2008

Cottonwood Establishment in a Gravel-Bed River

Claudio Ivan Meier
The University of Montana

COTTONWOOD ESTABLISHMENT IN A GRAVEL-BED RIVER

By

Claudio Iván Meier

B.Sc., Universidad de Concepción, Concepción, Chile, 1989
Civil Engineer, Universidad de Concepción, Concepción, Chile, 1990
M.Sc., Colorado State University, Fort Collins, Colorado, 1995

Dissertation
presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy in Biology

The University of Montana
Missoula, MT

Spring 2008

Approved by:

Dr. David A. Strobel, Dean
Graduate School

Dr. F. Richard Hauer, Chair
Flathead Lake Biological Station
Division of Biological Sciences

Dr. Paul B. Alaback
Department of Forest Management

Dr. James A. Burchfield
Department of Society and Conservation

Dr. Ray M. Callaway
Division of Biological Sciences

Dr. John S. Kimball
Flathead Lake Biological Station
Division of Biological Sciences

Dr. Jack A. Stanford
Flathead Lake Biological Station
Division of Biological Sciences

Meier, Claudio, Ph.D., Spring 2008 Biology

Cottonwood Establishment in a Gravel-Bed River

Chair: Dr. F. Richard Hauer

ABSTRACT

  I investigated the processes of establishment of the cottonwood *Populus trichocarpa* T.&G. along the pristine, 5th order, wandering floodplain of the gravel-bed Flathead River, Montana, USA. The focus of my research was to determine the mechanisms explaining successful recruitment on recently formed, unvegetated bars, covering a range of spatial scales from within-bar (~ 1 to 10 m) to across-reach (~ 1 to 10 km). Results are based on field observations and measurements over three growth seasons (2005 through 2007), as well as outdoor and laboratory experiments.

  At the within-bar scale, I used a paired-plot sampling design to compare closely-located sites with and without successful propagation, controlling for elevation and surface texture. I examined seedling response to soil texture in the root zone, thickness of the coarse surface layer of clean gravel, and depth to water. I found no effects of the vertical distance to water. On the other hand, the proportion of finer sediment (i.e., fine sand, very fine sand, and silt) within the matrix and the thickness of the coarse surface layer are controlling variables, that interact to explain both presence-absence and growth of seedlings. An evaporation experiment demonstrated that the coarse surface layer acts as mulch, strongly reducing evaporation and maintaining high soil moisture levels within the fines. I found that gravel bars are highly heterogeneous environments where the assumptions of horizontal and homogeneous water table and capillary fringe do not hold, and where cottonwood seedlings are essentially acting as facultative instead of obligate phreatophytes. Thus, some of the currently accepted concepts for cottonwood establishment do not apply in gravel-bed rivers.

  Based on my observations of seeds and germinants in the drift, on experimental results confirming that cottonwood seeds germinate, establish and grow under water, and on comparisons of seedling establishment limits with flow profiles, I am proposing the River Seeding Concept of cottonwood establishment in gravel-bed rivers. This conceptual model posits that hydrochory is the primary establishment mechanism creating recruitment bands and patches of seedlings. Wind-dispersed seeds fall on the water, are incorporated into the drift, and are deposited by receding floodwaters along shallow shorelines, where underwater establishment occurs.

DEDICATION

       This Ph.D. thesis is dedicated to the women in my life. My wife Margarita dropped jobs twice to follow me around the world in my academic pursuits. In both cases, she left her own career and personal interests behind in order to take care of our wonderful daughters and of myself, while I protractedly worked towards my doctorate. I am grateful for her constant love and care, and for supporting me in this endeavor. I trust that the opportunities that will derive from my having a Ph.D. will be reflected in our daily quality of life and in our family experiences. Deeply within myself, I know that I should have got my doctorate ten years ago, and am truly sorry for not having done so in a timely fashion. It has been the bane of my recent life; let us hope it is over.

       Our incredible daughters, Carla and Paula, probably took both the best, but also the brunt of this process. They learned English and had a fun time attending school in Polson, riding the yellow school bus, and swimming in Flathead Lake every day of the summer. On the other hand, no young girl should ever be separated from their father for ten months in a year. I hope I can be pardoned for having done so, and I swear that if I could go back in time, I would have arranged things in a way that would have not implied such lengthy separation periods. Indeed, I hereby solemnly promise never to leave my wife and my daughters alone again for any period longer than ten days, no matter how interesting the prospective trip might seem.

       My mother, Norma, has been helping me achieve my dreams since I was a kid. Now she helps us as a family. I am thankful for her support, particularly for her accommodating my family while our house was being rented and I was absent.

       Margarita, Carla, Paula, y Norma, esta tesis es gracias a Ustedes, por Ustedes, y para Ustedes.

       Con Amor,

       Claudio

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

Chapter 3: The River Seeding Concept for Cottonwood Establishment at the Reach-Scale

Chapter 4: Temperature and motion effects on underwater germination of cottonwood seeds

Chapter 5: Coarse Surface Layer Strongly Affects Moisture within Gravel Bars: Results from an Evaporation Experiment

Chapter 6: Conclusions

LIST OF FIGURES

**Chapter 2: Establishment of Cottonwood Seedlings in the Active Channel
of the Wandering Gravel-Bed Flathead River, Montana, USA**

**Chapter 3: The River Seeding Concept for Cottonwood Establishment
at the Reach-Scale**

**Chapter 4: Temperature and motion effects on underwater germination of
cottonwood seeds**

**Chapter 5: Coarse Surface Layer Strongly Affects Moisture within Gravel
Bars: Results from an Evaporation Experiment**

LIST OF TABLES

The Importance of Floodplain Forests

Pristine floodplain corridors of alluvial rivers are among the most dynamic, complex, diverse, productive, as well as endangered ecosystems, especially where the local climate and river hydrology allow for perennial flows and the occurrence of woody vegetation (Naiman and Décamps 1997, Tockner and Stanford 2002, Ward et al. 2002, Stanford et al. 2005).

Vegetation is the most important intermediary through which climate and land use affect geomorphological processes and landforms (Kirkby 1995). Fluvial landscapes are no exception to this rule: Riparian trees have a wide range of effects on the character and rates of the processes involved in creating fluvial landforms, mediated through changes in water budgets, soil moisture, resistance to flow, sediment deposition, bank erosion, channel and floodplain evolution, etc. (Gurnell 1997, Simon et al. 2004).

Until recently, riverine landscapes had been considered to be largely driven by hydrogeomorphic dynamics, with riparian vegetation taken to be only a secondary factor, a passive player within channel adjustment. However, Gurnell and Petts (2002) argue that vegetation has an active role, particularly in island-dominated reaches, as is the case in wandering (braided-meandering) gravel-bed rivers. Riparian vegetation not only exerts strong controls on many hydro-geomorphic processes; it is in turn dependent on many of those same processes, thus creating positive feedback loops (Gregory et al. 1991, Richards et al. 2002, Francis 2006). Tal et al. (2004), through field studies, flume experiments, and numerical modeling, confirm the role of riparian vegetation as a primary control on channel form, in the case of multi-thread gravel-bed rivers.

Riparian vegetation is also a fundamental driver of river ecology. The Shifting Habitat Mosaic (SHM) of Stanford et al. (2005; see also Stanford 1998 and Ward et al. 2002) is the unifying theory explaining the pattern and process of fluvial ecosystems in the case of alluvial rivers with a flood régime. It refers to the complex, heterogeneous, and ever-changing distribution of habitat patches within a floodplain, which is

dynamically used by the different life stages of aquatic and riparian organisms. This mosaic is driven by the flow, sediment, and large woody débris (LWD) régimes imposed from upstream, interacting with the floodplain vegetation and bed and bank materials along the reach. Specifically, the regeneration of pioneer riparian vegetation is one of the fundamental processes involved in changing the spatial distribution and availability of habitat patches over time, as bare sediments are colonized by woody vegetation.

Woody plants are one of the primary controls on the biophysical complexity of river-floodplain ecosystems. Riparian forest character and dynamics play important roles in explaining the structure and functioning of fluvial ecosystems (Gregory et al. 1991, Malanson 1993, Décamps 1996, Naiman and Décamps 1997, Naiman et al. 1998): They provide shade, allochthonous organic matter inputs, filtration of nutrients in shallow groundwater flows and of fine sediments in overland flows, and are a source of large woody débris (LWD) to aquatic ecosystems (Berg et al. 2003); they modify the microclimate and serve as corridor for movements of both animals and plants, and also as habitat for mammals and birds (Finch and Ruggiero, 1993).

Primary Succession in Floodplains

Even though the mechanisms of floodplain formation, and the rates at which they occur, can be quite different across river styles or patterns (Nanson and Croke 1992, Miall 1996), there is a fundamental principle which is valid for all alluvial channels: All landforms across a floodplain (but for features at the smallest spatial scales) are originally formed in the active part of the channel, the parafluvial zone (sensu Stanford et al. 2005, see also Lorang and Hauer 2006). As these younger habitats, formed by the physical processes of erosion and deposition -mediated by the presence of LWD (Gurnell et al. 2001 and 2005, Abbe and Montgomery 2003, Francis 2006), become colonized by vegetation, there is a shift towards a primary control by plant succession. In simpler terms, colonization of parafluvial surfaces must first happen in order for vegetated orthofluvial surfaces (sensu Stanford et al. 2005) to be built (Décamps 1996). The development of riparian forests starts then as a primary succession over bare sediment surfaces (Braatne et al. 1996, Mahoney and Rood 1998), controlled by allogenic

processes, whereas older stands on the orthofluvial are regenerated through autogenic processes such as competition and gap dynamics (Oliver 1981, Décamps 2005, Francis 2006).

Floodplain succession is thus initiated in the active part of the river corridor, the parafluvial zone, when woody plants colonize bare sediment surfaces. In gravel-bed rivers, these surfaces are normally associated with the creation of new bars. The most critical phase in floodplain forest succession can be assumed to be the early establishment of vegetation on bars, as plants need to survive the harsh conditions, involving frequent inundation, scouring by water and in some climates ice, and summertime desiccation (Mahoney and Rood 1998, Tabacchi et al. 1998, Stanford et al. 2005).

The initial colonization of gravel bars by pioneering vegetation is a process of the utmost importance, both from a morphological and ecological perspective, in understanding floodplain formation and habitat dynamics in alluvial rivers (Gregory et al. 1991, Décamps 1996, Bennett & Simon 2004). Once they are colonized by vegetation, bars trap fine sediment during floods, thus growing by vertical accretion. In a positive-feedback mechanism, the raised surface and deeper soil provide a better environment for vegetation growth, for example by decreasing the frequency of flooding and scouring disturbances, and by increasing water-holding capacity (Décamps 1996, Gurnell and Petts 2002, Francis 2006). In this way, the original bar becomes the new floodplain surface, allowing for succession to eventuate (Dykaar and Wigington 2000).

The establishment mechanisms of pioneering woody vegetation must be carefully studied, not only to understand floodplain creation, riparian forest succession, and the temporal and spatial dynamics of the SHM in alluvial river corridors (Décamps 1996, Stanford et al. 2005), but also in order to conduct meaningful river restoration, based on ecological science.

Riparian Cottonwoods

Species in the sections *Tacamahaca* and *Aigeiros* of the genus *Populus* L. (family Salicaceae), commonly known as cottonwoods or poplars, are important riparian trees throughout most of the Northern Hemisphere (Eckenwalder 1996, Rood et al. 2003a).

Together with willows, they are the main pioneer species colonizing bare, exposed sediments along corridors of alluvial rivers (Karrenberg et al. 2002). Cottonwoods are often the single dominant riparian tree along streams in semi-arid and arid environments, providing critical habitat (Finch and Ruggiero 1993, Friedman et al. 1997, Mahoney and Rood 1998), but they are usually replaced by later-successional species in wetter climates (Rood et al. 2003a).

Riparian cottonwoods are not only fundamental in trapping fine sediment during floods, thus creating deeper soils and forming the floodplain. They also help in stabilizing surfaces, protecting them from flood scour, and provide a major source of LWD. In all of these roles, they modify and create habitats, thus acting as ecosystem engineers (Jones et al. 1994, Lawton and Jones 1995). Cottonwoods can be categorized both as autogenic engineers, for example, when seedlings or fallen logs enhance sedimentation in their lee, and as allogenic engineers, e.g., when their root systems increase the mechanical resistance of river banks to scouring by floods.

The evolution of traits allowing colonization of the parafluvial by riparian tree species such as cottonwoods and willows is an example of biotic adaptation to disturbance. These pioneer species are not only one of the main drivers of the SHM of river ecosystems, but they in turn depend on the dynamic habitat régime provided by such environments (Karrenberg et al. 2002, Stanford et al. 2005). Within the Salicaceae, which are noted colonizers of bare sediments in fluvial landscapes, some species produce large numbers of short-lived seeds (Moss 1938), while others are also able to reproduce vegetatively (Karrenberg et al., 2002). Other species produce very few seeds, and mostly reproduce by vegetative propagation. Propagule dispersion can happen through many mechanisms; hydrochory – transport by water, is particularly relevant for riparian species (Gurnell et al. 2004), either for initial dispersion or for further mobilization of propagules that were initially dispersed into water by other mechanisms (e.g., by wind, anemochory).

The timing of propagule dispersal in relation to flow régime is important. Most species are seasonally specific in their time of propagule release, so that it occurs synchronously with particular hydrological régimes (Gurnell et al. 2004). For example, populations of cottonwoods in North America, and of other riparian *Populus* in the

Northern Hemisphere, have different phenologies of seed dispersal, reflecting environmental differences between plants growing at different elevations and latitudes.

The same variables affecting the timing of flowering and seed production also drive snowmelt, so that seed release usually occurs just after peak flows (Mahoney and Rood 1998). The fact that seed dispersal typically coincides with declining river flows, increases the probability that seeds will land on favorable microsites along the river channel (Braatne et al. 1996).

The riparian cottonwoods of North America include five species within sections *Tacamahaca* and *Aigeiros* (Eckenwalder 1996). In general, *Tacamahaca* species are found at higher elevations and latitudes (Braatne et al. 1996), and are considered to be adapted to colder conditions (Mazzoleni and Dickmann 1988). Cottonwoods hybridize easily, forming hybrid swarms. Montana and Alberta are centers of cottonwood diversity in North America, with four of the five species present (only *P. fremontii* of the US Southwest is absent), as well as a wide range of hybrids. These riparian trees are considered to be phreatophytic, i.e., they are tightly linked to alluvial aquifers for their water uptake (Busch et al. 1992, but see also Smith et al. 1998).

Cottonwoods are dioecious trees which bear flowers in catkins. Each adult tree produces large numbers of seeds, borne by cotton-like hairs (thus the name 'cottonwood'), which are dispersed by wind and water. This pappus surrounding cottonwood (and all Salicaceae) seeds favors retention on wet sites, ensuring that seeds landing on adequate, moist surfaces, remain attached there; on the other hand, seeds falling on dry sites keep tumbling until they reach a wet site to adhere to (Krasny et al. 1988). Seed viability is very short, lasting only a few weeks under natural moisture conditions (Moss 1938, Fenner et al. 1984). Once seeds get wet, they germinate in 2-3 days, and will be lost if they do not encounter adequate conditions (Braatne et al 1996). If seeds land on moist, mineral soil, without shading, and where surface moisture is maintained for a week or more, they germinate rapidly. Following dispersal, extensive mats of seedlings can thus be found on moist, exposed substrates within the parafluvial zone of alluvial rivers, in densities of more than 4000/m^2.

The growth and development of the seedlings is dependent on abundant sunlight, soil moisture, and direct contact with the mineral soil, as the seeds lack endosperm.

Cottonwood seedlings cannot really compete in vegetated sites, nor germinate well on plant litter. Root growth takes place slowly during the first month, and from there on occurs much more rapidly (Moss 1938). This is why soil moisture needs to be maintained during the initial weeks. Initial seedling establishment can be prolific; afterwards, the seasonal decline in the alluvial water-table determines seedling survival. As the hydrograph recedes, the roots strive to maintain contact with moist soil; the vast majority of the seedlings die of drought stress if root growth is unable to keep up with the rate of water table decline (Braatne et al. 1996, Mahoney and Rood 1998).

Cottonwood Establishment

Based on this research, and on ample field evidence on the deleterious effects that damming has had on riparian cottonwoods (Bradley and Smith 1986; Rood and Mahoney 1990, 1993, and 1995; Rood et al. 1995; Braatne et al. 1996; Cooper et al. 1999; Merritt and Cooper 2000; Williams and Cooper 2005), Mahoney and Rood (1991, 1993, 1998; see also Amlin and Rood 2002; Samuelson and Rood 2004; Rood et al. 2005) have proposed the Recruitment Box Model (RBM) for explaining cottonwood establishment. It states that there is an elevational range for recruiting seedlings, on recently exposed sediment surfaces along a river channel, where riparian trees are likely to become successfully established if the timing of flow peak and rates of recession are favorable. This model helps in defining stream stage patterns, and thus streamflow régimes, enabling successful establishment of riparian cottonwood seedlings. Their hypothesis is that (a) decreased flow peaks, (b) abrupt flow changes, particularly declines, and (c) insufficient late-summer flows have combined to reduce cottonwood establishment on dammed rivers, by decreasing disturbances that create new nursery sites, preventing initial establishment of seedlings at appropriate streambank elevations, and exaggerating drought stress. This has led to highly skewed age distributions of cottonwoods along many rivers in North America, with only old, remnant trees, but no young adults, saplings and seedlings. Most cottonwood species reach a maximum age of about 150 to 200 years, but *P. trichocarpa* can live upwards of 400 years (Rood and Polzin 2003). There is ample evidence that groundwater declines associated with decreased late-summer flows also

affect riparian cottonwoods negatively (Stromberg et al. 1996, Scott et al. 1999, Scott et al. 2000, Horton and Clark 2001, Horton et al. 2001, Rood et al. 2003a, Lite and Stromberg 2005), at least in effluent streams, which lose flow to the underlying alluvial aquifer.

It should be noted that some authors have actually described an increased recruitment of cottonwoods following damming (e.g., Johnson 1994, 2000), but this behavior seems restricted to fully braided sandy rivers, where regulated, stabilized flows decrease flood scour and ameliorate the original water-stress of summer. Webb and Leake (2006) also report flourishing cottonwood establishment in some streams of the Southwestern United States, over the last century.

The RBM focuses mainly on the need for: (a) large enough flood flows, in order to initiate cottonwood recruitment, by creating and/or wetting the barren nursery sites that are adequate for establishment, (b) the right timing for these peak flows and their subsequent recession to occur, based on the phenology of seed release, and (c) a survivable stage decline, based on root growth rates from the literature. Note that according to Noble (1979), and contrary to most recent research, a long period (> 2 weeks) with no recession is required for cottonwood establishment. In experimental applications of the RBM, across a suite of highly impacted rivers and streams, treatments have resulted in large differences in the age structure of riparian cottonwood corridors, clearly enhancing establishment and recruitment (Rood et al. 1998, Rood and Mahoney 2000, Kalischuk et al. 2001, Rood et al. 2003b, Rood et al. 2005).

Most of the field component of this previous research has focused on analyzing established cottonwoods, usually covering a broad range of ages and stages. Even though focusing on older trees is a good integrative measure of continued success through time, it also incorporates the additive effects of a wide range of environmental disturbances, such as floods, droughts, ice-drive events, etc., making it hard to pinpoint those specific mechanisms impeding or limiting early establishment. Because the most critical phase in floodplain forest succession can be assumed to be the early establishment of vegetation in the active channel, especially during its first season of growth, I decided to focus my investigation on establishment of cottonwood seedlings of the year (hereafter referred to as 0+ seedlings) on recent, unvegetated bars within the active channel.

Other researchers have shown that conditions favoring establishment, which are mostly related to hydrology, elevation, and soil texture, strongly depend on the geomorphological setting, specifically on the river pattern or style (Décamps 1996, Scott et al. 1996 and 1997, Friedman et al. 1997, Cooper et al. 2003). The Hydrogeomorphic Recruitment Model (HRM: Scott et al. 1996 and 1997, Friedman et al. 1997, Auble and Scott 1998, Friedman and Lee 2002) stresses that the relation between streamflow, the formation of establishment surfaces, and tree recruitment depends on the river pattern or style, because it determines how hydrologic and geomorphic processes create establishment sites and adequate conditions for cottonwoods. Not all processes apply in all geomorphic settings.

Specifically, establishment of riparian trees has been well-studied for meandering (e.g., Everitt 1968, Bradley and Smith 1986, Rood and Mahoney 1995), braided (e.g., Kollmann et al. 1999, Edwards et al. 1999, Johnson 1994 and 2000, Gurnell et al. 2001) and laterally constrained rivers (e.g., Baker 1990, Scott et al. 1996 and 1997, Auble and Scott 1998), but not for wandering systems. When Décamps (1996) claimed that "we need to concentrate more on the mechanisms which link water, landforms, and species in different landscape settings. In particular, we need to consider the various intermediate situations between meandering and braided rivers," he was referring exactly to the river style that I study herein.

Even though there have been applications of the RBM and HRM concepts in both fine and coarse substrate rivers, across a range of floodplain styles, none of the previously mentioned authors explicitly state whether their models apply indistinctly to both sand and gravel-bed streams. Cooper et al. (1999) proposed that cottonwood establishment on sand-bed rivers should be fundamentally different from that on rivers with a coarse, gravelly substrate. Several studies on cottonwood establishment were carried out on gravel-bed rivers (e.g., McBride and Strahan 1984, Merigliano 1998, Rood et al. 1998, Rood and Mahoney 2000, Francis et al. 2006), and there are conceptual models that account for establishment under diverse geomorphic settings (e.g., the above-mentioned HRM). Still, with the exception of Francis et al. (2006), no previous study on gravel-bed systems has considered the three dimensional structure of river deposits. Also, I know of no research that has actually looked at how some of the fundamental distinctions between

sand and gravel-bed alluvial streams could differentially affect riparian tree establishment.

Firstly, gravel beds show a bimodal distribution of grain sizes, whereby a gravel framework is partially or totally filled with a fine matrix of sand and silt (Church et al. 1987). Capillary effects can be presumed to be important, as proposed by Mahoney and Rood (1998). This matrix material can display a large variability in fine content, sediment caliber distribution, and continuity, at both the reach and bar scales. Consequently, the height of capillary rise from the alluvial water table should be expected to be variable at fine spatial scales, which should result in fine-scale patchiness in its ability to sustain vegetation (Alpert et al. 1999, Petts et al. 2000, Francis 2006). Secondly, these mixed sediment deposits are usually covered with clean gravel and cobbles. These act as mulch, i.e., as a layer of coarse material that strongly decreases evaporation from the soil surface, retaining moisture within the matrix. Thirdly, the presence of layers of open-framework gravels with large hydraulic conductivity can result in preferential flow pathways (Huggenberger et al. 1998) and strong downwelling. Both effects mean that the usual assumptions that the alluvial water-table is horizontal and connected to the river stage cannot be sustained in most alluvial gravel-bed rivers. Finally, bar height is larger in gravel-bed rivers than in sand streams. As proposed by Cooper et al. (1999) and Bhattacharjee et al. (2006), it is not possible for seedlings located in high bars to maintain root contact with the receding water table or capillary fringe during the initial years of growth. Indeed, Cooper et al. (1999) state that "the mechanism of seedling establishment on rivers with large stage change is unclear".

In this work, I study the mechanisms enabling establishment of cottonwood seedlings of the year in the active channel (the parafluvial, sensu Stanford et al. 2005) of a wandering, gravel-bed river, focusing on the differences with sand-bed channels.

Thesis Structure

In Chapter 2, I focus on the factors affecting establishment of cottonwood seedlings in bars of a gravel-bed river during their first season of growth, at the within-the-bar scale. Specifically, I study how the thickness of the coarse surface layer, the

texture characteristics of the fine matrix, and the difference in elevation between establishment site and water, explain 0+ seedling presence-absence, density, as well as growth. I question the usual assumption that cottonwood seedlings are obligate phreatophytes. My hypotheses are that: (i) the presence of a coarse surface layer (acting as rock mulch) improves establishment success, by protecting moisture within the bar, (ii) if this coarse surface layer is too thick, seeds will not be able to establish, (iii) finer matrix material within the root zone leads to higher establishment success, by holding more capillary water, and (iv) as suggested by the RBM, the vertical distance to water is inversely correlated with establishment success.

In Chapter 3, I look at cottonwood establishment at the reach scale. I question the currently accepted paradigm that seedlings form well-defined bands because of desiccation of individuals located at higher elevations. Instead, I propose the "River Seeding Concept", a new hypothesis that explains the occurrence of seedling bands and patches as a result of hydrochory: Cottonwood seeds are disseminated by the river's waters, and the recruitment bands (and patches) on bars are simply the riverbed area uncovered by the receding stage over the period of seed availability, during which the flow is carrying and depositing seeds.

Chapter 4 reports the results of laboratory experiments conducted in support of the River Seeding hypothesis, in which I tested the effects of water temperature and motion on cottonwood seed germination. My hypotheses are that: (i) immersion under cold water delays germination and there is a cost in vitality associated with such delay, (ii) germination has a functional dependence on both water temperature and time under water, which can thus be parametrized in terms of cumulative degree-days, (iii) germinating seeds and seedlings are adapted to withstand water motion, and (iv) seeds with their plume (or pappus) mostly float when falling on quiet waters.

In Chapter 5, I document the results of an outdoor evaporation experiment, in which I tested the hypothesis that the coarse surface layer of clean gravel and cobble found on bars of gravel-bed rivers acts as rock mulch, decreasing evaporation and maintaining high soil moisture levels in the underlying finer material. These results lend support to some of the main findings from Chapter 2.

Chapter 6 summarizes the conclusions of this thesis, and discusses some of its broad implications with respect to the restoration of riparian forests and river conservation in general.

The larger goals of this work involve (i) testing whether the RBM, which was seemingly developed for sand-bed streams, is also applicable to gravel-bed rivers at the bar and reach scale, (ii) understanding the mechanisms underlying cottonwood establishment in a hydrologically and morphologically intact wandering gravel-bed river, and (iii) generating information specific to the black cottonwood *P. trichocarpa*, a species that has been much less studied than the *Aigeiros* section species, for example, *P. deltoides* (sensu lato, cf. Eckenwalder 1996), according to Braatne et al. (2007).

Understanding cottonwood seedling recruitment more thoroughly within the context of these goals will help guide river restoration attempts in systems that have been modified by human activity.

References Cited

Abbe, T.H., and D.R. Montgomery. 2003. Patterns and processes of wood débris accumulation in the Queets River basin, Washington. *Geomorphology*, **51**, 81-107.

Alpert, P., F.T. Griggs, and D.R. Peterson. 1999. Riparian forest restoration along large rivers: Initial results from the Sacramento River Project. *Restoration Ecology*, **7**, 360-368.

Amlin, N.M., and S.B. Rood. 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands*, **22**, 338-346.

Auble, G.T., and M.L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the Upper Missouri River, Montana. *Wetlands*, **18**, 546-556.

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

Bennett, S.J., and A. Simon. 2004. *Riparian Vegetation and Fluvial Geomorphology*. Water Science and Application series No8, American Geophysical Union, Washington, DC.

Berg, D.R., A. McKee, and M.J. Maki. 2003. Restoring floodplain forests. Pp. 248-291 in D.R. Montgomery, S. Bolton, D.B. Booth, and L. Wall, Editors, *Restoration of Puget Sound Rivers*. University of Washington Press, Seattle.

Bhattacharjee, J., J.P. Taylor, Jr., and L.M. Smith. 2006. Controlled flooding and staged drawdown for restoration of native cottonwoods in the Middle Rio Grande Valley, New Mexico, USA. *Wetlands*, **26**, 691 – 702.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. Pp. 57-85 in R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley, Editors, *Biology of* Populus *and its Implications for Management and Conservation*, Natural Research Council of Canada Press, Ottawa.

Bradley, C.E., and D.G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany*, **64**, 1433-1442.

Busch, D.E., N.L. Ingraham, and S.D. Smith. 1992. Water uptake in woody riparian phreatophytes of the Southwestern United States: A stable isotope study. *Ecological Applications*, **2**, 450-459.

Church, M.A., D.G. McLean, and J.F. Wolcott. 1987. River bed gravels: Sampling and Analysis. In *Sediment Transport in Gravel-Bed Rivers*. Edited by C.R. Thorne, J.C. Bathurst, and R.D Hey. John Wiley and Sons, Chichester. Pp. 43-88.

Cooper, D.J., D.M. Merritt, D.C. Andersen, and R.A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the Upper Green River, USA. *Regulated Rivers: Research and Management*, **15**, 419-440.

Décamps, H. 1996. The renewal of floodplain forests along rivers: a landscape perspective. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **26**, 35-59.

Décamps, H. 2005. The 'why?' and the 'so what?' of riverine landscapes. Pp. 248-256 in J.A. Wiens and M.R. Moss, Editors, *Issues and Perspectives in Landscape Ecology*, Cambridge University Press.

Dykaar, B.B., and P.J. Wigington, Jr. 2000. Floodplain formation and cottonwood colonization patterns on the Willamette River, Oregon, USA. *Environmental Management*, **25**, 87-104.

Eckenwalder, J.E. 1996. Systematics and evolution of *Populus*. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 7-32.

Edwards, P.J., J. Kollmann, A.M. Gurnell, G.E.Petts, K. Tockner, and J.V. Ward. 1999. A conceptual model of vegetation dynamics on gravel bars of a large alpine river. *Wetlands Ecology and Management*, **7**, 141-153.

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

Fenner, P., W.W. Brady, and D.R. Patton. 1984. Observations on seeds and seedlings of Fremont cottonwood. *Desert Plants*, **6**, 55 - 58.

Finch, D.M., and L.R. Ruggiero. 1993. Wildlife and biological diversity in the Rocky Mountains and Northern Great Plains. *Natural Areas Journal*, **13**, 191-203.

Francis, R.A. 2006. Allogenic and autogenic influences upon riparian vegetation dynamics. *Area*, **38**, 453-464.

Francis, R.A., A.M. Gurnell, G.E. Petts, and P.J. Edwards. 2006. Riparian tree establishment on gravel bars: interactions between plant growth strategy and the physical environment. In *Braided rivers: process, deposits, ecology and management.* Edited by G. Sambrook-Smith, J. Best, C. Bristow, and G.E. Petts. International Association of Sedimentologists Special Publication 36. Blackwell, Oxford. Pp. 361–380.

Friedman, J.M., M.L. Scott, and G.T Auble. 1997. Water management and cottonwood forest dynamics along prairie streams. Pp.49-71 in F.L. Knopf and F.B. Samson, Editors, *Ecology and Conservation of Great Plains Vertebrates*. Springer, New York.

Friedman, J.M., and V.J. Lee. 2002. Extreme floods, channel change and riparian forests along ephemeral streams. *Ecological Monographs*, **72**, 409-425.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience*, **41**, 540-551.

Gurnell, A.M. 1997. The hydrological and geomorphological significance of forested floodplains. *Global Ecology and Biogeography Letters*, **6**, 219-229.

Gurnell, A.M., G.E. Petts, D.M. Hannah, B.P.G. Smith, P.J. Edwards, J. Kollmann, J.V. Ward, and K. Tockner. 2001. Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. *Earth Surface Processes and Landforms*, **26**, 31-62.

Gurnell, A.M., and G.E. Petts. 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. *Freshwater Biology*, **47**, 581-600.

Gurnell, A.M., J.M. Goodson, P.G. Angold, I.P Morrissey, G.E. Petts, and J. Steiger. 2004. Vegetation propagule dynamics and fluvial geomorphology. Pp. 209-219 in Bennett and Simon (2004).

Gurnell, A.M., K. Tockner, P. Edwards, and G.E. Petts. 2005. Effects of deposited wood on biocomplexity of river corridors. *Frontiers in Ecology and the Environment*, **3**, 377-382.

Horton, J.L., and J.L. Clark. 2001. Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. *Forest Ecology and Management*, **140**, 239-247.

Horton, J.L., T.E. Kolb, and S.C. Hart. 2001. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications*, **11**, 1046-1059.

Huggenberger, P., E. Hoehn, R. Beschta, and W. Woessner. 1998. Abiotic aspects of channels and floodplains in riparian ecology. *Freshwater Biology*, **40**, 407-425.

Johnson, W.C. 1994. Woodland expansion in the Platte River, Nebraska: Patterns and causes. *Ecological Monographs*, **64**, 45-84.

Johnson, W.C. 2000. Tree recruitment and survival in rivers: Influence of hydrological processes. *Hydrological Processes*, **14**, 3051- 3074.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos*, **69**, 373-386.

Kalischuk, A.R., S.B. Rood, and J.M. Mahoney. 2001. Environmental influences on seedling growth of cottonwood species following a major flood. *Forest Ecology and Management*, **144**, 75-89.

Karrenberg, S., P.J. Edwards, and J. Kollmann. 2002. The life-history of Salicaceae living in the active zone of floodplains. *Freshwater Biology*, **47**, 733-748.

Kirkby, M. 1995. Modelling the links between vegetation and landforms. *Geomorphology*, **13**, 319-335.

Kollmann, J., M. Vieli, P.J. Edwards, K. Tockner, and J.V. Ward. 1999. Interactions between vegetation development and island formation in the Alpine river Tagliamento. *Applied Vegetation Science*, **2**, 25-36.

Krasny, M.E., K.A. Vogt, and J.C. Zasada. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Holarctic Ecology*, **11**, 210-219.

Lawton, J.H., and C.G. Jones. 1995. Linking species and ecosystems: Organisms as ecosystem engineers. Chapter 14, pp. 141-150, in C.G. Jones and J.H. Lawton (Eds.), *Linking Species and Ecosystems*, Chapman and Hall, New York.

Lite, S.J., and J.C. Stromberg. 2005. Surface water and groundwater thresholds for maintaining *Populus-Salix* forests, San Pedro River, Arizona. *Biological Conservation*, **125**, 153-167.

Lorang, M.S., and F.R. Hauer. 2006. Fluvial geomorphic processes. Chapter 7 in F. R. Hauer and G. A. Lamberti (Eds.) 2nd Edition. *Methods in Stream Ecology*. Academic Press/Elsevier. San Diego.

Mahoney, J.M., and Rood, S.B. 1993. A model for assessing the effects of altered river flows on the recruitment of riparian cottonwoods. Pages 228-232 in B. Tellman, H.J. Cortner, M.G. Wallace, L.F. DeBano, and R.H. Hamre, editors. "*Riparian Management: Common Threads and Shared Interests*", USDA Forest Service General Technical Report RM-226.

Mahoney, J.M., and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment – An integrative model. *Wetlands*, **18**, 634-645.

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

Mazzoleni, S., and D.I. Dickmann. 1988. Different physiological and morphological responses to of two hybrid *Populus* clones to water stress. *Tree Physiology*, **4**, 61-70.

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

Merigliano, M.F. 1998. Cottonwood and willow demography on a young island, Salmon River, Idaho. *Wetlands*, **18**, 571-576.

Merritt, D.M., and D.J. Cooper. 2000. Riparian vegetation and channel change in response to river regulation: A comparative study of regulated and unregulated streams in the Green River Basin, USA. *Regulated Rivers: Research and Management*, **16**, 543-564.

Miall, A.D. 1996. *The geology of fluvial deposits*. Springer, Berlin.

Moss, E.H. 1938. Longevity of seed and establishment of seedlings in species of Populus. *Botanical Gazette*, **99**, 529-542.

Naiman, R.J., and H. Décamps. 1997. The ecology of interfaces – riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621-658.

Naiman, R.J., K.L. Fetherston, S.J. McKay, and J. Chen. 1998. Riparian forests. Pp. 289-323 in R.J. Naiman and R.E. Bilby, Editors, *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*. Springer-Verlag, New York.

Nanson, G.C., and J.C. Croke. 1992. A genetic classification of floodplains. *Geomorphology*, **4**, 459-486.

Noble, M.G. 1979. The origin of *Populus deltoides* and *Salix interior* zones on point bars along the Minnesota River. *American Midland Naturalist*, **102**, 59-67.

Oliver, C.D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management*, **3**, 153-168.

Petts, G.E., A.M. Gurnell, A.J. Gerrard, D.M. Hannah, B. Hansford, I. Morrissey, P.J. Edwards, J. Kollmann, J.V. Ward, K. Tockner, and B.P.G. Smith. 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems*,**10**, 249–266.

Richards, K., J. Brasington, and F. Hughes. 2002. Geomorphic dynamics of floodplains: ecological implications and a potential modeling strategy. *Freshwater Biology*, **47**, 559–579.

Rood, S.B., and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. *Environmental Management*, **14**, 451-464.

Rood,S.B., and J.M. Mahoney. 1993. River damming and riparian cottonwoods: Management opportunities and problems. Pages 134-143 in B. Tellman, H.J. Cortner, M.G. Wallace, L.F. DeBano, and R.H. Hamre, editors. "*Riparian Management: Common Threads and Shared Interests*", USDA Forest Service General Technical Report RM-226.

