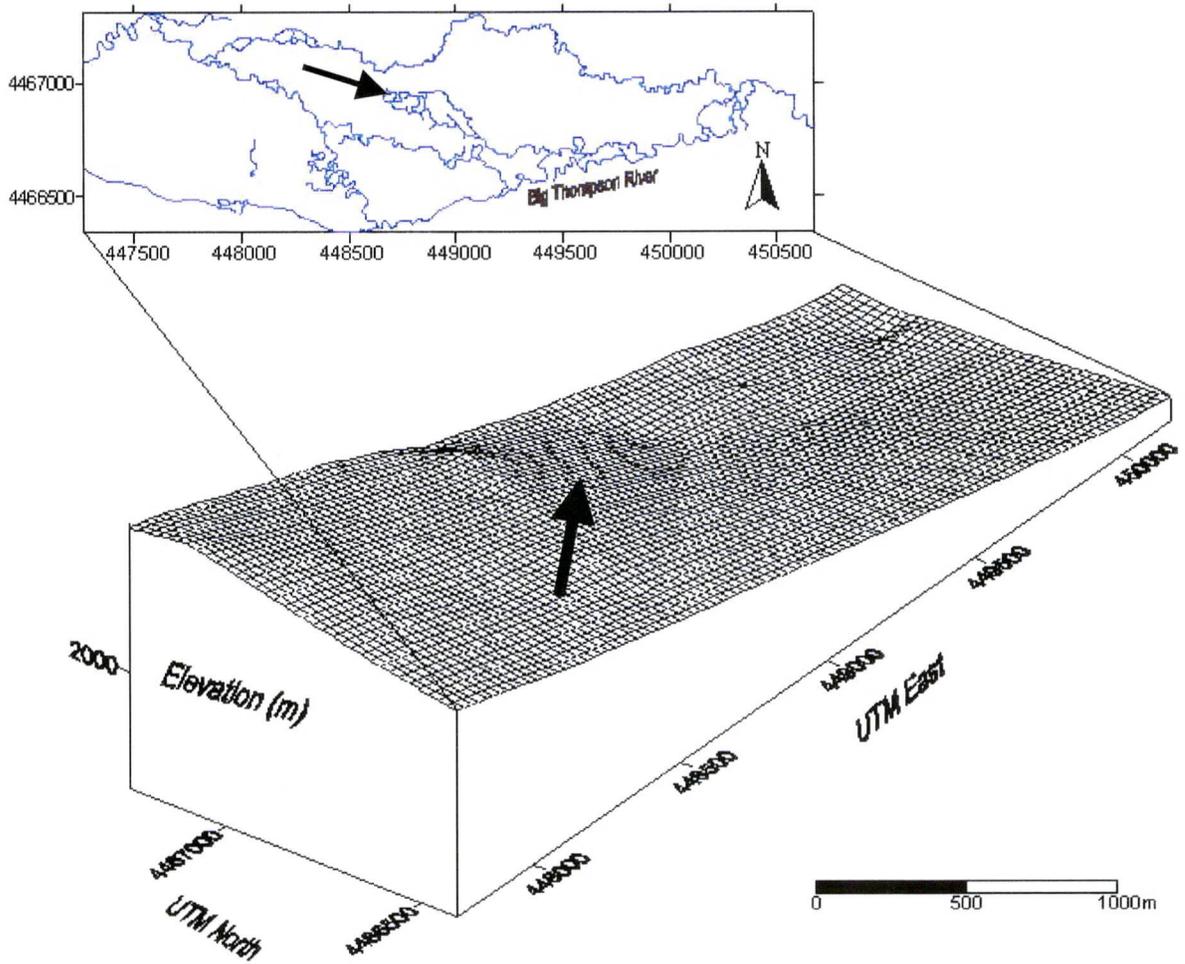
Figure 10. Interpolated water table surface (m asl) for Moraine Park generated using ground water monitoring well data from June 28, 2001
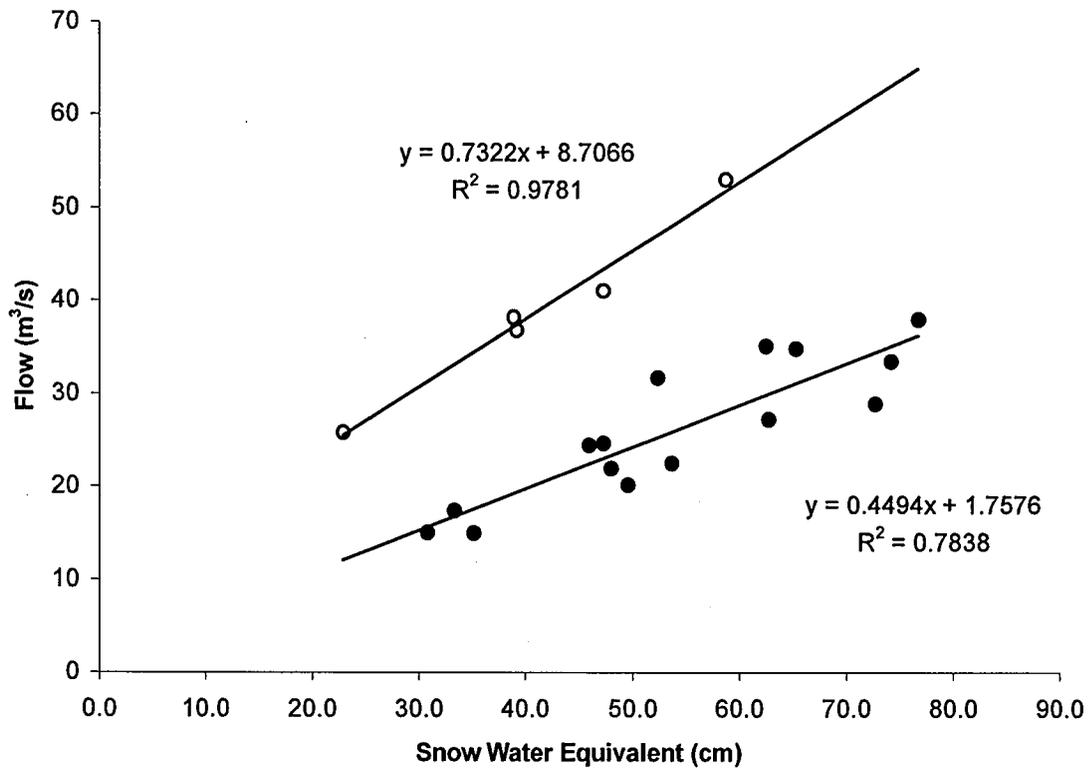
Figure 14. Relationship of May 1 SWE to instantaneous peak flow. Normal meltout (●) occurs in the majority of years and is represented by the lower line. The upper line shows the relationship in years where rapid warming or large precipitation events coincide with snowmelt (○), resulting in rapid snowpack melting and a peak flow nearly twice as high as that predicted by the relationship of normal snowmelt years.

Appendix 1. Calculation of return interval for flows measured at the Big Thompson at Estes Park gauge, based on data from 1950-1998.

Year	Instantaneous Peak Flow (m^3/s)	Rank	Return Interval (years)
1950	15.54	18	2.78
1951	19.62	6	8.33
1952	21.07	4	12.50
1953	20.15	5	10.00
1954	5.35	49	1.02
1955	7.15	45	1.11
1956	13.43	24	2.08
1957	21.47	3	16.67
1958	15.67	17	2.94
1959	13.43	24	2.08
1960	12.08	32	1.56
1961	12.58	30	1.67
1962	10.68	39	1.28
1963	11.33	37	1.35
1964	7.36	44	1.14
1965	21.60	2	25.00
1966	5.62	48	1.04
1967	11.38	35	1.43
1968	12.41	31	1.61
1969	14.22	23	2.17
1970	14.49	22	2.27
1971	16.07	16	3.13
1972	13.43	24	2.08
1973	15.41	20	2.50
1974	12.80	28	1.79
1975	12.75	29	1.72
1976	8.20	42	1.19
1977	7.70	43	1.16
1978	18.70	9	5.56
1979	16.72	13	3.85
1980	19.36	7	7.14
1981	11.10	38	1.32
1982	11.38	35	1.43
1983	19.09	8	6.25
1984	16.33	14	3.57

1985	17.78	10	5.00
1986	15.54	18	2.78
1987	12.02	33	1.52
1988	11.47	34	1.47
1989	6.97	47	1.06
1990	14.75	21	2.38
1991	17.12	12	4.17
1992	6.99	46	1.09
1993	16.20	15	3.33
1994	10.21	40	1.25
1995	24.63	1	50.00
1996	13.43	24	2.08
1997	17.65	11	4.55
1998	9.36	41	1.22

CHAPTER 5. SURVIVAL OF ROOTED AND UNROOTED WILLOW STEM CUTTINGS, MORAINE AND HORSESHOE PARKS, ROCKY MOUNTAIN NATIONAL PARK, COLORADO

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Preformed root primordia commonly occur on stems of many members of the *Salicaceae* including willows (*Salix* spp.) (Carlson 1938; Carlson 1950; Haissig 1970). These represent an important adaptation to life in wetland and riparian environments, which enable plants to form adventitious roots under saturated soil conditions and survive inundation and sedimentation associated with flooding. Many willow species are capable of vegetative reproduction, either through clonal expansion (Douglas 1991; Ottenbreit and Staniforth 1992) or establishment from stem cuttings, which is often facilitated by the feeding and building activities of beavers (*Castor canadensis*) (Cottrell 1995). Vegetative willow plantings have long been employed to promote bank stabilization (Carriere 1976; Watson et al. 1997) and improve wildlife habitat (Densmore et al. 1987). Though willow use in restoration (Densmore and Zasada 1978; Cooper and MacDonald 2000) and bioengineering (Shields et al. 1995a; Shields et al. 1995b; Pezeshki et al. 1998) has been extensively studied, few data exist on the range of water table depth environments, or cutting treatments, that limit survival of montane willow species in the Rocky Mountains. Our objectives were to: (1) test the feasibility of establishing unrooted and rooted cuttings in the study areas, (2) quantify the groundwater depths where willow cutting survival is highest, and (3) based upon water table depth investigations, provide a coarse delineation of areas within Moraine Park where willows could be established using the methods tested.

METHODS

Experimental design

In early May 2000, prior to leaf out, approximately 500 stem cuttings 30 cm long and ~1cm in diameter were collected using pruning shears from the interior of 10 Salix monticola plants; six in Moraine Park and four in Horseshoe Park. Only tall morphotype willows were selected, consequently all individuals were from either the western end of Moraine Park or from the

Endovalley area of Horseshoe Park. 250 cuttings were randomly selected and planted, with 2/3 of the stem below the soil surface in 6.4 cm x 30.5 cm Zipset® planting containers (Monarch Manufacturing Co., Salida, CO) filled with a loam soil mix. The containers were immersed in ~20 cm of water for approximately 6 weeks to induce rooting. The remaining cuttings were stored in water until planted.

Forty plots were established along a gradient of elevation and soil textures in different locations across Moraine and Horseshoe Parks (Figure 1). In June of 2000, seven unrooted and five rooted cuttings were planted into each plot. Twelve paired plots were established to test the hypothesis that competition with herbaceous vegetation may inhibit cutting survivorship. Herbaceous vegetation in one plot of each pair was clipped to within 2 cm of the ground surface every two weeks throughout the summer of 2000. Wire exclosures were placed over plots to prevent herbivory by elk.

All plots were established adjacent to ground water monitoring wells or staff gauges. Relative elevations of plots and wells were determined using a total station and surveyor's rod. Soil samples were collected from each plot for soil texture analysis using the hydrometer method (modified from Gee and Bauder 1986). Cutting survival was assessed at the end of the 2000 season, and in the spring and fall of 2001.

Statistical analyses

Paired t-tests were used to compare the effects of clipping on willow cutting survival and compare survival on different dates (Proc TTEST; SAS Institute 2000). Stepwise logistic regression was used to model the influence of late-summer water table depth and the percentage silt and clay in soils (Proc LOGISTIC; SAS Institute 2000) on cutting survivorship. All first-, second-, and third-order polynomials were also evaluated. Only variables with a ≥ 0.05 significance level or those required to maintain model hierarchy were retained in the final model.

131

Separate analyses were run examining cutting survivorship after one and two seasons. Overall

model fit was assessed using the chi-square likelihood ratio statistic and McFadden's ρ^2, an

analogue to the coefficient of determination in linear regression.

Identification of sites suitable for willow planting

A broad-scale map of sites suitable for willow planting was generated for Moraine Park

where we had suitable water table depth measurements and land surface elevation data. Suitable

areas for planting were qualitatively delineated within ArcView 3.2 (ESRI Inc., 1999) using

aerial photographs, water table maps, and data from ground water monitoring well cross-

sections. Areas estimated to have a mean August 2000 water table depths ≤ 90 cm (see below)

were considered suitable for the planting of both rooted and unrooted cuttings.

RESULTS

Cutting survivorship was highly variable across all plots, ranging from 0 to 100% for both

rooted and unrooted cuttings. Survival after the first season in clipped treatments did not differ

significantly from controls (t = 1.60, p = 0.128). Therefore, clipping was discontinued after the

summer of 2000 and plots were pooled in subsequent analyses. Rooted cuttings survived at a

significantly higher rate than unrooted cuttings after both one (t = 2.27, p = 0.026) and two

seasons of growth (t = 2.58, p = 0.012) (Table 1). The greatest cutting mortality occurred during

the summer of 2000, and to a lesser extent, over the first winter. Both rooted and unrooted

survival declined <5% between June and September of 2001, suggesting that most cuttings

surviving the first winter were fairly well established.

Although there was significant variability in cutting survival across the water table depth

gradient, there appeared to be a late-summer water table depth threshold of ~90cm, beyond

which little cutting survivorship occurred (Figure 2). Logistic regression models indicate that

132

late-summer water table depth is a critical determinant of cutting survival. Mid-August water table depths along with several polynomial terms were significant in the selected models after one and two seasons of growth for both rooted and unrooted cuttings (Table 2). In contrast, the percentage of silt and clay in soil samples was not significant predictor of cutting survival in any model.

Identification of sites suitable for willow planting

A map of areas within Moraine Park suitable for planting of willow cuttings was produced using data from ground water monitoring wells, staff gauges, topographic data, aerial photographs and knowledge regarding study area physiography (Figure 3). Delineated areas fell principally along the major stream channels, although extensive areas in the interior of Moraine Park were also judged suitable. Boundaries are approximate, and many small low-lying areas outside of the main polygon may also be suitable for planting; conversely, there may be areas within the main polygon that are unsuitable due to variation in local topography.

DISCUSSION

Results from this experiment suggest that depth to water table is a critical variable influencing patterns of willow stem cutting survival. Few cuttings, either rooted or unrooted, were able to survive in areas with late-summer water table depths greater than ~90 cm. In addition to directly influencing water availability during hot and dry summer months, water table depths early in the season influence initial patterns of root formation in cuttings. The higher survival observed for rooted cuttings, particularly in plots with deeper water tables, suggests that early root formation strongly influences the ability of cuttings to tolerate drier soil conditions in late summer (Schaff et al. 2002). Prolonged inundation has been demonstrated to reduce cutting growth and survivorship in several different willow species (Talbot et al. 1987, Pezeshki et al.

133

1998), suggesting that both drought and prolonged flooding can reduce planting success. However, none of the plots in this study were inundated for more than one week, and no decrease in survival was observed in plots with deep water table depths. Soil texture was not a significant predictor of cutting survival, probably due to the sandy and gravelly soils present throughout the study area, which typically have little water holding capacity and have little capillarity.

Although small exclosures placed around cutting plots prevented direct mortality due to elk herbivory, elk were able to browse the ends of shoots growing beyond exclosure edges, with unknown effects on cutting survival. Direct mortality due to small mammal herbivory was observed in several of the drier plots in Moraine Park, indicating another factor potentially influencing the success of plantings. However, all plots affected by small mammal herbivory were at the driest end of the water table gradient, in sites with low cutting establishment based on hydrologic conditions alone.

Pronounced differences in rooting potential among different willow species have been demonstrated by several researchers (Talbot et al. 1987; Cottrell 1993). Survivorship in the *Salix monticola* cuttings used in this experiment suggests that this species may be appropriate for restoration efforts, although other species present in the study areas may be more or less suitable, for example *Salix geyeriana, S. bebbiana, S. planifolia, S. lasiandra* ssp. *lucida*, and *S. gracilis*. Additional factors that have been demonstrated to influence planting success include the length and diameter of cuttings and planting depth (Hoag 1992). Presumably, longer cuttings planted more deeply into the soil would exhibit greater survival in areas with deeper water tables.

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Table 1. Mean percent cutting survival (+/- std. error) through September of 2000 and 2001. Test statistics are from paired t-tests of rooted and unrooted survival on each date.

Date	Rooted		Unrooted		t	df	p
Sep. 2000	55.2	(5.9)	36.5	(6.1)	2.27	77	0.026
Sep. 2001	44.5	(5.2)	26.1	(4.9)	2.58	77	0.012

Table 2. Logistic regression results from analysis of rooted and unrooted cutting survivorship after one and two growing seasons. The variable WTD in logistic models refers to mid-August 2000 water table depth, and the term M represents the probability of mortality.

	Type	Logistic model	χ^2	df	$p > \chi^2$	ρ^2
Sep 00	*Rooted*	Logit(M)= -1.01 − 0.03[WTD] + 0.0005[WTD]^2	85.3	2	<0.001	0.36
	Unrooted	Logit(M)= -2.16 + 0.18[WTD] − 0.004[WTD]^2 +0.00002[WTD]^3	70.3	3	<0.001	0.22
Sep 01	*Rooted*	Logit(M)= 0.22 + 0.31[WTD] + 0.02[WTD]^2	63.9	2	<0.001	0.28
	Unrooted	Logit(M)= -2.94 + 0.33[WTD] − 0.007[WTD]^2 +0.00004[WTD]^3	53.0	3	<0.001	0.17