Rood, S.B., and J.M. Mahoney. 1995. River damming and riparian cottonwoods along the Marias River, Montana. *Rivers*, **5**, 195- 207.

Rood, S.B., and J.M. Mahoney. 2000. Revised instream flow regulation enables cottonwood recruitment along the St Mary River, Alberta, Canada. *Rivers*, **7**, 109-125.

Rood, S.B., J.M. Mahoney, D.E. Reid, and L. Zilm. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. *Canadian Journal of Botany*, **73**, 120-1260.

Rood, S.B., A.R. Kalischuk, and J.M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands*, **18**, 557-570.

Rood, S.B., and M.L. Polzin. 2003. Big old cottonwoods. *Canadian Journal of Botany*, **81**, 764-767.

Rood, S.B., J.H. Braatne, and F.M.R. Hughes. 2003a. Ecophysiology of riparian cottonwoods: Stream flow dependency, water relations, and restoration. *Tree Physiology*, **23**, 1113-1124.

Rood, S.B., and nine authors. 2003b. Flows for floodplain forests: A successful riparian restoration. *Bioscience*, **53**, 647-656.

Rood, S.B., G.M. Samuelson, J.H. Braatne, C.R. Gourley, F.M.R. Hughes, and J.M. Mahoney. 2005. Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment*, **73**, 193-201.

Samuelson, G.M., and S.B. Rood. 2004. Differing influences of natural and artificial disturbances on riparian cottonwoods from prairie to mountain ecoregions in Alberta, Canada. *Journal of Biogeography*, **31**, 435-450.

Scott, M.L., J.M. Friedman, and G.T. Auble. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology*, **12**, 327-339.

Scott, M.L., G.T. Auble, and J.M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications*, **7**, 677-690.

Scott, M.L., P.B. Shafroth, and G.T. Auble. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environmental Management*, **23**, 347-358.

Scott, M.L., G.C. Lines, and G.T. Auble. 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. *Journal of Arid Environments*, **44**, 399-414.

Simon, A., S.J. Bennett, and V.S. Neary. 2004. Riparian vegetation and fluvial geomorphology: Problems and opportunities. Pp. 1- 10 in Bennett and Simon (2004).

Smith, S.D., D.A. Devitt, A. Sala, J.R. Cleverly, and D.E. Busch. 1998.Water relations of riparian plants from warm desert regions. *Wetlands*, **18**, 687-696.

Stanford, J.A. 1998. Rivers in the landscape: introduction to the special issue on riparian and groundwater ecology. *Freshwater Biology*, **40**, 402–406.

Stanford, J.A., M.S. Lorang, and F.R. Hauer. 2005. The shifting habitat mosaic of river
ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und
Angewandte Limnologie*, **29**,123-136.

Stromberg, J.C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian
vegetation of semiarid regions: The San Pedro, Arizona. *Ecological Applications*, **6**, 113-
131.

Tabacchi, E., D.L. Correll, F.R. Hauer, G. Pinay, A.M. Planty-Tabacchi, and R.C. Wissmar.
1998. Development, maintenance and role of riparian vegetation in the river landscape.
Freshwater Biology, **40**, 497- 516.

Tal, M., K. Gran, A.B. Murray, C. Paola, and D.M. Hicks. 2004. Riparian vegetation as a primary
control on channel characteristics in multi-thread rivers. Pp. 43-58 in Bennett and Simon
(2004).

Tockner, K., and J.A. Stanford. 2002. Riverine flood plains: Present state and future trends.
Environmental Conservation, **29**, 308-330.

Ward, J.V., K. Tockner, D.B. Arscott, and Claret. 2002. Riverine landscape diversity. *Freshwater
Biology*, **47**, 517-539.

Webb, R.H., and S.A. Leake. 2006. Ground-water surface-water interactions and long-term
changes in riverine riparian vegetation in the southwestern United States. *Journal of
Hydrology*, **320**, 302-323.

Williams, C.A., and D.J. Cooper. 2005. Mechanisms of riparian cottonwood decline along
regulated rivers. *Ecosystems*, *8*, 382-395.

<u>Introduction</u>

Species in sections *Tacamahaca* and *Aigeiros* of the genus *Populus* L. (family Salicaceae), commonly known as cottonwoods or poplars, are important riparian trees throughout most of the Northern Hemisphere (Eckenwalder 1996, Rood et al. 2003). Together with willows, they are the main pioneer species colonizing bare, exposed sediments along corridors of alluvial rivers (Karrenberg et al. 2002). Cottonwoods are often the single dominant tree species along streams in semi-arid and arid environments, providing critical habitat (Friedman et al. 1997, Mahoney and Rood 1998), but they are usually replaced by later-successional species in wetter climates (Rood et al. 2003). The initial colonization of gravel bars by pioneering vegetation is a process of the utmost importance, both from a morphological and ecological perspective, in understanding floodplain formation and habitat dynamics in alluvial rivers (Gregory et al. 1991, Décamps 1996, Bennett & Simon 2004). Once they are colonized by vegetation, bars trap fine sediment during floods, thus growing by vertical accretion. In a positive-feedback mechanism, the raised surface and deeper soil provide a better environment for vegetation growth, for example, by decreasing the frequency of flooding and scouring disturbances, and by increasing water-holding capacity (Décamps 1996, Gurnell and Petts 2002, Francis 2006). In this way, the original bar becomes the new floodplain surface, allowing for succession to eventuate (Dykaar and Wigington 2000). This underscores that the establishment mechanisms of pioneering woody vegetation must be carefully studied not only in order to understand floodplain creation, riparian forest succession, and the temporal and spatial habitat dynamics in alluvial river corridors (Décamps 1996, Stanford et al. 2005), but also to conduct meaningful river restoration, based on ecological science.

Many studies have documented sustained declines in cottonwood recruitment along dammed rivers, throughout western North America (see reviews in Rood and Mahoney 1990 and Braatne et al. 1996). Attempts to revert such losses have driven much

research on cottonwood establishment (Braatne et al. 1986, Mahoney and Rood 1998, Rood et al. 2003). Most of the field component of this previous research has focused on analyzing established cottonwoods, usually covering a broad range of ages and stages. Even though focusing on older trees is a good integrative measure of continued success through time, it also incorporates the additive effects of a wide range of environmental disturbances, such as floods, droughts, ice-drive events, etc., making it harder to pinpoint those specific mechanisms impeding or limiting early establishment. The most critical phase in floodplain forest succession can be assumed to be the initial establishment of vegetation in the active channel, especially in the first season of growth, as seedlings need to survive the harsh conditions, involving frequent inundation, scouring by water and in some climates ice, and summertime desiccation (Mahoney and Rood 1998, Tabacchi et al. 1998, Dixon 2003, Stanford et al. 2005). Thus, I decided to focus my investigation on establishment of cottonwood seedlings of the year (hereafter referred to as 0+ seedlings) on recent, unvegetated bars within the active channel.

Braatne et al. (1996), Mahoney and Rood (1998), Rood et al. (2003), and Francis et al. (2006) summarize the current knowledge about cottonwood establishment in river corridors. The accepted concepts for cottonwood establishment at the reach and bar scale are the Recruitment Box Model (RBM: Mahoney and Rood 1991, 1993, 1998; Amlin and Rood 2002; Samuelson and Rood 2004; Rood et al. 2005), and the Hydrogeomorphic Recruitment Model (HRM: Scott et al. 1996 and 1997, Friedman et al. 1997, Auble and Scott 1998, Friedman and Lee 2002).

These models are complementary: The RBM states that recruitment occurs through a range of elevations on recently exposed sediment surfaces along a river channel, forming bands of seedlings. This only happens if the timing of flow peak with respect to seed release, and the subsequent rates of recession in river stage are favorable. The HRM stresses that the relation between streamflow, the formation of adequate surfaces, and tree recruitment depends on how hydrologic and geomorphic processes interact to create establishment sites for cottonwoods; not all processes apply in all geomorphic settings. Even though none of these authors explicitly state whether their models apply indistinctly to both sand and gravel-bed streams, there have been applications of these two concepts in both fine and coarse substrate rivers. Both models

also assume that cottonwood seedlings are obligate phreatophytes (sensu Smith et al. 1998): their growing roots must continuously maintain contact with either the alluvial water table or the capillary fringe, defined as the tension-saturated zone located immediately above the groundwater. Further assumptions are that the water table is horizontal (or very close to horizontal) and connected to the river stage, and that the capillary fringe is parallel to it (see for example Figure 4 in Mahoney and Rood, 1998).

Cooper et al. (1999) proposed that cottonwood establishment on sand-bed rivers should be fundamentally different from that on rivers with a coarse, gravelly substrate. Quite a few of the previous studies on cottonwood establishment were carried out on gravel-bed rivers (e.g., McBride and Strahan 1984, Merigliano 1998, Rood et al. 1998, Rood and Mahoney 2000, Francis et al. 2006), even though most of them were either meandering or fully braided. Only the study by Merigliano (1998) was on a wandering gravel-bed river. Still, with the exception of Francis et al. (2006), none of these investigations consider the three dimensional structure of river deposits. In summary, I know of no research that has actually looked at how some of the fundamental distinctions between sand and gravel-bed alluvial streams could differentially affect riparian tree establishment. Also, most work on gravel-bed rivers has been on meandering or fully-braided systems, but not on floodplains with an intermediate, wandering river pattern (Nanson and Croke, 1992).

What are the main differences between sand and gravel-bed rivers that should affect riparian tree establishment? Firstly, gravel beds show a bimodal distribution of grain sizes, whereby a gravel framework is partially or totally filled with a fine matrix of sand and silt (Church et al. 1987). Capillary effects can be presumed to be important within such deposits, as proposed by Mahoney and Rood (1998). This makes it necessary to look at how the spatial variability in particle size distribution, both horizontally and vertically, can affect establishment. In a sand-bed stream, the spatial variability in bed material diameter will usually lie within one order of magnitude, resulting in a more or less homogeneous capillary fringe along and across the active channel; in gravel beds, on the other hand, the bars can be composed of exceedingly non-uniform material, ranging from silts (< 63 μm) to cobbles and boulders (hundreds of mm), a range of four orders of magnitude or more (Simons and Simons 1987). The matrix material can display a large

variability in fine content, sediment caliber distribution, and continuity, at both the reach and bar scales. Consequently, the height of capillary rise from the alluvial water table should be expected to be highly variable at fine spatial scales, which should result in fine-scale patchiness in its ability to sustain vegetation (Alpert et al. 1999, Petts et al. 2000, Francis 2006). Secondly, these mixed sediment deposits are usually covered with clean gravel and cobbles. These act as a mulch, i.e., as a layer of coarse material that strongly decreases evaporation from the soil surface, retaining moisture within the matrix (see Chapter 5). Because of their magnitude, these effects must be considered when studying riparian tree establishment in gravel-bed rivers. Thirdly, there can be a high spatial variability in the sedimentary architecture of a bar, reflecting the legacies of alluvial cut and fill processes. Specifically, the presence of layers of open-framework gravels with large hydraulic conductivity can result in preferential flow pathways (Huggenberger et al. 1998) and strong downwelling. Both effects mean that the usual assumptions that the alluvial water-table is horizontal and connected to the river stage cannot be sustained in most alluvial gravel-bed rivers. At my study site, I have observed that most bars with successful establishment are downwelling, and that the lateral slope of the water table can reach 15% or more. This means that the vertical distance between establishment site and some low water reference stage (LWRS) in the nearest channel cannot be used as a surrogate variable for the actual distance to the water table. Correct evaluation of the vertical distance to water requires the installation of observation wells. Finally, bar height is larger in gravel-bed rivers than in sand streams; along my study reach, successful seedlings established on bar ridges can be at more than 2.5 m above LWRS. As proposed by Cooper et al. (1999) and Bhattacharjee et al. (2006), it is not possible for these seedlings to maintain root contact with the receding water table or capillary fringe during the initial years of growth. Indeed, Cooper et al. (1999) state that "the mechanism of seedling establishment on rivers with large stage change is unclear".

From frequent and spatially extensive observations at my study reach, in the years 2005 to 2007, I observed that 0+ cottonwood seedlings established every year on some of the unvegetated bars within the active channel along the reach, forming establishment bands as described in the literature (e.g., Everitt 1968, Bradley and Smith 1986, Rood et al. 1998). On the other hand, in any given year, I found that there were many more bars

that did not get any seedlings established at all, even though they were similar to those getting recruitment in all seemingly relevant aspects, such as elevational range above LWRS and surface texture. Also, the establishment bands showed clear discontinuities along some of the bars, at locations without any obvious changes in elevation or texture. All of these observations led me to consider the hypothesis that there must be some other variable explaining successful cottonwood establishment along gravel-bed rivers. Most studies on riparian tree establishment have singled out the vulnerability to drought stress as the most important factor affecting seedling recruitment. As clearly explained by Francis (2006), the elevation above water table and the size distribution of the sediments within the bar are the two main factors affecting water availability. Up to now, there has been little consideration of the influence that the sediment within the bar can have on cottonwood establishment. The exceptions are studies by Alpert et al. (1999) on planting success at restored sites on the Sacramento river, Cooper et al. (1999, 2003) on the establishment of Fremont cottonwood (*P. deltoides* Marshall subsp. *wislizenii* (Watson) Eckenwalder) in the sandy Green river, and by Francis and collaborators (Francis et al. 2004, 2006; Francis and Gurnell 2006), on the establishment of the European black poplar (*P. nigra* L.) in the Alpine Tagliamento river.

In this investigation, I focus on the factors affecting establishment of cottonwood seedlings in bars of a gravel-bed river, during their first season of growth, at the reach and within-bar scales. Specifically, I study how the thickness of the coarse surface layer, the texture characteristics of the fine matrix within the bar, and the difference in elevation between establishment site and groundwater, explain 0+ seedling presence-absence, abundance, as well as growth. My hypotheses are that: (i) the presence of a coarse surface layer (rock mulch) improves establishment success, by protecting moisture within the bar, (ii) if this coarse surface layer is too thick, seeds will not be able to establish, (iii) finer matrix material within the root zone leads to higher establishment success, by holding more capillary water, and (iv) as proposed by the RBM, the vertical distance to water is inversely correlated with establishment success. In order to test these hypotheses, I used a paired-plot sampling design, analyzing seedling response to variability in matrix grain size, thickness of the coarse surface layer and depth to water.

My larger goals involve (i) testing whether the RBM, which was seemingly developed for sand-bed streams, is also applicable to gravel-bed rivers at the bar and reach scale, (ii) finding if spatial variability at the within-bar scale (in the order of magnitude of 1 ~ 10 m) has relevant effects in explaining establishment of riparian vegetation, (iii) understanding the mechanisms underlying cottonwood establishment in a hydrologically and morphologically intact wandering gravel-bed river, in order to guide restoration attempts in systems that have been modified by human activity, and (iv) generating information specific to the black cottonwood *P. trichocarpa*, a species that has been much less studied than *P. deltoides* (sensu lato, cf. Eckenwalder 1996), according to Braatne et al. (2007). Understanding cottonwood seedling recruitment more thoroughly within the context of these goals will help guide river restoration attempts in systems that have been modified by human activity.

Methods

Study area

The study site was the wandering Nyack Floodplain, located on the Middle Fork of the Flathead River, a fifth order gravel-bed river with headwaters in the Bob Marshall-Great Bear Wilderness Complex, forming the southwest boundary of Glacier National Park in western Montana, USA (Figure 1). The study reach is between 8 and 9 km long, with a floodplain that is 1 to 2 km wide. The average channel slope in the reach is 2.4 ‰. Anthropogenic effects on the floodplain are minimal, with a highway and railroad corridor along its southwest edge, rip-rap embankments at a few locations at the top of the floodplain, and some agriculture. All of these effects occur primarily in the passive part of the orthofluvial zone (sensu Stanford et al. 2005). The catchment area is 2920 km^2, as measured at the USGS gauging station located 9.5 km below the end of the reach, in West Glacier, Montana (USGS Station Number 12358500: Middle Fork of the Flathead River near West Glacier, Montana). The elevation ranges from 1000 masl at the downstream end of the study reach, to about 2900 masl, at the highest point in the basin.
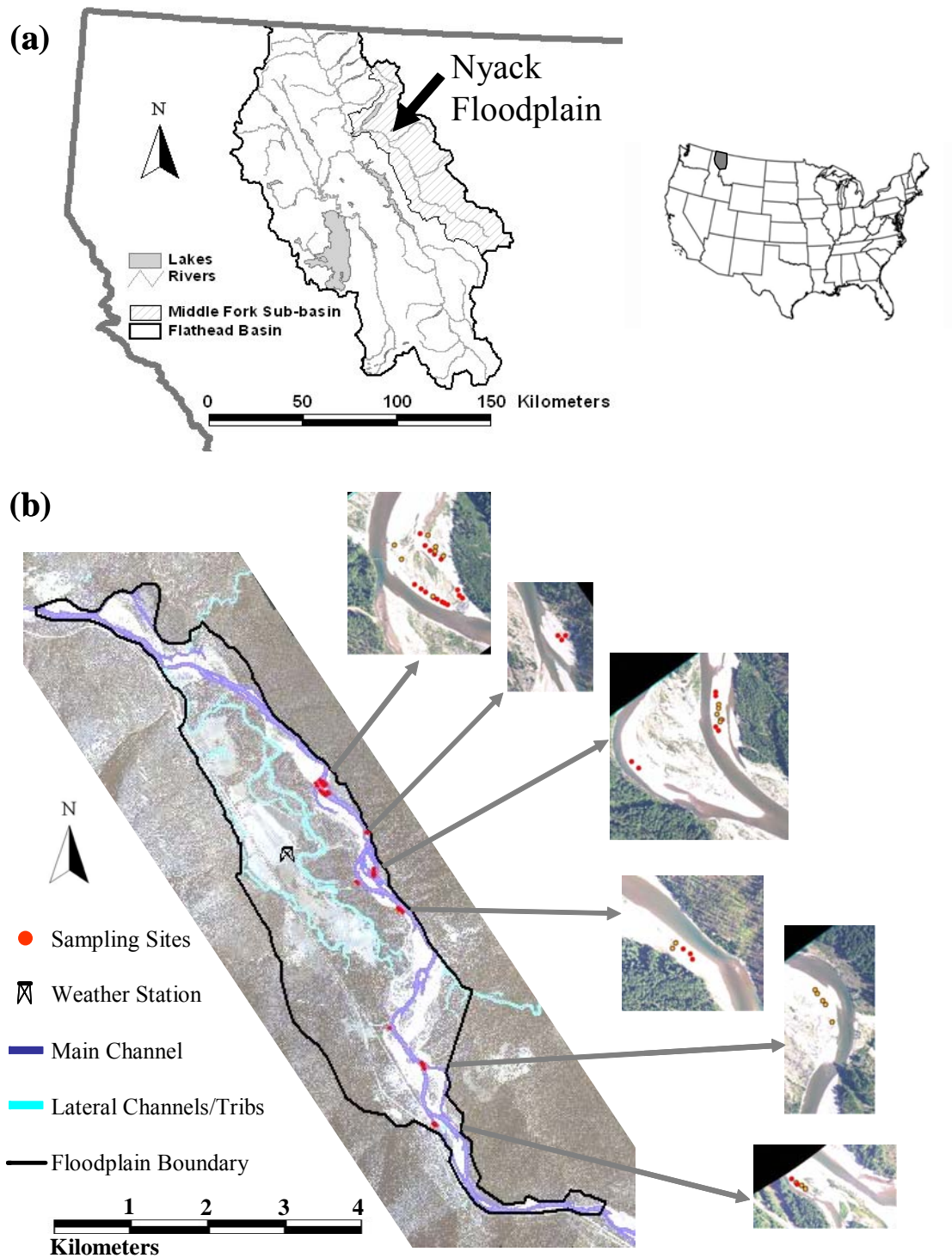
Figure 1. (a) Map of the Flathead River Basin in western Montana (black arrow indicates site of Nyack Floodplain) and (b) Satellite image of the Nyack Floodplain showing sampling locations (insets).

The mean annual flow for the period 1940-2007 was 81.1 m^3/s; June is the month with the highest mean flow, 282 m^3/s, while January and February have the lowest mean flows, at 20.2 m^3/s. The mean annual flood is 645 m^3/s, while the maximum recorded annual flow is almost 4,000 m^3/s in 1964, even though historical records mention that the 1894 flood was much larger. The floodplain is bounded laterally by valley walls, and has bedrock knick points at both its upper and lower ends. The river is a typical gravel-bed wandering channel along the length of the floodplain, with low-order braiding and the presence of vegetated islands and recent gravel bars within the active channel. The more mature, orthofluvial floodplain forest and agricultural pasture is to the southwest. During low flow periods, over 30% of the incoming flow is lost to the aquifer at the upstream end of the floodplain and various gaining and loosing reaches have been documented (Stanford et al. 2005) and modeled (Poole et al. 2006) throughout the floodplain. The poplar species present at my study site is the black cottonwood, *Populus trichocarpa* T. & G., within the *Tacamahaca* section of the genus *Populus*. The site has been the focus of research by the Flathead Lake Biological Station for over 20 years, and additional site description is offered in Stanford et al. (1994).

Location of sampling sites

During the first two months of the 2006 and 2007 growth seasons, mid-June to mid-August, the whole active channel corridor through my study reach was repeatedly surveyed, and the occurrence of 0+ cottonwood seedlings was mapped on recently acquired high-resolution aerial images. Establishment patches with more than 20 seedlings were measured, and sampling sites were selected on these bands, with a stratified random design based on the following criterion: one site on patches less than 10 m in length, two sites on patches 10 to 30 m in length, three sites on patches 30 to 60 m in length, four patches on sites 60 to 100 m in length, and five sites on patches longer than 100 m. The focus of the research was the initial colonization of recent, previously unvegetated gravel bars; thus, establishment on sand deposits, always located at the downstream end of large, vegetated islands or in backwaters, was not considered. At each randomly-determined site, the nearest grouping of three or more 0+ seedlings was chosen as the "seedling" plot for sampling. The corresponding "no-seedling" plot was chosen as

25

the closest location where one could place a 1 m^2 quadrat without enclosing any seedling. In order to control for other variables that could affect plant success, the "no-seedling" plots were always located at the same elevation above river stage as their matching "seedling" plots. At each sampling site, I assumed that both closely located plots would be at about the same vertical distance from groundwater. Finally, I chose the "no-seedling" plots to be similar in surface texture to their "seedling" counterparts.

In 2006, I initially considered 28 sampling sites with paired "seedling" and "no-seedling" plots, but an unseasonably large flood in early November erased most evidence before I could complete digging all of the pits, so that I ended up with 19 to 28 pairs of data (depending on the variable of interest) for that year, distributed over seven different bars. In 2007, I added another 33 sampling sites with paired "seedling" and "no-seedling" plots, also on seven different bars. In total, my analyses are based on a minimum of 52 pairs of plots, located on nine different bars along the study reach.

Field Sampling and Measurements

At each "seedling" plot, at the end of the 2006 growth season (i.e., late October), I measured plant abundance by counting the number of seedlings established within a 1 m^2 quadrat, centered on the seedling group defining the plot location. I computed a spatially weighed average of the size of successful plants, L, by measuring the length of the five tallest seedling shoots located in each quarter of the quadrat (i.e., the quadrat was divided in four 0.5 x 0.5 m sectors) and then averaging the values for these 20 plants. I sampled leaves from seedlings in all four quadrat quarters for leaf chemistry (carbon, nitrogen, and phosphorus; C-N-P) analyses. The distance between paired plots was measured to the nearest decimeter. After carefully removing the coarse surface layer of clean gravel and cobble, and measuring its approximate thickness T to the nearest 0.5 cm, I dug pits at both the "seedling" and the "no-seedling" plots. For the former, the seedlings were excavated with their root systems. Vertically integrated samples of the fine matrix material were collected at depths from 0 to 25 and from 25 to 50 cm below the top of the matrix. In each sampled bar, either earlier in the season or immediately after digging the pits, I installed wells for observing groundwater levels, following Baxter et al. (2003); a total of 48 wells were driven. These were made of CPVC pipe, 1.51 m in length and with

an internal diameter of 18.4 mm. Wells were usually installed to a depth of 1.40 to 1.45 m into the ground. Water levels in wells installed earlier in the season were checked approximately every month; wells installed after digging the pit were sampled immediately. The sampling and measurements were repeated in 2007. However, after analysis of the 2006 data, I made the following modifications to sampling protocols: (i) I decided not to sample leaf tissue for C-N-P analyses, (ii) I dug pits only for the first horizon (from 0 to 25 cm below the top of the fine matrix), (iii) I did not excavate seedlings, and (iv) I did not install additional observation wells.

In September 2007, I surveyed the sampled bars with a Leica 5000 survey-grade differential GPS, obtaining the elevations for the sampling sites, well locations, and the river shore at low water reference stage (LWRS). For the purposes of this study, the LWRS at any location along my study reach was taken as the stage corresponding to a streamflow of 14.1 ± 1 m^3/s, as recorded at the USGS gaging station at West Glacier. This value was chosen as it is the flow exceeded with 85 % probability, according to the duration curve of mean daily flows for the period 1940-2007. This means that there are on average 55 days per year (15% of the time) with flows lower than 14.1 m^3/s.

Laboratory analyses

The fine matrix samples were sieved in a Ro-Tap sieving machine in order to obtain the weight proportion in each of the following size classes: gravel (sieve diameter above 2 mm), very coarse sand (between 2000 and 1000 μm), coarse sand (between 1000 and 500 μm), medium sand (between 500 and 250 μm), fine sand (between 250 and 125 μm), very fine sand (between 125 and 63 μm), and silt (finer than 63 μm).

Leaf samples were dried at 70°C to constant weight and were then homogenized in a ball mill (SPEX SamplePrep Model 5100-115); 5 to 8 mg of plant tissue was analyzed for C and N leaf chemistry analyses in a CHN Analyzer (Fisons Model NA1500) using atropine (CAS# 51-55-8) as a calibration standard (Pella 1990). For tissue P analysis, after drying and homogenizing, 2 to 4 mg of dried sample was combusted in a 500 ml test tube at 500 degrees C for two hours in a muffle furnace (Thermolyne, Model F-A1740). Upon cooling, 2 ml of 1 N HCl was added and the sample was incubated for 30 minutes at 80 C; 50 ml of deionized water was added and

the solution was analyzed with a standard ascorbic acid colorimetric method for phosphate (APHA 4500-P B(1) E; APHA 2007).

The excavated plants were cleaned and dried to constant weight at 70°C. Dried shoot and root biomass were then obtained by weighing. Mean dry shoot biomass, SW, mean dry root biomass, RW, and shoot-to-root biomass ratio, S/R, were computed for each "seedling" plot, by averaging over the excavated plants.

Data analyses

I computed an index of matrix fineness (FI) for each soil matrix sample, as the percentage in weight of the fine material (defined as everything finer than 2.0 mm, i.e., sand and silt) finer than 250 μm. In other words, FI is the proportion of the fines made up of fine sand, very fine sand, and silt:

$$FI = (material\ finer\ than\ 250\ μm) / (material\ finer\ than\ 2.0\ mm) * 100\quad (\%)$$

The vertical distance to water, Z_w, was obtained directly from well readings, in the rare occasions when these were available. At most sampling sites the wells were dry upon installation, i.e., the water table was deeper than the well depth of about 1.4 m. At such locations, Z_w was estimated as the maximum value between the well depth and the difference in elevation between the establishment site and the river stage at the nearest shoreline. Some of the sampling sites did not have wells located nearby, and in such cases Z_w was computed as the difference in elevation between the site and the river stage. When the sampling sites were located close to a pond, the water surface elevation in the pond was used instead of river stage.

In order to explain presence-absence of 0+ cottonwood seedlings, differences in T, the thickness of the coarse surface layer, and FI were compared with paired t-tests between the "seedling" and "no-seedling" plots. The effects of FI, T, and of the vertical distance to water, Z_w, on plant response (density, growth, and leaf chemistry) were analyzed with stepwise multiple linear regressions on the original or log-transformed data. I also explored possible relationships between C, N, and P content, as well as C/N and N/P ratios, and the other variables.

Presence-absence of seedlings

Plots with seedling establishment had a greater proportion of finer sediments than the corresponding plots without cottonwood seedlings. The mean index of fineness (FI) across all locations with seedlings was 44.8 % (n = 57, range: 6.53 – 92.4 %, standard deviation = 20.1 %). In contrast, the mean of FI was 34.1 % (n = 53, range: 0 – 95.3 %, standard deviation = 19.8 %) at those locations without establishment of cottonwood seedlings. When comparing FI values between the paired plots, it is clear that at most sampling sites, the FI at "seedling" plots is higher than that at the corresponding "no-seedling" plots (Figure 2). A paired t-test among all available data pairs (n=52) indicated that at locations with 0+ seedlings, the fine matrix has a significantly higher proportion of finer material than at closely located matching sites without cottonwood establishment (difference in means = 9.39 %, df = 51 , t = 3.528, p = 0.001).
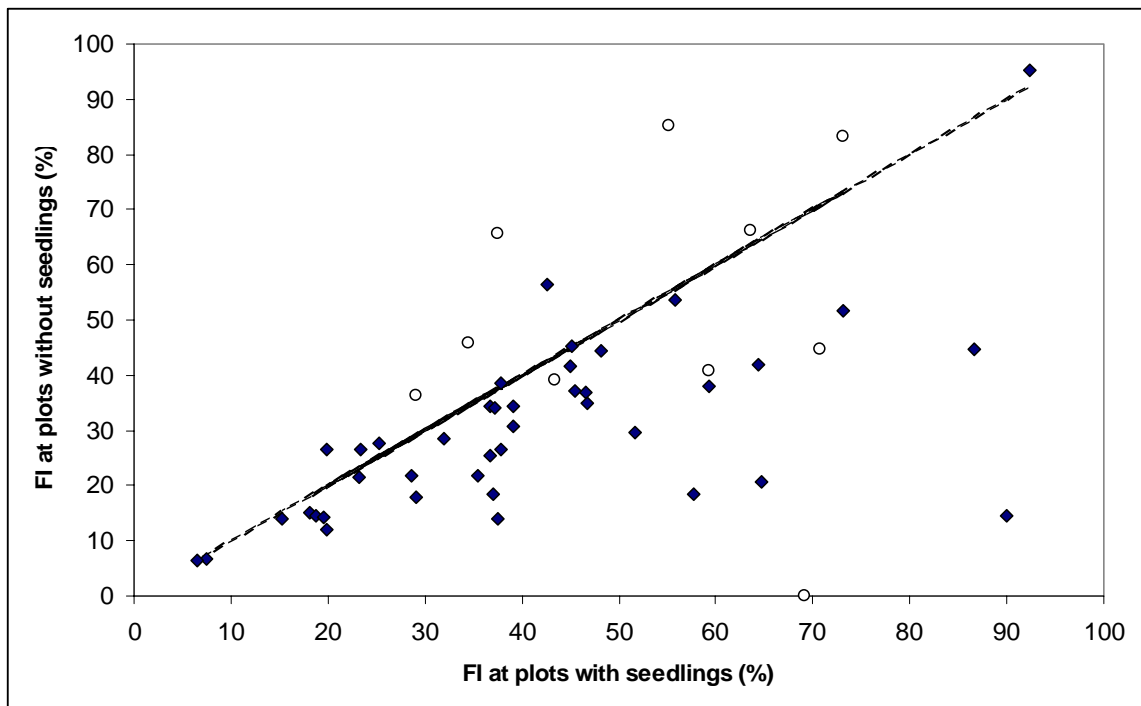
Figure 2. Index of fineness (FI, in %) at plots without seedlings versus the value at the corresponding plots with seedlings, for the 52 sampling sites. The black line is the 45° (one-to-one correspondence) line. The open circles represent sites where the thickness of the coarse surface layer at the "no-seedling" plot was equal or larger than 6.0 cm.

Notwithstanding the previous result, there were a few sampling sites for which FI was noticeably larger at the "no-seedling" plot than at the corresponding location with seedlings. A cursory analysis of the data indicated that many such sites had a thick coarse surface layer. This suggested a threshold mechanism, whereby a thicker coarse surface layer could impede establishment, even at locations with a high proportion of finer sediment. In order to account for this effect, I repeated the statistical analyses excluding those 10 sampling locations at which the thickness of the coarse surface layer on the "no-seedling" plot was equal to, or larger than 6.0 cm (the open circles in Figure 2). In such case, the mean FI for locations without seedlings decreased to 30.2 % (n = 43, range: 6.51 – 95.3 %, standard deviation = 16.4 %), while the paired t-test resulted in an even more significant difference in FI: locations with seedlings had a value of FI that was 10.9% higher, on average, than the corresponding locations without any seedlings (df = 41, t = 4.424, p < 0.0001).

The thickness of the coarse layer T was significantly larger at locations without seedlings than at the corresponding paired plots with seedlings (paired t-test: difference in means = 1.77 cm, df = 60, t = 3.404, p = 0.001). The mean value of T at locations with seedlings was 3.24 cm (n = 61, range: 1.0 – 6.5 cm, standard deviation = 1.21 cm), while it was 5.01 cm (n = 61, range: 1.0 to more than 30 cm, standard deviation = 4.30 cm) at the sampling locations without cottonwood establishment. However, at the sampling site with an FI value of zero for the "no-seedling" plot (see Figure 2), the pit was dug to 30 cm without encountering a fine matrix. Formally, I only know here that T is larger than 30 cm, but I had to set T = 30 cm in order to compute the mean and run the test. I repeated the statistical analysis discarding this location, as it clearly is an outlier; in such case, the mean of T at plots without seedlings is much lower (4.59 cm, n = 60, range: 1.0 – 13.5 cm, standard deviation = 2.84 cm), while the paired t-test indicates that the difference in means is highly significant (difference = 1.37 cm, df = 59, t = 4.099, p < 0.0001).

Effects on plant density

There was an average of 51.4 seedlings/m^2 at the locations with establishment (n = 60, range: 6 – 194 seedlings/m^2, standard deviation = 38.1 seedlings/m^2). A linear

regression explaining plant density as a function of FI had a very low coefficient of determination (n = 57, adjusted R^2 = 0.0183) and a slope not significantly different from 0 (p = 0.158). A similar result was obtained when regressing plant density against T (n = 59, adjusted R^2 = 0.0136). In this latter case, the upper data envelope in the plot of plant density versus T (Figure 3) does suggest a decrease in density with a thicker coarse surface layer, even though the slope of the regression is not significantly different from zero (p = 0.185). The plot could also suggest a Gaussian distribution, with higher densities for intermediate thicknesses of the surface layer. I can not test for this though, as no data were collected at locations with T < 1 cm.
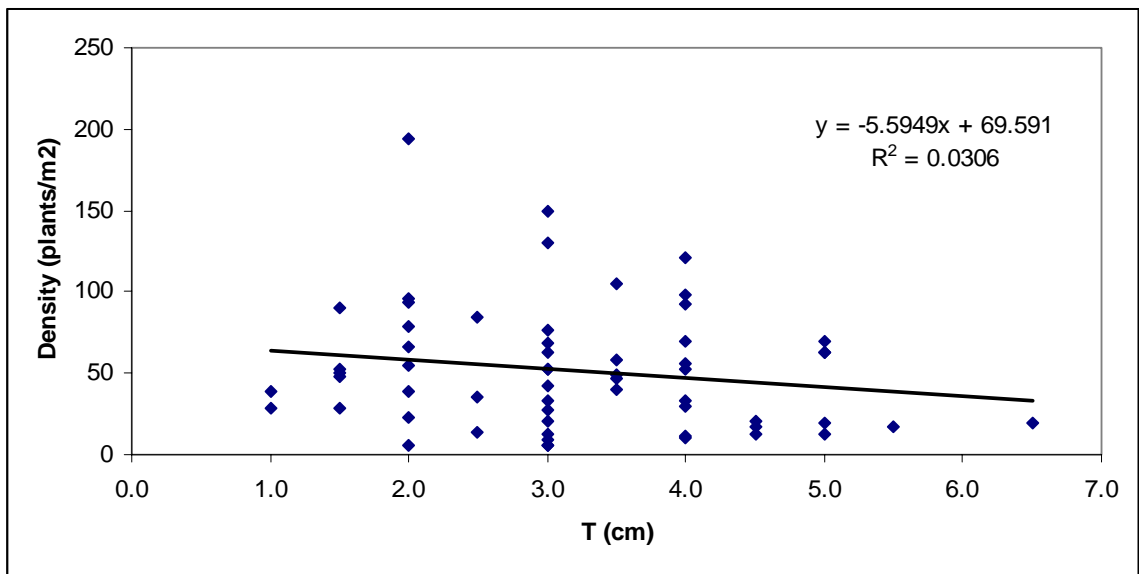
Figure 3. Plot of plant density (in seedlings/m^2) versus the thickness of the coarse surface layer, T (in cm).