138
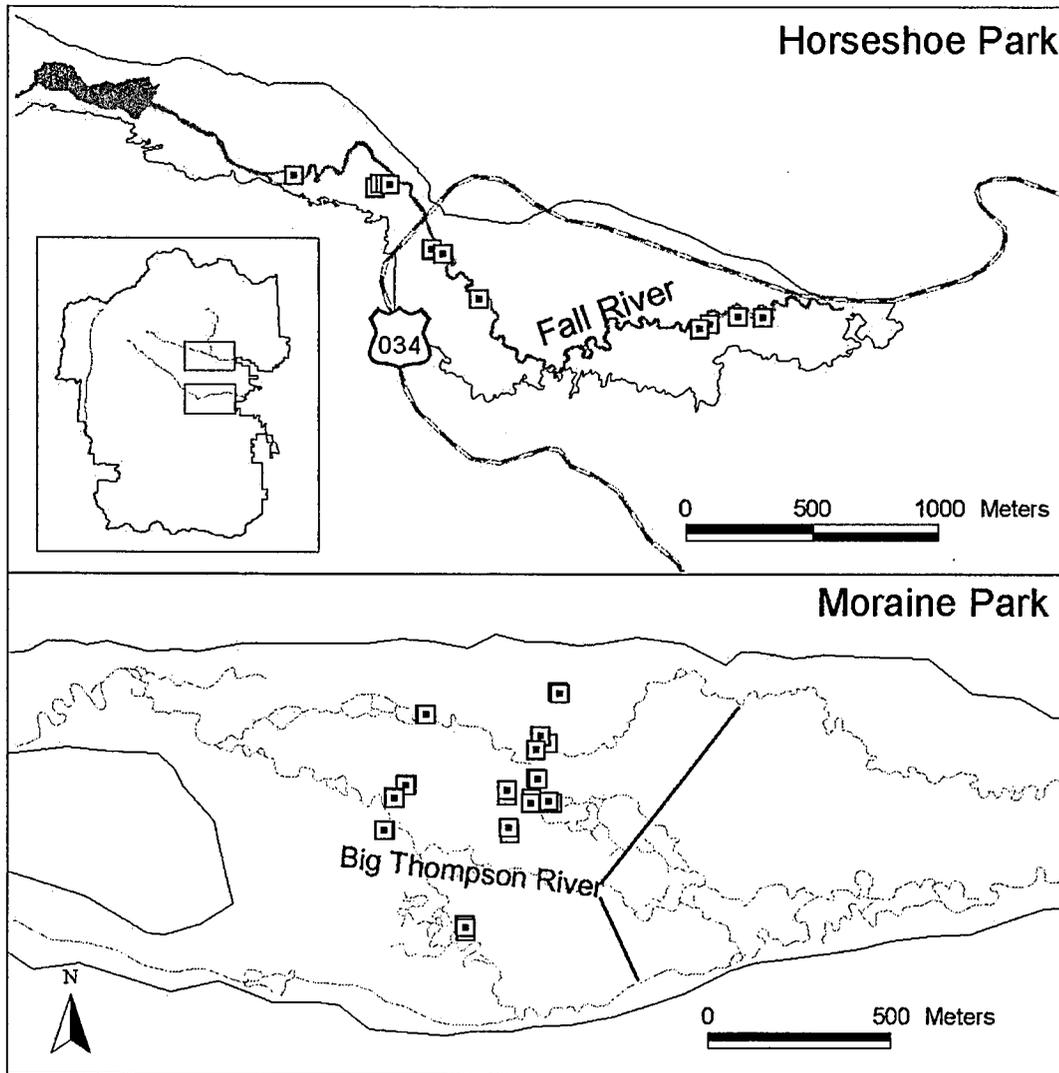
Figure 1. Map of cutting plot locations in the study area. Cutting plots were established in two principal settings: bare mineral point bars and vegetated meadows adjacent to active stream channels.
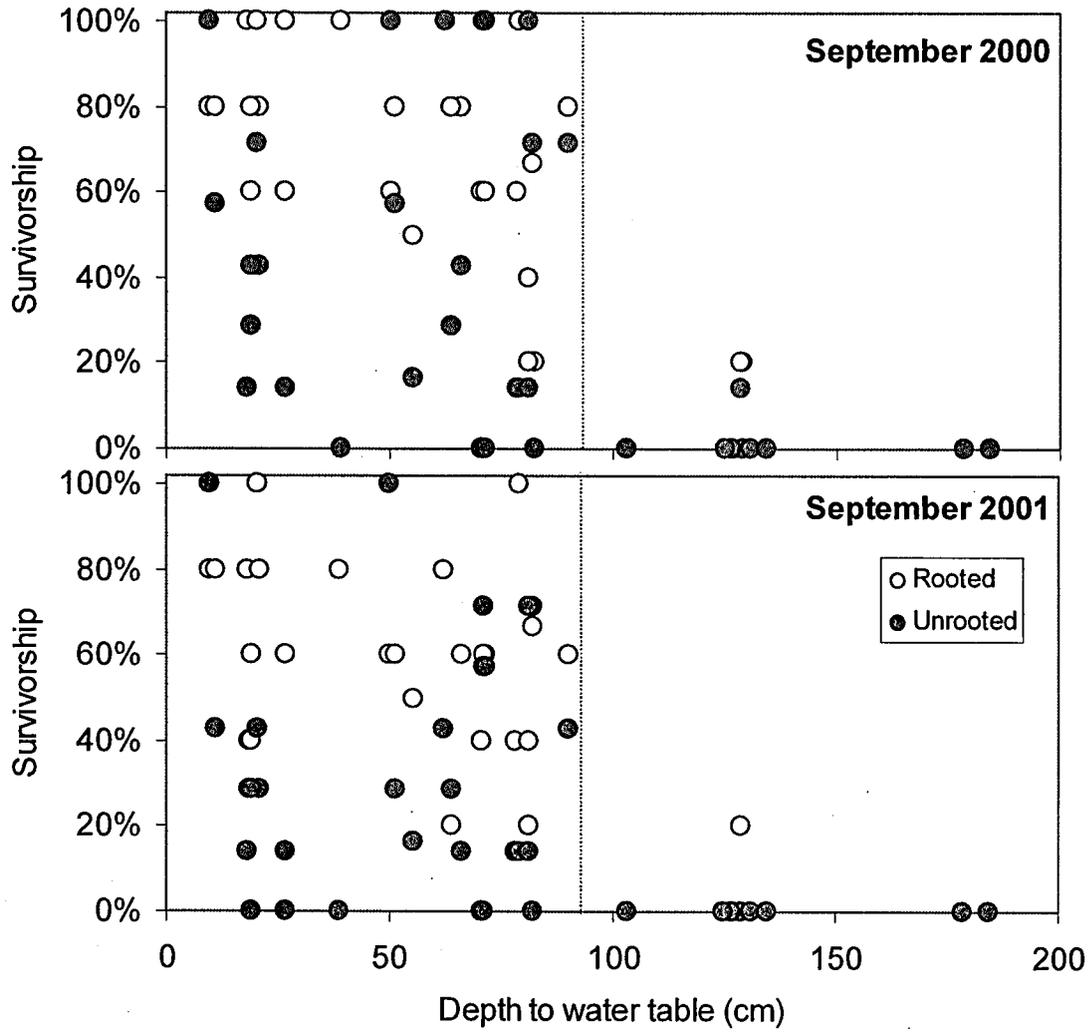
Figure 2. Mean survivorship for rooted and unrooted cuttings after one (top) and two (bottom) growing seasons. Dashed line represents approximate water table depth threshold for cutting survivorship.

Figure 3. Locations in Moraine Park with suitable hydrologic conditions for potentially establishing willows from cuttings. Boundaries are approximate and represent only a broad outline of potential sites.

CHAPTER 6. SURFACE AND GROUND WATER FLOW AND INTERACTIONS IN MORAINE AND HORSESHOE PARKS

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INTRODUCTION

Patterns of surface and ground water flow can control the establishment and survival of riparian willows in montane landscapes. We analyzed stream flow and its effects on ground water levels in Moraine and Horseshoe Park to assist us in understanding the hydrologic processes that create suitable conditions for willow persistence in these areas. We used two types of measures in our analysis. We quantified surface water patterns using staff gauges to measure stream stage, which we correlated with our stream flow measurements in these study areas as well as flow measured at the Big Thompson River at Estes Park, USGS gauge. We also installed ground water monitoring wells to quantify the depth to water table, water table elevation, and ground water dynamics throughout Moraine Park, and in portions of Horseshoe Park. We were particularly interested in analyzing the interaction of surface and ground water, to determine how stream stage influences ground water levels. This information can be used to conceptualize how the presence or absence of beavers, whose dams raise stream stage, may have historically influenced surface and ground water levels in the study sites.

METHODS

A network of ground water monitoring wells and staff gauges were installed in the study areas beginning in May of 2000. A total of nine transects were installed in north to south transects in Moraine Park and Horseshoe Parks (Figures 1 and 2). Each transect consisted of 3-15 monitoring wells extending from forest edge to forest edge with a staff gauge installed at major stream crossings. Staff gauges consisted of rebar or fence posts driven into the streambed along meander bends. Ground water monitoring wells were hand-augered and cased with 1.25-inch diameter slotted PVC pipe. Water depths and stage heights were measured weekly from May through late September in 2000 with an electric tape, and approximately every 2 weeks during the summer of 2001.

The x-y coordinates and elevations of wells and staff gauges were surveyed using a Total station and surveying rod, and converted into a local datum by National Park Service Water Resources Division staff, using previously established benchmarks. To characterize ground water flow patterns across the study areas, inverse distance weighting was used to interpolate point estimates of water table depth using Surfer 7.0 software (Boss International Inc., Madison, WI). In addition, cross-sectional profiles of well transects and well hydrographs for individual monitoring wells were generated.
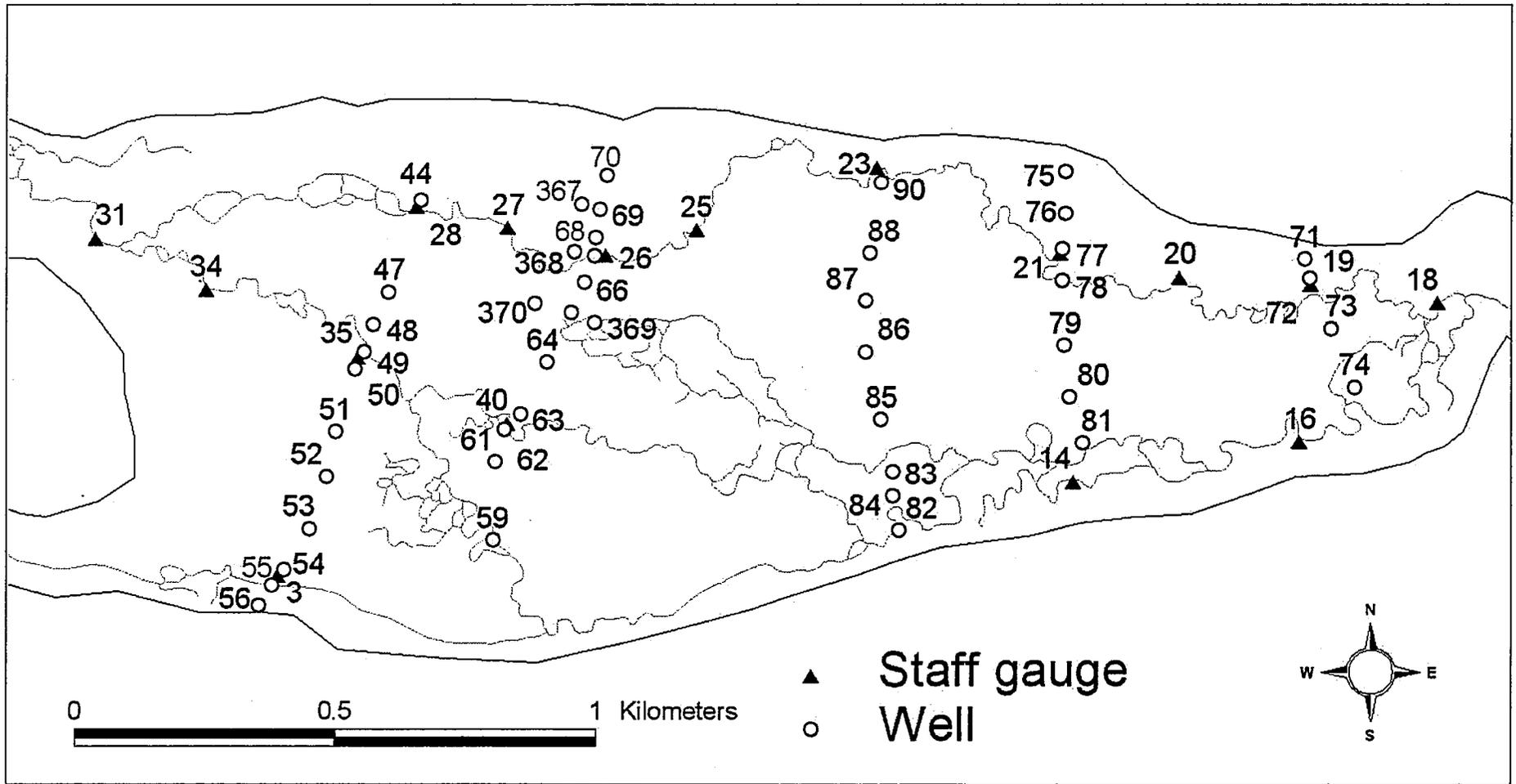
Figure 1. Location of ground water monitoring wells (**O**) and staff gauges (**▲**) in Moraine Park.
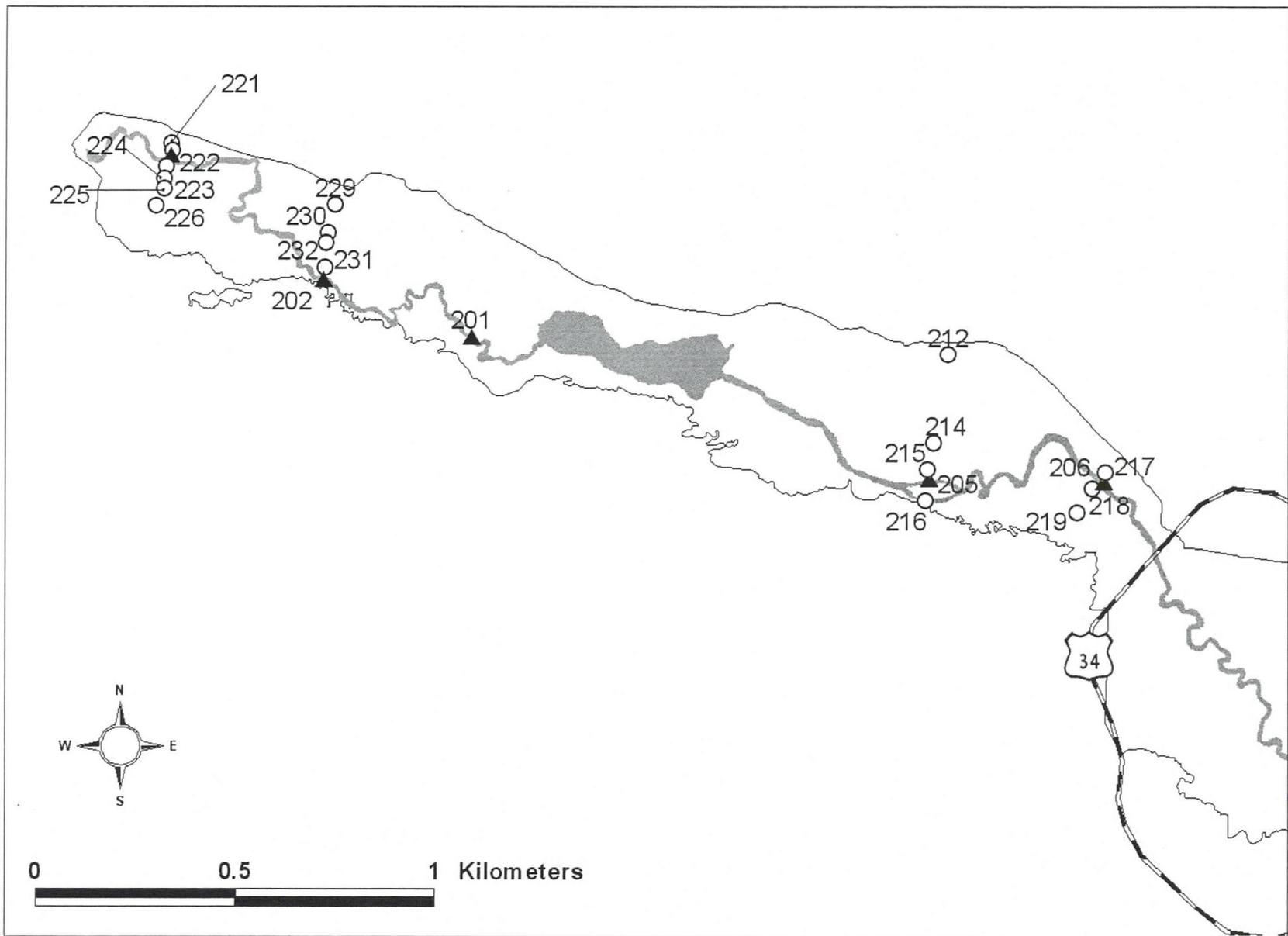
Figure 2. Location of ground water monitoring wells (**O**) and staff gauges (▲) in Horseshoe Park.