The mean of the vertical distance to water Z_w was 1.23 m (n = 55, range: 0.64 – 2.89 m, standard deviation = 0.514 m). I found that plant density was positively correlated with Z_w (n = 55, p = 0.0014, adjusted R^2 = 0.160; Figure 4), even though the coefficient of determination was low. On the other hand, it is clear that the five data points with Z_w > 2 m, from the two bars that had a higher relief, are driving the positive slope of the regression line. Discarding such points yielded a regression equation with a marginally significant negative slope, and with a very low coefficient of determination (n = 50, adjusted R^2 = 0.0737, p = 0.032).

Effects on plant growth

The percentage of finer sediment in the matrix was highly correlated with cottonwood seedling size and biomass. For each sampling location, I computed three different plant responses that can be considered to be representative of growth and establishment success: (i) weighed mean shoot size for the 20 largest plants on the quadrat, L, (ii) mean dry biomass of the shoots of excavated seedlings, SW, and (iii) mean dry biomass of the root systems of excavated seedlings, RW. L had a mean of 5.29 cm (n = 60, range: 1.61 -16.4 cm, standard deviation = 3.40 cm), SW of 0.38 g (n = 22, range: 0.05 – 0.77 g, standard deviation = 0.236 g), and RW of 0.53 g (n = 22, range: 0.10 – 1.13 g, standard deviation = 0.298 g).
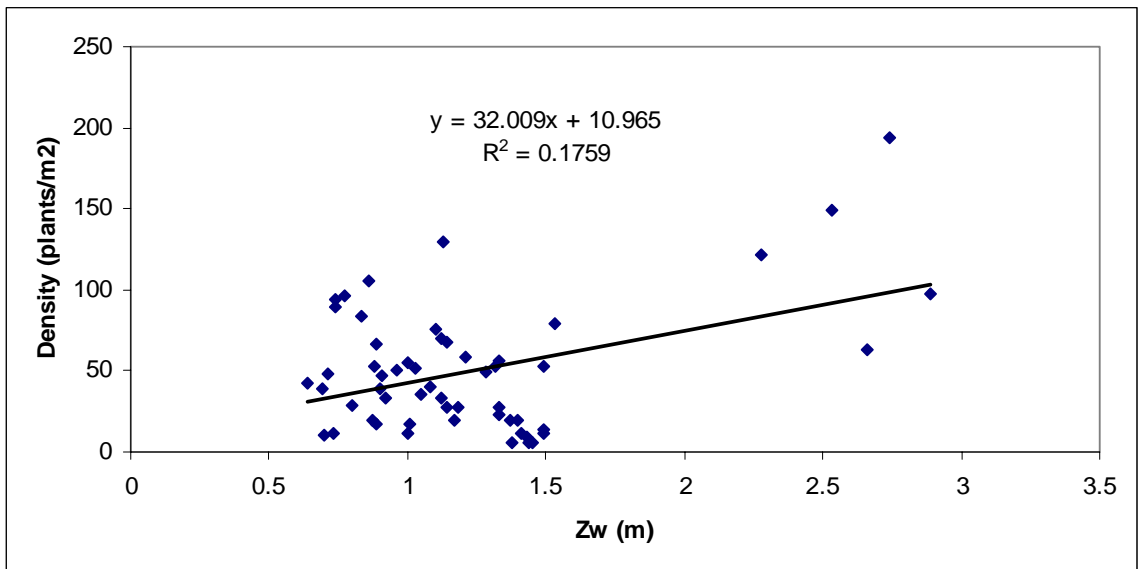
Figure 4. Plot of density (seedlings/m^2) versus the vertical distance to water, Z_w (in m).

I found that regressions explaining these variables as a function of FI were all highly significant: the variability in FI explained nearly 50% of that in mean plant size L (Figure 5, where n = 55, adjusted R^2 = 0.486, and p < 0.0001), and that in log FI explained 52.4 % of that in shoot biomass SW (Figure 6, where n = 22, adjusted R^2 = 0.524, and the slope was significantly different than 0 with p < 0.0001). In the case of the root biomass, regressing log RW versus log FI yielded an adjusted R^2 of 0.543 (Figure 7, n = 22, p < 0.0001). I also computed S/R, the shoot-to-root biomass ratio, which had a mean of 0.71 (n = 22, range: 0.33 – 1.09, standard deviation = 0.203). Regressions of S/R

32

against FI and T had very low values of adjusted R^2 and were not significant. The relationship between L and Z_w was marginally significant only when the three data points with $Z_w > 2m$ were discarded (Figure 8, adjusted $R^2 = 0.216$, n = 16, p = 0.04).
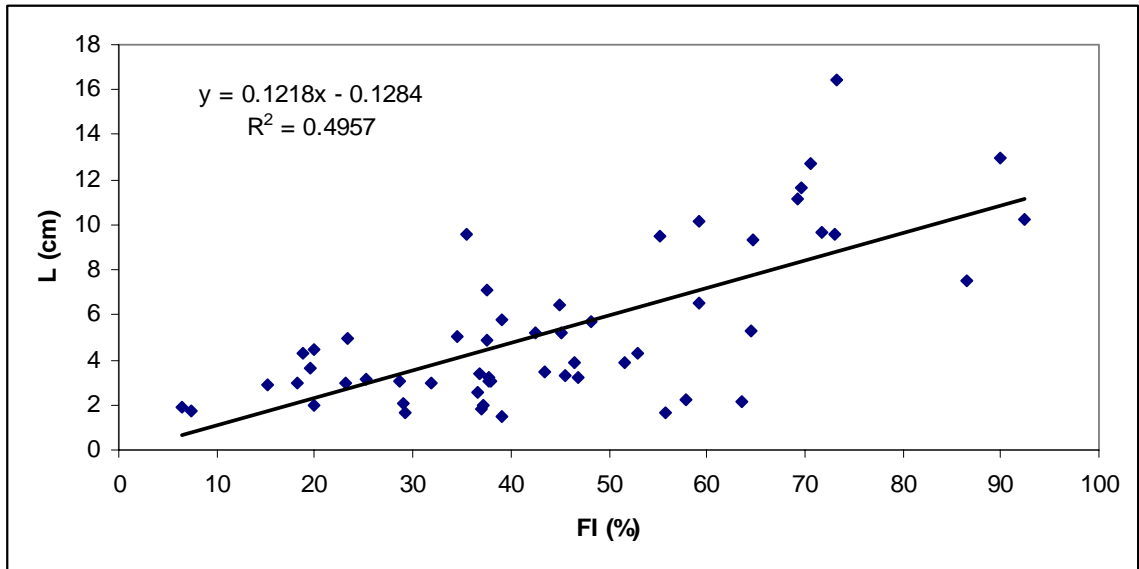
Figure 5. Plot of weighed mean shoot length over 20 largest plants in quadrat, L (in cm), against the index of fineness FI (in %).
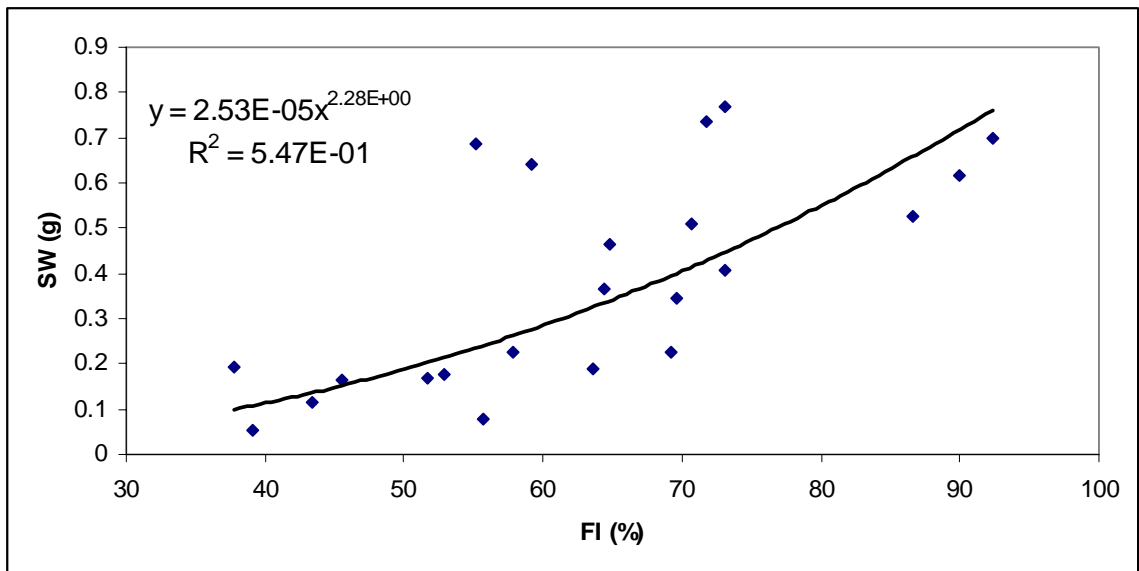
Figure 6. Plot of mean dry shoot weight of excavated plants, SW (in g), against FI (in %).

Preliminary, simple regression analyses indicated that FI was strongly correlated with plant growth, Z_w had an intermediate effect, and T was not correlated. I found no

significant linear correlations between FI and T, or T and Z_w, but FI and Z_w were linearly correlated, with $r = 0.621$ ($n = 46$, discarding five outliers). Thus, I conducted stepwise linear regression with partial correlation to explain L as a function of the three independent variables. The model had an adjusted R^2 of 0.534, and only the effect of FI was significant ($p < 0.0001$).
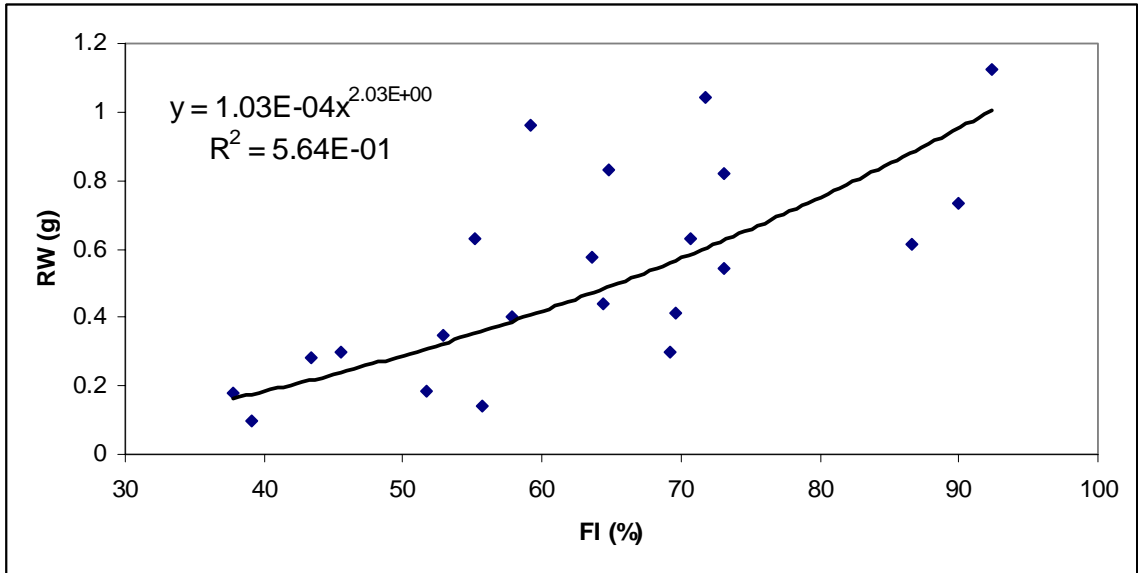
Figure 7. Plot of mean dry root weight of excavated plants (in g) versus FI (in %).
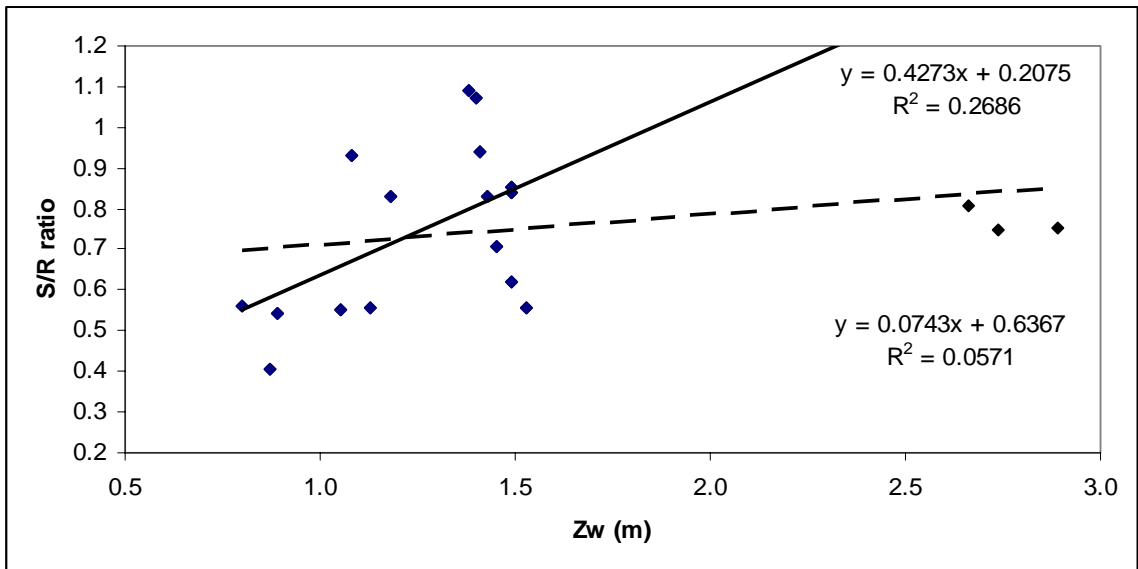
Figure 8. Plot of the shoot-to-root biomass ration against the vertical distance to water. The dotted line is the regression equation when the 3 data points to the right are included.

Effects on leaf chemistry

I tested all pairwise combinations of effects of the independent variables FI, T, and Z_w on the different leaf chemistry variables (C, N, and P content, as well as C/N and N/P ratios). Carbon content displayed a bimodal distribution: Samples from 3 bars had a mean of 33.45 μmol/mg (n = 9, range: 33.00 – 33.89 μmol/mg, standard deviation = 0.339 μmol/mg), while those from the other 6 sampled bars had a much higher mean of 38.94 μmol/mg (n = 29, range: 38.38 – 39.77 μmol/mg, standard deviation = 0.327 μmol/mg). Nitrogen concentration had a mean of 1.81 μmol/mg (n = 29, range: 1.49 – 2.07 μmol/mg, standard deviation = 0.131 μmol/mg). Phosphorus content had a mean value of 0.0546 μmol/mg (n = 29, range: 0.0404 – 0.0721 μmol/mg, standard deviation = 0.00768). The molar C/N ratio ranged from 17.2 to 24.74, with a mean of 20.86 and a standard deviation of 1.80, while the N/P ratio ranged from 25.19 to 45.26, with a mean of 33.71 and a standard deviation of 4.73 (n = 29 for both). All linear relationships had very low adjusted R^2 and were not significant, except for the regression explaining N content (in μmol/mg) as a function of vertical distance to water, Z_w, which was highly significant (Figure 9, n = 20, adjusted $R^2 = 0.461$, p = 0.0006).
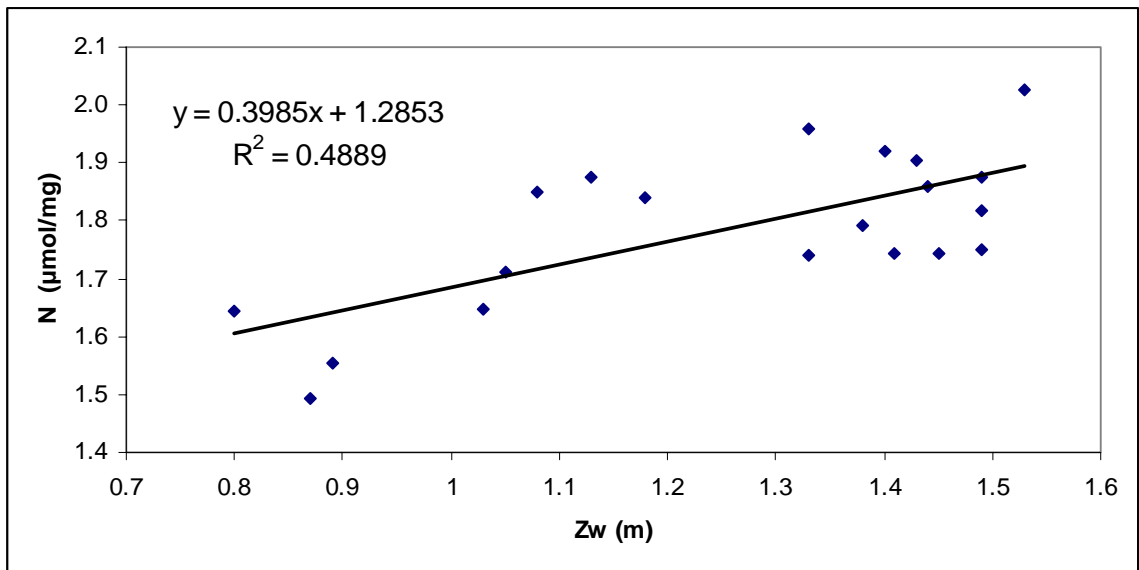
Figure 9. Plot of foliar nitrogen concentration (in μmol/mg) against vertical distance to water, Z_w (in m), excluding three outliers (n = 20).

Spatial variability of the explanatory variables

On average, the paired plots were located at 2.58 m of each other (n = 45, range: 0.8 – 6.0 m, standard deviation = 1.32 m). The absolute values of the difference in index of fineness FI and the thickness of the coarse surface layer T between the "seedling" and the "no seedling" plots were plotted against the corresponding distance between paired plots to analyze spatial effects.

The difference in finer material, ΔFI, computed as FI at the "seedling" plot minus FI at the corresponding "no seedling" plot, ranged from -30.0 to 75.4 %, and its standard deviation was 19.2 %, more than twice its mean value of 9.39 %. Regressing the absolute values of ΔFI against the distance between plots resulted in a positive relationship (n = 44, adjusted R^2 = 0.051, p = 0.076). Even when one outlier was discarded, this relationship remained largely unchanged (n =43, adjusted R^2 = 0.058, p = 0.066). In the case of the thickness of the coarse surface layer, the differences in T ranged from -3.0 to 10.5 cm, excluding the outlier at the plot where T was larger than 30 cm. The standard deviation of ΔT was 2.58 cm, as compared to a mean of 1.37 cm. As was the case for FI, the regression of the absolute values of the differences versus the distance between paired plots resulted in a positive relationship (n = 45, adjusted R^2 = 0.065, p = 0.054).

Discussion

Effects of fine material

I find extensive evidence that the proportion of finer material in the matrix is a key controlling variable explaining establishment success of cottonwood seedlings on gravel bars. At locations with seedlings, the matrix material has a significantly higher index of fineness (i.e., higher content of fine sand, very fine sand, and silt), than at the corresponding plots without successful establishment. The proportion of finer material is also significantly correlated with seedling growth: FI explains about half of the variability in seedling shoot length, shoot dry weight, and root dry weight.

As reported by Alpert et al. (1999), Cooper et al. (1999, 2003), Francis et al. (2004, 2006) and Francis (2006), the particle size of the matrix material must be highly influential in determining establishment success, as it controls water holding capacity by

capillarity. In this context, it is important to note that all previous research on cottonwood seedling establishment, both in the field and in rhizopods in the laboratory, has only reported the type of material ('sand', 'gravel', etc.), its general class size ('fine sand', 'medium sand', etc.), or at most the mean or median size of the particles. Because the capillary behavior of a soil depends on the range of pore sizes (the pore size distribution), it is important to obtain the complete distribution of particle sizes (e.g., see Chapter 5). In this case, I used a two-parameter approach, describing the soil at each sampling plot by an index which includes two size thresholds (2 mm and 250 μm). Note that hydraulic conductivity at saturation, K_{sat}, also depends on the pore size distribution, but I do not think of K_{sat} as a relevant variable in cottonwood establishment, as was proposed by Mahoney and Rood (1992) and Francis et al. (2006). In effect, K_{sat} is a parameter which only indicates the ease of flow through a porous medium, whereas what really matters for plants is the water holding capacity of the soil in the root zone, as this determines water availability through dry periods. Indeed, K_{sat} will be higher for larger, uniformly-sized particles, conditions which result in a much lower water-holding capacity. Finally, most studies up to now have reported only surface texture; my findings strongly suggest that what matters the most is the particle size distribution within the root zone. This should be expected, as this is where the seedlings acquire the water they need to survive and grow.

The spatial variability in FI is high, as reflected in the comparison between the "no-seedling" and the corresponding "seedling" plots. Over the range of distances between matching plots (0.8 to 6.0 m, with a mean of 2.58 m and a standard deviation of 1.32 m), ΔFI increased with distance; its standard deviation was also much larger than its mean. All of this indicates that there is a large variability in this controlling variable, even at short, within-bar spatial scales. These results confirm the findings of Alpert et al. (1999) and Francis et al. (2006) that plant growth is significantly affected by fine-scale variability in soil texture, so that bars need to be treated as patchy environments.

Effects of the coarse surface layer

Three lines of evidence in my data support the hypothesis that a thick coarse surface layer will impede establishment (see also Chapter 5): (i) "No-seedling" plots have a significantly thicker coarse surface layer than the corresponding plots with established

37

seedlings. (ii) There were a few sampling sites where FI was clearly larger in the "no seedling" than in the paired "seedling" plot, contrary to the above- discussed, expected effects of FI. Most such sites shared a common characteristic: a coarse surface layer thicker than 6 cm (the open circles in Figure 2). This suggests that there is a threshold value for T, above which cottonwood seeds cannot germinate and establish, possibly because of the shading effect of the coarse material overlying the matrix surface, and the difficulty that the seed radicle has in reaching the fine material. The largest value of T at my "seedling" plots (n = 61) was 6.5 cm, so I propose that this value should be a good approximation for this threshold. (iii) Even though the regression between plant density and T is not significant, the negative slope of this relation and the behavior of the upper envelope to the data points (Figure 3) suggest that a thicker coarse surface layer results in decreased establishment.

As shown in Chapter 5, the coarse surface layer of clean gravel and cobble found on bars of gravel-bed rivers acts as rock mulch. This decreases evaporation and maintains soil moisture in the underlying finer material, with thicker layers resulting in higher moisture levels. I did not find any effect of T on seedling growth though, contrary to my expectations. McBride and Strahan (1984) did report that Fremont cottonwoods (*P. fremontii*) established more densely on areas with intermediate and large sized sediments (0.2 to 1 cm), but they explained this because areas with finer particles where under water during seed release, and not as a function of the possible effects of the coarse surface layer.

As was the case for FI, T is highly variable spatially: ΔT increases with distance and its standard deviation is much larger than its mean. Because the coarse surface layer acts as a threshold mechanism, impeding establishment if it is too thick, its fine-scale variability partly explains the patchiness in presence-absence of 0+ seedlings that I observed over bars with overall successful establishment.

Effects of the vertical distance to water

I attempted to measure Z_w directly, with observation wells, as I knew that the alluvial water table under the bars was not horizontal and at the same elevation than river stage. This did not really work though, as the groundwater was deeper than the average

1.4 m depths of the wells at most of the sampling locations. Thus, I ended up estimating Z_w as the difference in elevation between the establishment point and the LWRS. By digging pits or installing wells close to the shore, I qualitatively established that most of the establishment patches that I sampled were on downwelling bars, with an alluvial water table sloping down steeply, away from the river. This means that my estimates of Z_w are negatively biased, i.e., I am underestimating the vertical distance to water.

Unexpectedly, Z_w did not have any effect on establishment success, as reflected in seedling density or growth. Thus, based on the evidence at hand, I reject the hypothesis that establishment success is inversely correlated with the vertical distance to water, as proposed by the RBM. Another way of looking at this issue is by comparing maximum root depth with the position of the water table (and the capillary fringe), at the end of the growth season. The longest roots in the seedlings I excavated occurred at six different sampling plots, all located on downwelling bars, and were between 54 and 56 cm long in the second half of October. At each one of these locations, the observation wells, which were driven between 1.38 and 1.49 m into the ground, were all dry upon installation in July, just a month after establishment. From July until September or October, river stage fell by at least another 50 cm at all of my sites. This means that the water table at these plots with the longest root growth (which, incidentally, also exhibited the longest and heaviest shoots) would have been located at the very least at about 2 m below the surface (recall that I am underestimating Z_w).

Thus, my findings fully agree with those of Cooper et al. (1999) and Bhattacharjee et al. (2006), in that it is not possible for seedlings located at higher elevations to maintain root contact with the receding water table, or the capillary fringe, during their first year of growth. Following Cooper et al. (1999), I therefore propose that cottonwood seedlings are not obligate phreatophytes, at the very least during their first year of growth. Instead, they behave as facultative phreatophytes (sensu Smith et al. 1998), using alluvial groundwater if it is readily available, or tapping other sources of moisture, e.g., capillary or vadose water from the soil, when possible.

The only strong effect of Z_w was on the nitrogen content of leaf tissue: Plants located at higher elevations with respect to groundwater had a significantly higher N concentration.

Cottonwood establishment at the reach scale

Over the three summer seasons that I surveyed 0+ seedlings across the active channel corridor at my study site, I always found many more bars without any establishment than bars with patches of successfully recruited cottonwoods. This was so, even though all of these bars seemed to be similar in landscape position, elevational range, and surface texture. They would also have had similar recession rates, as they were all located in the same reach (subjected to the same flows), and occupied hydraulically similar positions. This indicates that the Recruitment Box Model for cottonwood establishment (RBM, Mahoney and Rood 1998) and other similar models, which are based only on elevation with respect to stage and on recession rates (and how these are timed in comparison with seed release) are not describing all of the variability in presence-absence of successfully established 0+ seedlings. Actually, such models seem to be much better at explaining where the seedlings will not be able to establish (i.e., those areas falling outside of the recruitment box), than the actual probability of establishment within the band. For example, the results in Shafroth et al. (1998, see Table 1 on page 583) show that there was a vast agreement when predicting areas that would not sustain establishment, but only a very modest success rate when attempting to determine which areas would actually get cottonwood recruitment.

According to most literature (as reviewed in Mahoney and Rood 1998), adequate conditions for successful cottonwood establishment occur on average only once every 5 to 10 years. However, at my study site, I witnessed recruitment on some bars each one of the three years I spent on the field. Successful seedlings occurred either as elevational bands around bars, or as continuous patches, covering some bars from the ridge-top, down to the lower establishment limit. Even though I did not mark seedlings to follow their trajectory in time, I noticed that most seedling patches observed in 2005 and 2006 were still doing very well in 2007. The only exception was at a location where bar ablation was taking place, due to lateral migration of the channel. Many of the point bars, located on the inner side of bends, had aggraded, and the seedlings at such sites had been able to survive perfectly well.

Seedling densities on my gravel bars, with a mean of 51.4 and a maximum of 194 plants/m^2, were in the lower end of the range of 20 to 4000 seedlings/m^2 that has been

reported in the literature (Braatne et al. 1996). Most of the larger values come from sand-bed streams, though, and my densities are similar, within one order of magnitude, to those reported for other gravel-bed reaches. At my study site, I have observed (but not measured) very high seedling densities on sandy deposits; these generally occur in backwater sectors, at the lee of large vegetated islands or in disconnected side-channels, and result from the wind blowing seeds over the water surface, which then accumulate in bands along the shore.

Adequacy of existing models

All existing models for establishment of cottonwood assume that seedlings are obligate phreatophytes, so that their roots need to continuously maintain contact with the receding alluvial water table, or the tension-saturated capillary fringe. At my study site, I find that the proportion of finer material within the matrix and the thickness of the coarse surface layer are important controlling variables when explaining 0+ seedling presence-absence and growth. On the other hand, the vertical distance to water seems to play no role. Thus, I suggest that cottonwood seedlings growing on gravel bars are facultative phreatophytes (sensu Smith et al. 1998), as proposed by Cooper et al. (1999) for the case of seedlings on high bars of a constrained sand-bed river. If groundwater is available, either as a water table or a saturated capillary fringe, they will take advantage of it, but if the saturated zone is too deep, they will still be able to establish and grow by using floodwater and rain held by capillarity within the fine matrix. The results of Cooper et al. (1999) and Bhattacharjee et al. (2006) support this conclusion.

The two factors that allow cottonwood seedlings to establish without relying on direct contact with groundwater - a fine matrix with a wide range of particle sizes and the presence of a coarse surface layer - are typical of gravel-bed rivers. Even though sand-bed streams usually have a fairly narrow range of particle sizes, the sand can be fine enough to hold moisture by capillarity, as suggested by Cooper et al. (1999). In such case though, evaporation from the soil surface will be much higher because of the absence of a coarse surface layer (see Chapter 5), so that the mechanisms invoked by the RBM should take place.

I propose that the Recruitment Box Model should be an adequate representation of the processes allowing early cottonwood establishment in sand-bed streams with a horizontal water table and capillary fringe, and homogeneously sized sand. For gravel-bed streams though, the assumption that seedlings are obligate phreatophytes should be relaxed. The concept could also be expanded to that of a "Recruitment Cube", in order to emphasize the important effects that the bar sedimentary structure has on early establishment of cottonwood seedlings, and possibly on that of other riparian species. Finally, the very important role played by the coarse surface layer should also be incorporated into any conceptual model of riparian tree establishment in gravel-bed rivers.

The processes and effects discussed in this study are general, and apply not only to wandering rivers. Thus, I propose that my results can be broadly extrapolated to other alluvial gravel-bed rivers in the Northern Hemisphere that sustain populations of riparian poplars within sections *Tacamahaca* and *Aigeiros*.

Implications for management

Previous literature on reduced cottonwood establishment below dams has focused on the effects of altered hydrographs (Bradley and Smith 1986, Mahoney and Rood 1998, Rood and Mahoney 2000, Rood et al. 2005). Rood and Mahoney (1990, 1995) suggested that the silt shadow below dams could affect recruitment because of a decrease in bar formation. My findings strongly suggest that the proportion of finer material within the matrix is a driving variable for 0+ seedling success on gravel bars, while the coarse surface layer acts as a threshold, impeding establishment if it is too thick. The upstream presence of a dam should then affect cottonwood recruitment at least in two ways, in addition to those impacts caused by changes in the flow régime: (i) A varying proportion of the fine bed material originally carried by the river will deposit in the impoundment, depending on its size, depth, and shape, on the incoming and outgoing flows and their temperature, on the depth of the intake structure(s), and on the type of material. This could limit the amount of fines in the matrix at downstream locations. (ii) Unnaturally steep drawdown rates during flood recession could result in the formation of coarse

sediment deposits lacking a fine matrix. More research will be needed in order to

elucidate how these mechanisms affect cottonwood recruitment downstream of dams.

<u>References Cited</u>

Alpert, P., F.T. Griggs, and D.R. Peterson. 1999. Riparian forest restoration along large rivers: Initial results from the Sacramento River Project. *Restoration Ecology*, **7**, 360-368.

Amlin, N.M., and S.B. Rood. 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands*, **22**, 338-346.

APHA. 2007. *Standard methods for the examination of water and wastewater*, On-Line. American Public Health Association, Washington, District of Columbia.

Auble, G.T., and M.L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the Upper Missouri River, Montana. *Wetlands*, **18**, 546-556.

Baxter, C., F.R. Hauer, and W.W. Woessner. 2003. Measuring groundwater–stream water exchange: New techniques for installing minipiezometers and estimating hydraulic conductivity. *Transactions of the American Fisheries Society*, **132**, 493-502.

Bennett, S.J., and A. Simon. 2004. *Riparian Vegetation and Fluvial Geomorphology*. Water Science and Application series N°8, American Geophysical Union, Washington, DC.

Bhattacharjee, J., J.P. Taylor, Jr., and L.M. Smith. 2006. Controlled flooding and staged drawdown for restoration of native cottonwoods in the Middle Rio Grande Valley, New Mexico, USA. *Wetlands*, **26**, 691 – 702.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 57-85.

Braatne, J.H., R. Jamieson, K.M. Gill, and S.B. Rood. 2007. Instream flows and the decline of riparian cottonwoods along the Yakima river, Washington, USA. *River Research and Applications*, **23**, 247-267.

Bradley, C.E., and D.G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany*, **64**, 1433-1442.

Brierley, G.J., T. Cohen, K. Fryirs and A. Brooks. 1999. Post-European changes to the fluvial geomorphology of Bega catchment, Australia: Implications for river ecology. *Freshwater Biology*, **41**, 839-848.

Church, M.A., D.G. McLean, and J.F. Wolcott. 1987. River bed gravels: Sampling and Analysis. In *Sediment Transport in Gravel-Bed Rivers*. Edited by C.R. Thorne, J.C. Bathurst, and R.D Hey. John Wiley and Sons, Chichester. Pp. 43-88.

Cooper, D.J., D.M. Merritt, D.C. Andersen, and R.A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the Upper Green River, USA. *Regulated Rivers: Research and Management*, **15**, 419-440.

Cooper, D.J., D.C. Andersen, and R.A. Chimner. 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. *Journal of Ecology*, **91**, 182-196.

Décamps, H. 1996. The renewal of floodplain forests along rivers: a landscape perspective. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **26**, 35-59.

Dixon, M.D. 2003. Effects of flow pattern on riparian seedling recruitment on sandbars in the Wisconsin river, Wisconsin, USA. *Wetlands*, **23**, 125-139.

Dykaar, B.B., Wigington Jr., P.J., 2000. Floodplain formation and cottonwood colonization patterns on the Willamette River, Oregon, USA. *Environmental Management*, **25**, 87–104.

Eckenwalder, J.E. 1996. Systematics and evolution of *Populus*. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 7-32.

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

Fenner, P., W.W. Brady, and D.R. Patton. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. *Journal of Range Management*, **38**, 135-138.

Francis, R.A. 2006. Allogenic and autogenic influences upon riparian vegetation dynamics. *Area*, **38**, 453-464.

Francis, R.A., A.M. Gurnell, and G.E. Petts. 2004. Survival and growth response of *Populus nigra* fragments to differing hydrogeomorphological conditions. In B. Webb, M. Acreman, C. Maksimovic, H. Smithers, and C. Kirby (eds.). *Hydrology: Science and Practice for the 21st Century*. Volume II. British Hydrological Society, London, UK. Pp. 80-89.

Francis, R.A., A.M. Gurnell, G.E. Petts, and P.J. Edwards. 2006. Riparian tree establishment on gravel bars: interactions between plant growth strategy and the physical environment. In *Braided rivers: process, deposits, ecology and management.* Edited by G. Sambrook-Smith, J. Best, C. Bristow, and G.E. Petts. International Association of Sedimentologists Special Publication 36. Blackwell, Oxford. Pp. 361–380.

Francis, R.A., and A.M. Gurnell. 2006. Initial establishment of vegetative fragments within the active zone of a braided gravel-bed river (river Tagliamento, NE Italy). *Wetlands*, **26**, 641-648.

Friedman, J.M., M.L. Scott, and G.T. Auble. 1997. Water management and cottonwood forest dynamics along prairie streams. In *Ecology and Conservation of Great Plains Vertebrates*. Edited by F.L. Knopf and F.B. Samson. Springer –Verlag, New York.

Friedman, J.M., and V.J. Lee. 2002. Extreme floods, channel change and riparian forests along ephemeral streams. *Ecological Monographs*, **72**, 409-425.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience*, **41**, 540-551.

Gurnell, A.M., and G.E. Petts. 2002. Island dominated landscapes of large floodplain rivers, a European perspective. *Freshwater Biology*, **47**, 581- 600.

Helsel, D.R., and R.M. Hirsch. 1992. *Statistical Methods in Water Resources*. Studies in Environmental Science 49, Elsevier, Amsterdam. 530 pages.

Hillel. 1998. *Environmental Soil Physics*. Academic Press. San Diego.

Huggenberger, P., E. Hoehn, R. Beschta, and W. Woessner. 1998. Abiotic aspects of channels and floodplains in riparian ecology. *Freshwater Biology*, **40**, 407-425.

Hughes, F.M.R., and S.B. Rood. 2003. Allocation of river flows for restoration of floodplain forest ecosystems: A review of approaches and their applicability in Europe. *Environmental Management*, **32**, 12-33.

Karrenberg, S., P.J. Edwards, and J. Kollmann. 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology*, **47**, 733-748.

Mahoney, J.M., and S.B. Rood. 1991. A model for assessing the impact of altered river flows on riparian poplars in Southwestern Alberta. In *The Biology and Management of Southern Alberta's Cottonwoods*. Edited by S.B. Rood and J.M. Mahoney. Proceedings of the University of Lethbridge Conference, May 4 to 6, 1990. University of Lethbridge, Alberta. Pp. 99-111.