RESULTS

Surface Water Flow and Flow/Stage Relationships

The Big Thompson River splits into a north and south channel in the western part of Moraine Park, and these channels join before the stream exits Moraine Park. The north channel (measured at gauge 21) carries more water than the south channel (measured at gauge 14) (Figure 3) although at low flows summer the difference is slight. Flow of Fall and Big Thompson Rivers are similar (Figure 4). The flow-stage relationship for the south Big Thompson River channel in Moraine Park (Figure 5) was perfectly linear ($R^2 = 1.00$), while for the north channel a polynomial was fit to the data ($R^2 = 0.99$) (Figure 6). The regression lines for both channels fit the data well indicating a very tight relationship of flow to river stage, with 1 m^3/s of flow raising stage at gauge 14 by ~ 13 cm, and at gauge 21 by ~10 cm. Thus, higher river flows definitely increase river stage.
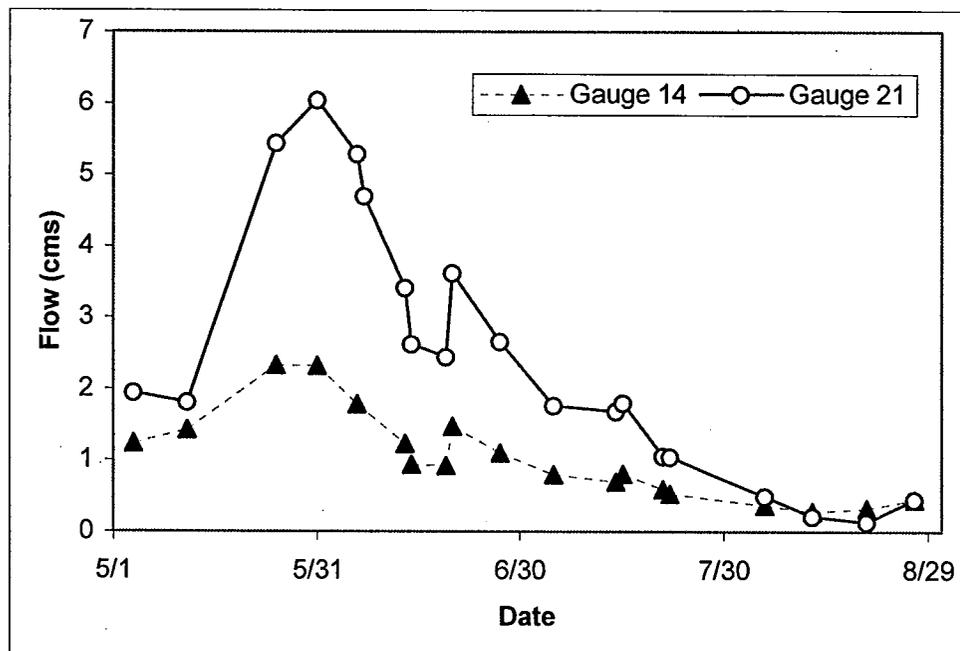
Figure 3. Stream flow (cubic meters per second) for the north (gauge 21) and south channels (gauge 14) of the Big Thompson River in Moraine Park during 2000.
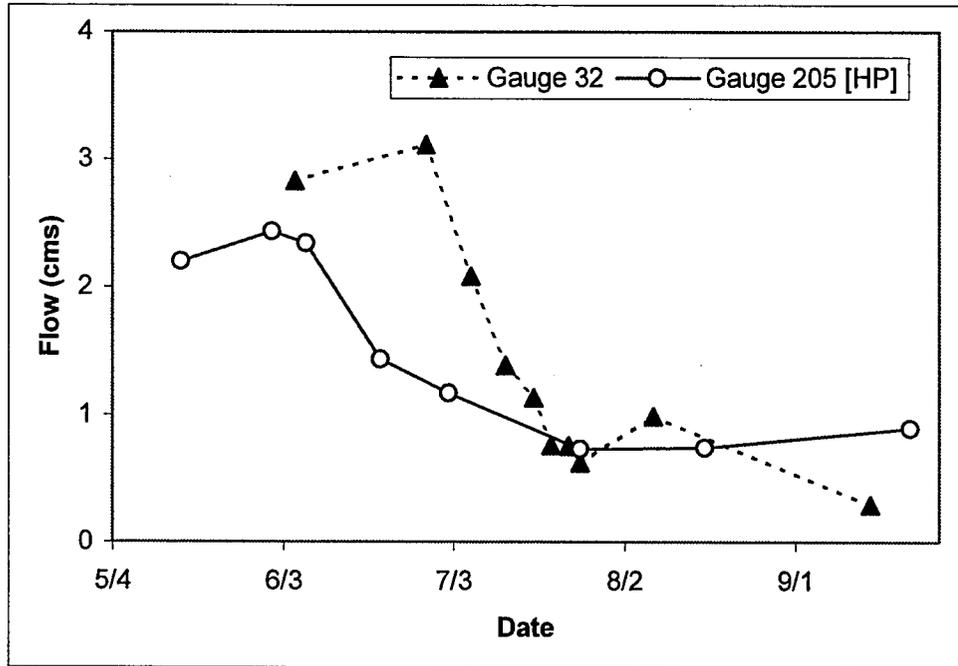
Figure 4. Flow (cubic meters per second) of Big Thompson (Gauge 32) and Fall Rivers (Gauge 205) during 2000.
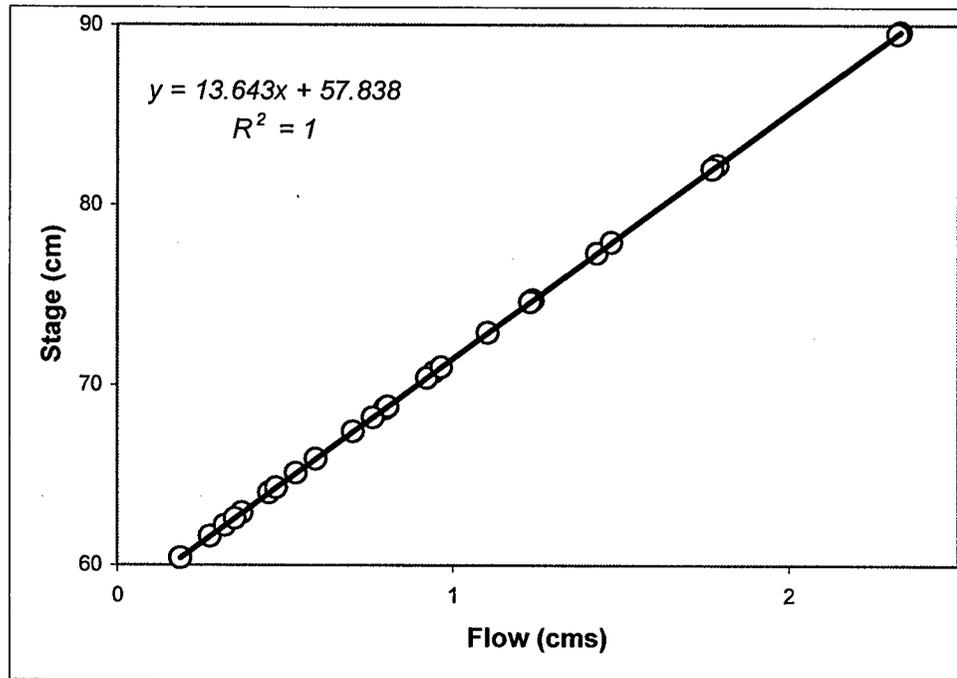
Figure 5. Flow-stage relationship at staff gauge 14, the south channel of the Big Thompson River in Moraine Park for 2000 and 2001.
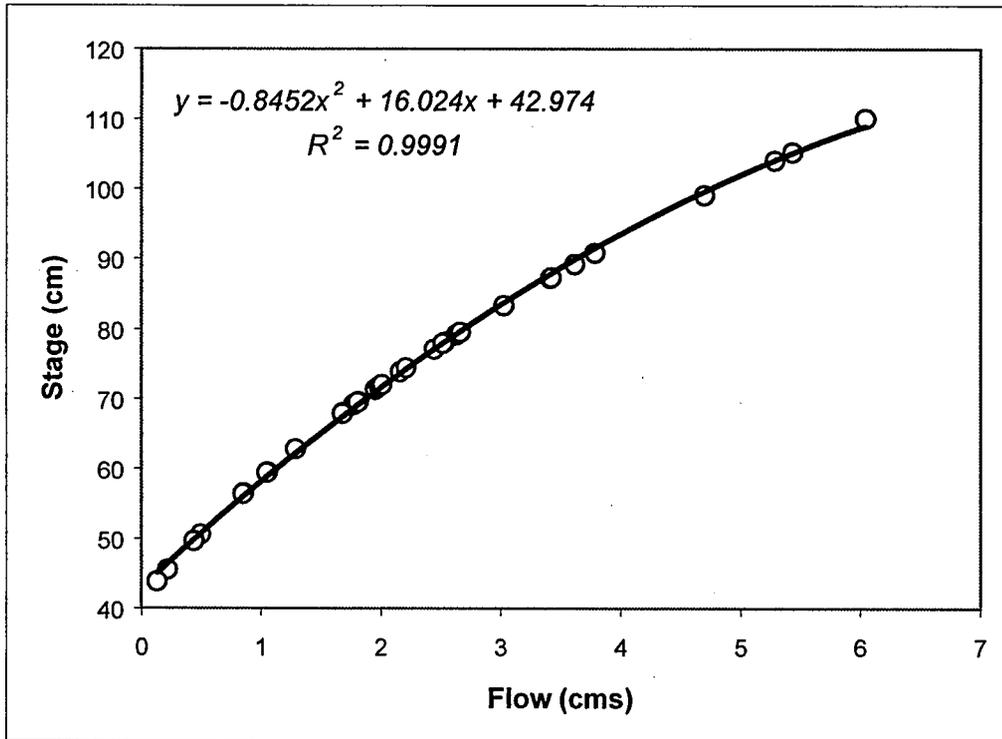
Figure 6. Flow-stage relationship at staff gauge 21, the north channel of the Big Thompson River in Moraine Park for 2000 and 2001.

SURFACE WATER GROUND WATER INTERACTIONS

Stream flow controlled ground water levels throughout most of Moraine Park

(Figures 7, 8, 9). For example, along our western most transect of wells (Figure 1) staff

gauge 28 had an stage change of ~40 cm during 2000, and many monitoring wells, e.g.

44, 47, 48, had a nearly identical change in ground water level with similar timing of rise

and fall as the Big Thompson River (Figure 7). Wells located farther from the river, e.g.

wells 52 and 53, had their seasonal high coincide with the timing of Big Thompson River

stage peak, but had a larger drop in ground water level than wells closer to the river.

Similar patterns of river control of the timing and amount of ground water level rise and

fall can be seen for monitoring wells along two other transects illustrated on Figures 8 and 9.

However, the patterns of ground water level were not completely related to stream stage in all monitoring wells. For example, ground water level in well 70 (Figures 1, 8) rises with river stage, but its decline is much sharper and deeper than other wells. This is likely due to the unusual ground water recharge patterns on the north of the Big Thompson River where recharge is most effective at high river stages. Once river stage declines, ground water levels rapidly decline, likely due to greatly reduced ground water recharge. The other exception occurs in the vicinity of well 65 (Figures 1, 8) where the large granite bedrock outcrop in the center of Moraine Park blocks ground water flow, forcing water to the ground surface where it discharges in numerous springs. Water tables are maintained very close to the soil surface. This pattern can also be seen on the block diagram in Figure 10, where the upward arrow identifies the location of ground water discharge. Ground water levels in this spring complex rise with peak river stage in early summer, but fall much less, 20-25 cm, than other wells or river stage, 40-60 cm. This spring complex has peat soil in areas with perennially saturated soils.

Soil surface and ground water level profiles across Moraine and Horseshoe Parks (Figures 12 and 13) indicate that the river surface elevation is generally the highest water level. Across transect 4 in Moraine Park (Figure 13) the entire central portion of the site is a ground water mound, with lower water levels on the valley edges. Ground water levels are nearly flat across Horseshoe Park (Figure 14) indicating a relatively simple equilibrium between stream gaining and losing, and ground water elevations.

149
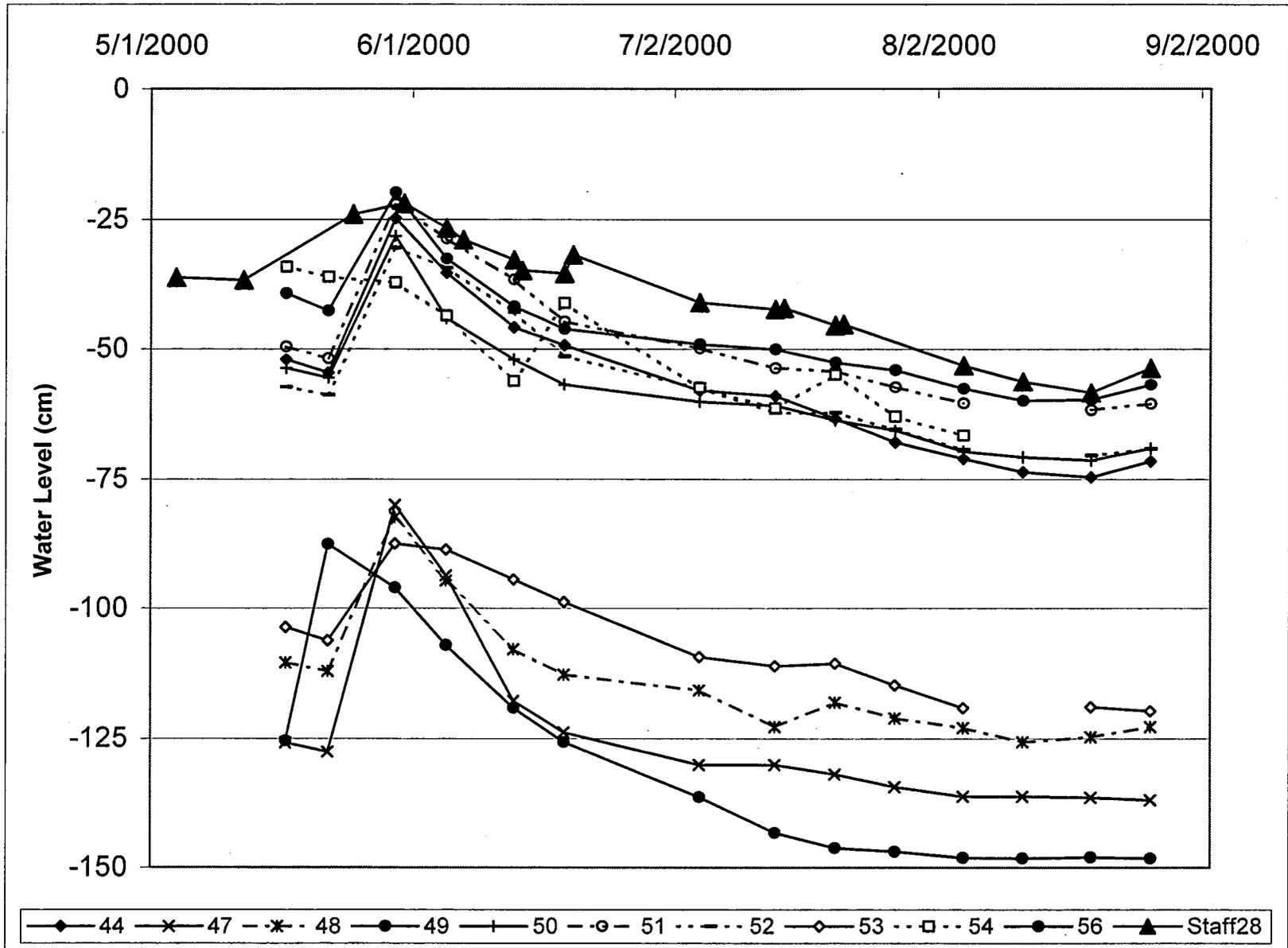
Figure 7. Stage of the Big Thompson River (staff gauge 28) and depth to water table in monitoring wells in Moraine Park.