Mahoney, J.M., and S.B. Rood. 1992. Response of a hybrid poplar to water table decline in different substrates. *Forest Ecology and Management*, **54**, 141-156.

Mahoney, J.M., and Rood, S.B. 1993. A model for assessing the effects of altered river flows on the recruitment of riparian cottonwoods. Pages 228-232 in B. Tellman, H.J. Cortner, M.G. Wallace, L.F. DeBano, and R.H. Hamre, editors. "*Riparian Management: Common Threads and Shared Interests*", USDA Forest Service General Technical Report RM-226.

Mahoney, J.M., and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment – An integrative model. *Wetlands*, **18**, 634-645.

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

Merigliano, M.F. 1998. Cottonwood and willow demography on a young island, Salmon River, Idaho. *Wetlands*, **18**, 571-576.

Montgomery, D.R. and S.M. Bolton. 2003. Hydrogeomorphic variability and river restoration. Pages 39-80 in R.C. Wissmar and P.A. Bisson, editors. *Strategies for Restoring River Ecosystems: Sources of Variability and Uncertainty in Natural and Managed Systems*. American Fisheries Society, Bethesda, Maryland.

Naiman, R.J., and H. Décamps. 1997. The ecology of interfaces – riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621-658.

Nanson, G.C., and J.C. Croke. 1992. A genetic classification of floodplains. *Geomorphology*, **4**, 459-486.

Pella, E. 1990. Elemental organic analysis. Part 2. State of the Art. *American Laboratory*, **22**, 28–32.

Petts, G.E., A.M. Gurnell, A.J. Gerrard, D.M. Hannah, B. Hansford, I. Morrissey, P.J. Edwards, J. Kollmann, J.V. Ward, K. Tockner, and B.P.G. Smith. 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **10**, 249–266.

Poole, G.C., J.A. Stanford, S.W. Running and C.A. Frissell. 2006. Multiscale geomorphic drivers of groundwater flow paths: subsurface hydrologic dynamics and hyporheic habitat diversity. *Journal of the North American Benthological Society*, **25**, 288-303.

Rood, S.B., and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. *Environmental Management*, **14**, 451-464.

Rood, S.B., J.M. Mahoney, D.E. Reid, and L. Zilm. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. *Canadian Journal of Botany*, **73**, 120-1260.

Rood, S.B., and J.M. Mahoney. 1995. River damming and riparian cottonwoods along the Marias River, Montana. *Rivers*, **5**, 195-207.

Rood, S.B., A.R. Kalischuk, and J.M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands*, **18**, 557-570.

Rood, S.B., and J.M. Mahoney. 2000. Revised instream flow regulation enables cottonwood recruitment along the St Mary River, Alberta, Canada. *Rivers*, **7**, 109-125.

Rood, S.B., J.H. Braatne, and F.M.R. Hughes. 2003. Ecophysiology of riparian cottonwoods: Stream flow dependency, water relations, and restoration. *Tree Physiology*, **23**, 1113-1124.

Rood, S.B., G.M. Samuelson, J.H. Braatne, C.R. Gourley, F.M.R. Hughes, and J.M. Mahoney. 2005. Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment*, **73**, 193-201.

Samuelson, G.M., and S.B. Rood. 2004. Differing influences of natural and artificial disturbances on riparian cottonwoods from prairie to mountain ecoregions in Alberta, Canada. *Journal of Biogeography*, **31**, 435-450.

Scott, M.L., J.M. Friedman, and G.T. Auble. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology*, **12**, 327-339.

Scott, M.L., G.T. Auble, and J.M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications*, **7**, 677-690.

Shafroth, P.B., G.T. Auble, J.C. Stromberg, and D.T. Patten. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands*, **18**, 577-590.

Simons, D.B., and R.K. Simons. 1987. Differences between gravel- and sand-bed rivers. In *Sediment Transport in Gravel-Bed Rivers*. Edited by C.R. Thorne, J.C. Bathurst, and R.D Hey. John Wiley and Sons, Chichester. Pp. 3-15.

Smith, S.D., D.A. Devitt, A. Sala, J.R. Cleverly, and D.E. Busch. 1998.Water relations of riparian plants from warm desert regions. *Wetlands*, **18**, 687-696.

Stanford, J.A., J.V. Ward and B.K. Ellis. 1994. Ecology of the alluvial aquifers of the Flathead River, Montana, pp. 367-390. In Gibert, J., D.L. Danielopol, J.A. Stanford (ed.), *Groundwater Ecology*. Academic Press, Inc., San Diego, California. 571 pp.

Stanford, J.A., M.S. Lorang, and F.R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **29**, 123-136.

Tabacchi, E., D.L. Correll, F.R. Hauer, G. Pinay, A.M. Planty-Tabacchi, and R.C. Wissmar. 1998. Development, maintenance and role of riparian vegetation in the river landscape. *Freshwater Biology*, **40**, 497- 516.

Tockner, K., and J.A. Stanford. 2002. Riverine flood plains: Present state and future trends. *Environmental Conservation*, **29**, 308-330.

Ward, J.V., K. Tockner, D.B. Arscott, and Claret. 2002. Riverine landscape diversity. *Freshwater Biology*, **47**, 517-539.

CHAPTER 3: THE RIVER SEEDING CONCEPT FOR COTTONWOOD

ESTABLISHMENT AT THE REACH-SCALE

<u>Introduction</u>

Background

It is well known that along alluvial river reaches, riparian cottonwoods (*Populus spp.*, Salicaceae) establish on sediment bars during the recession of the snowmelt hydrograph, creating bands that are referred to as arcuate (Everitt 1968, Bradley and Smith 1986, Braatne et al. 1996). Such bands are generally formed on point bars, along the inner part of bends in meandering rivers. They can have other shapes in the case of medial bars, usually found on braided rivers. The Recruitment Box Model (RBM), which is the currently accepted conceptual framework for cottonwood establishment (Mahoney and Rood 1991 and 1998, Braatne et al. 1996), proposes that the occurrence of such recruitment bands depends on the combination of two mechanisms. First, dispersal of cottonwood seeds by wind results in germination over all moist bar surfaces exposed above the receding river stage (for example, see Figure 6 in Braatne et al. 1996). Second, continued flow recession limits success to those seedlings established at lower elevations, such that their roots can keep continuous contact with the receding alluvial water table, or with the associated capillary fringe above it, during the first season of growth. Seedlings located at higher elevations desiccate and die. As discussed in detail in Chapter 2, these concepts are based on the assumptions that: (i) cottonwood seedlings are obligate phreatophytes (sensu Smith et al. 1998), (ii) the groundwater under river bars is horizontal (or very close to it) and connected to the river stage, and (iii) the capillary fringe is parallel to the water table (see Figure 4 in Mahoney and Rood, 1998).

As part of a broader investigation on cottonwood ecology, I have found that none of these assumptions hold for my study reach, on the Nyack Floodplain of the gravel-bed Flathead River, Montana, USA (see Chapter 2). I have strong evidence that cottonwood seedlings established in 2006 and 2007 were facultative, not obligate phreatophytes. If groundwater was available, either as a water table or a saturated capillary fringe, they

took advantage of it. At the many locations with successful establishment and growth, but where the saturated zone was too deep, they used floodwater and rain held by capillarity within the matrix of fine sediment, wherever such fine material had enough water-holding capacity. The results of Cooper et al. (1999) and Bhattacharjee et al. (2006) support this conclusion. The coarse surface layer found on all gravel-bed rivers (Church et al. 1987) helps maintain capillary moisture within the fine matrix through dry periods, as shown later in Chapter 5.

Alluvial water tables are not horizontal under bars in gravel-bed rivers. At my study site, most of the bars where I documented successful establishment were in "losing reaches" (i.e., those having a negative vertical hydraulic gradient) and the water tables deepened steeply away from the channel, with transversal (to the longitudinal, main flow direction) slopes of 15% or more. I have found lateral groundwater slopes of similar magnitude in gravel-bed rivers in Chilean Patagonia, as has Datry on the Selwyn River, in Canterbury, New Zealand (Thibault Datry, CEMAGREF, Lyon, France, personal communication, February 2006).

For the capillary fringe to be parallel to the alluvial water table (as depicted for example in Figure 4, Mahoney and Rood 1998, and in Figure 1.a herein), the fine matrix would need to be continuous in space and highly homogeneous (i.e., made up of particles of the same size everywhere across the bar). As proposed in Chapter 2, such conditions could be achieved in sand-bed streams. In gravel-bed systems though, it is well known that the enormous spatial and temporal variability in sedimentary processes results in deposits that are discontinuous and exhibit a high heterogeneity over a wide range of spatial scales (for example, see Huggenberger et al. 1998, Powell 1998, Lunt et al. 2004, and references therein). In my study reach, I found high spatial variability in fine content, sediment caliber range, and matrix continuity at small, within-the-bar scales, in the order of 1 m (see Chapter 2). Thus, the height of capillary rise from the alluvial water table should be expected to be highly variable at such spatial scales, which should result in fine-scale patchiness in the sediment's ability to sustain moisture, and thus seedling vegetation. The results of Alpert et al. (1999), Petts et al. (2000), and Francis et al. (2006), from other gravel-bed systems, clearly support my observations. Some of these important differences between gravel and sand systems are depicted in Figure 1.

The generality of the above results and observations indicates that the three assumptions of (i) obligate phreatophyte behavior of cottonwood seedlings of the year, (ii) horizontal alluvial water table, and (iii) horizontal capillary fringe, do not hold for gravel-bed rivers, in general. Nonetheless, over three summers, I observed and documented successful seedling establishment on some of the gravel-bars located in my reach.

a. Homogeneous sand-bed stream

b. Heterogeneous gravel-bed river
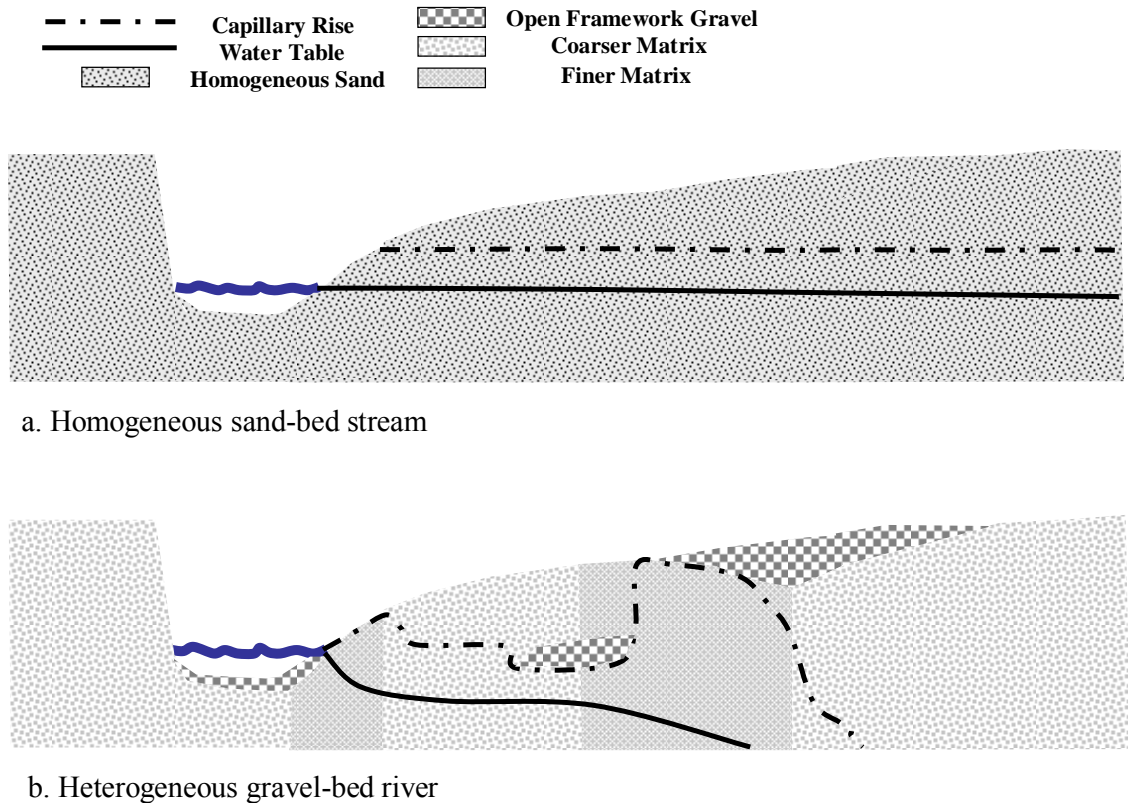
Figure 1. Cartoons depicting the different behavior of the alluvial water table and associated capillary fringe in the case of (a) sand-bed streams and (b) gravel-bed rivers. Please note that both depictions, but mostly (b), are gross oversimplifications as compared to the natural heterogeneity found in fluvial sedimentary deposits.

In two of those years (2005 and 2007), I observed clearly delineated bands of recruiting cottonwood seedlings around both medial and point bars. In 2006, medial bars were completely covered with successful seedlings, above a sharply delimited lower establishment line. In all cases, the lower and upper bounds appeared to closely follow

contour (elevation) lines. This begs the questions: If the basic assumptions of the RBM do not hold for gravel-bed rivers, what then are the actual mechanisms driving cottonwood establishment at the reach scale? In other words, what alternative processes, not described heretofore, result in the formation of the bands of cottonwood seedlings that have been recurrently mentioned in the literature? Why is it that in some years cottonwoods establish in patches, covering whole bars, while in others recruitment on the same bars only occurs in bands? The goal of this paper is to present evidence supporting a new hypothesis which in my opinion explains all of these, as well as previous observations and results, in a parsimonious way: the River Seeding Concept for cottonwood establishment at the reach-scale.

Specifically, at my study reach, for the 2006 and 2007 growth seasons, I determined the period of seed release, mapped the occurrence of bands of cottonwood seedlings of the year (0+ seedlings from now on) on bare gravel bars, and compared the lower and upper establishment limits with flow profiles for different discharges. I also sampled the drift for cottonwood seeds and germinants, and did experiments in order to determine the settling velocity of cottonwood seeds with different hydration times.

The River Seeding Concept

I propose herein that hydrochory (i.e., water dispersal of seeds) is the fundamental mechanism creating recruitment bands of cottonwood seedlings along gravel-bed rivers, thus explaining their spatial distribution (and possibly that of other riparian Salicaceae) on alluvial floodplains. According to this hypothesis, anemochory (wind dispersal) results in large numbers of seeds falling on the water surface. These seeds are incorporated into the drift, and subsequently deposit wherever their settling velocity is larger than the vertical component of the instantaneous flow velocity, just as any sediment particle would. Such conditions are found along sloping shorelines, in shallow flows over gravel and cobble beds. This is where the small flow depth and high relative roughness, usually with particle protrusion, result in decreased turbulence. In turn, the reduced fluctuations in the instantaneous vertical velocity (as turbulence is proportional to both flow velocity and depth; see Dingman 1984) allow for shoreline settling of the hydrated seeds.

In this way, as the river stage drops, following the receding limb of the hydrograph, the flow deposits seeds and germinants on bars and banks. The upper establishment limit is given by the position of the shoreline at that moment when seeds start becoming available in the flow. The lower limit corresponds to the river stage when seeds stop being available in the drift. Both the beginning and the end of seed availability in the flow are clearly related to the phenology of seed dispersal from the trees (i.e., to the moments at which the release of seeds starts and ends, respectively). Still, these times should not be expected to be exactly the same. In effect, the diffusion inherent to transport processes in rivers must slightly delay (by minutes or hours) the beginning of seed availability, while shifting the end by at least a few days or maybe weeks, as seeds falling in upper reaches within the basin, where trees flower and release their seed later, travel towards a given location downstream.

Because flow profiles in flooding alluvial rivers are gradually-varied in space (Henderson 1966, Dingman 1984), the resulting establishment bands should have highly regular lower and upper limits. These limits should not exactly follow elevation contour lines: Because flow profiles have a downstream slope, they must also decrease in elevation in the downstream direction, matching the slope of the water surface.

As implied by the name of my hypothesis, I am simply proposing that it is the river that does the seeding, and that initial establishment of cottonwoods occurs under water. The implications of this idea are manifold. In any given year, if the receding stage were low when seeds start being available in the flow, the upper establishment limit would be at a low elevation. Such a situation would result in low, narrow establishment bands along bars and banks. This could happen either because the peak flow was low, or because it occurred early in the season with respect to the beginning of seed availability. On the other hand, if a large peak flow, above bank-full, were to occur simultaneously with seed availability, the receding waters would be able to seed cottonwoods over a much broader range of elevations. Medial bars would be seeded from the ridge-top down, to the lower limit of seed establishment, while point bars would get much wider establishment bands, resulting in broader recruitment. In such case, medial bars would exhibit seedling patches, not the typical bands, as the flow would have seeded the whole

bar, from the ridge-top down to the lower limit for establishment, instead of only a fringe surrounding the base of the bar.

Even though the specific mechanisms behind this concept are quite different than those espoused by the RBM (Braatne et al. 1996, Mahoney and Rood 1998), the management implications are fundamentally the same: Floods are needed with sufficient magnitude, appropriate timing, and adequate rates of recession, in order to ensure successful recruitment of cottonwoods. If the flood is not synchronized with the period of seed availability (which in turn depends on the phenology of seed release, but also on the transport times in the river), cottonwoods will not be able to establish well.

Note also that the ideas presented in this work are only applicable to alluvial gravel-bed rivers, of any pattern or style. Sand-bed rivers tend to have a more constant depth across their width, the bed material is in continuous motion, even at low flows, and the banks are in constant flux. It would be harder for seeds to find conditions fostering deposition in such environments, and even if they did deposit, the movable bed would impede underwater establishment. I think that wind dispersal of seeds upon moist sand bars is the main mechanism explaining establishment in sand-bed streams, and that the ideas embodied in the RBM are fully applicable. Furthermore, it appears that the RBM was first developed in such sand-bed streams, even though this is not explicitly stated by its authors (Mahoney and Rood 1991 and 1998).

Methods

Study area

This research was conducted at the Nyack Floodplain, located on the Middle Fork of the Flathead River, a fifth order wandering gravel-bed river with headwaters in the Bob Marshall-Great Bear Wilderness Complex, forming the southwest boundary of Glacier National Park in western Montana, USA (Figure 2). The study reach is between 8 and 9 km long, with a floodplain that is 1 to 2 km wide. The average channel slope in the reach is 2.4 ‰.
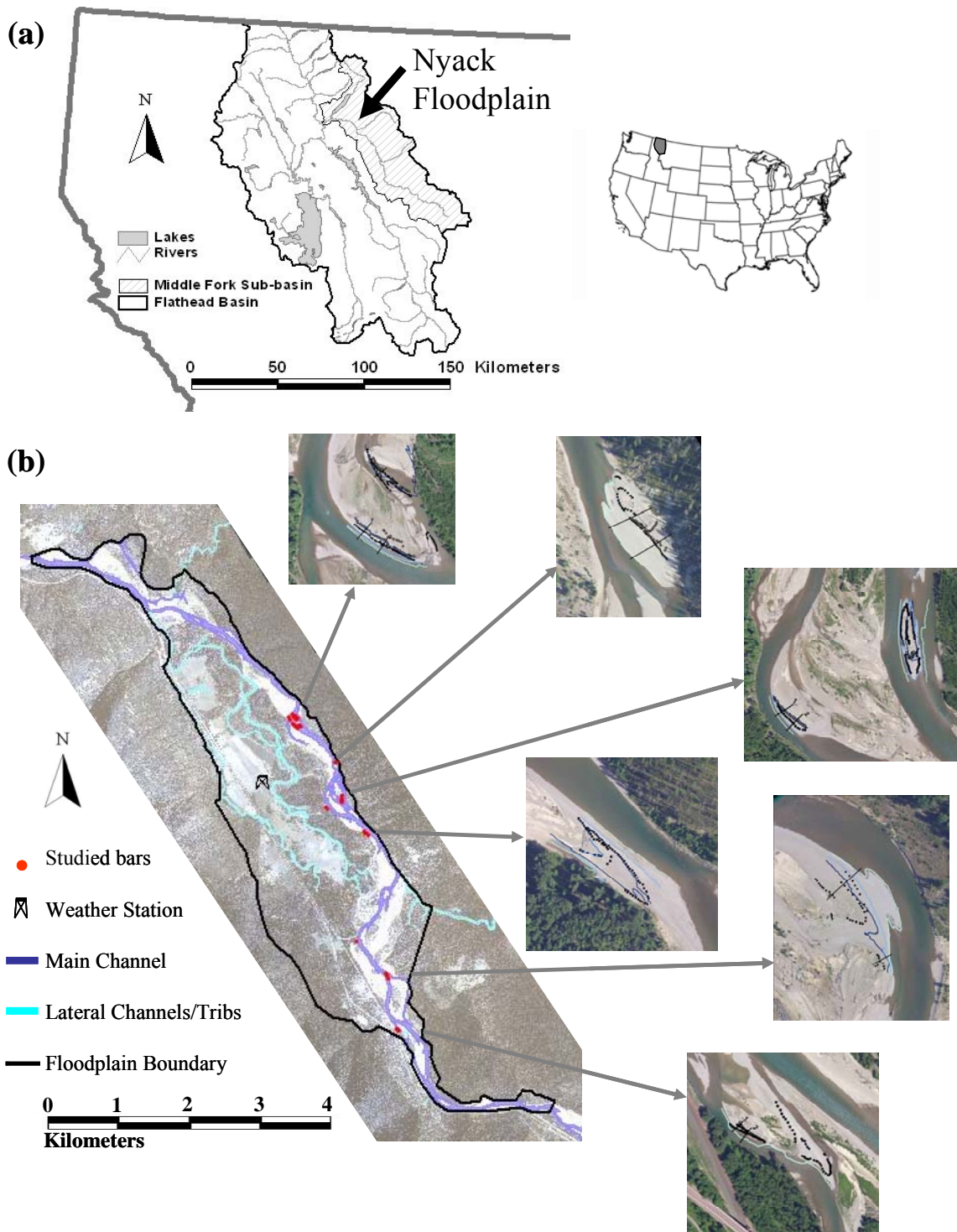
Figure 2. (a) Map of the Flathead River Basin in western Montana (black arrow indicates site of Nyack Floodplain) and (b) Satellite image of the Nyack Floodplain showing the eight study bars (insets).

Anthropogenic effects on the floodplain are minimal, with a highway and railroad corridor along its southwest edge, rip-rap embankments at a few locations at the top of the floodplain, to protect the railway, and some agriculture. All of these effects occur primarily in the passive part of the orthofluvial zone (sensu Stanford et al. 2005). The catchment area is 2920 km^2, as measured at the USGS gaging station located 9.5 km below the end of the reach, in West Glacier, Montana (USGS Station Number 12358500; Middle Fork of the Flathead River near West Glacier, Montana). The elevation ranges from 1000 masl at the downstream end of the study reach, to about 2900 masl, at the highest point in the basin.

The mean annual flow for the period 1940-2007 was 81.1 m^3/s; June is the month with the highest mean flow, 282 m^3/s, while January and February have the lowest mean flows, at 20.2 m^3/s. The mean annual flood is 645 m^3/s, and the maximum recorded annual flood is almost 4,000 m^3/s in 1964, even though historical records mention that the 1894 flood was much larger. In most years, annual floods are caused by snowmelt, or rain over snow, and occur in May or June. On some occasions, the annual flood can be caused by rain in the fall. The floodplain is bounded laterally by valley walls, and has bedrock knick points at both its upper and lower ends. The river along the length of the floodplain is a typical gravel-bed wandering reach, with low-order braiding and the presence of vegetated islands and recent gravel bars within the active channel. The more mature, orthofluvial floodplain forest and agricultural pasture is to the southwest.

The poplar species present at my study site is the black cottonwood, *Populus trichocarpa* T. & G., within the *Tacamahaca* section of the genus *Populus* (taxonomy follows Eckenwalder 1996). The site has been the focus of research by the Flathead Lake Biological Station of the University of Montana for over 20 years, and additional site description is offered in Stanford et al. (1994).

Timing of seed dispersal

In the years 2006 and 2007, I placed seed traps at different locations on the floodplain. This was done in early June, before the beginning of the seed release period, in order to document its timing as well as the temporal variation in the magnitude of the seed rain. I also interviewed the local landowners and asked them to record the exact date

when seed dispersal began. In 2006, I used rectangular plastic containers (dishpans, with maximum outside dimensions of 33.5 x 29.2 x 13.7 cm), filled with 5 cm of water, as traps. The exposed, collecting surface area was 828 cm^2. In order to minimize collection of seeds tumbling along the ground, the containers were placed on horizontal tables with narrow legs, 30 cm above the surface. Trapped seeds were counted weekly. This set-up gave only qualitative results, as the maximum number of seeds ever collected was only 5 per week (corresponding to a rate of 8.6 seeds/d/m^2). This was most probably due to the pans not being filled closer to their rim, as the turbulence induced by the pan walls was observed to reduce the seed catch. Thus, in 2007 I selected much larger, round plastic pans, which were also placed on horizontal tables 30 cm above ground surface. These were 69.5 cm in diameter and 6.4 cm in height, and were filled with water up to 0.5 cm from the rim, exposing a trapping surface of 3728 cm^2. I placed traps at four different locations on my study floodplain, always in closely-located pairs, in order to test how consistent the measurements were. Traps were never placed directly under trees, to avoid whole seedpods or branches falling by gravity.

Seeds were collected every three days from the traps, and counted. I then computed the seed rain as seeds per day per unit area. The data concurrently collected at pairs of traps were compared with Pearson's correlation coefficient.

High Resolution Aerial Photographs

High resolution digital photographs of the study reach were collected from a plane on different dates, using a standard professional digital camera (14.8 megapixels) mounted with an autofocus 50 mm lens. The images were taken from an altitude of approximately 1000 m, and have a pixel resolution of ≈ 10 cm at the ground. Those images selected for the study were georectified in ERDAS Imagine 9.0 using ground control (i.e., geo-referencing) points collected with a Leica 5000 survey-grade differential GPS. The mean RMS error for all images was 0.4 m. The dates and corresponding flows of those images used for building stage-discharge relationships at my study sites are given in Table 1.

Table 1. Collection dates for high-resolution digital images of the floodplain, and corresponding mean daily flows at the USGS gaging station in West Glacier, Montana.

Date	Flow (m^3/s)
August 11, 2007	21.9
July 21, 2006	47.3
June 28, 2007	97.1
June 25, 2006	173.0

Mapping of 0+ seedlings

In the months of July and August, both in 2006 and 2007, I repeatedly surveyed the whole active channel corridor through my study reach, looking for 0+ seedlings. The focus of the research was the colonization of recent, previously unvegetated gravel bars. Thus, establishment on sand deposits, always located at the downstream end of vegetated islands or in backwaters, was not considered. In late August and early September, after all successfully established seedlings of the year had had enough time to grow and become visible among the gravel and cobble beds, I mapped the occurrence of any patch or band of 0+ seedlings. This was done on large scale, high-resolution aerial images, taken at the most 1 month before the mapping date. I took great care in identifying all occurrence of establishment, even down to patches with only a few 0+ seedlings. In September 2007, as part of a topographic survey of my study sites, I delineated the lower and upper establishment limits of all identified seedling bands and patches, for both those seedlings established in 2007 (0+ seedlings), and those established in 2006 (1+ seedlings).

Topographic surveying

I surveyed my study bars the first week of September 2007, using a Leica 5000 survey-grade differential GPS. I obtained *(x,y,z)* coordinates for a large number of points

on each bar (about 400 on average), on a grid of about 5 x 5 m. I also surveyed a series of clearly visible landscape features, to use as geo-referencing or ground control points when rectifying aerial images. The water surface elevation (WSE from now on) in the river (or pond if any site was located closer to a pond) on the day of the survey was noted. Where possible, I also surveyed flood marks, such as floating débris lines on bars or on vegetation. Only points collected with a vertical GPS error lower than 2 cm were used in further analyses.

Hydrology

My study reach corresponds to a wandering gravel-bed river, with low-order braiding, presence of gravel bars and vegetated islands, and multiple channels. During low flow periods, over 30% of the incoming flow is lost to the aquifer at the upstream end of the floodplain (and recovered at its downstream end), and various gaining and loosing reaches have been documented (Stanford et al. 2005) and modeled (Poole et al. 2006) throughout the floodplain. The occurrence of braiding, whereby flows get split into multiple channels, and the fact that flows change in the longitudinal direction due to downwelling, make it extremely difficult to obtain stage-discharge relationships at every studied bar. The only way to do so would be to install and operate independent flow gaging stations on each one of the channels next to each study bar.

In order to avoid such complications, I referred all of my stage determinations to the flow concurrently recorded at the USGS gaging station located 9.5 km below the end of the reach, in West Glacier, Montana. In this way, every time I report a river stage at any given study bar, and associate it to a given discharge, it is the WSE at that location, corresponding to the flow measured on the same day at the USGS gage. This means that my stage-discharge relationships are not representing the hydraulic link between the flow actually conveyed at a given cross-section and the corresponding river stage. They are just indexing the conditions observed at any moment, at any given bar, by the flow passing through the whole reach, as measured at the gaging station. The mean daily flow data for the study period (Figure 5) were downloaded from the USGS website at http://waterdata.usgs.gov/nwis/uv/?site_no=12358500&agency_cd=USGS.

Digital Elevation Models of Gravel Bars

The data collected with the differential GPS were used to create high resolution (0.2 m horizontal) digital elevation models (DEMs) of my study gravel bars. The GPS points were converted to a GIS coverage and DEMs were created in ArcMap 9.2 (ESRI 2007) using the tensioned spline interpolation method. Cross-sections were created from the gravel bar DEMs to describe the lower and upper seedling establishment levels, as well as the river stages corresponding to different flows.

Stage-discharge relationships

For each gravel bar, several images representing discharges at different dates (as measured at the USGS gaging station) were overlaid. Using the information from the DEMs, I estimated the inundation stages corresponding to the different flows. At those locations which had suffered obvious geomorphic changes, such as bar ablation or vertical accretion, between the date of the aerial picture and that of the surveying, I was only able to use the two most recent sets of images, acquired after the June 2007 flood. The inundation stages corresponding to each flow were noted and then used to develop a stage-discharge equation for each bar, with a power regression. Where available, flood marks were also used to add further information to the stage-discharge relationship. The errors in the stage estimations are most probably in the range from 5 to 10 cm, and are mainly due to possible changes in the bed morphology.

The stage-discharge equations were then used to back-calculate the flows corresponding to the upper and lower seedling establishment limits.

Drifting seeds and germinants

In order to get "proof of concept" that seeds are indeed transported by the drift, I placed drift nets and screened tubes at different locations, both at my study reach, as well as in reaches and tributaries located further upstream in the basin. The screened tubes had an inside diameter of 10.2 cm and were usually placed at three to six locations, in order to have replicates. Sampling time was recorded and I used a Gurley Price current-meter to measure the velocity of the flow at the mouth of the drift nets, in order to estimate the

volume of water sampled. Screened tubes were always placed in shallow areas, where velocity could not be measured with the current meter. Drift samples were analyzed under a dissecting microscope, counting the number of closed cottonwood seeds and of germinants. Germination stages were as used in Chapter 4, so that I distinguished closed seeds, initial germination (length of radicle plus hypocotyl equal to, or smaller than the overall seed size), and full germination (length of radicle plus hypocotyl longer than the seed). I also counted the number of open, empty seed capsules, as well as willow seeds.

Settling velocity of hydrated seeds

Batches of cottonwood seeds were placed in vials with water and were gently shaken for 30 seconds to ensure they all sank. In order to simulate the hydration process that takes place when seeds get incorporated into the drift, they were left in water for 9 different periods, ranging from 15 minutes to 2 days. The seeds were then dropped at the top surface of a graduated glass cylinder, filled with water at room temperature ($21.0 \pm 0.3°C$). The time required for the seeds to travel between two different marks on the graduated cylinder was recorded with a stop-watch. The selected starting mark was located about 10 cm below the water surface, to ensure that steady-state flow conditions had been reached around each seed when the measurement started. The mean settling velocity for each individual seed was computed by dividing the distance between the starting and ending marks by the travel time. The data were tested for normality and homogeneity of variances with Shapiro-Wilks and Levene tests, respectively. Differences in settling velocity due to hydration time were then analyzed with one-way ANOVA, and post-hoc tests were used for significant models.

Results

Seed dispersal

I obtained only qualitative results in 2006, as the smaller pans collected too few seeds to conduct statistical analyses of the data. Seed dispersal that year began on June 12 or 13 (Chris Dalimata, landowner, personal communication, June 2006) and ended by the second week of July. I found no seeds in the traps after July 14.

During 2007, I used the larger pans (as described in the Methods section), filling them almost to the rim. A maximum of 404 seeds (corresponding to a rate of 372 seeds/d/m^2) were trapped over one 3-day sampling interval. Seed dispersal in 2007 began on June 7 (John Dalimata, landowner, personal communication, June 2007), and lasted approximately until mid July. I terminated seed collections on July 10, as the numbers had fallen to less than 5% of those trapped at the moment of maximum seed release. An animal overturned one trap before the second measurement. After the third measurement date, the traps at one of the sites were continuously vandalized, so that there were only 6 traps from the fourth period on. The temporal behavior of the seed rain in 2007 is shown in Figure 3. The time distribution is clearly skewed, with the maximum occurring just a few days after the beginning of the dispersal period, and a long tail to the right.

There was a highly significant correlation (n = 29, Pearson's r = 0.984, p < 0.0001) between the seeds measured at the closely-located pairs of traps (Figure 4), indicating that the methodology that I devised can be trusted for estimating rain of
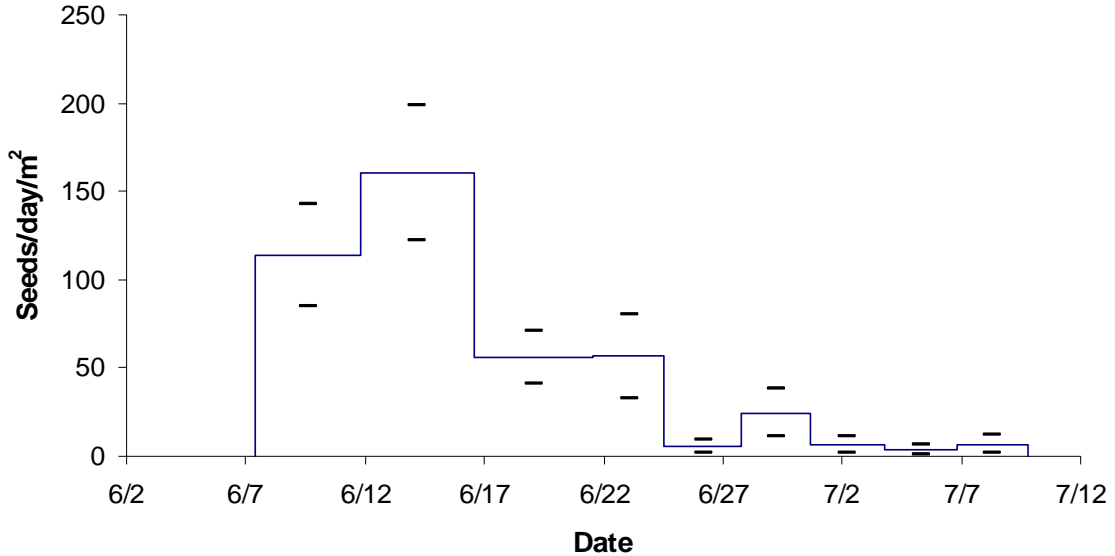
Figure 3. Temporal behavior of the seed rain (mean ± standard deviation) in 2007. The mean is computed from 8 measurements for the first and third dates, 7 for the second, and 6 at all other times.
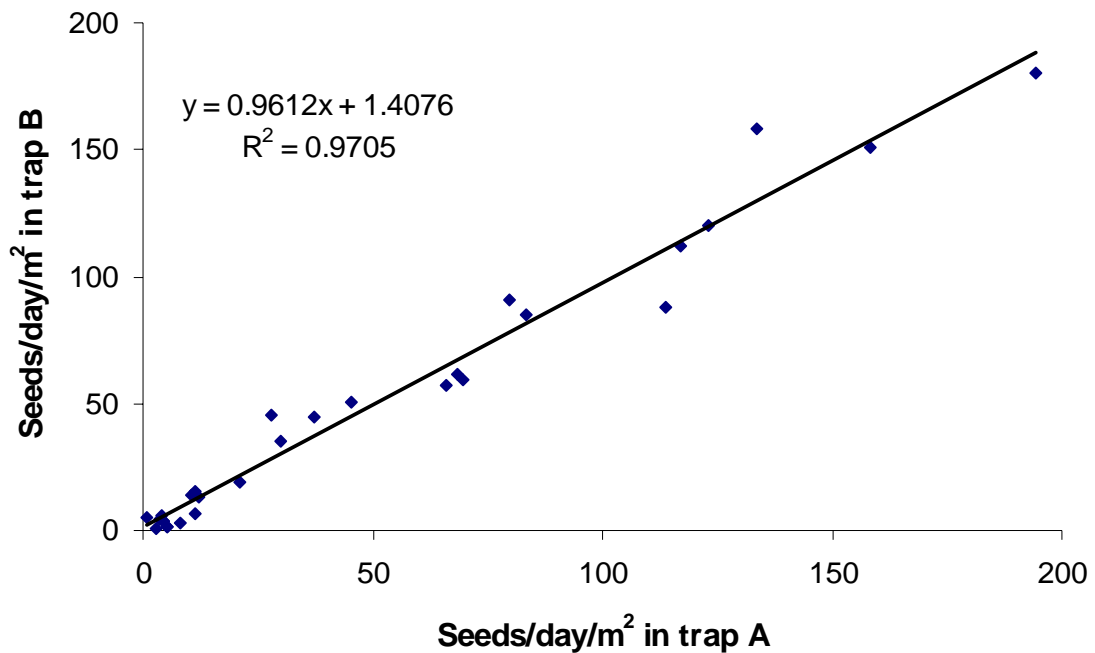
Figure 4. Correspondence between the seed rain at closely-located pairs of traps (n = 29).

plumed cottonwood seeds. The average number of seeds collected per m^2 over the duration of the seed dispersal period amounted to 1842, i.e., 18 million seeds per hectare.