150
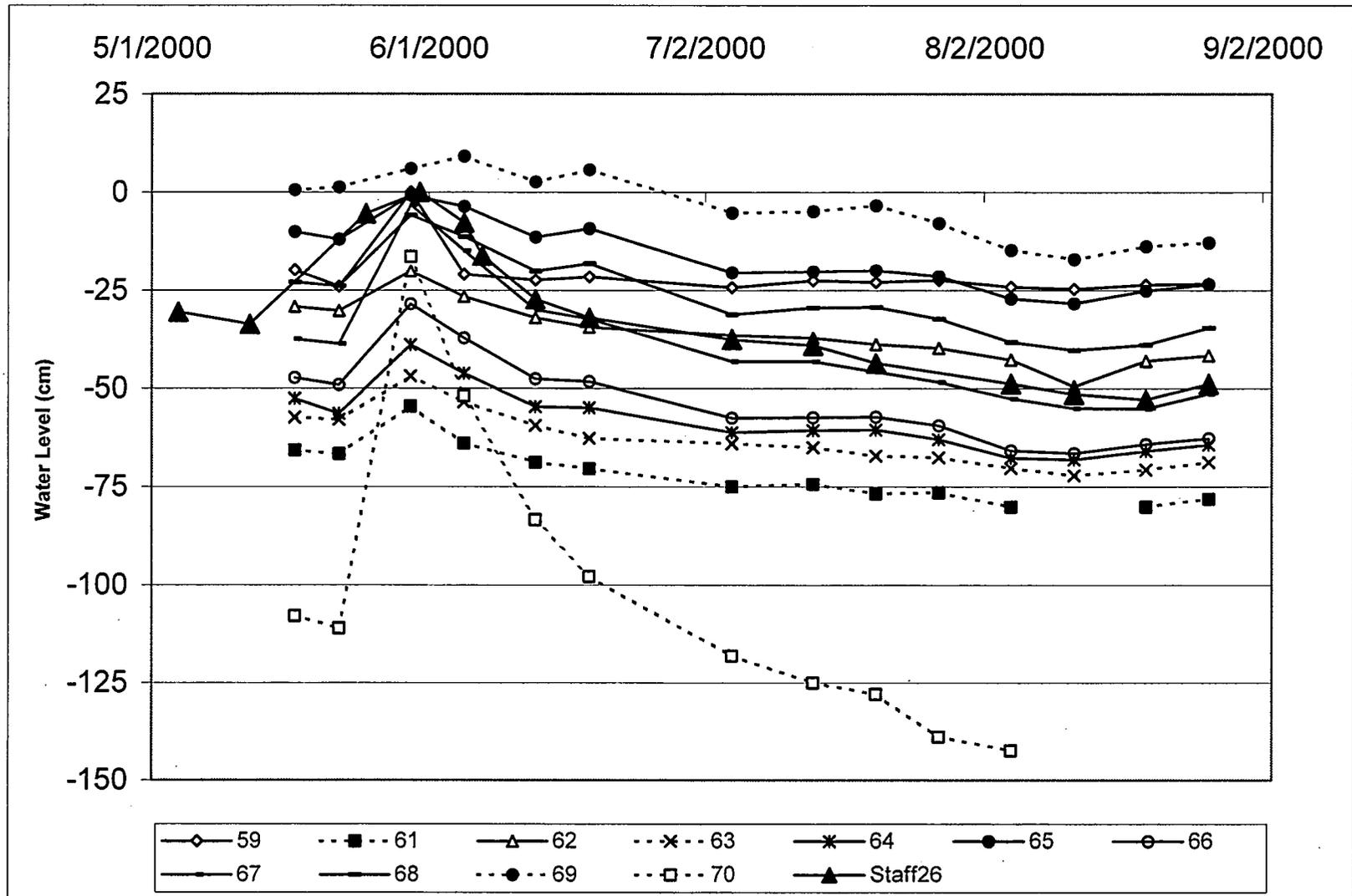
Figure 8. Stage of the Big Thompson River (staff gauge 26) and depth to water table in monitoring wells in Moraine Park.
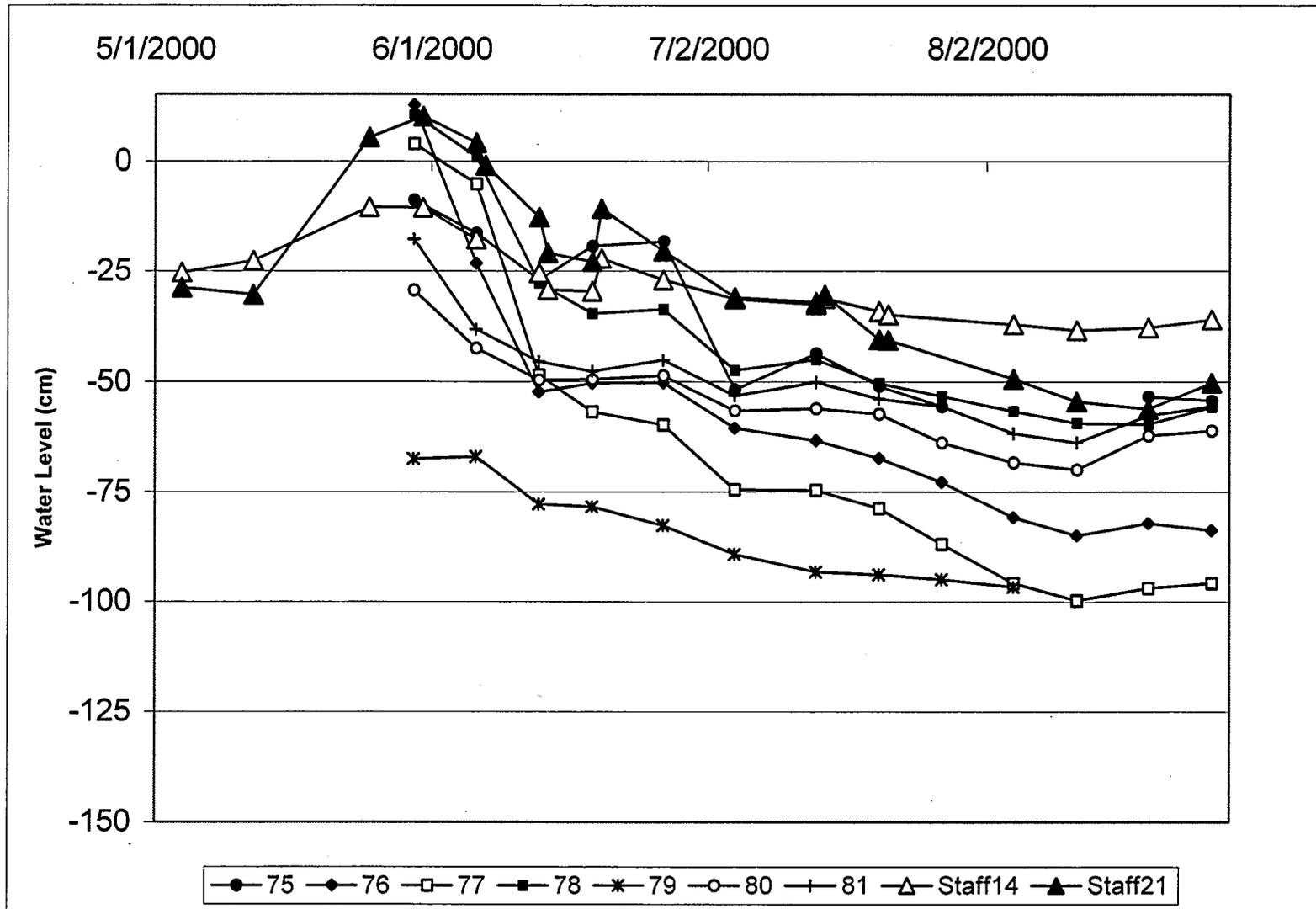
Figure 9. Stage of the Big Thompson River (staff gauge 21 and south channel gauge 14) and depth to water table in monitoring wells in Moraine Park.
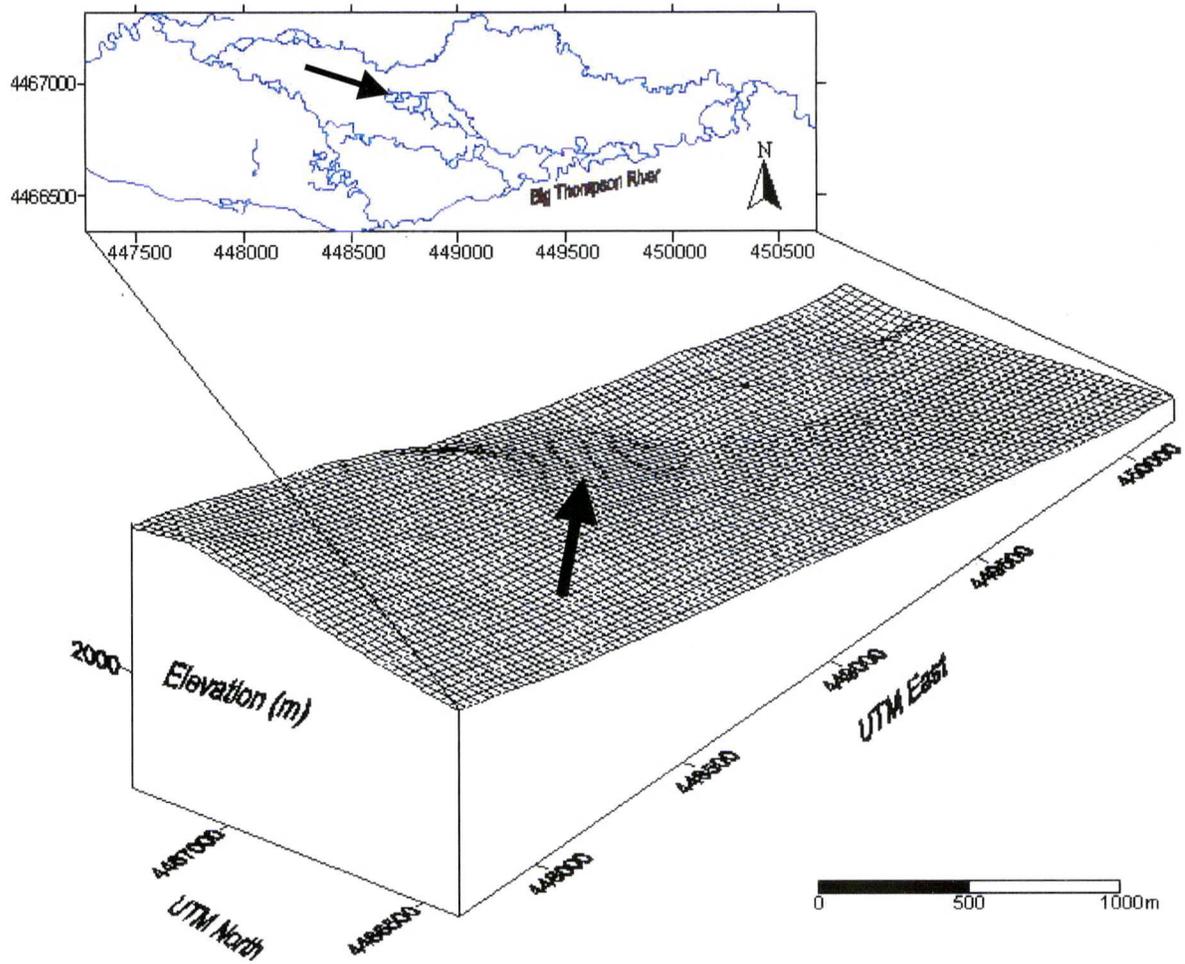
Figure 10. Interpolated water table surface (m asl) for Moraine Park generated using ground water monitoring well data from June 28, 2001
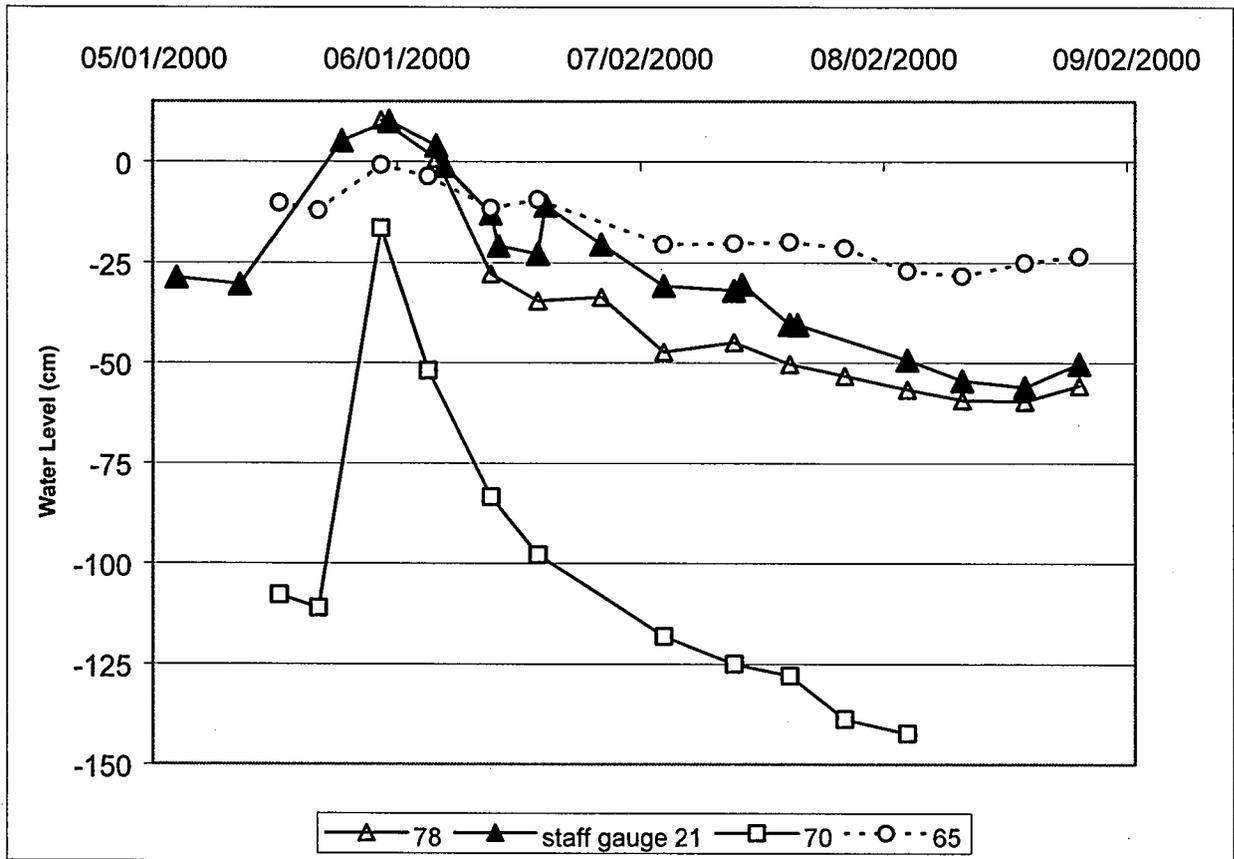
Figure 11. Three types of well hydrographs in Moraine Park, relative to the stage of the Big Thompson River (Staff 21). Ground water levels in well 78 mirrors stage of the Big Thompson River, while water levels in well 78 reflect extreme patterns of recharge and drainage, while well 65 has relatively consistent water levels all summer. Annual ground water level changes are 25, 50 and >100 cm for wells 65, 78 and 70.