Mapping of seedlings

In both years of mapping (2006 and 2007), as well as in 2005, when I conducted only qualitative observations of cottonwood recruitment along my study reach, I found that there were many more bars without any 0+ seedlings, than with successful establishment. Over the two growth seasons with detailed mapping, along a 9 km-long floodplain with hundreds of different gravel unit bars, I only found 18 such sedimentary units with more than 20 seedlings of the year. Of those, only 10 had significant numbers (in the hundreds) of 0+ seedlings, with ample spatial coverage by the recruiting plants, and I studied all but two of them. The locations of seedling bands and patches on the 8 different study bars are shown in Figure 8, a series of images where I delineate the lower and upper establishment limits, both in plan views and in selected cross-sections.

Hydrology

The river hydrograph over the period of study is given in Figure 5. Note that this is a plot of mean daily flows, so that the instantaneous peaks are somewhat larger, as indicated in the caption. In both 2006 and 2007, the recessions from the snowmelt peak were highly regular through the growth season, as there were no large-scale rainfall events. A very flashy, unseasonably large flood of 538 m^3/s, caused by heavy rainfall occurring over a short duration, occurred in the fall of 2006, just after the end of the growth season.
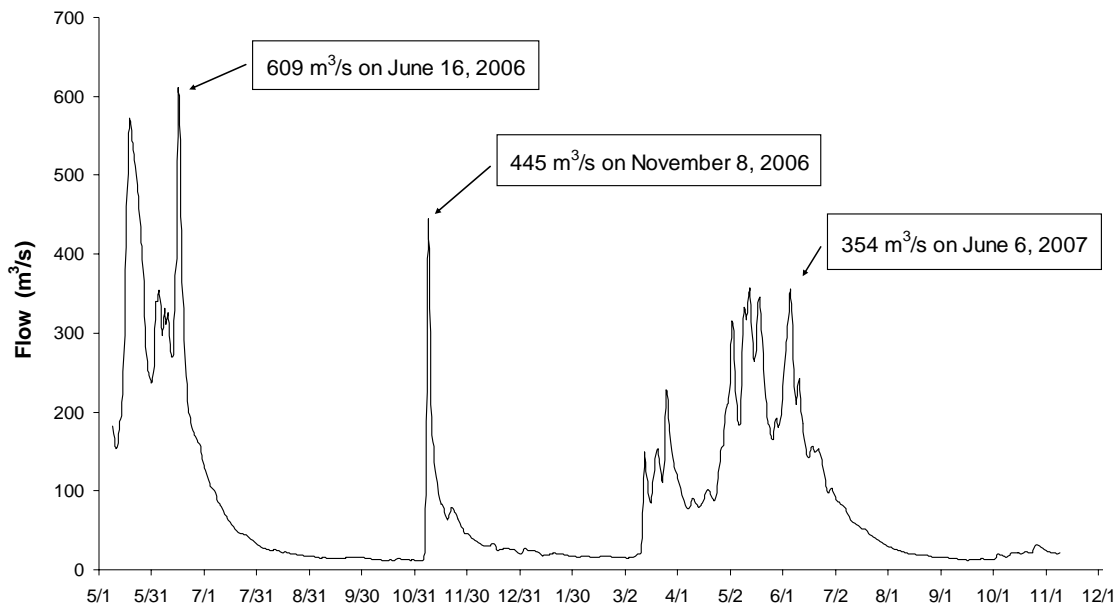
Figure 5. Mean daily flows over the study period, as measured at USGS Station Number 12358500, Middle Fork of the Flathead River near West Glacier, Montana. The corresponding instantaneous peaks are 637 m^3/s on June 16, 2006, 538 m^3/s on November 8, 2006, and 371 m^3/s on June 6, 2007.

For 2006, the mean daily flow on the initial date of seed release was 271 m^3/s on June 12 and 13. The instantaneous peak of 637 m^3/s occurred a few days later, when seed dispersal was already under way. In 2007, on the other hand, seed dispersal started on June 7, at the very beginning of the receding limb of the hydrograph, when the flow was at 242 m^3/s, down from the annual peak of 371 m^3/s.

63

Stage-discharge relationships

Most of the flood marks I collected were difficult to interpret, for multiple reasons. Because the snowmelt flood of 2007 (371 m^3/s on June 6) was quite smaller than the large rainfall flood of November 8, 2006 (538 m^3/s), it was not able to erase the still recent flood marks. A summary hydraulic computation indicated that the difference in flood stage between these two events was only somewhere between 20 and 30 cm. Thus, I ended up finding multiple marks at many of my study locations, covering a range of stages, and was not able to discriminate between the two most recent floods. Also, the November flood was large enough, so that most of my study bars, which are recently deposited, relatively low landforms, were under water. Of course, in such case there was no record of the maximum flood stages. This meant that the only way to acquire reliable flood marks was by getting on the floodplain, far from my sites on the active channel. Any stage-discharge relationship derived with such data was bound to be affected by a much larger error. Thus, I decided to obtain stage-discharge equations (Figure 6) only for the two study bars for which I had reliable flood mark information, in the form of débris rack-lines left by the June 2007 flood.

The flow corresponding to the high establishment limit for 2007 seedlings was estimated at 327 m^3/s on "End of Road" bar, and at 216 m^3/s on "Wally Side Channel" bar. In the case of the low establishment limit for 0+ seedlings (i.e., those established in 2007), the river stage corresponded to 180 m^3/s at "End of Road", and to 138 m^3/s at "Wally Side Channel". At "End of Road" bar I also had establishment in 2006 (1+ seedlings), which covered the bar's ridge, starting at a lower limit corresponding to a flow of 236 m^3/s.

For both bars, the river stage corresponding approximately to the November 2006 flood, with an instantaneous peak flow of 538 m^3/s (not included in the stage-discharge relationships), would have been clearly above the bar's ridge. Indeed, this was the case for all of the studied bars.

(a)

High 0+ limit: 327 m^3/s

Low 1+ limit: 236 m^3/s

Low 0+ limit: 180 m^3/s

$Q = 135.1 \ (H - 997)^{1.811}$

$R^2 = 0.998$

Stage (masl)

(b)

High 0+ limit: 216 m^3/s

Low 0+ limit: 138 m^3/s

$Q = 88.15 \ (H - 995.5)^{2.719}$
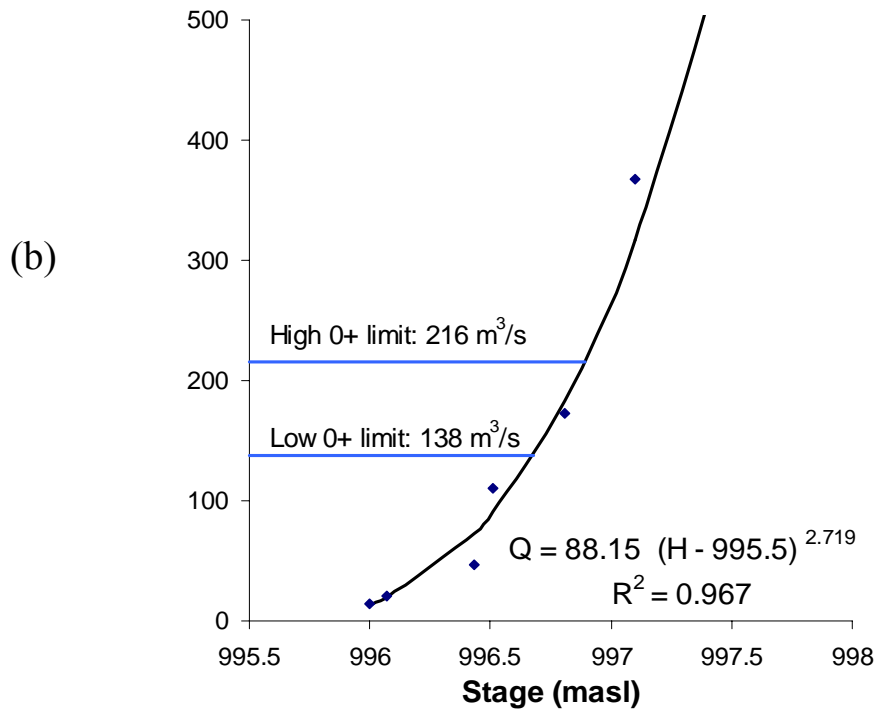
$R^2 = 0.967$

Stage (masl)
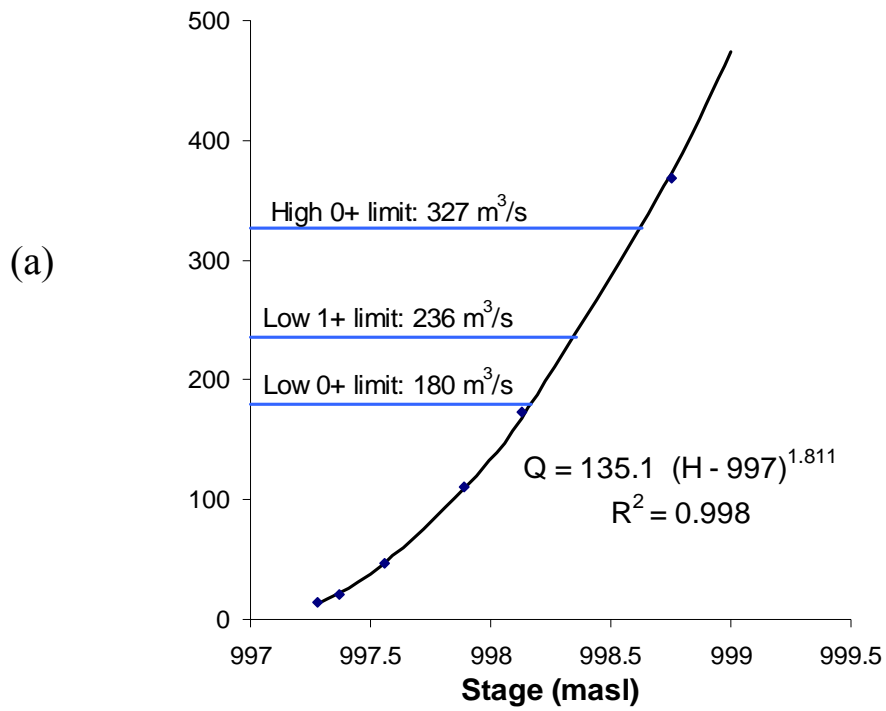
Figure 6. Stage-discharge equations for (a) Cross-section 1 on "End of Road" bar, and (b) Cross-section 1 on "Wally Side Channel" bar. Cross-sections are shown in Figure 8.

Seeds and germinants in the drift

These results can not really be compared to each other, as the sampling was synoptic in nature: I covered eight different locations over a period of 11 days (from June 23 to July 3, 2007), with two distinct sampling devices (screened tubes and drift nets) and with widely different sampling times. At most locations, and with both methods, I collected drifting cottonwood seeds in all stages of germination, as well as seeds and germinants from some undetermined willow species. The results for the screened tubes are presented in Table 2, while those for the drift nets are in Table 3. The locations for the different sampling sites are in Table 4. Results for screened tubes were not normalized by sampling time, because the mesh would rapidly clog, causing observable reflux.

Even though I sampled after the period of maximum seed dispersal at my study floodplain had already passed, I still collected sizable numbers of cottonwood and willow seeds and germinants from the drift, suggesting that this is indeed a common dispersal mechanism. It is evident from the screened tube data that I collected more seeds in the drift at the higher locations in the basin, where seed dispersal was still underway, than at my study site, where it was waning (compare with dates on Figure 3).

The drift net data collected along the study reach indicate that cottonwood seeds stopped being available in the drift sometime during the last week of June. On the other hand, willow seeds became more common. On June 25, 2007, the flow in the Middle Fork of the Flathead was 127 m^3/s (as recorded at the USGS station). With the data in Table 3, I estimated that on that date, the total cottonwood seed flux for the river was 2.7 seeds/s, of which 1.4 were closed seeds, 0.9 were seeds in the initial germination stage, and 0.3 were fully germinated. For willow seeds, the total flux was 0.8 seeds/s, of which 0.3 were closed, 0.1 were in initial germination, and 0.5 were fully germinated. On June 30, though, with a river flow of 104 m^3/s, I did not detect cottonwood seeds in the drift, but estimated a total willow seed flux of 11 seeds/s, of which 8.4 were closed seeds, 0.7 were in initial germination, and 1.8 were full germinants. Please note that all of these are very rough estimates, and the totals do not exactly match because of rounding off.

Table 2. Average seed catch with the screened tubes (seeds per tube). C = closed cottonwood seeds, I = initial germination cottonwood seeds, F = full germination cottonwood seeds, E = empty cottonwood seed capsules, CS = closed willow seeds, IS = initial germination of willow seeds, FS = full germination willow seeds.

Site and date	Seeds in air	n	Water T° (C)	Time (hr)	Average catch per tube (seeds)
Bear Ck. upstream of bridge on US2 06.23.07	yes	3	13.5	1.0	3.0 C – 0.67 I – 1.0 F – 5.0 CS – 3.67 FS
Bear Ck. upstream of Giefer Ck. 06.23.07	yes	1	13.0	1.0	3C – 1F – 4CS – 3 FS
Giefer Ck. upstream of Bear Ck. 06.23.07	yes	1	13.5	1.0	12 C – 3 I – 1 FS
Middle Fk. Flathead at Paola Ck. 06.23.07	few	5	12.0	1.0	1.2 C – 0.4 I – 0.2 F – 0.4 CS – 0.2 FS
Middle Fk. Flathead, at Monster Bar 06.23.07	yes	6	13.0	3.0	0.17 E – 0.17 CS – 0.33 FS
Middle Fk. Flathead, End of Road Bar 06.23.07	few	6	13.0	3.5	0.17 E - 0.17 I – 0.17 F – 1.0 FS
Middle Fk. Flathead, End of Road Bar 06.24.07	few	6	10.5	9.7	0.34 E – 0.17 I – 0.34 F
Middle Fk. Flathead, at Monster Bar 06.24.07	few	6	11.5	14.4	0.17 C – 0.17 I
Bear Ck. at Devil Ck. Campground 06.24.07	yes	6	9.0	3.2	0.83 C – 0.50 I – 0.67 CS – 0.17 FS
Giefer Ck. upstream of Bear Ck. 06.24.07	yes	3	13.0	1.8	0.33 E – 4.67 C – 0.83 I – 0.33 F
Bear Ck. upstream of Giefer Ck. 06.24.07	yes	3	-	1.8	0.33 E – 21.3 C – 5.67 I – 0.33 F
Bear Ck. at Devil Ck. Campground 06.25.07	no	6	9.0	22.8	0.83 C
Bear Ck. at Middle Fk. Flathead 06.25.07	no	6	10.0	23.2	3.0 C

Table 3. Average seed catch with the drift nets (seeds/m^3). Nomenclature is as above.

Site and date	Seeds in air	n	Water T° (C)	Average catch (seeds/m^3)
Middle Fk. Flathead, End of Road Bar 06.25.07	few	2	12.0	0.0111 C - 0.0074 I – 0.0027 F – 0.0563 FS – 0.0022 CS – 0.0006 IS – 0.0037 FS
Middle Fk. Flathead, End of Road Bar 06.30.07	no	3	11.5	0.0324 E – 0.0854 CS – 0.0065 IS- 0.0178 FS

Table 4. Location of the sites where I sampled seeds in the drift. The last two sites are on my study floodplain, the others are in the upper part of the basin.

Site	Latitude	Longitude	Elevation (masl)
Bear Ck. upstream of Giefer Ck.	48°16'14.8"	113°26'12.9"	1348
Giefer Ck. upstream of Bear Ck.	48°16'12.6"	113°26'12.0"	1348
Bear Ck. upstream of bridge on US2	48°16'11.9"	113°26'16.5"	1348
Bear Ck. at Devil Ck. Campground	48°15'54.2"	113°28'18.1"	1312
Bear Ck. at Middle Fk. of the Flathead	48°14'00.2"	113°33'38.9"	1188
Middle Fk. Flathead at Paola Ck. Access	48°20'37.7"	113°38'24.9"	1094
Middle Fk. Flathead at Monster Bar	48°26'05.4"	113°48'02.2"	1031
Middle Fk. Flathead at End of Road Bar	48°27'29.6"	113°48'19.7"	1016

Settling velocities of hydrated seeds

The mean settling velocities (± one standard deviation) for each one of the different hydration times are shown in Figure 7. Shapiro-Wilks tests for normality were carried out for each one of the 9 treatments (duration of seed hydration). In all cases but one, the null hypothesis that the data are normally distributed was not rejected at a significance level of $\alpha = 0.10$. The normality hypothesis was only rejected for the 1-hr hydration time data (df = 49, p = 0.035). I used Levene's test to check for equality of error variances and rejected the null hypothesis that the error variance of the cumulative water losses was equal across the different groups (p < 0.0001). Because the sample size was quite different across treatments (n ranged from 34 to 58) I decided not to rely on the robustness of ANOVA, and used non-parametric tests instead. I conducted an exact Kruskal-Wallis test and found a significant difference due to the treatments (df = 8, p < 0.0001). To compare treatments, I conducted a one-way ANOVA on the ranks, with post-hoc tests. I rejected again the hypothesis of equal variances (Levene's F = 3.103, p = 0.002). The model was highly significant (F = 11.932, p < 0.0001) even when

considering robust tests of equality of means (Welch's statistic = 12.719, p < 0.0001; Brown-Forsythe statistic = 11.849, p < 0.0001). The results of conducting Tamhane's T2 post-hoc tests are given in Table 5.

Table 5. Significance values for the post-hoc comparisons between ranks of settling velocities, for the different hydration times (in hours).

	0.25	0.5	1.0	2.0	4.0	8.0	12.0	24.0	48.0
0.25		0.947	1.000	0.006	0.009	0.059	1.000	1.000	1.000
0.5	0.947		0.914	<.0001	<.0001	<.0001	0.111	1.000	1.000
1.0	1.000	0.914		<.0001	<.0001	0.007	0.999	1.000	1.000
2.0	0.006	<.0001	<.0001		1.000	1.000	0.054	<.0001	<.0001
4.0	0.009	<.0001	<.0001	1.000		1.000	0.074	<.0001	<.0001
8.0	0.059	<.0001	0.007	1.000	1.000		0.402	0.002	<.0001
12.0	1.000	0.111	0.999	0.054	0.074	0.402		0.743	0.421
24.0	1.000	1.000	1.000	<.0001	<.0001	0.002	0.743		1.000
48.0	1.000	1.000	1.000	<.0001	<.0001	<.0001	0.421	1.000	
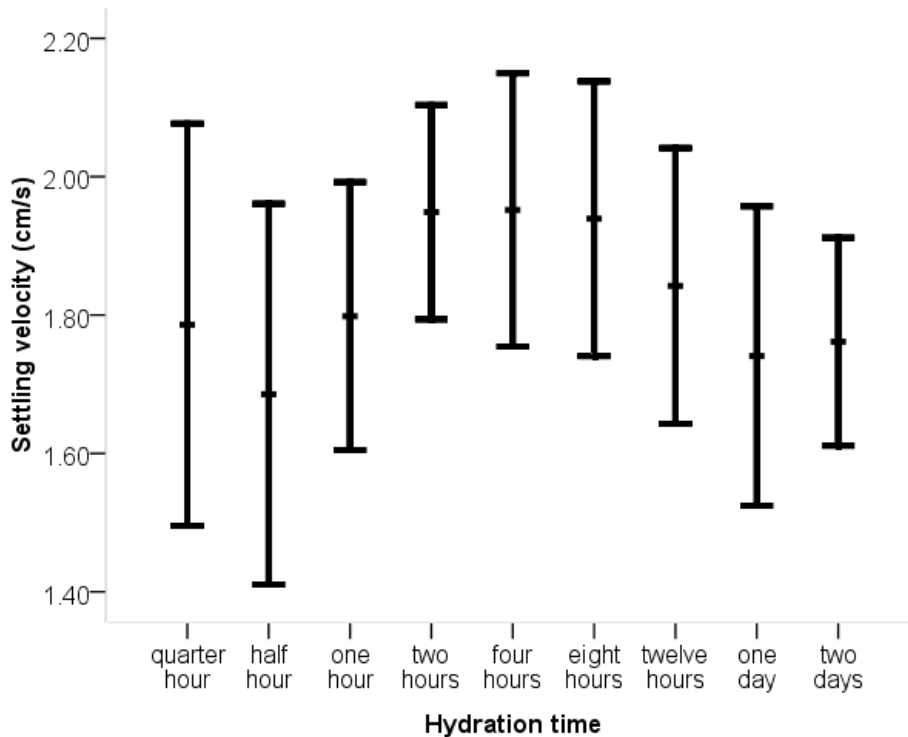
Figure 7. Mean (± standard deviation) of the settling velocities, for each one of the different hydration times.
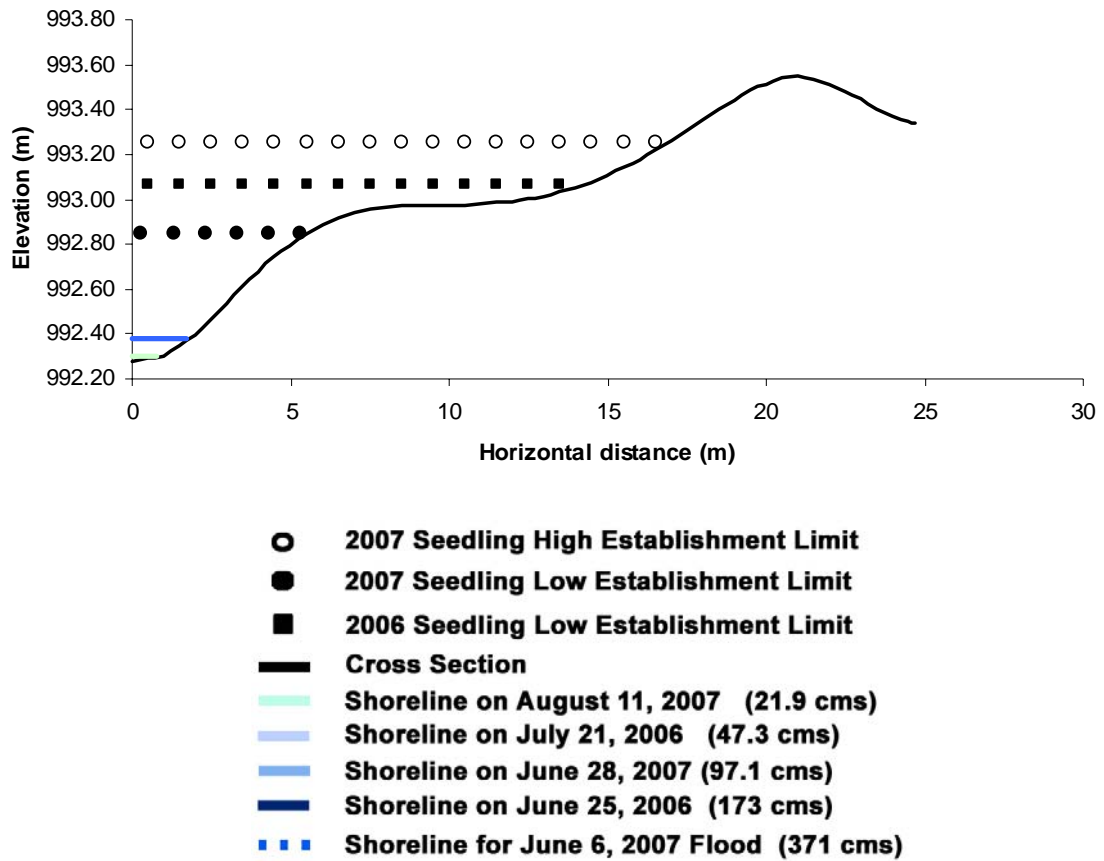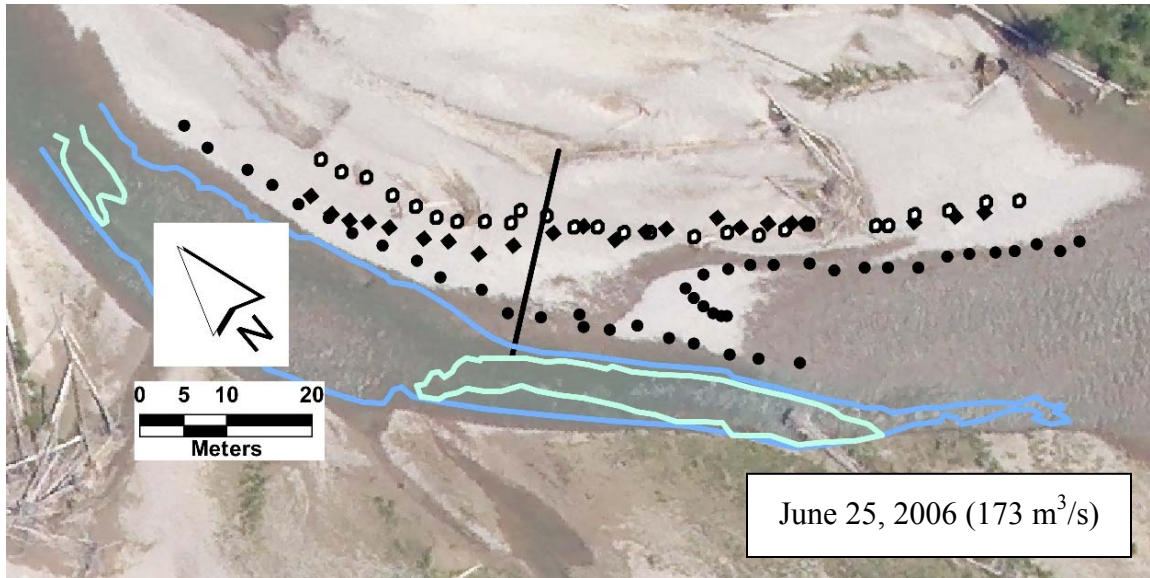
Figure 8. Plan view and cross-sections of all of the studied bars, showing the upper and lower establishment limits, as well as the shorelines and stages corresponding to the different flows, as given in the aerial photographs. The flow in all pictures is from right to left. Cross-sections are shown as seen from upstream. The legend applies to all bars.

June 25, 2006 (173 m³/s)

Cross-section 1

Cross-section 2

June 28, 2007 (97.1 m³/s)

Cross-section 1

Cross-section 2

June 28, 2007 (97.1 m³/s)

Cross-section 1

Cross-section 2

June 28, 2007 (97.1 m³/s)

Cross-section 1

Cross-section 2

June 28, 2007 (97.1 m³/s)

Cross-section 1

Cross-section 2

June 28, 2007 (97.1 m^3/s)

Cross-section 1

Cross-section 2

June 28, 2007 (97.1 m^3/s)