154
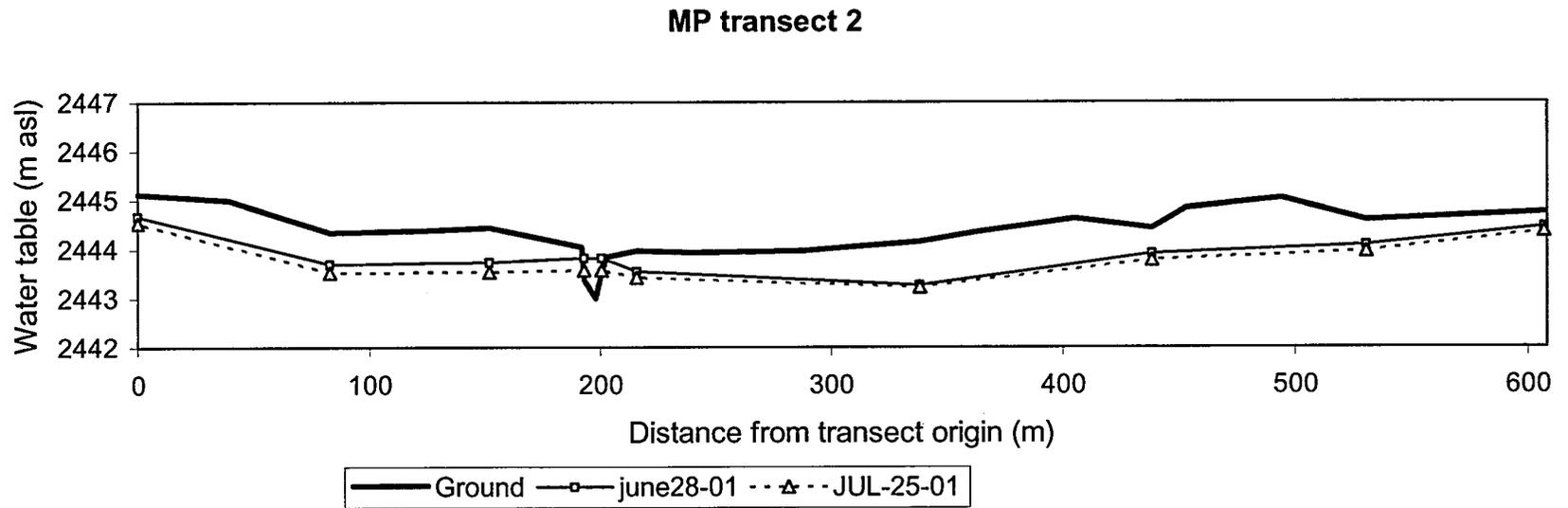
MP transect 2

Figure 12. Ground surface and ground water elevations on 28 June 2001 and 25 July 2001 for well transect 2 in Moraine Park.
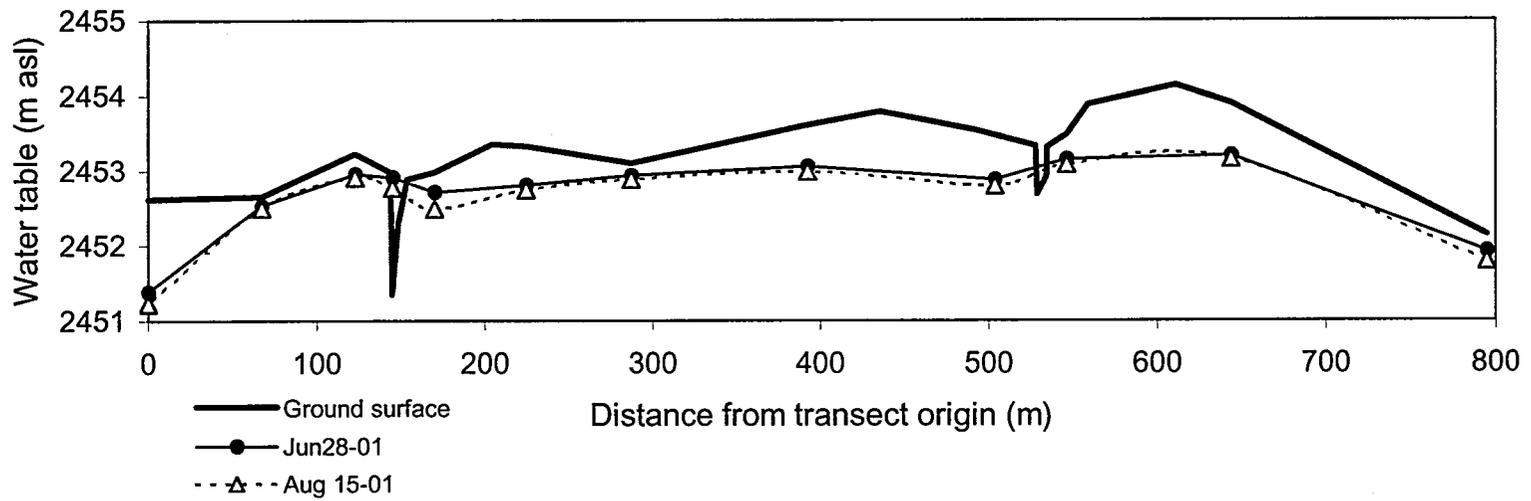
Figure 13. Ground surface and ground water elevations on 28 June 2001 and 15 August 2001 for well transect 4 in Moraine Park.
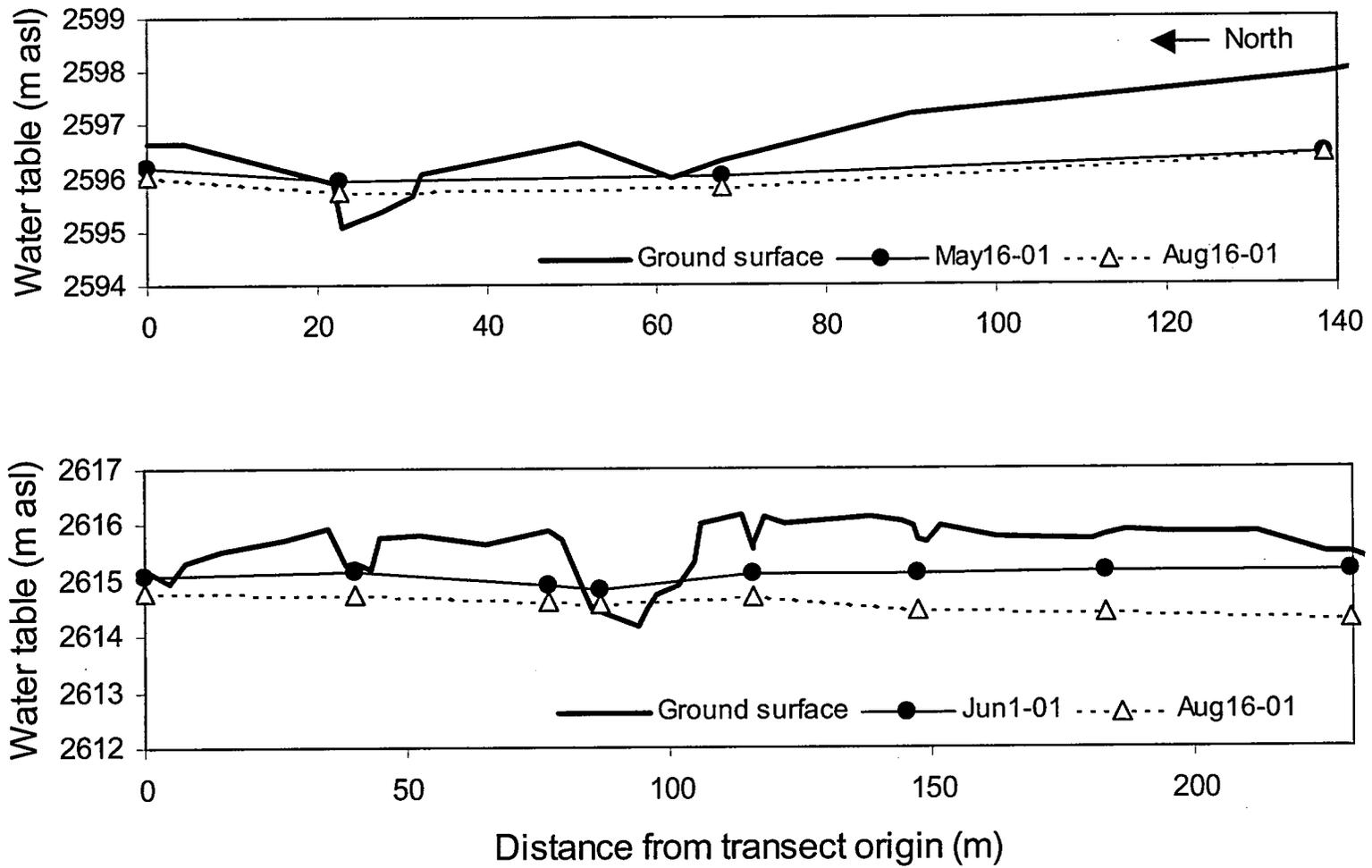
Figure 14. Water table elevation along transects #1 (above) and #4 (below) in Horseshoe Park

DISCUSSION

Stream flow is highly correlated (R^2 = 0.99 to 1.00) with stream stage in Moraine Park. Thus, increases in flow create predictable increases in stream stage. Stream stage is also strongly related to the pattern and magnitude of ground water rise in the study areas. In Moraine Park the Big Thompson River provides important ground water recharge to the large park and is the high point in the surface/ground water system. Because the surface and ground water systems are so well coupled in most areas, higher river flow or higher river stage would produce higher rates of ground water recharge throughout Moraine Park, raising ground water levels. The presence of beaver ponds would also raise river stage and result in higher rates of ground water recharge and high ground water levels in areas influenced by that portion of the river.

The large bedrock outcrop in the center of Moraine Park creates a large upwelling of groundwater on its western and southwestern side. This water flows around the southern side of the outcrop, or into the Big Thompson River on the north, and produces a large dry area with deeper water tables to the east of the outcrop. The ground water discharge area has the most shallow and stable water levels in the central portion of Moraine Park, with highly organic soils.

The surface water and ground water data provide a useful baseline for water levels during the study period and could be monitored regularly in the future to determine the depth to water table in the study areas during years with larger snowpack and higher peak flows than occurred during 2000 and 2001. In addition, if beavers occupy portions of Moraine Park, these wells would provide a data set to compare how beaver dams influence ground water levels at different distances from the Big Thompson River. We recommend that all monitoring wells remain in place, and they are equipped with heavy aluminum tags that should last a decade or more making the wells useful for a long time to come. .