Cross-section 1

Cross-section 2
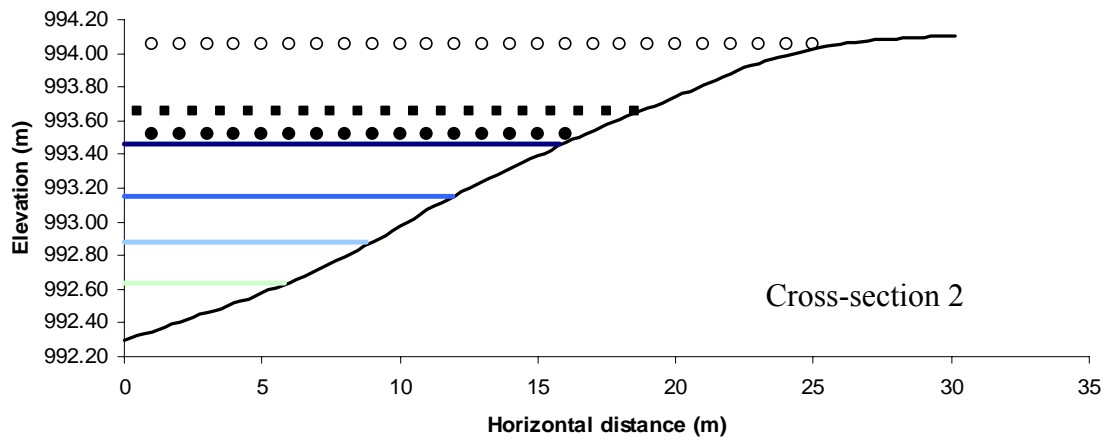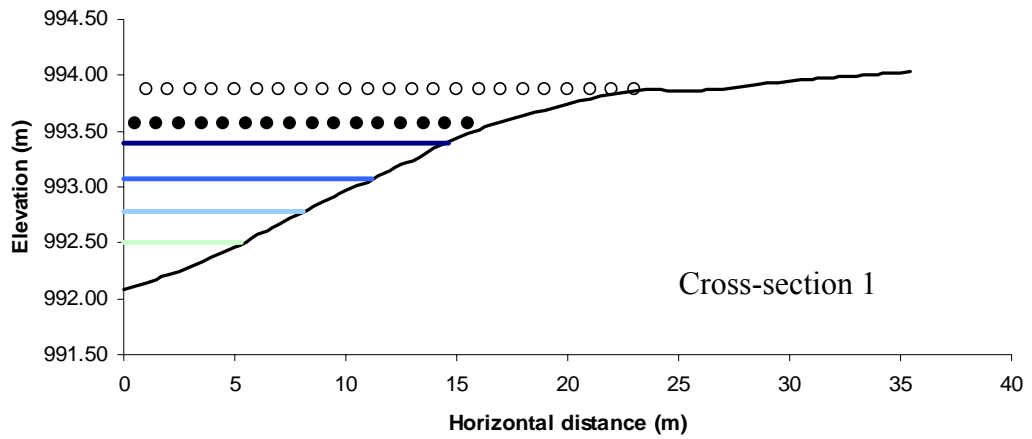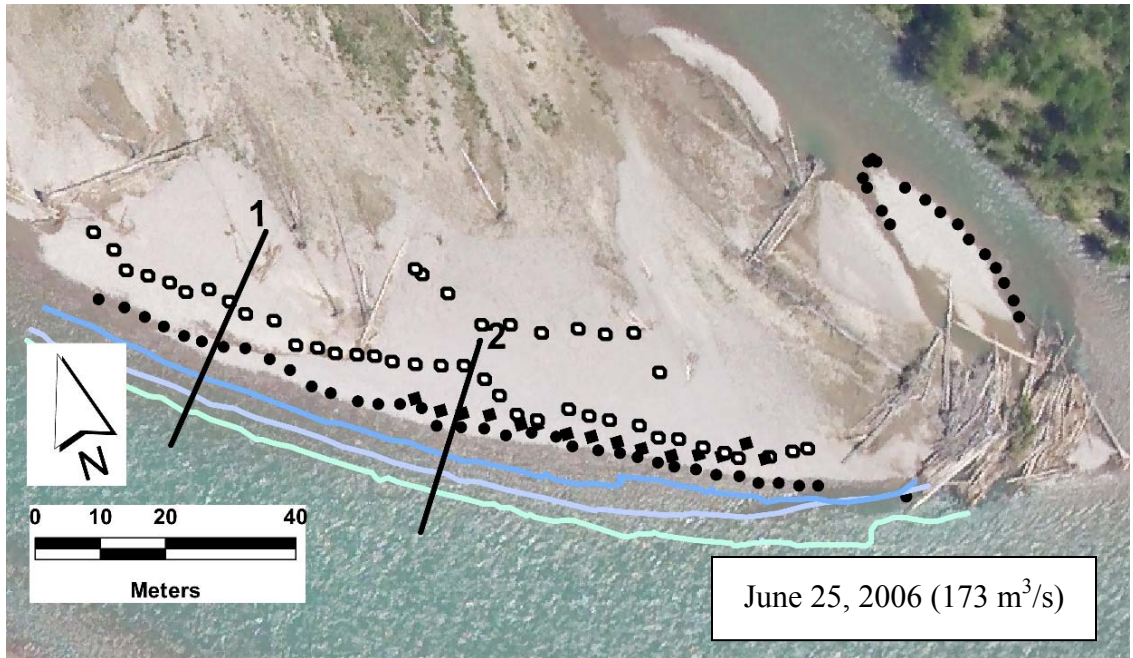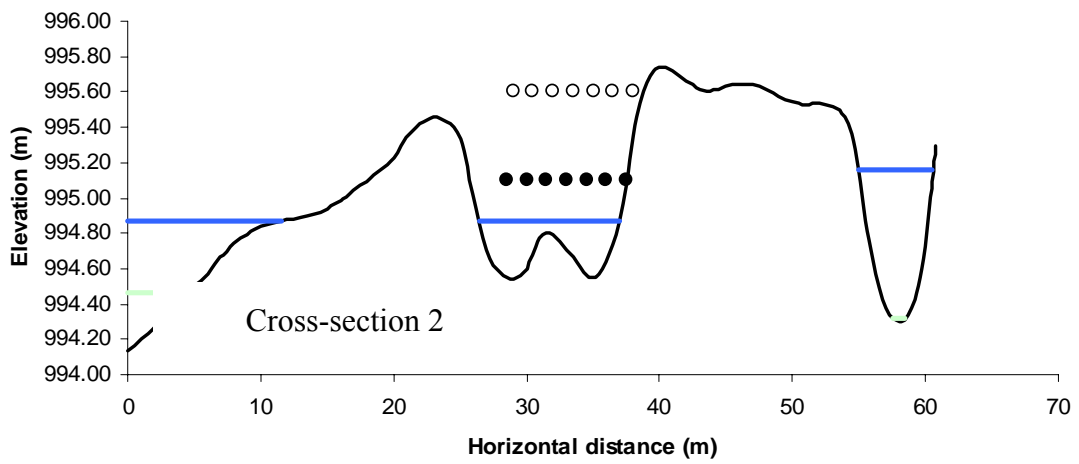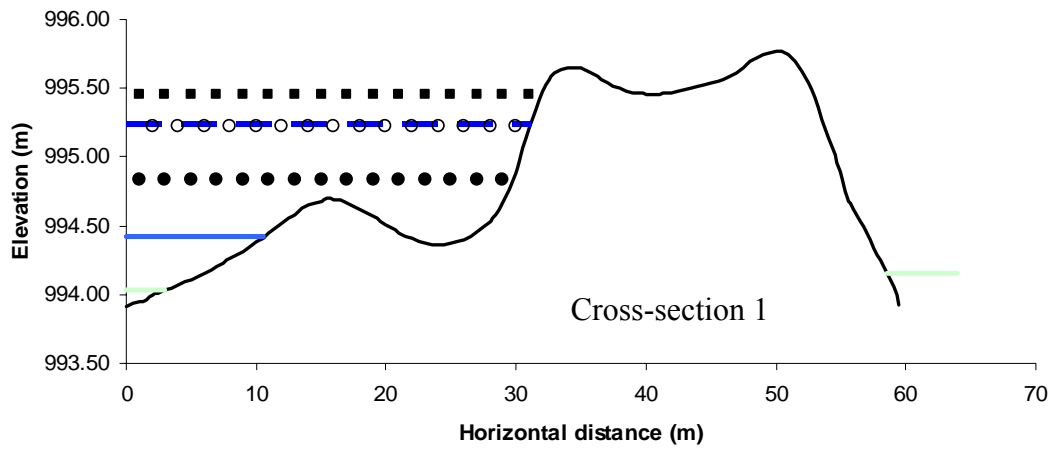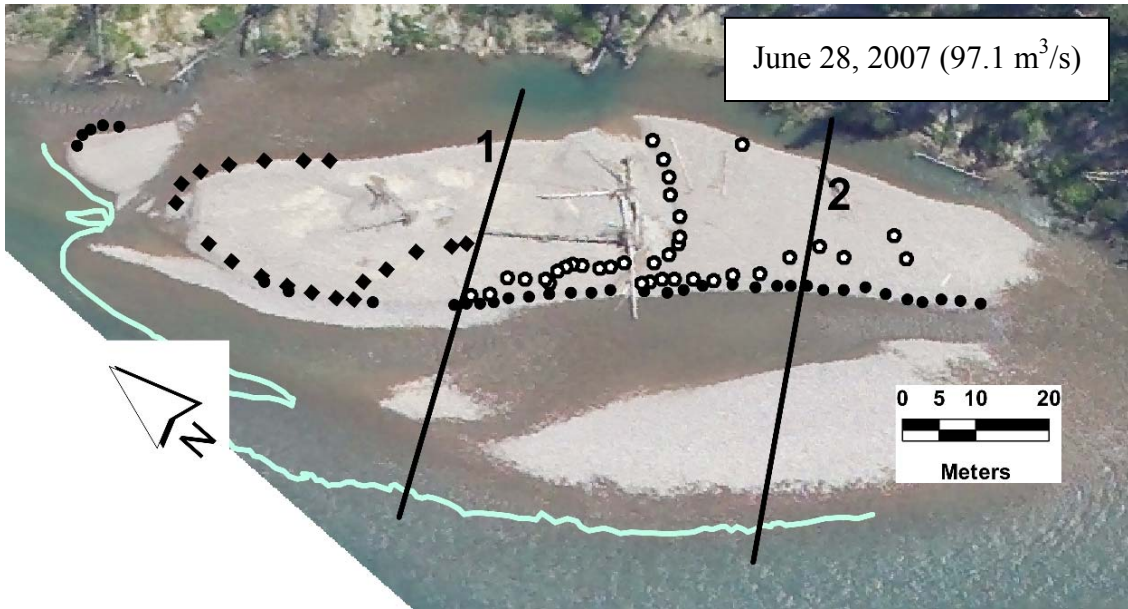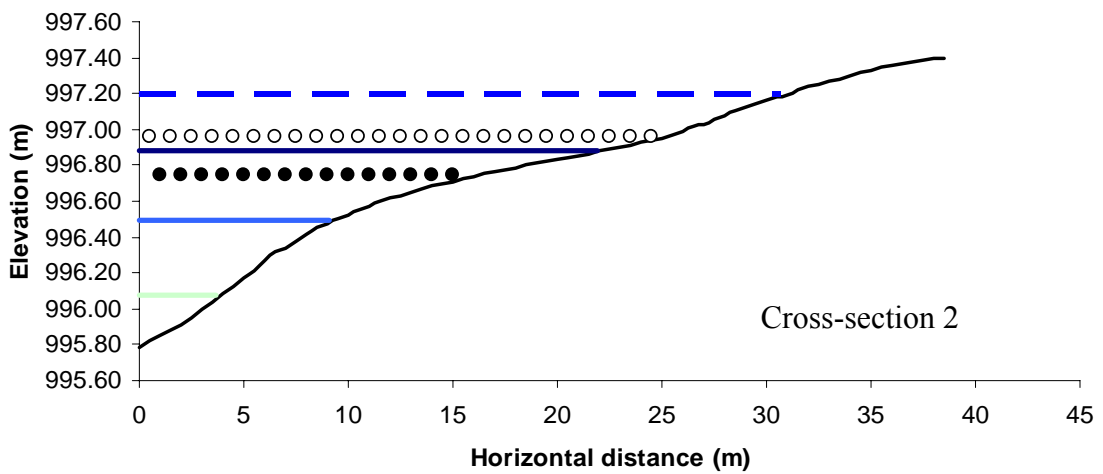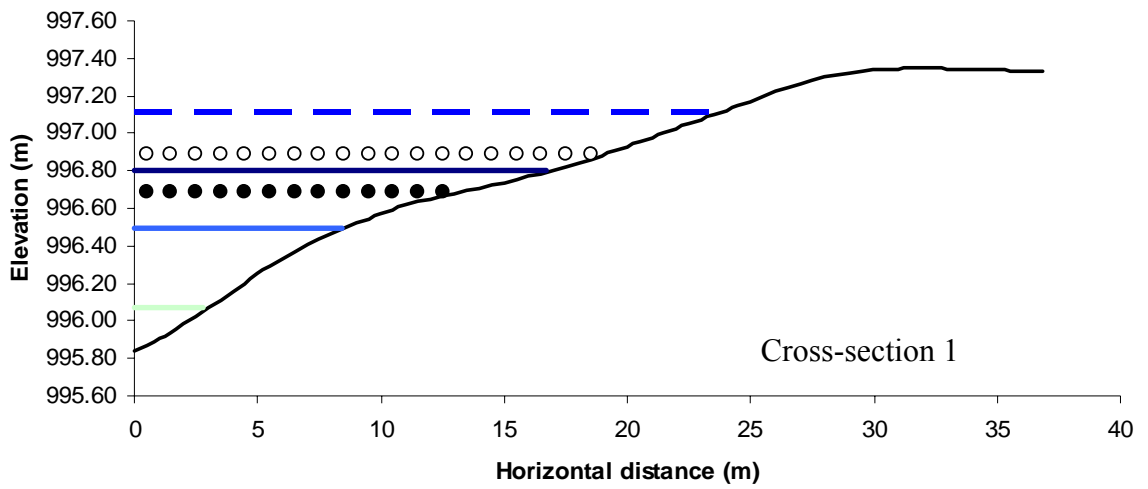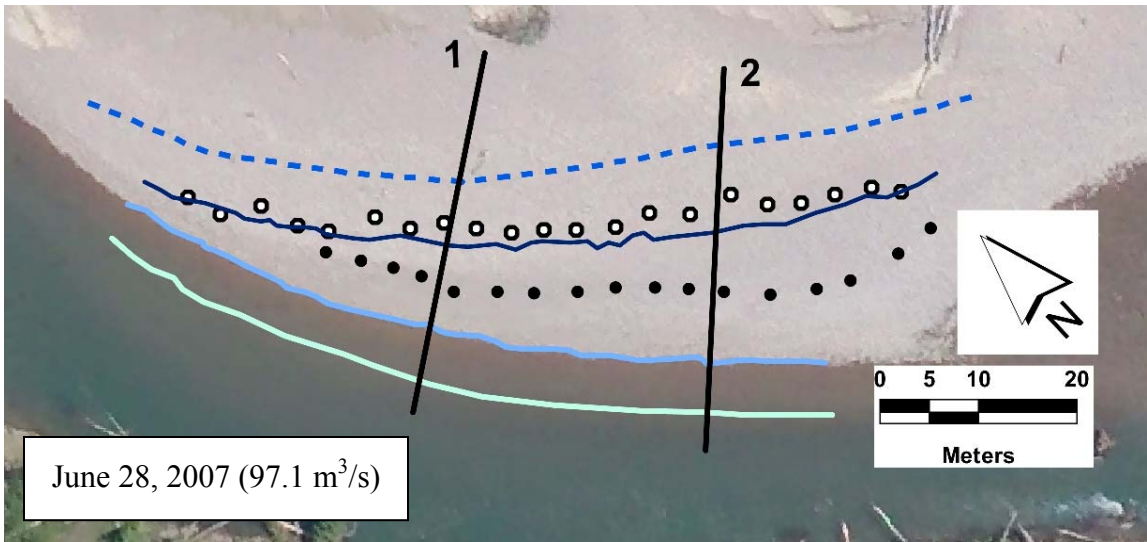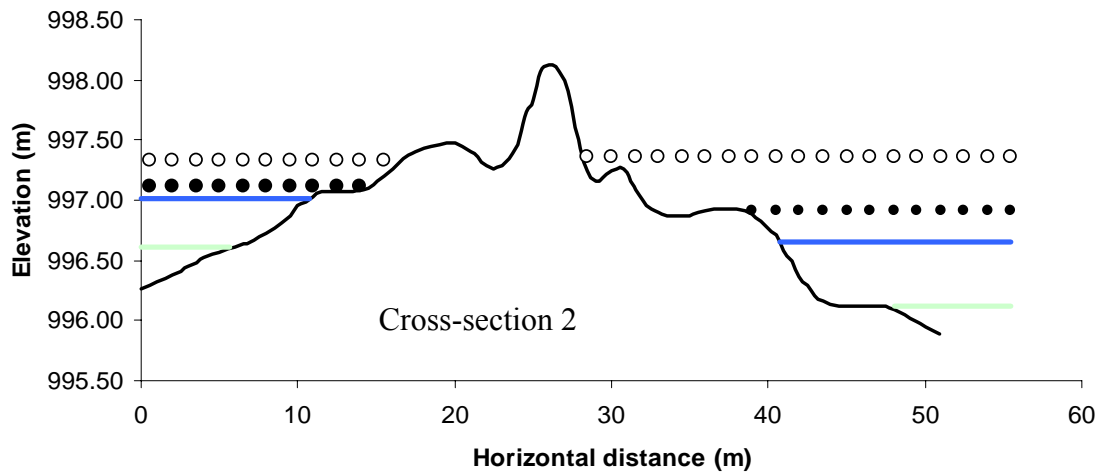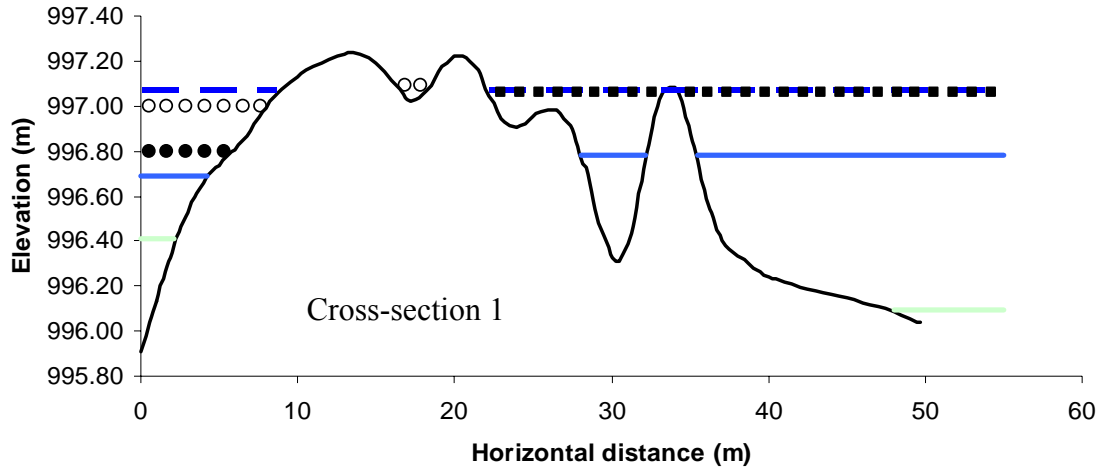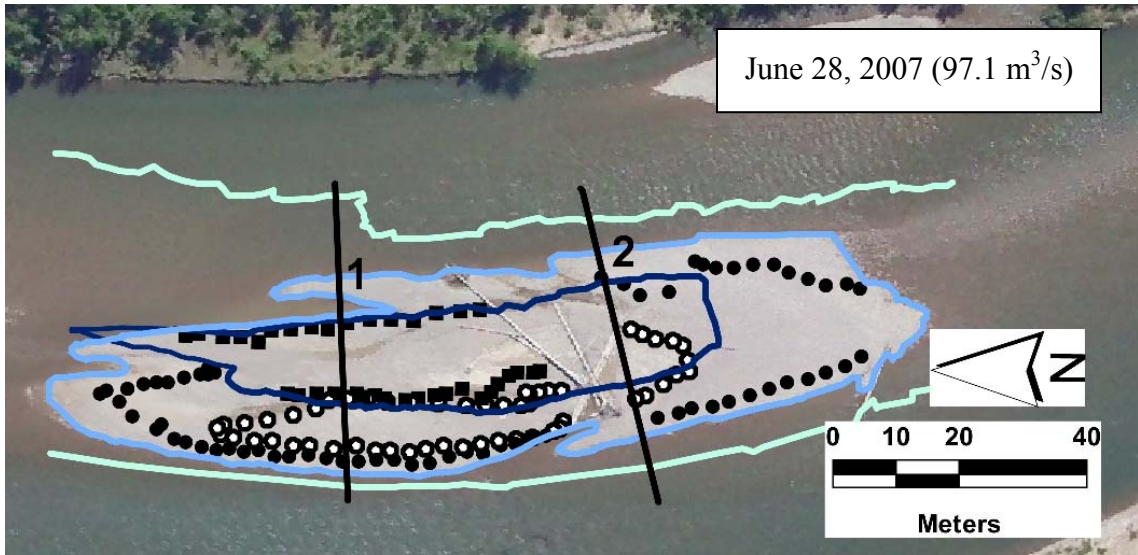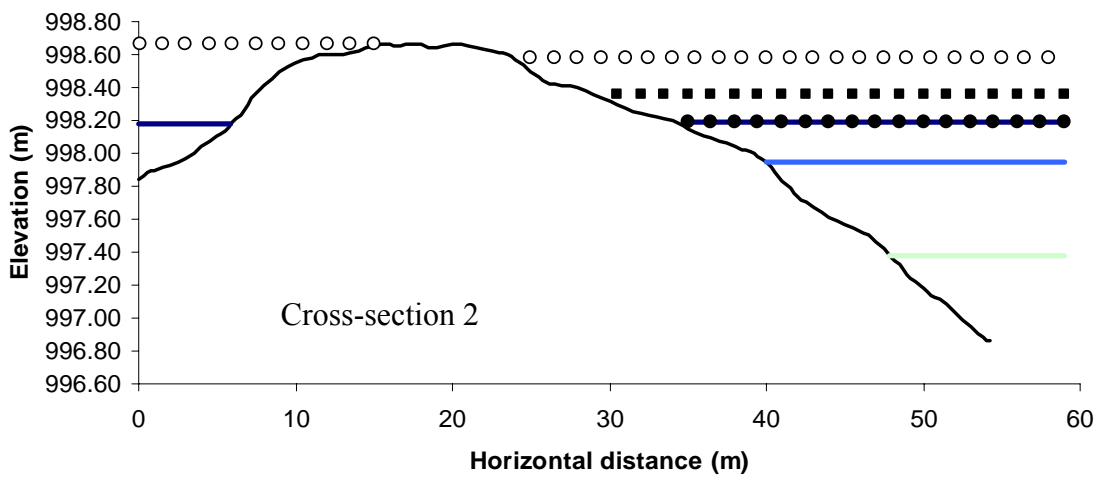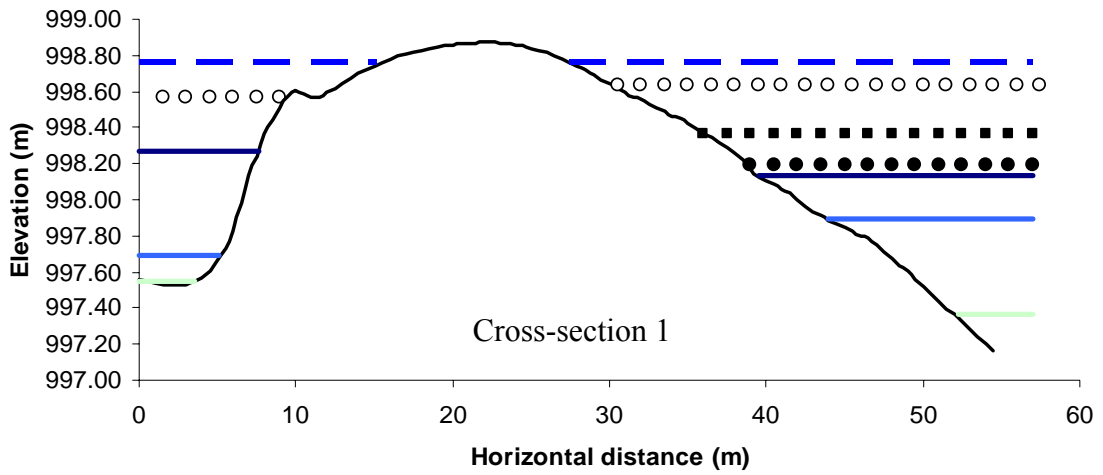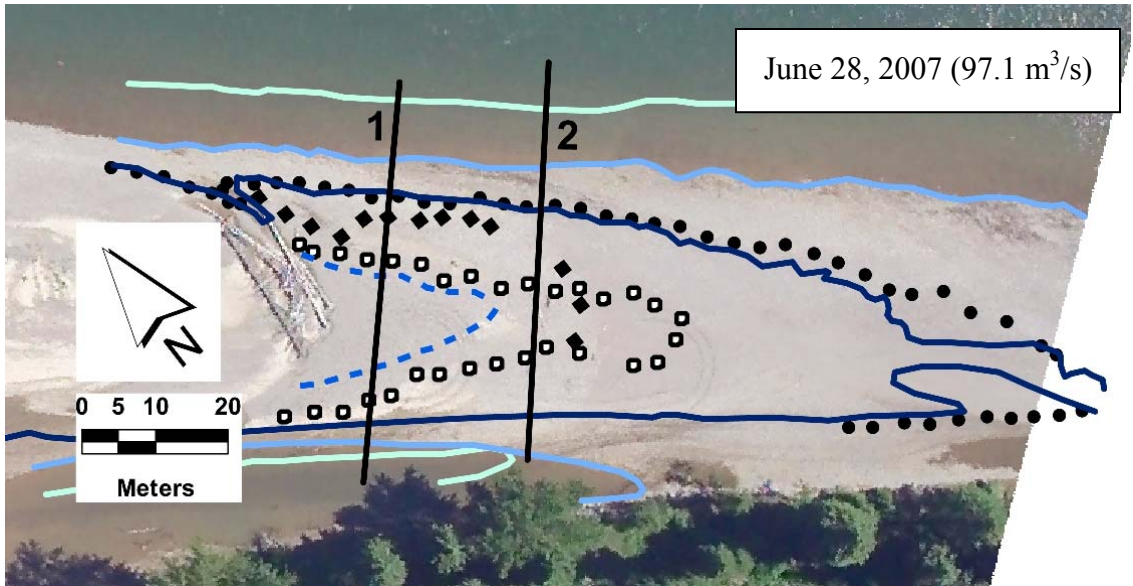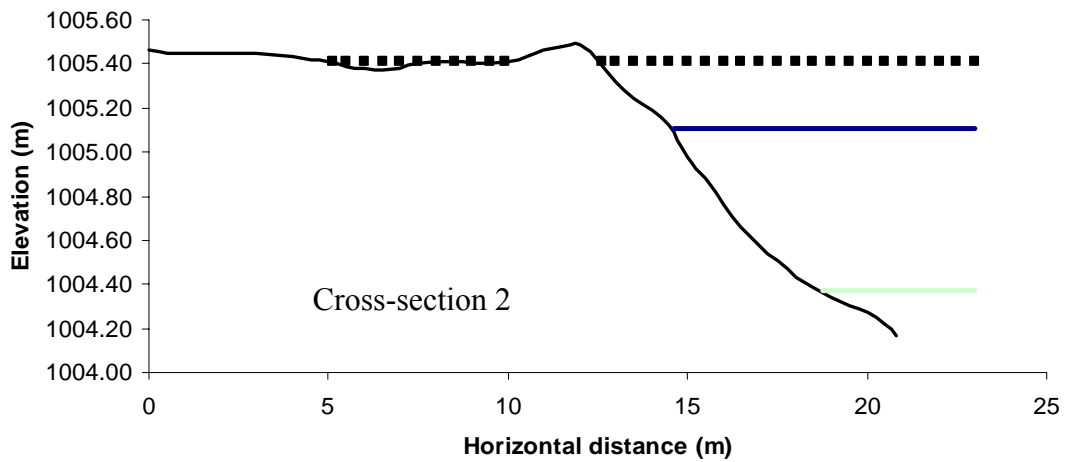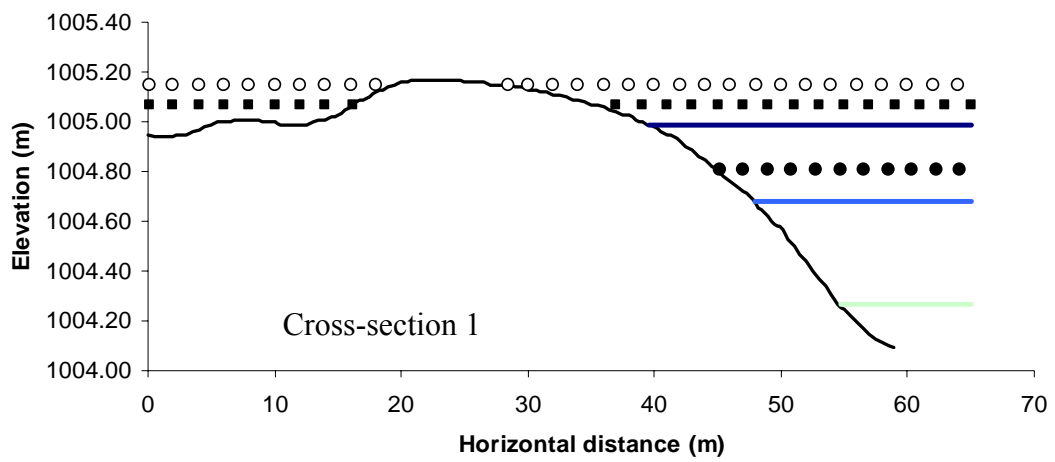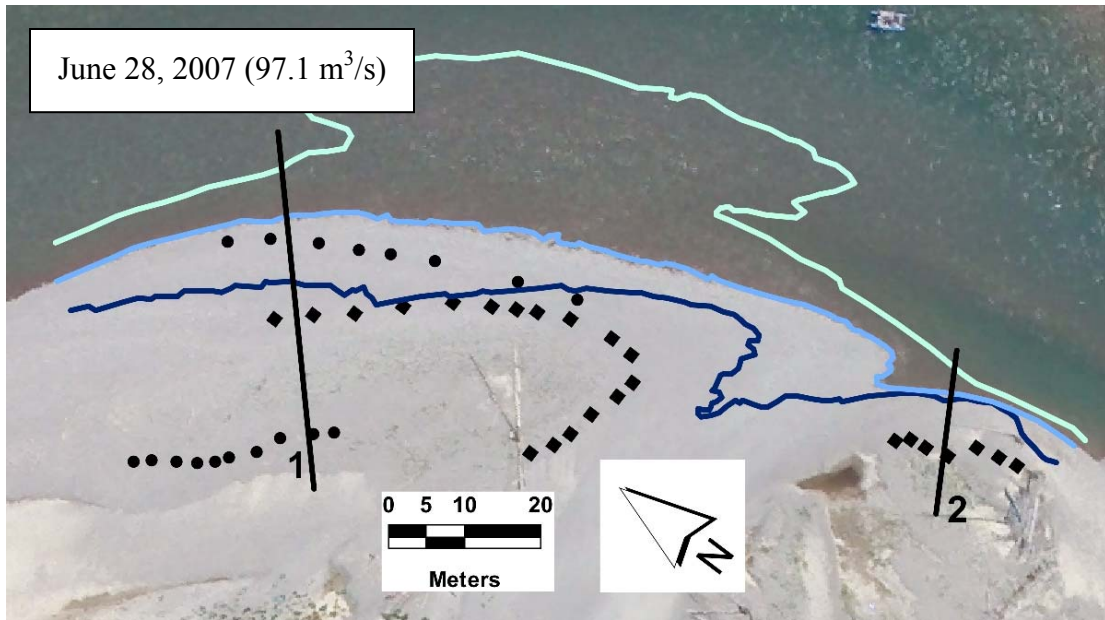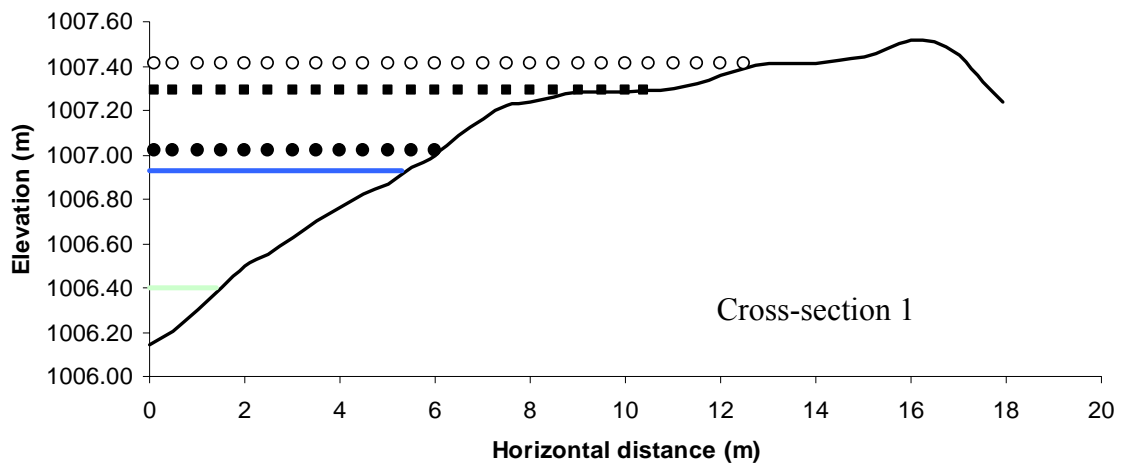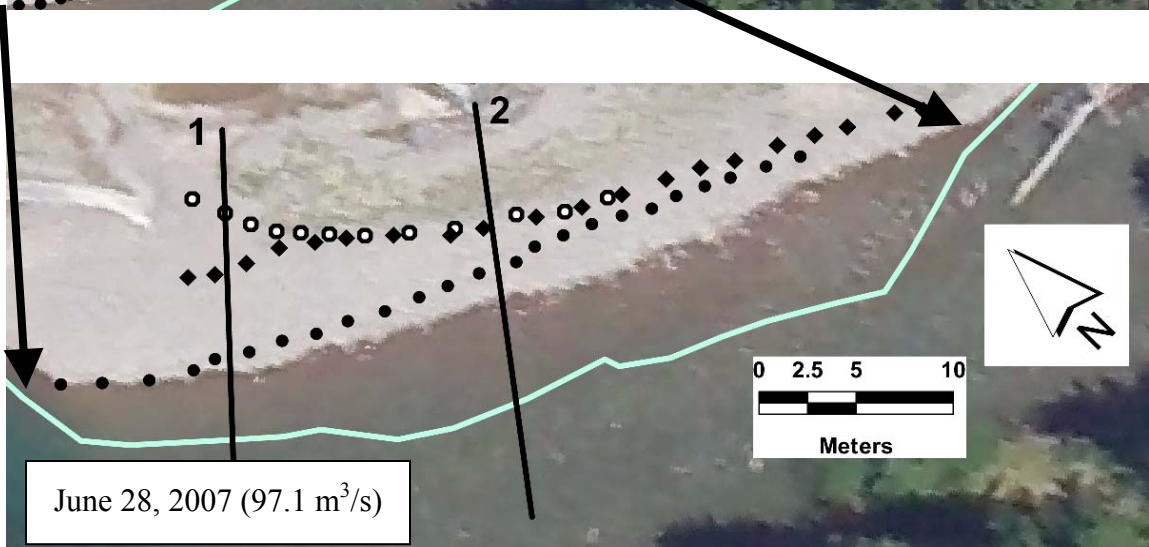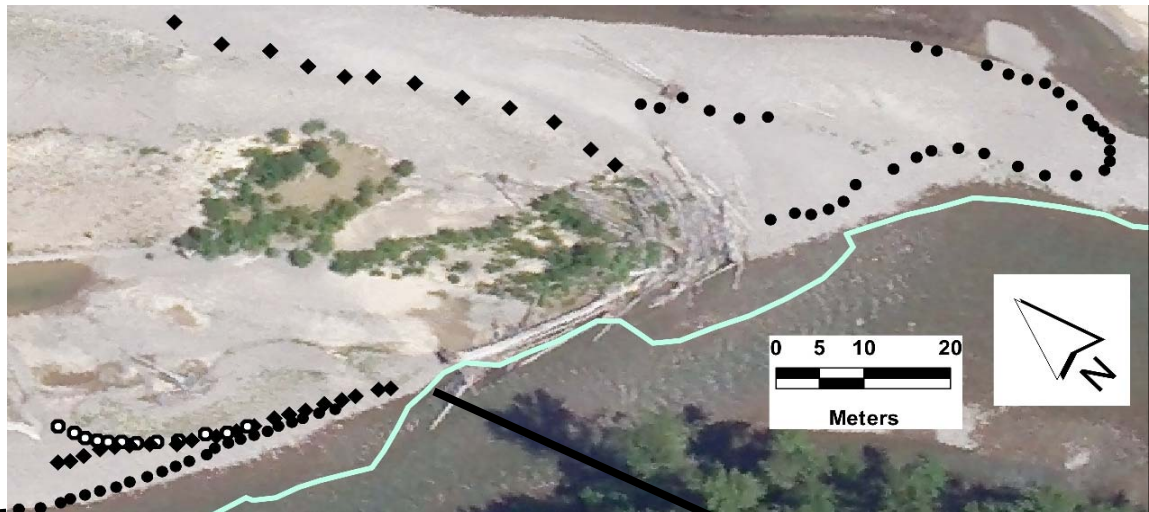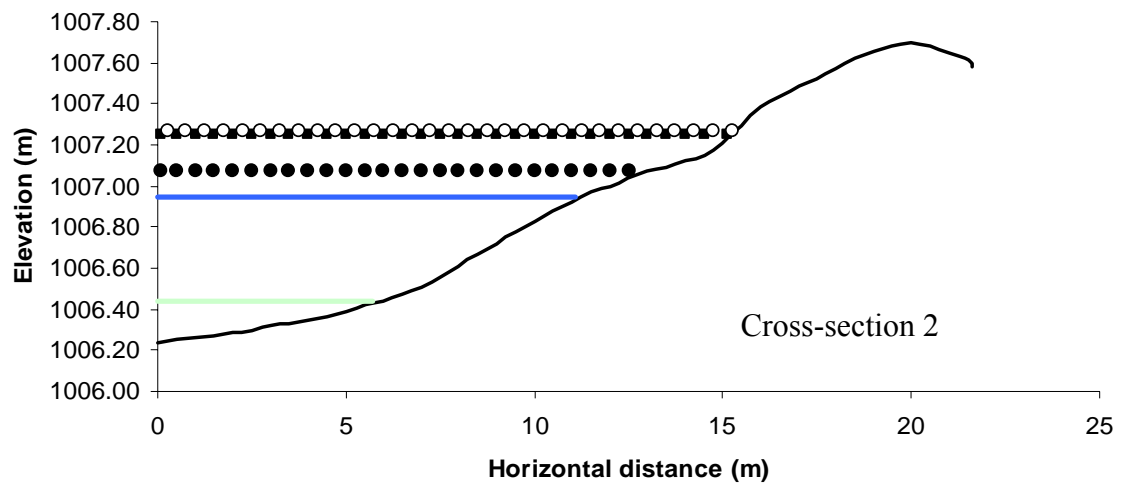
Discussion

Seed dispersal

The tight and highly significant correlation between seed rain measured at closely-located pairs of traps, separated by about 5 to 10 m, indicates that the methodology used in 2007 is an effective way of quantitatively measuring the density of falling cottonwood seeds. The single highest measurement of 372 seeds/d/m^2, and the maximum mean of 160 seeds/d/m^2 (from 8 seed traps) compare very well with the 362 and 120 seeds/d/m^2 measured by Cooper et al. (1999) for *P. deltoides*. Integrating the temporal distribution of seed rain, I obtained an average of 1842 seeds/m^2 over the 5-week long period of seed dispersal. This value is higher, but within the same order of magnitude than the 833 seeds/m^2 reported by Barsoum (2002) for *P. nigra*, over a much longer seed release period, in a European river.

I found that *P. trichocarpa* at my study floodplain have a pronounced peak in their temporal distribution of seed dispersal. In other words, the distribution is highly skewed. Even though seed release started quite early in 2007 (John Dalimata, landowner, personal communication, June 2007), a full 68% of the total seeds dispersed over the 5 week-long season had been released in the first 9 days, and more than 83% in the first two weeks. As stressed by Guilloy-Froget et al. (2002), this is a strategy that results in

very high rates of recruitment, or no regeneration at all, depending on whether the released seeds find adequate environmental conditions or not.

It is worthwhile mentioning that the collaboration of the landowners was fundamental in pinpointing the exact beginning of the seed release period. Natural recession rates in snowmelt driven rivers are very large in the first few days following the annual peak, and errors of just one or two days in estimating the beginning of seed dispersal would have translated into large differences in flow, and thus in river stage.

Settling velocity of seeds

In other experiments (see Chapter 4), I found that most plumed seeds will stay afloat for at least 3 days, when falling on quiet water, but that agitation will rapidly separate the pappus from the seed, and incorporate the latter in the flow. It is of fundamental importance for my hypothesis that cottonwood seeds sink, and the experiments show that they do so. The mean settling velocity in quiet water at 21°C was 1.83 cm/s for the 448 seeds I tested. According to Stokes' Law (see, e.g., Julien 1995), this corresponds to the settling velocity of a sand grain with a diameter of 0.23 mm, i.e., a particle of fine sand. Of course, because of differences in size, shape, and density, which affect the hydrodynamics in actual flows, this does not mean that cottonwood seeds will sediment under the same conditions as 0.23 mm sand grains do.

I found highly significant, albeit small differences in settling velocities, as a function of hydration times. Statistically homogeneous groupings can be formed, with the 15 min, 30 min, and 1 hr data, which have a mean of 1.76 cm/s; the 2 hr, 4 hr, and 8 hr data, with a faster mean settling velocity of 1.95 cm/s; and the 12 hr, 24 hr, and 48 hr, with a mean of 1.78 cm/s. I hypothesize that the most logical explanation for such differences is that seeds recently immersed tend to have a lower density, because their tissues are still dry and air can be entrapped within the seed capsule. Thus, they have a low settling velocity. After enough hydration, the incorporation of water results in an increase in density, and faster settling rates. If seeds are kept for too long in water, though, they swell. The increased size results in a larger drag, and a corresponding reduction in settling velocity. I doubt that these rather small differences have much of an ecological relevance. Their main effect would be to increase the chances of deposition for

seeds which have spent an intermediate amount of time (2 to 8 hours according to my experiments) in water. The increased floatability of recently fallen seeds would help in dispersing them further downstream, away from the parents.

Seedling establishment and hydrology

I think that the images of bars shown in Figure 8 make it quite clear that the lower and upper establishment limits (i.e., the spatial boundaries of seedling patches and bands), are highly regular in the longitudinal direction, and correspond very well with the flow profiles of the river stages, at different flows. Even though I also show the presence of seedlings established in 2006, I mostly base the following discussion on the establishment patterns for the cottonwood recruitment that took place in 2007. I am particularly confident in the 2007 data (establishment limits and aerial imagery), because there were no floods between seedling establishment in June, and the moment in which I surveyed the bars, in September. This way, I ensure that the DEMs for the bars correspond very well with the topography on the dates the aerial images were acquired, and that the observed spatial distribution of seedlings has not been affected by disturbances such as morphological change or prolonged flooding.

At all locations, the lower limit for cottonwood establishment in 2007 was higher than the flow of 97.1 m^3/s observed on June 27, 2007. This is clearly seen in Figure 8, both in the plane views and on the cross-sections. At some of those locations where the morphology did not change much, allowing me to use the aerial images acquired in 2006, the lower limit for establishment in 2007 coincides quite well with the flow of 173 m^3/s observed on June 25, 2006 (e.g., see the first and second photographs in Figure 8). For the two locations in which I had enough information to derive stage-discharge equations, I conducted a retrospective analysis that demonstrated that the flows corresponding to the lower establishment limit were 180 and 138 m^3/s. The best floodmark data for the June 2007 flood were those for "End of Road" Bar, in the form of a very clearly visible rack-line (i.e., floating débris that had accumulated on the bar's ridge). Thus, I tend to give more credence to the results from this site. All of this evidence suggests that the flow profile (i.e., the river stage) corresponding to the lower establishment limit for cottonwood in 2007 was caused by a flow ranging between 140 and 180 m^3/s, with a

most probable value around 160 or 170 m^3/s, as measured at the USGS gaging station in West Glacier.

Seed release in 2007 began on June 7. On that day, the river had a mean daily flow of 295 m^3/s, and was rapidly receding from the peak flow of 371 m^3/s that had occurred the previous day. The hydrograph thereafter (see Figure 5) had a very regular recession, without floods, and reached 180 m^3/s sometime on June 13, 165 m^3/s on June 14, and 140 m^3/s on June 16, and then again on June 24, after a small increase. As was said above, the flow of 97.1 m^3/s on June 27, when images were acquired, results in a flow profile that is consistently below the lower limit of establishment, at all of my study bars. Because the hydrograph recession was basically monotonous from June 19 on, until late September (except for two very slight fluctuations < 5 m^3/s, see Figure 5), I can ascertain that the flow associated to the low limit for establishment could not have happened after June 27, and most probably occurred sometimes between June 13 and June 24.

Comparing these dates with the phenology of seed release given in Figure 3, I observe that the lower limit for establishment, which corresponds to the end of the period of seed availability in the drift according to my hypothesis, is associated with the end of the peak in seed dispersal. In other words, the long tail to the right of the temporal distribution of seed release, with low densities of seed rain lasting until mid-July, does not affect at all the position of the lower limit of cottonwood establishment.

As was discussed in the Introduction, I expected that the lower limit of establishment would be related to the end of the seed dispersal period, or would even last longer, considering that cottonwoods located upstream in the basin flower and release their seed at a later date. Nonetheless, all evidence suggests that, at least for my study floodplain, successful cottonwood establishment on river bars takes place only during the peak of the seed dispersal period. This further suggests that the pronounced peak in seed dispersal that I observed (see also Guillloy-Froget et al. 2002) could very well represent an adaptation derived in order to ensure that a large enough concentration of seeds is present in the drift, so that successful colonization of gravel bars can take place.

The upper establishment limit in 2007 corresponds to a river stage just under the annual flood of 371 m^3/s, on June 6. According to the stage-discharge relationships, the

flow associated to this establishment boundary lies between 327 and 216 m^3/s. Again, I trust the first value (from "End of Road" Bar) more. Such range of flows occurred in the river between June 6 and June 9, i.e., immediately after the peak. On the other hand, the beginning of seed dispersal was on June 7. Thus, I conclude that the upper limit for establishment in 2007 coincides with the beginning of the seed dispersal period.

In 2006, seed dispersal started later, and the lower limit for establishment was noticeably higher than in 2007. At all of the study sites which had establishment in both 2006 and 2007, the lower limit for recruitment in 2006 was located above that for 2007, but at the same time, below the upper 2007 limit. Thus, a probable range of flows associated to the lower 2006 limit is from 160 to 330 m^3/s, with a most probable value about 240 m^3/s. In that year's highly regular and absolutely monotonous recession, after the peak of 609 m^3/s on June 16, the river reached 330 m^3/s on June 19, 240 m^3/s between June 20 and 21, and 160 m^3/s on June 28. I do not have detailed seed dispersal data for 2006 but do know that it started on June 12 or 13. If the receding stage formed the lower establishment limit somewhere between 330 and 160 m^3/s, that could only have happened between June 19 and 28 (i.e., during the second week of the seed release period). Thus, I find again that the lower establishment limit is associated with the end of the peak in seed dispersal, and not with the long tail. In 2006, seed dispersal ended sometime in mid-July, when flows in the river were much lower, about 50 to 60 m^3/s.

I believe this is an important observation, because it means that the initial establishment of cottonwoods, when the seeds are being deposited on river bars, coincides with the steepest part of the hydrograph, immediately after the peak. According to the model, a fast recession rate should increase the potential area for establishment, because the receding waters will uncover a much larger surface area during the time of seed availability in the drift. On the other hand, a constant stage or very slow recession should result in narrow establishment bands. This is exactly the situation that Noble (1979, Figure 2) found along the lower Minnesota River. In such case, the seedlings will have water available for a long period, which should increase establishment success, as was also proposed by Noble (1979). In regions with dry summers, a fast rate of recession means that the established seedlings will be left far above the river waters. As proposed in Chapter 2, such seedlings will only be able to survive if there is enough fine material,

with an adequate water-holding capacity, and the presence of a coarse surface layer to decrease soil evaporation.

I have no observations of an upper establishment limit for 2006, as all of the bars with successful recruitment were covered with seedlings from the ridge down. In other words, in this season I did not observe any establishment in bands, only in patches that completely covered the bar tops. Everitt (1968), Braatne et al. (1996), and Karrenberg et al. (2002) propose that the occurrence of bands is typical on point bars of meandering systems. Karrenberg et al. (2002, see Figure 2) also mention that Salicaceae in braided reaches establish mainly in mid-bar patches. I think that their views come mostly from their experience in the fully braided Tagliamento River in Italy. Such river systems tend to have a large sediment supply, which results in an overall lower relief, and much flatter bar surfaces. They also have flashier hydrographs. My study floodplain is wandering, i.e., low-order braided, and as can be seen in the cross-sections (Figure 8), the bars have more relief and well-defined ridges. In such a system, my data indicate that establishment in a given bar can happen both as recruitment bands or as patches, depending on the peak magnitude, recession rates, and timing of the flood with respect to the seed dispersal period.

River seeding by receding floodwaters is also a good explanation for the commonly observed zonation of salicaceous species along river banks (van Splunder et al. 1995, Karrenberg et al. 2002). Co-habiting species with sequential periods of seed dispersal would form spatially-segregated bands of seedlings if my hypothesis were correct, as the receding waters would sequentially sow lower elevations along bars and riverbanks.

Many researchers have studied the relationship between hydrology and cottonwood establishment, stressing the role of large floods, with return periods between 5 and 10 years (see reviews in Braatne et al. 1996, Mahoney and Rood 1998, Rood et al. 2003). The need for large, infrequent floods has been justified on the grounds that they create extensive areas with deposition of bare sediment, which can then be colonized by cottonwoods (e.g., see Bovee and Scott 2002, Polzin and Rood 2006). In my view, most gravel-bed rivers do not lack areas of bare sediment that could serve as potential nursery grounds, unless they have a very regular flow régime such as that found in reaches

located downstream of large lakes, which would allow for vegetation encroachment (Petts 1984). In reaches with enough energy, previous floods and the occurrence of avulsions always ensure the presence of an active channel with bare gravel-beds. I think that floods are indeed very important for cottonwood establishment, but for a different reason altogether: they carry cottonwood seeds in their flow, and deposit them at the elevations that they are able to reach. As was mentioned in the introduction, larger floods, with a higher flood stage, are thus able to deposit seeds over a much larger area of the active channel, replenishing cottonwood populations.

Anemochory versus hydrochory

Most of the literature on cottonwood and willow establishment indicates that seeds are dispersed on river bars both by wind and water (e.g., Noble 1979, Bradley and Smith 1986, Krasny et al. 1988, Braatne et al. 1996, Karrenberg et al. 2002, Guilloy-Froget et al. 2002). Still, and probably due to the very small size of cottonwood seeds, actual evidence to support such claim is surprisingly scant. I know of no studies that have compared these two processes, or proposed the actual mechanisms under which one or the other might prevail.

In Chapter 4, I perform a series of experiments and review the literature, in order to show how seeds from cottonwoods, and other species of riparian Salicaceae, possess the incredible ability to germinate, establish, and grow under water without any negative effects, for periods of up to 42 days. I argue that for a group of plants to have developed such adaptations, it must be the case that water dispersal is indeed a fundamental aspect of their life-histories.

Based on my observations at the Nyack floodplain and on an ample literature review, I propose that hydrochory is the fundamental mechanism explaining establishment and thus the spatial distribution of cottonwoods (and other riparian Salicaceae, in general) in gravel-bed rivers. These observations and results from previous researchers include: (i) the occurrence of clearly delimited bands and patches of successfully recruited cottonwood and willow seedlings of the year, (ii) the fact that such regular features occur across all types of gravel-bed rivers, over bars and banks with large fine-scale spatial variability in fine sediment content and caliber, surface texture, distance

to water table, and width of the capillary fringe, (iii) the clear correspondence between establishment limits and flow profiles along the bars, (iv) the fact that on repeated surveys I never observed dying seedlings on gravel bars, at elevations above the upper establishment limit, (v) the occurrence of zonation bands for salicaceous species with sequential flowering and seed release periods, (vi) the fact that seeds from riparian Salicaceae get incorporated in turbulent flows, where they can later deposit if they find adequate sedimentary environments, and are able to germinate, establish, and grow under water, (vii) my observations of closed seeds, germinants, and empty seed capsules of both cottonwood and willow in the drift, and (viii) the evidence that cottonwood successfully recruit over a wider range of elevations, and thus over a larger proportion of the active channel, after the occurrence of large floods with the right timing, as compared with seed release.

I think that many of the observations and results previously published on establishment of Salicaceae neatly fall within this broad idea, and thus can be explained in light of the River Seeding Concept.

Nonetheless, it should be noted that alternative hypotheses based on anemochory could be devised in order to explain some, but not all, of the above observations. For example, I have observed in the field and laboratory that wind-dispersed seeds falling on quiet waters float for long periods. In gravel-bed rivers, stagnant water conditions only happen in ponds and in backwaters in disconnected lateral channels or at the downstream end of large compound bars or vegetated islands. In such environments, I have repeatedly observed how floating seeds get skimmed by the wind, accumulating in bands on the shoreline, at enormous densities. It is interesting to note that usually, the hydraulic conditions at these habitats coincidentally foster deposition of fine sediments. Thus, I think that this alternative mechanism for establishment can be quite common on gravel-bed rivers, but only at those few locations with sand deposits. As I mentioned in the Introduction, I feel that the concepts of the Recruitment Box Model apply very well in such cases. At my study site, I have repeatedly observed how bands of seedlings established at higher locations on sand bars, through this mechanism, desiccate as the summer progresses, while those located closer to the capillary fringe successfully survive.

Another possible mechanism, which would rely only on wind dispersal but would still involve the need for receding flow profiles, would be for seeds to attach themselves to the moist fringe left along bars and banks by floodwaters, as stage gradually declines. Krasny et al. (1988) stated that "The pappus surrounding Salicaceae seeds appears to favor retention on wet sites, thereby ensuring that seeds falling on these favorable surfaces will make contact with the surface. In contrast, seeds landing on dry sites tumble in a manner reminiscent of tumbleweed until they reach wet sites." My own observations certainly agree with this description. On the other hand, I have consistently observed that gravel bars dry very quickly. For example, after summer thunderstorms, it only takes a matter of minutes for the stone surfaces to dry. Thus, I think that most tumbling seeds would ultimately reach water, instead of a gravel surface.

It should be noted that the management implications of the River Seeding Concept would be quite similar for these two alternative mechanisms, because all three pathways for establishment would still depend on the peak flow, subsequent rates of recession, and timing of the flood as compared with seed dispersal phenology. Indeed, as was mentioned before, the recommendations for conservation of Salicaceae in regulated rivers will be quite similar using either the Recruitment Box Model or the River Seeding Concept. I just feel that this hypothesis explains in a more parsimonious way both my own observations, and the ample literature on establishment of Salicaceae in gravel-bed rivers.

<u>References Cited</u>

Alpert, P., F.T. Griggs, and D.R. Peterson. 1999. Riparian forest restoration along large rivers: Initial results from the Sacramento River Project. *Restoration Ecology*, **7**, 360-368.

Barsoum, N. 2002. Relative contributions of sexual and asexual regeneration strategies in Populus nigra and Salix alba during the first years of establishment on a braided gravel bed river. *Evolutionary Ecology*, **15**, 255-279.

Bhattacharjee, J., J.P. Taylor, Jr., and L.M. Smith. 2006. Controlled flooding and staged drawdown for restoration of native cottonwoods in the Middle Rio Grande Valley, New Mexico, USA. *Wetlands*, **26**, 691 – 702.

Bovee, K.D., and M.L. Scott. 2002. Implications of flood pulse restoration for *Populus* regeneration on the upper Missouri river. *River Research and Applications*, **18**, 287-298.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 57-85.

Bradley, C.E., and D.G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany*, **64**: 1433-1442.

Church, M.A., D.G. McLean, and J.F. Wolcott. 1987. River bed gravels: Sampling and Analysis. In *Sediment Transport in Gravel-Bed Rivers*. Edited by C.R. Thorne, J.C. Bathurst, and R.D Hey. John Wiley and Sons, Chichester. Pp. 43-88.

Cooper, D.J., D.M. Merritt, D.C. Andersen, and R.A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the Upper Green River, USA. *Regulated Rivers: Research and Management*, **15**, 419-440.

Dingman, S.L. 1984. *Fluvial Hydrology*. Freeman and Co., San Francisco.

Eckenwalder, J.E. 1996. Systematics and evolution of *Populus*. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 7-32.

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

Francis, R.A., A.M. Gurnell, G.E. Petts, and P.J. Edwards. 2006. Riparian tree establishment on gravel bars: interactions between plant growth strategy and the physical environment. In *Braided rivers: process, deposits, ecology and management.* Edited by G. Sambrook-Smith, J. Best, C. Bristow, and G.E. Petts. International Association of Sedimentologists Special Publication 36. Blackwell, Oxford. Pp. 361–380.

Guilloy-Froget, H., E. Muller, N. Barsoum, and F.M.R. Hughes. 2002. Dispersal germination, and survival of *Populus nigra* L.(Salicaceae) in changing hydrologic conditions. *Wetlands*, **22**, 478-488.

Henderson, F.M. 1966. *Open Channel Flow*. McMillan, New York.

Huggenberger, P., E. Hoehn, R. Beschta, and W. Woessner. 1998. Abiotic aspects of channels and floodplains in riparian ecology. *Freshwater Biology*, **40**, 407-425.

Julien, P.Y. 1995. *Erosion and Sedimentation*. Cambridge University Press. Cambridge.

Karrenberg, S., P.J. Edwards, and J. Kollmann. 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology*, **47**, 733-748.

Krasny, M.E., K.A. Vogt, and J.C. Zasada. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Holarctic Ecology*, **11**, 210-219.

Lunt, I.A., J.S. Bridge, and R.S. Tye. 2004. A quantitative, three-dimensional depositional model of gravelly braided rivers. *Sedimentology*, **51**, 377-414.

Mahoney, J.M., and S.B. Rood. 1991. A model for assessing the impact of altered river flows on riparian poplars in southwestern Alberta. Pp 99-104 In S.B. Rood and J.M. Mahoney (eds.). *Proceedings of the Biology and Management of Southern Alberta's Cottonwoods Conference*. University of Lethbridge, Lethbridge, Alberta, Canada.

Mahoney, J.M., and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment – An integrative model. *Wetlands*, **18**, 634-645.

Noble, M.G. 1979. The origin of *Populus deltoides* and *Salix interior* zones on point bars along the Minnesota River. *American Midland Naturalist*, **102**, 59-67.

Petts, G.E. 1984. *Impounded Rivers: Perspectives for Ecological Management*. Wiley, Chichester, U.K.

Petts, G.E., A.M. Gurnell, A.J. Gerrard, D.M. Hannah, B. Hansford, I. Morrissey, P.J. Edwards, J. Kollmann, J.V. Ward, K. Tockner, and B.P.G. Smith. 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **10**, 249–266.

Polzin, M.L., and S.B. Rood. 2006. Effective disturbance: seedling safe sites and patch recruitment of riparian cottonwoods after a major flood of a mountain river. *Wetlands*, **26**, 965-980.

Poole, G.C., J.A. Stanford, S.W. Running and C.A. Frissell. 2006. Multiscale geomorphic drivers of groundwater flow paths: subsurface hydrologic dynamics and hyporheic habitat diversity. *Journal of the North American Benthological Society*, **25**, 288-303.

Powell, D.M. 1998. Patterns and processes of sediment sorting in gravel-bed rivers. *Progress in Physical Geography*, **22**, 1-32.

Rood, S.B., J.H. Braatne, and F.M.R. Hughes. 2003. Ecophysiology of riparian cottonwoods: Stream flow dependency, water relations, and restoration. *Tree Physiology*, **23**, 1113-1124.

Smith, S.D., D.A. Devitt, A. Sala, J.R. Cleverly, and D.E. Busch. 1998.Water relations of riparian plants from warm desert regions. *Wetlands*, **18**, 687-696.

Stanford, J.A., J.V. Ward and B.K. Ellis. 1994. Ecology of the alluvial aquifers of the Flathead River, Montana, pp. 367-390. In Gibert, J., D.L. Danielopol, J.A. Stanford (ed.), *Groundwater Ecology*. Academic Press, Inc., San Diego, California. 571 pp.

Stanford, J.A., M.S. Lorang, and F.R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **29**, 123-136.

van Splunder, I., H. Coops, L.A.C.J. Voesenek, and C.W.P.M. Blom. 1995. Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination characteristics and water level fluctuations. *Acta Botanica Neerlandica*, **44**, 269–278.

CHAPTER 4: TEMPERATURE AND MOTION EFFECTS ON UNDERWATER

GERMINATION OF COTTONWOOD SEEDS

Introduction

Even though Putnam (1951) proposed that "no seeds can germinate under water", Hosner (1957) found experimentally that after being immersed for four days, all viable seeds of plains cottonwood (*Populus deltoides* Marsh.) had germinated. He also reported that being in water did not slow nor delay the rate of seed germination, as compared with seeds placed on moist beds. Hosner (1957) also found that no additional germination could be had after four days, and that many of the water-germinated seedlings were doing fine after spending 32 days under water. He obtained similar results with black willow (*Salix nigra* Marsh.) seed, even though sample sizes were smaller. Hosner's goal was to study the selective effects of flooding upon regeneration of different riparian trees, and he did not pursue this part of his research further.

Krasny et al. (1988) corroborated these results for four other species within Salicaceae: balsam poplar (*Populus balsamifera* L.), feltleaf willow (*Salix alaxensis* (Anderss.) Cov.), sandbar willow (*Salix interior* Rowlee), and trembling aspen (*Populus tremuloides* Michx.). Seeds from all of these species germinated under water, and more than 50% of the seedlings survived when immersed for 42 days. In the case of the only cottonwood species, balsam poplar, the seedlings had even produced true leaves. Krasny et al. (1988) were looking at how the differences in regeneration niche explained the spatial distribution of these four species on a floodplain, but they did not focus on this specific life-history trait.

In an article about the life history of riparian Salicaceae, Karrenberg et al. (2002) mention this interesting trait, but do not discuss its implications nor adaptive value. In their complete review of the life history of North American riparian cottonwoods, Braatne et al. (1996) state that "once a seed becomes wet, viability will be lost in 2-3 d if a favorable microsite is not encountered." In light of the previously mentioned

89

observations, it is clear that when a cottonwood seed becomes wet and stays wet, it will simply germinate under water, instead of loosing its viability after 2 or 3 days.

As part of a comprehensive study of the factors determining successful establishment of black cottonwood, *Populus trichocarpa* T.&G. in a gravel-bed river, I installed seed traps at different locations on the floodplain (see Chapter 3). The traps consisted of wide plastic pans filled with water, and were checked every three or four days. During each collection, I noted that a large percentage of the seeds had germinated under water. Also, as observed by Hosner (1957) and Krasny et al. (1988), and contrary to the statement by Braatne et al. (1996), the seedlings established under water and kept growing for many days after collection in water- filled jars. Furthermore, I noted that seeds brought to the laboratory in jars within a cooler with ice would not germinate, but they would do so after taking the jars out of the cold and exposing them to room temperature. The same observations also applied to the seeds of some unidentified willow species located at two of my seed trapping sites.

As part of a study into cottonwood ecology, I am proposing the "River Seeding Concept" for cottonwood seedling establishment (see Chapter 3). Many researchers have noted that cottonwoods establish in regular, arcuate bands (Everitt 1968), and have proposed conceptual models to explain such banding (Mahoney and Rood 1998, Rood et al. 2003), which are based on wind dispersal of cottonwood seeds. The "River Seeding Concept" states that hydrochory (i.e., water transport), is fundamental in creating recruitment bands of poplar seedlings along gravel-bed rivers, and thus in explaining their spatial distribution on floodplains. If cottonwoods in particular, and other riparian Salicaceae in general, do rely predominantly on water dispersal, they should have special adaptations to facilitate this. These observations on underwater germination and on possible temperature effects led me to believe that this overlooked life history trait might be a fundamental mechanism employed by the species in seed dispersal, and an important characteristic of the regeneration niche of riparian salicaceous trees. With exception of the cursory notes by Hosner (1957) and Krasny et al. (1988), I was unable to find any literature on the subject.

In order to look at water temperature and motion effects on *P. trichocarpa* seed germination, I conducted a series of experiments in the laboratory. Assuming that seeds

do germinate under water, and that seedlings can grow immersed, my hypotheses were that: (i) immersion under cold water delays germination and there is a cost in vitality associated with such delay, (ii) germination has a functional dependence on both water temperature and time under water, which can be parametrized in terms of cumulative degree-days, (iii) germinating seeds and seedlings are adapted to withstand water motion, and (iv) seeds with their plume (or pappus) mostly float when falling on quiet waters.

<u>Methods</u>

I conducted four different experiments in order to test my hypotheses. In the first experiment, I placed seeds in cold water for varying durations, and then put them at room temperature, still under water. I checked the progress in germination on a daily basis. The second experiment was similar, but I used a wider range of water temperature, and only looked at final germination rates. The third experiment consisted of a comparison in germination rates between seeds immersed in quiet water and seeds maintained in motion. The fourth analyzed the flotation capacity of plumed seeds.

Experiment 1: Germination progress after immersion in cold water

Seeds were collected on July 7, 2007 from one female tree located on Bear Creek, within the Flathead River Basin, in northwestern Montana, USA. This corresponds to the time for natural dispersal at this elevation. The site was located along US Highway 2, near Marias Pass, at an elevation of 1360 m and at coordinates 48°16'33" N and 113°25'50" W. Seeds were manually separated from the pappus. Potentially viable seeds were selected, based on their size, shape, and color. Good seeds tend to be larger, fuller or plumper, and have a clear tan color. Very small, shriveled, and darker seeds were separated, as they are usually unviable, and were not used in the experiments. Lots of 50 seeds were randomly selected from the batch of potentially viable seeds, and placed in 200 ml glass jars. The jars were filled with 150 ml of tap water, closed, and then shaken for about 30 s, in order for all seeds to sink. The occasional seeds that would not sink were replaced. The jars were then opened and placed in the temperature baths.

I used a factorial design, with two different temperatures and four durations for the immersion in the cold water baths. Three 50 seed lots were randomly chosen as replicates for each treatment. After completing their duration in cold water, the jars were placed in water at room temperature. The jars were kept in the dark for the duration of the experiment, except when taken out for assessing germination. Upon withdrawal from the cold bath, and every day afterwards for a period of 10 days, I checked the germination status of the seeds. This involved examination under a dissecting microscope by transferring the contents of each jar to a Petri dish and counting the numbers of closed seeds, seeds with initial germination, and seeds with final germination.

Because cottonwood seedlings establish under conditions of receding river stage, speed of germination can be critical to recruitment success. This is why I consider two different measures of germination for my experiments: full germination refers only to germinants which have attained a larger size, which would presumably correspond to a higher probability of survival. Total germination is always larger or equal than full germination, as it also includes seeds which are just starting to germinate. The criterion for initial germination was the presence of the radicle, and that the combined length of the radicle and hypocotyl did not surpass the length of the seed. When the length of the radicle plus hypocotyl clearly exceeded the seed size, I considered the seed to be fully germinated. Total germination rates were simply computed as the sum of initial plus full germination. All germination rates were expressed as percentage.

The treatments included two water temperatures, 3 and 7° C (± 0.1°C) , chosen to be colder than, and at the low limit of the natural range of river water temperatures found during snowmelt. There were four durations for the cold baths: 1, 2, 4, and 8 days. All treatments were run concurrently, in order to control for differences in seed vitality. In order to have a control for comparison, I also determined seed vitality in water at room temperature. Three replicates of 50 seeds each were placed in jars maintained at 21.5°C (± 1.5°C), and their germination was checked daily over a 10 day period. At the end of the experiment, after the last determination of germination rate, both the root and the hypocotyl length were measured to the nearest millimeter. Two-way analyses of variance and post-hoc tests (Tukey's Honestly Significant Difference test and Tamhane's T2 test, depending on homogeneity of variances) were used to determine significant differences

in final (i.e., after 10 days) full and total germination rates, root length, and hypocotyl length, among the treatments and the control, due to bath temperature and bath duration. When no significant differences occurred across treatments, t-tests were used to compare means between pooled treatment data and the control. Because of the small sample size, I also conducted non-parametric tests to corroborate the results from the ANOVAs. Kruskal-Wallis tests were used to look at differences in means due to bath temperature and bath duration. I carried out exact Wilcoxon-Mann-Whitney tests to compare means between pooled treatment data and the control, whenever there were no significant differences among treatments.

Non-linear regression was used to determine the relationship between germination rates and time. I used a logistic equation with 3 parameters, of the form:

$$G(t) = A\ e^{(B+Ct)} / (1+e^{(B+Ct)})$$

Where G is the germination rate in % (either full or total, depending on which variable is being modeled), t is the time elapsed since the seeds were taken out of the cold bath and placed at room temperature, and A, B, and C are the parameters to be calibrated. For each treatment, I averaged the germination rates over the three replicates at each time step, before fitting the model.

Experiment 2: Water temperature effects on germination

Because of the long time involved in separating the pappus, the need for more than three replicates, and the lack of sufficient seeds, I decided to purchase seeds for this experiment. Seeds were obtained from Quality Seed Collections, Ltd., in Kamloops, British Columbia. These *P. trichocarpa* seeds were collected in 2007 near Brookmere, British Columbia, Canada. The collection site is located at 49°51' N and 120°54' W, at an elevation of 905 m, and is within the Coquihalla River basin, a tributary to the Fraser River. The seed preparation and experimental steps were identical to those described for experiment 1, except that in this case I used five replicates of 50 seeds each per treatment, instead of three. Also, I did not check germination daily, determining germination rates only on three occasions: when the jars where removed from the baths, 4 days after placing them at room temperature, and 8 days after initiating each experiment (i.e., after wetting the seeds).

93

The treatments involved six different water temperatures, covering the natural range that can be found in snowmelt-fed rivers from early to mid-summer: 7.5, 10.0, 12.5, 15.0, 17.5, and 20.0°C (± 0.1°C, in each case). For each temperature, the jars were kept in the bath either 12, 24, 48, or 96 hours, before being placed in water at room temperature of 22.5°C (± 2.5°C), until a total of 8 days of immersion was reached. For control, I also determined germination rates for six replicates placed for 4 days at room temperature. Because I could only run two temperature baths simultaneously, it took me over a month to complete the whole experiment. In order to maintain seed vitality through the duration of the experiment, seeds were maintained in a freezer, in air-tight plastic bags, as recommended by Schreiner (1974) and Krasny et al. (1988). The sequence of bath temperatures was randomly chosen: the experiments at 10.0 and 15.0°C were conducted first, followed by those at 12.5 and 20.0°C, finalizing with those at 7.5 and 17.5°C. The control at room temperature was run concurrently with the 12.5 and 20.0°C experiments.

The data were checked for normality with Shapiro-Wilks tests, and for equality of variances with Levene's test. One-way analysis of variance was used to determine bath temperature effects on the germination rates after 4 days of immersion. In the case of significant models, pairwise comparisons were conducted with post-hoc tests (Tukey's Honestly Significant Difference (HSD) test or Tamhane's T2 test, depending on homogeneity of variances). Two-way analyses of variance and the same post-hoc pairwise comparisons were used to test for differences in final germination rates (measured 8 days after initiating each experiment), due to bath temperature and bath duration.

In interpreting the results of this experiment, there was a problem related to the comparison of germination rates for seeds which had been exposed to water at different temperatures, for varying durations. The question was: when analyzing bath temperature effects, should germination rates be compared after the same duration immersed under water –independently of the duration of the exposure at room temperature, or after the same duration at the higher, room temperature –independently of the duration of the colder bath? The only way to deal with this issue was using some integral measure of the time spent at different temperatures. Thus, I computed cumulative degree-days above

seven different thresholds (0, 2.5, 5, 7.5, 10, 12.5, and 15°C), as an overall measure of the time and temperature to which the seeds had been cumulatively exposed. I then fitted regressions to the relationships between germination rate and water temperature, and between germination rate and cumulative degree-days.

Experiment 3: Water motion effects on germination

Seeds used for this experiment were of the same origin as those used in experiment 1. I used Plexiglas chambers originally designed by Hauer and Benke (1987) for providing current in the rearing of blackfly larvae (also described in Hauer and Resh 1996). A curtain of air bubbles maintained a constant water circulation within the chambers. The treatments involved placing 50 seeds in the chambers with water at room temperature (22.5 ± 2.5°C), and letting them germinate under motion for periods of 2, 4, and 5 days. The control was similar in all respects, but the seeds were left to germinate in quiet water. I used three replicates per treatment, and also for the control. At the end of the treatment duration, I assessed the rates of initial, full, and total germination, and also measured the length of the radicle and hypocotyl of all fully germinated seeds.

As I only had three circulation chambers, I could not run the experiments for different durations simultaneously. Thus, I randomized the order in which I ran the experiments for different durations. I started the 5-day experiment on 07.13, the 2-day experiment on 07.20, and the 4-day experiment on 07.23. In the meanwhile, the seeds that were to be used in the later experiments were kept at ambient, room conditions. A preliminary assessment of the results indicated that the seeds had clearly lost vitality over this 10 day period, so that the effects of duration could not be investigated in this experiment.

For each experimental duration, I tested for differences in germination rates due to treatment (motion or control) by conducting non-parametric Wilcoxon-Mann-Whitney tests. The seedling radicle and hypocotyl lengths had highly skewed distributions, so that I also had to use Wilcoxon-Mann-Whitney tests to investigate treatment effects. In this latter case, I pooled all seedlings from the different replicates for each duration and treatment, in order to work with larger sample sizes.

Experiment 4: Seed floatation over quiet water

In order to test whether plumed cottonwood seeds float or not, and for how long they will do so, I carefully placed seeds with their pappus on trays filled with quiet water at room temperature. There were 50 seeds per tray, and three replicates. Trays were checked once daily for 6 days, counting how many seeds had sunk. Seeds for this experiment were of the same origin as those used in experiments 1 and 3.

<div align="center">Results</div>

Experiment 1: Germination progress after immersion in cold water

No seeds germinated while in the cold baths, with the exception of 1 seed out of 50, in two of the replicates for the treatments with the higher temperature (7°C) and the two longest bath durations (4 and 8 days). In other words, out of the 1200 seeds that were tested in the different treatments (2 temperatures times 4 bath durations times 3 replicates times 50 seeds per replicate), only 4 had germinated (0.33%) when taken out of the cold baths.

The corresponding total germination rates for the control at room temperature ($\pm$ one standard deviation), where 34.0% ($\pm$ 6.56%), with only initial germination (i.e., no full germination), after 1 day; 40.8% ($\pm$ 13.4%), with 23.8% full germination, after 2 days; 63.3 % ($\pm$ 3.53 %), with 42.4% full germination, after 4 days; and 76.2 % ($\pm$ 7.73 %), with 59.2% full germination, after 8 days. The means are shown in Figure 1. All of these results clearly support the hypothesis that immersion in cold water delays cottonwood seed germination.

The total germination data for the treatments at 3°C are also shown in Figure 1. The data for 7°C are shown in Figure 2, which has a different time axis. The behavior through time suggests that a logistic curve would be a good fit for all treatments, except for the first few days in the treatment with 3°C and a 2 day bath.

Figure 1. Mean of the total germination rate for three replicates, plotted against the time elapsed since the seeds were placed in the 3°C bath, for the 4 different bath durations and the room temperature control.

Levene's test indicated that total germination data had similar variances across treatments (F = 2.168, p = 0.095). Normality was not tested, as there were only three replicates per treatment. A full factorial two-factor ANOVA with bath temperature and bath duration as between-subject factors was not significant (F = 1.413, p = 0.267, adjusted R^2 = 0.112). The data for all treatments were then grouped, and compared with the total germination rates for the control, at room temperature, with a t-test. Assuming equal variances (Levene's F = 1.730, p = 0.200), the total germination rates for the control were significantly larger, by 29.9%, than those for the data pooled across all treatments (t = - 4.146, df = 25, p < 0.0001).

In the case of the full germination data, the two-way factorial ANOVA was not significant either (F = 1.730, p = 0.172, adjusted R^2 = 0.182). Grouping the data for all treatments and comparing with the control with a t-test yielded a difference in means of 37.0%, which is highly significant (t = - 5.429, df = 25, p < 0.0001).

The results are qualitatively similar for the radicle and the hypocotyl length. In both cases, the statistical models are not significant (F = 0.505, p = 0.817, and the adjusted R^2 = -0.177 for the radicle length; F = 1.238, p = 0.339, and the adjusted R^2 = 0.068 for the hypocotyl length). Radicle length is significantly smaller for the grouped

97

data for all treatments than for the control (mean difference = 0.427 mm, t = -5.123, df = 25, p < 0.0001). On the other hand, hypocotyl length does not exhibit any significant difference (mean difference = 0.724 mm, t = -0.952, df =25, p = 0.350).

The non-parametric tests gave results that were fully consistent with those from the ANOVAs and t-tests. Kruskal-Wallis tests for differences due to bath temperature gave p-values ranging from 0.139 to 1.000, while those for bath duration resulted in $0.163 \leq p \leq 0.948$. Thus, for all four variables (full and total germination, radicle and hypocotyl length) there were no significant differences across treatments, as shown in Figure 2 for the rate of total germination. After pooling all of the treatment data, the Wilcoxon-Mann-Whitney tests indicated highly significant differences between the treatment and the control for all variables (p = 0.001), except for the hypocotyl length (p = 0.160).

Thus, I can assert that there is a significant cost in seed vitality associated with a period of immersion in cold water, but the small sample size used in this experiment (only three replicates) does not allow me to discriminate possible differences among the treatments.

The logistic equation provided a very good fit to the average germination data for the 8 different treatments, with all R^2 values above 0.974. In the case of the control, R^2 was 0.951 for the full germination data, and 0.956 for the total germination data. These two cases are shown in Figure 3. I also checked the fit of the logistic equation to the six individual replicates for the treatments at 3°C with durations 1 and 2 day. R^2 values were all above 0.947.

Experiment 2: Water temperature effects on germination

I first compared the germination rates after 96 hours in a constant temperature bath. Shapiro-Wilks tests for normality were carried out for both the full and total germination data, for the six different treatment temperatures (n = 5 in each case), as well as for the control (room temperature) data (n = 6). I used a significance level α = 0.10, as recommended by Helsel and Hirsch (1992) for small sample sizes, in order to increase power to detect non-normality.
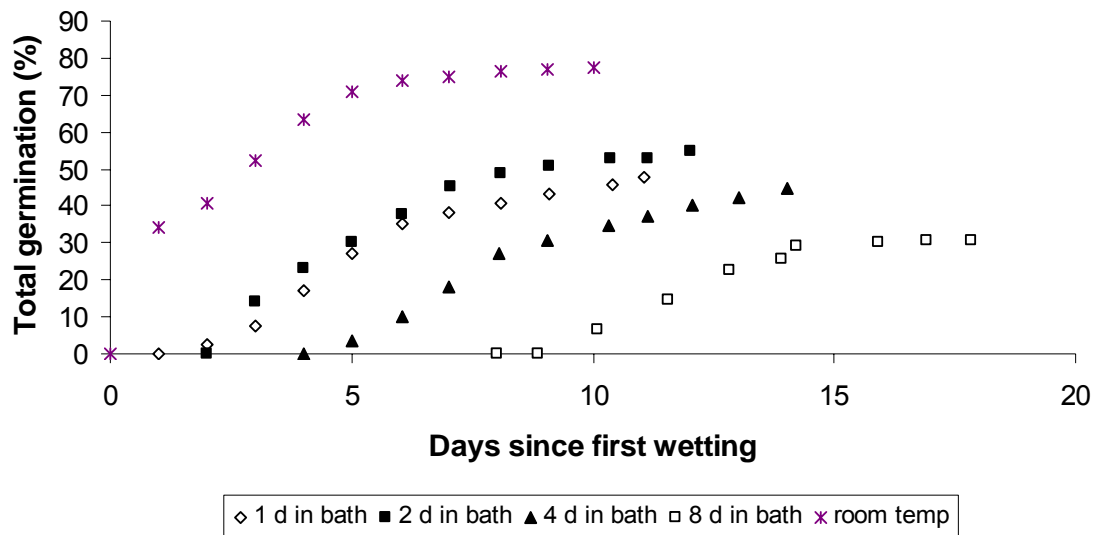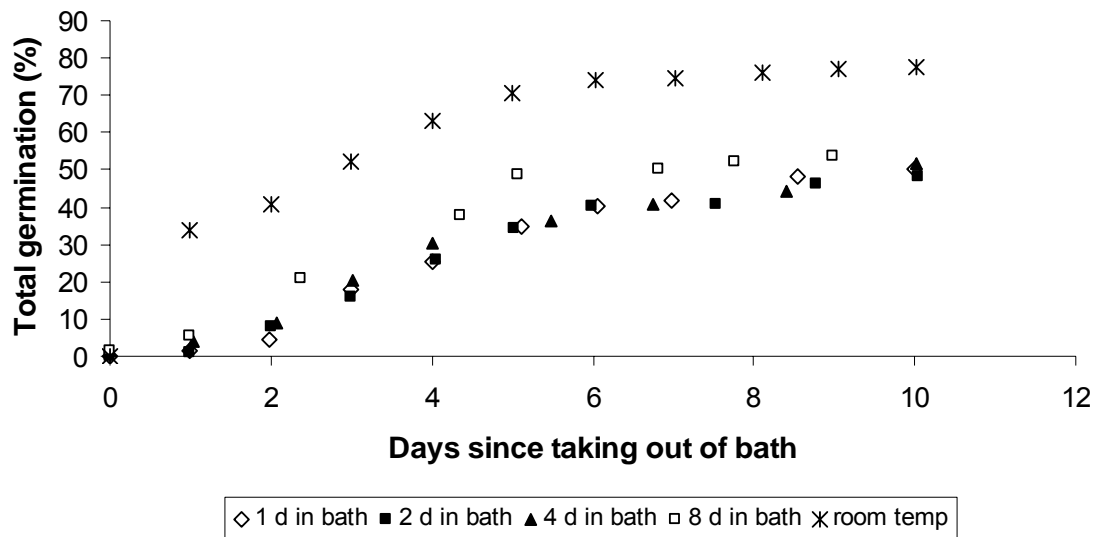
Figure 2. Mean of the total germination rates for three replicates, plotted against the time elapsed since taking the seeds out of the 7°C bath.
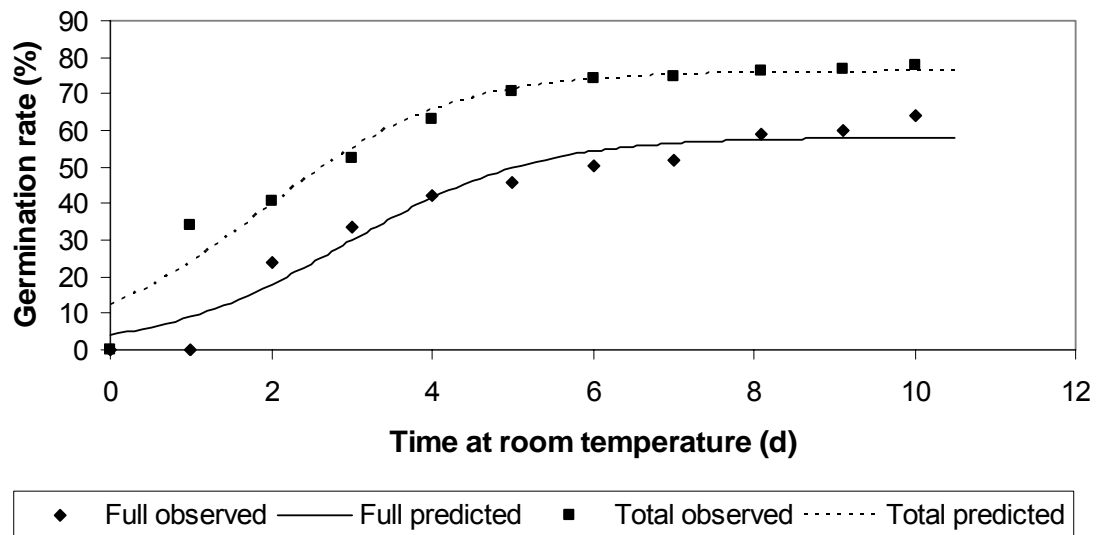
Figure 3. Temporal behavior of the mean of the full and total germination rates (3 replicates), for the control at room temperature, also showing the fitted logistic regressions.

In all but four cases, the null hypothesis that the data are normally distributed was not rejected. Those cases involved the full germination at the four lower temperatures (7.5, 10.0, 12.5, and 15.0°C), where there were so many zero values that the distribution could obviously not be Gaussian.

I used Levene's test to check for equality of error variances. For the full germination data, I rejected the null hypothesis that the error variance of the cumulative

water losses was equal across the different groups (Levene's F = 15.571, p < 0.0001). Again, this was due to the presence of many zero values in the data. Because of this, I used the non-parametric Kruskal-Wallis test for the full germination data. Even though two of the required assumptions for analysis of variance were not met in the case of the full germination data, I still relied on the robustness of one-factor ANOVA when sample sizes are the same (or very similar), as was the case here. This way, for significant models, I conducted post-hoc comparisons using Tamhane's T2 test, developed for the case of significantly different variances across groups. On the other hand, the variances were not significantly different for the total germination data (Levene's F = 1.349, p = 0.268). Thus, I tested for differences in means by conducting a one-way ANOVA, with post-hoc pairwise comparisons using Tukey's HSD tests, in the case of significant models.

The Kruskal-Wallis test for the full germination data was highly significant (χ^2= 31.848, df = 6, exact p < 0.0001), as was the one-way ANOVA (F = 36.84, df = 6, p < 0.0001). The post-hoc pairwise comparisons indicated three clear homogeneous subsets within the data, for α = 0.05: 7.5, 10.0, 12.5, and 15.0°C, with respective means of 0.0, 0.0, 0.4, and 1.6 % (overall group mean of 0.5%); 17.5 and 20°C, with means of 16.8 and 19.2 %, respectively, and a subset mean of 18.0%; and the control at room temperature (22.5°C), with a mean of 35.7% (see Figure 4).

For the total germination data, the ANOVA was even more significant (F = 59.96, df = 6, p < 0.0001). Tukey's HSD post-hoc tests defined four homogeneous subsets at α = 0.05: 7.5 and 10.0°C, with means of 3.2 and 16.8%, respectively (group mean = 10.0%); 10.0, 12.5, and 15.0°C, with respective means of 16.8, 19.6, and 24.0% (overall mean = 20.1%); 17.5 and 20.0°C, with means of 50.4 and 56.0%, and a group mean of 53.2%; and finally a group including the 20.0°C and the control data, with means of 56.0 and 67.0%, for an overall subset mean of 61.5%.

These results strongly support the hypothesis that water temperature affects the germination of immersed cottonwood seeds. In order to obtain the functional relationship between germination at 4 days and water temperature, I conducted logistic non-linear regression.
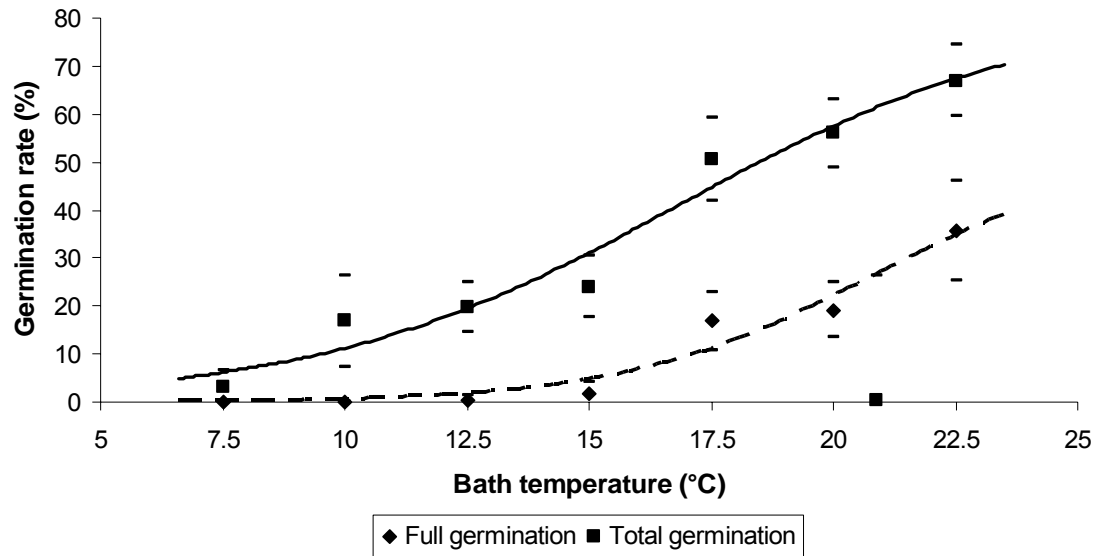
Figure 4. Full and total germination rates (± 1 standard deviation) after 4 days in a water bath at a given temperature. Each data point is the mean of 5 replicates, except for the control at 22.5°C, which has 6 replicates. Best fit logistic regressions are also shown.

The best fit equations for full and total germination (see Figure 4) were as follows:

$$FG_4 (T) = 52.82 \ e^{(-8.202 + 0.394 \ T)} / (1 + e^{(-8.202 + 0.394 \ T)}), \ R^2 = 0.953, \ n = 7$$

$$TG_4 (T) = 81.92 \ e^{(-4.541 + 0.270 \ T)} / (1 + e^{(-4.541 + 0.270 \ T)}), \ R^2 = 0.963, \ n = 7$$

Where FG_4 and TG_4 are the full and total germination rates in %, respectively, after 4 days immersed in water, and T is the bath temperature in °C. In these models, the first parameter corresponds to the asymptotic maximum germination rate, reached for very large temperature values. I computed T_{99}, the temperature needed to reach 99% of the maximum germination rate, obtaining 32.5 and 33.9°C for the full and total germination, respectively. T_{50}, the temperature needed to reach 50% of the maximum germination rate (note that this is different from a 50% germination rate), was 20.9 and 16.8°C for full and total germination, respectively.

A two-way ANOVA was run on the final full germination data, with bath temperature (7.5, 10.0, 12.5, 15.0, 17.5, and 20.0°C) and bath duration (12, 24, 48, and 96

101

hours) as between-subject factors. Levene's test indicated homogeneous variances across the different treatments (F = 0.907, p = 0.589). The model was highly significant (F = 3.757, df = 23, p < 0.0001, adjusted R^2 = 0.348), with a strong effect of the temperature (p < 0.0001) and of the interaction between temperature and bath duration (p = 0.003). Bath duration was not significant on its own (p = 0.161). Post-hoc comparisons conducted with Tukey's HSD test indicated the existence of 3 homogeneous subsets of data, which cut across temperature without any clear trend: a first group with the data for 7.5, 12.5, and 17.5°C, which had means of 18.95, 16.51, and 20.54%, respectively (overall mean = 18.66%); a second group with the data for 7.5, 10.0, 17.5, and 20.0°C, with respective mean full germination rates of 18.95, 23.20, 20.54, and 23.50%, and an overall mean of 21.55%; and a third group with the data for 10.0, 15.0, and 20.0°C, which had means of 23.20, 27.00, and 23.50%, respectively, for a grand mean of 24.57% (see Figure 5).
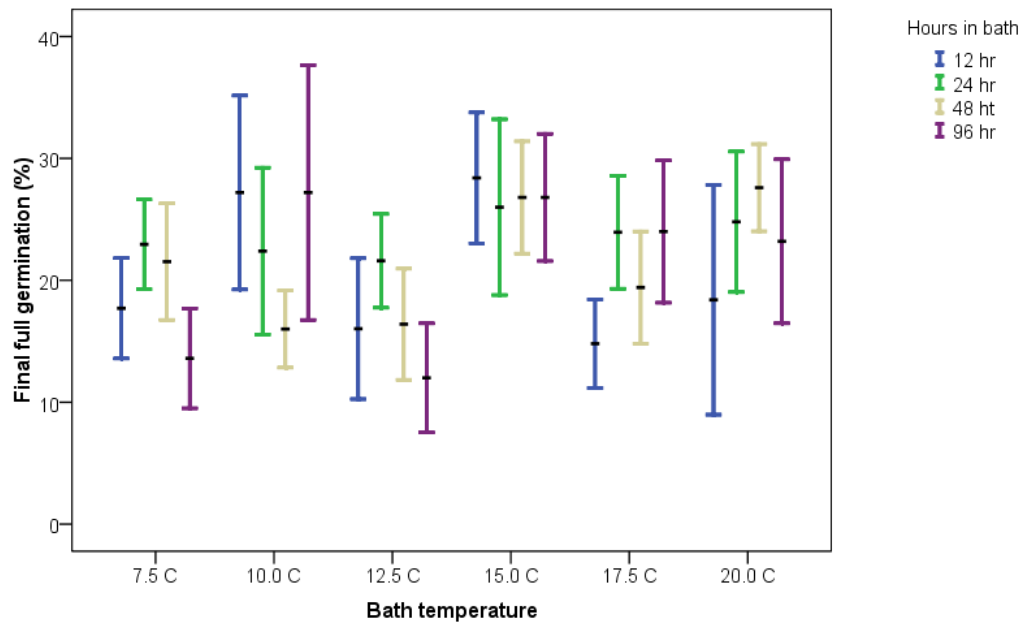
Figure 5. Final full germination rates in % (± 1 standard deviation), 8 days after initiating the experiments, for the different bath temperatures and durations.

The results for the total germination data at the end of the experiments were very similar to those for full germination. Variances across the different treatments were

homogeneous (Levene's F = 1.169, p = 0.292), and the ANOVA was highly significant (F = 3.286, df = 23, p < 0.0001, adjusted R^2 = 0.306). There was a strong effect of the temperature (p < 0.0001) and of the interaction between temperature and bath duration (p = 0.004), but bath duration was not significant (p = 0.481). Again, the post-hoc Tukey tests indicated the existence of homogeneous subsets without a clear trend in temperature (see Figure 6): A first group with the 7.5, 12.5, and 17.5°C data had means of 43.74, 48.44, and 45.05%, respectively, with an overall mean of 45.75%; a second one with the 10.0, 12.5 and 17.5°C data had respective mean total germination rates of 50.8, 48.44, and 45.05%, with a grand mean of 48.10%; and finally, a subset with the data from the treatments at 10.0, 12.5, 15.0, and 20.0°C had means of 51.76, 48.44, 52.80, and 55.00%, respectively, for an overall mean of 51.7%.
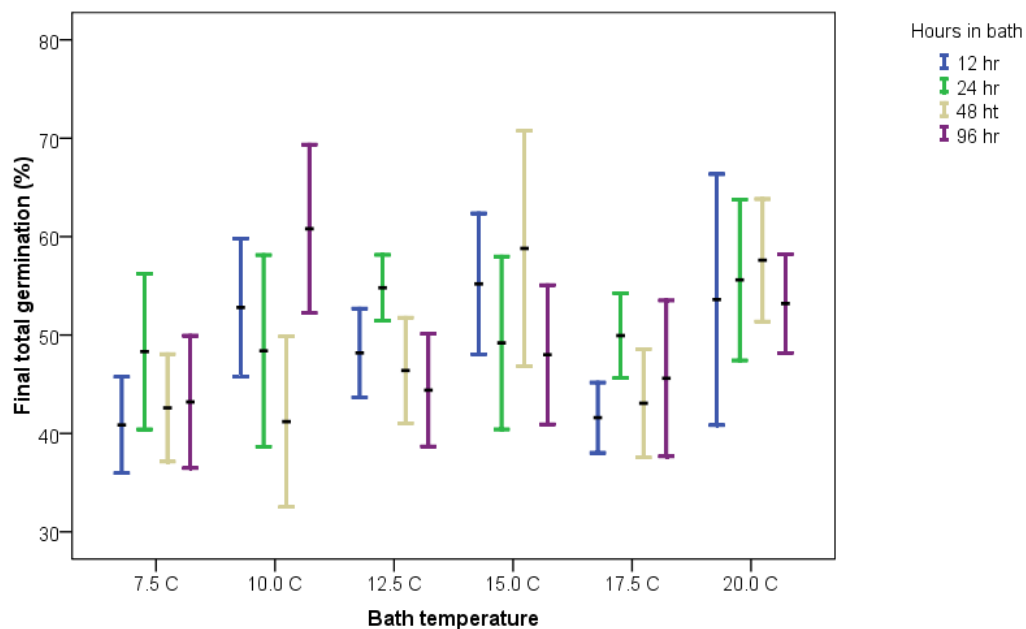
Figure 6. Final total germination rates in % (± 1 standard deviation), 8 days after initiating the experiments, for the different bath temperatures and durations.

A plot of total germination rate versus cumulative degree-days above a threshold of 0°C (dd_0 from now on), for all measurements (n = 336), shows a clear pattern of increasing germination, until a plateau is reached at a cutoff of about 90 dd_0 (Figure 7).

The plot was similar for the full germination data, but there were many more zero germination values in the lower range of cumulative degree-days.
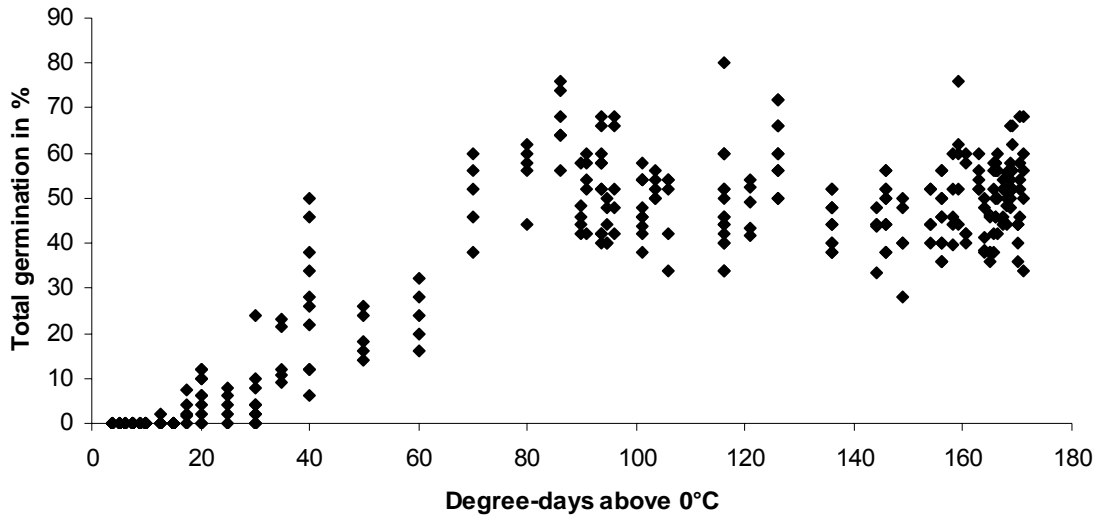
Figure 7. Total germination rates (in %) plotted against cumulative degree-days above a threshold of 0°C.

These plots suggest that a fit with two straight lines, one sloping and the other constant (which I will loosely term a double linear regression model from now on), would explain most of the variability in the relationship between germination rate and accumulated degree-days. The fact that the sloping line would clearly have a negative intercept, and that there are many zero germination values for positive dd_0 values, suggests in turn that the fit could be improved by using a higher threshold for defining the cumulative degree-days, especially for the full germination data. I fitted a suite of 124 double linear regression models to both the full and total germination data, forcing the sloping line to go through the origin. I used 7 different thresholds for computing degree-days, and a range of 7 to 14 different values for the cutoff point, where the two lines meet. The main criterion for choosing the best models was the goodness of fit of the sloping line as given by the coefficient of determination R^2, but I also required that a regression line fitted to the data above the cutoff be as constant as possible. The best models for full and total germination are shown in Figure 8.

104
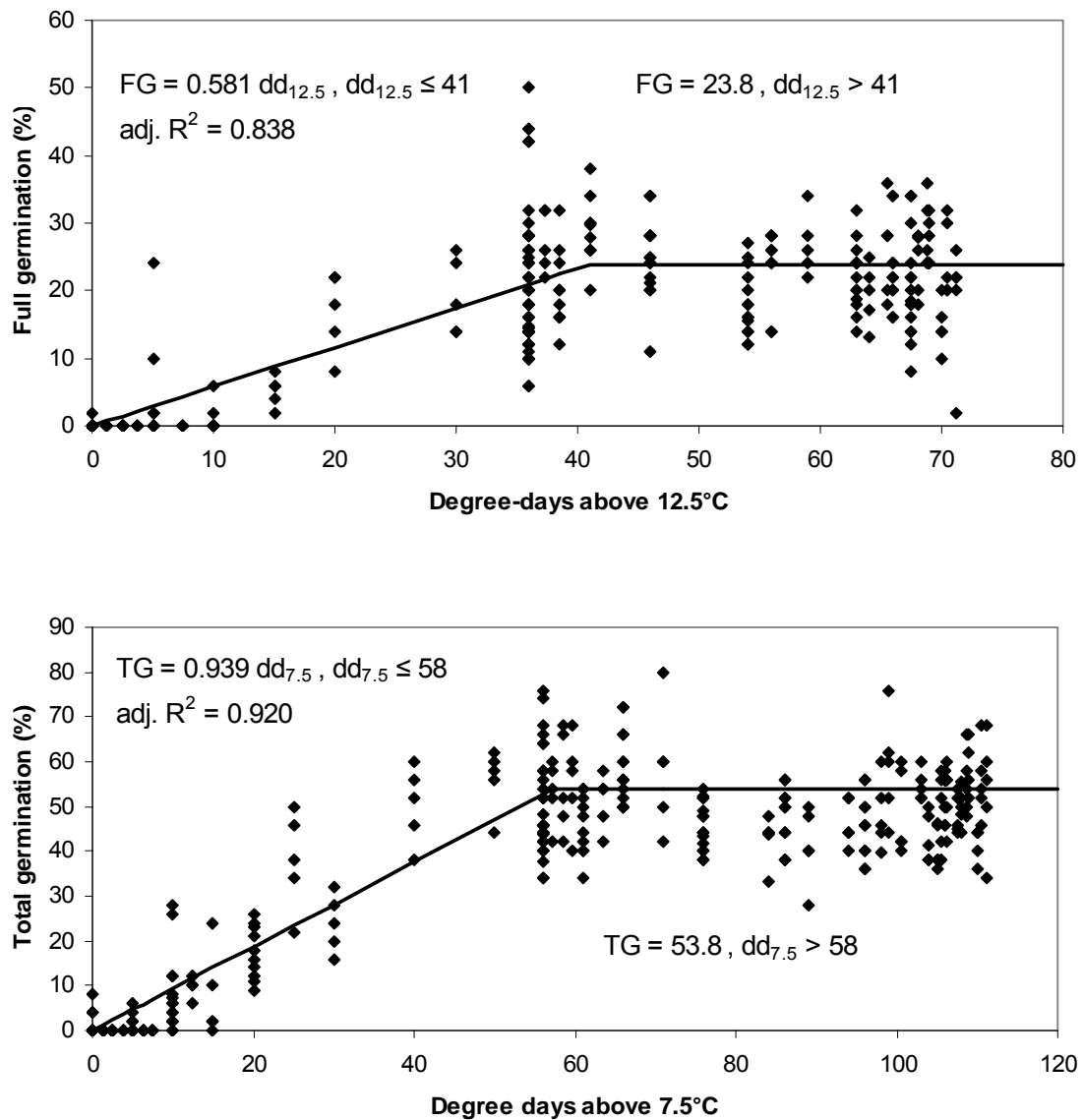
Figure 8. Best fit models for full (above) and total (below) germination data, as a function of cumulative degree-days.

Experiment 3: Water motion effects on germination

According to the Mann-Wilcoxon-Whitney tests, there were no significant differences in germination rate between the control and the treatment replicates, for all durations, and for both full and total germination rates (see Table 1 and Figures 9 and 10).

Table 1. Comparison of full and total germination rates (in %) for the different durations of the motion experiments. Control = quiet water, treatment = motion.

			Duration of the experiment		
			2 days	4 days	5 days
Full germination	mean	control	64.19	52.67	97.93
		treatment	65.10	58.13	94.41
	St. dev.	control	15.31	6.11	0.02
		treatment	3.01	12.06	1.16
	Z-value		-0.218	-0.655	-1.993
	p-value		1.000	0.700	0.100
Total germination	mean	control	78.91	68.00	98.63
		treatment	75.16	67.22	96.48
	St. dev.	control	15.32	10.00	1.19
		treatment	2.48	7.25	1.28
	Z-value		-0.655	-0.218	-1.348
	p-value		0.700	1.000	0.300

In the light of these results, I concluded that there is no effect of water movement on cottonwood seed germination rates.

I did find significant effects of the motion treatment, both on hypocotyl and radicle lengths, for the two longer experimental durations (4 and 5 days). Hypocotyls were somewhat shorter, and radicles were much shorter in the motion treatment, with respect to the quiet water control (Table 2 and Figure 10).

Experiment 4: Seed floatation over quiet water

Out of the 150 seeds with their pappus that were tested (three replicates of 50 seeds each), only two seeds sank, in one of the trays. One did so between the 1st and the 2nd observation (i.e., after more than 1 day but less than 2 days), and the second between the 4th and 5th. Thus, 100% of the seeds were still floating after 1 day, 99.3% after 3 days,

and 98.7% at the end of the experiment, after 6 days. Most of the seeds rode high on the water, did not touch its surface, and thus never germinated. The mean total germination rate for the three replicates, at the end of the experiment, was 23.3%, with a standard deviation of 16.5%.
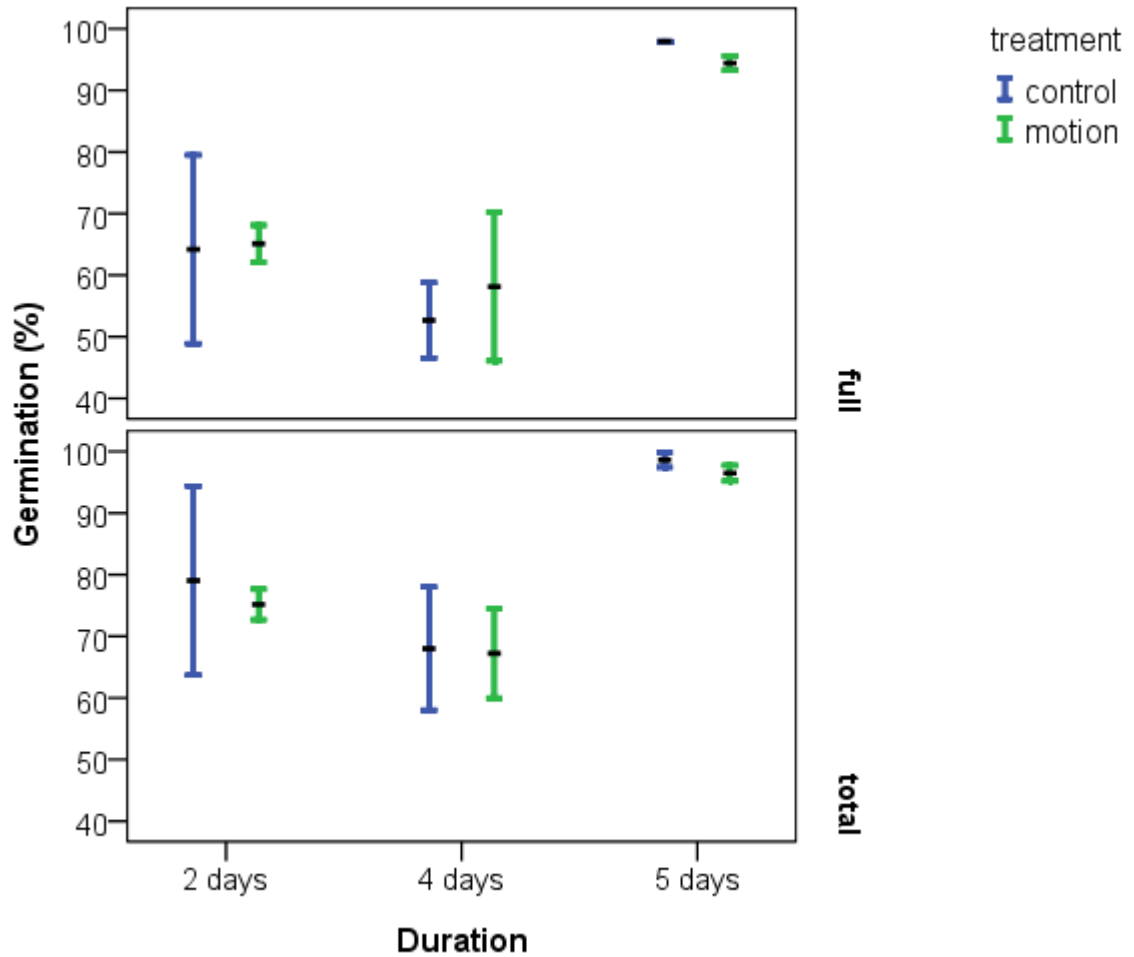
Figure 9. Full and total germination rates (mean of 3 replicates ± standard deviation) for the different durations of the motion experiments.

Table 2. Comparison of hypocotyl and radicle length between the control and the treatment, for the three different experimental durations.

			Duration of the experiment		
			2 days	4 days	5 days
Hypocotyl length	n	control	95	79	142
		treatment	97	84	136
	mean	control	2.05	2.43	6.38
		treatment	1.99	3.30	4.97
	St. dev.	control	0.690	1.22	2.20
		treatment	0.757	1.73	2.05
	Z-value		-0.797	-3.117	-5.188
	p-value		0.432	0.002	<0.0001
Radicle length	n	control	95	79	142
		treatment	97	84	136
	mean	control	1.93	2.52	9.07
		treatment	1.98	3.52	0.912
	St. dev.	control	0.914	1.71	3.68
		treatment	0.854	2.22	0.745
	Z-value		-0.881	-2.949	-13.466
	p-value		0.380	0.003	<0.0001

<u>Discussion</u>

The results strongly support each one of my hypotheses. As observed by Hosner (1957) for *P. deltoides*, and by Krasny et al. (1988) for *P. balsamifera*, seeds of *P. trichocarpa* do germinate under water, and the seedlings are perfectly able to grow fully immersed. Note that my experiments were not designed to compare germination rates between immersed seeds and seeds establishing on moist media.
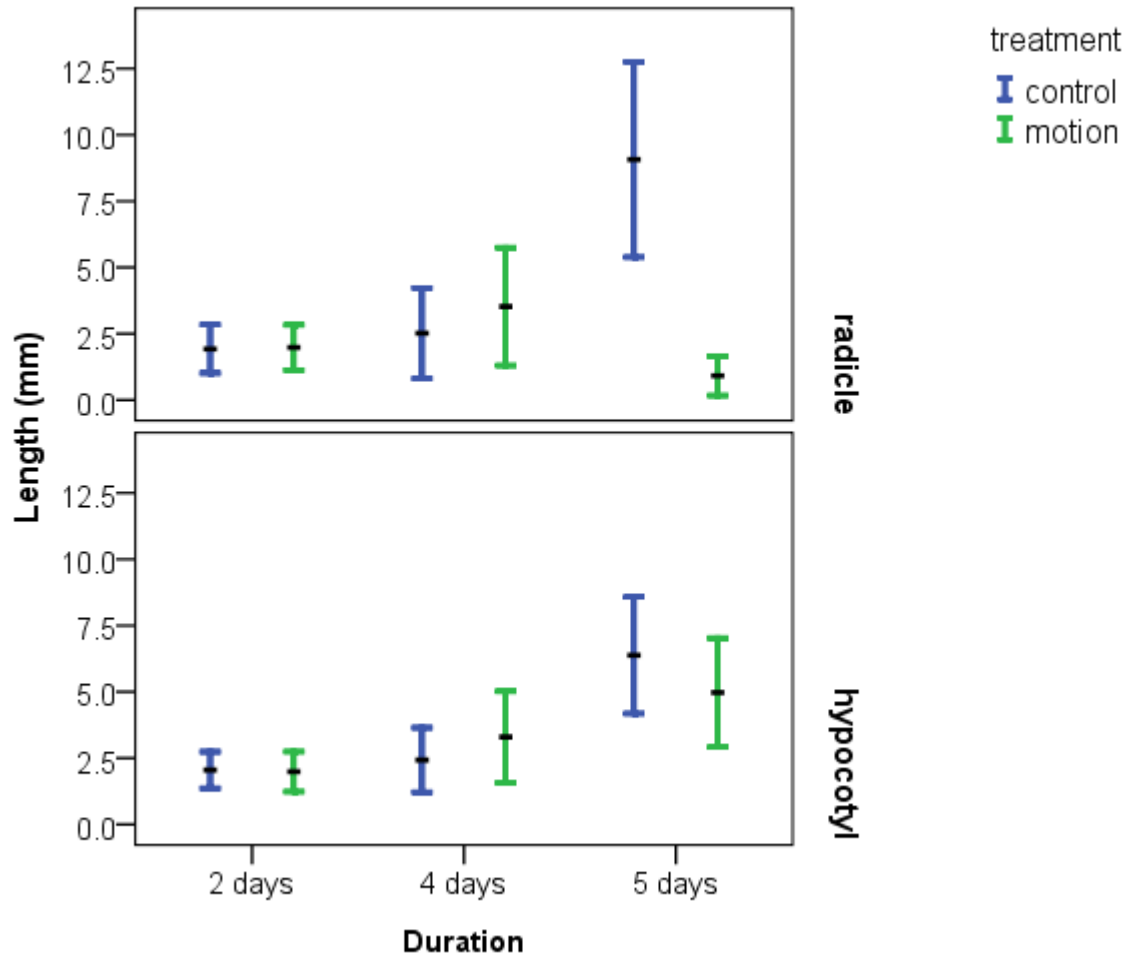
Figure 10. Hypocotyl and radicle length (± standard deviation) for the different experimental durations of the motion experiments.

Still, my qualitative observations in the field, where all freshly released seeds falling in traps with water germinated, as well as my laboratory data for seeds from two different sources, clearly indicate that a large proportion of seeds placed under water germinate successfully. In my experiments, seeds were submerged for periods of up to 10 days, and I never observed a fully germinated seed dying. I did note that some of the late-germinating seeds, which had reached only the initial germination stage after a few days, could be smothered by fungi. Indeed, fungal growth was a problem in some of my longest-running experiments. I recommend the use of some anti-fungal solution, in any further research, in order to control for this factor.

Underwater germination has a functional dependence on both water temperature and time of immersion. At higher temperatures and longer immersion times, germination rates are higher, and the seedlings grow faster. After 2 days under water, no seeds germinated at 7.5°C, and only a few did at 10.0 and 12.5°C. After 4 days, some germination occurred at 7.5°C, and many seeds exposed to water at 10.0 and 12.5°C germinated. Still, for these temperatures, basically no seeds reached full germination even after 4 days under water. This joint effect of water temperature and immersion time is clearly exposed when one considers germination rate as a function of cumulative degree-days (Figure 8). Hosner (1957) conducted his experiments at a "relatively constant temperature" of 15.6°C, and noted that no further germination could be had after 4 days. I observed a similar behavior (Figure 8), whereby germination reached a plateau after seeds had been exposed to a sufficient number of cumulative degree-days. Hosner (1957) did not define what he meant by germination, but I will assume here that he was referring to what I have termed total germination. In such case, the plateau would have been reached after exposure to 32.4 $dd_{7.5}$, which is quite low compared to my finding of a cutoff at 58 $dd_{7.5}$. The difference could be specific: seeds of *P. deltoides* may have a lower degree-day threshold for germination than those of *P. trichocarpa*. Krasny et al. (1988) mention previous research indicating that no further germination of willows, aspens, and poplars occurs after 4 days, at 20°C. In this case, the cutoff would be at 50 $dd_{7.5}$, which is closer to my results.

The relationships between germination and water temperature (Figure 4) can be extrapolated beyond the experimental range. Doing so, I obtained temperatures of 32.5 and 33.9°C for reaching maximum germination asymptotically. These may seem rather large, but my field observations confirm them: Water in the seed-collecting pans, made of black plastic, easily reached temperatures between 35 and 40°C during hot summer days. This did not affect germination negatively; on the contrary, all of the seeds falling into the traps germinated, and the seedlings grew very quickly at high water temperatures.

As pointed out by Farmer and Bonner (1967), speed of germination could be more fundamental than total germination rates in explaining cottonwood establishment success. This idea is also implicit in currently accepted models of cottonwood establishment (Braatne et al. 1996, Mahoney and Rood 1998, Rood et al. 2003), which stress the need

for seedlings' roots to grow as fast as groundwater levels recede. My results suggest that the probability of success of an ungerminated seed deposited by the river at a suitable location depends on previous conditions, such as how much time it was in the flow, and what the temperature of the water was.

According to these results, seeds could travel many days with the flow, without germinating, if the water were cold enough. Upon being deposited at an adequate location, with higher water and/or air temperature (as the flow recedes, a seed deposited under water will be quickly uncovered), such a seed would still have a noticeable probability of germination, but it would have lost some germination energy (Figure 1). In the upper reaches of the Flathead River, Montana, USA, where I conducted my larger investigation of cottonwood establishment, maximum seed release covers a two-week period starting in early to mid-June. During this period, water temperatures in snowmelt-fed rivers range from a low of 7°C to a high of about 12°C. This means that my findings are ecologically relevant: cottonwood seeds falling in snowmelt waters and transported downstream by the flow will have their germination delayed until they reach more favorable temperatures. According to my motion experiments, even if germination did happen while the seeds are being washed downstream, it would not cause any detrimental effects.

This possibility raises the prospect of long-distance hydrochorous seed dispersal in *P. trichocarpa*, and maybe in other riparian *Populus* and Salicaceae in general, in the downstream direction along the longitudinal axis of a river. This was hypothesized by Krasny et al. (1988) when they stated "Germinants from seeds landing on the river may be transported downstream and subsequently washed up onto river bars". The prevalence of such a mechanism over wind dispersal could be tested with genetic investigations: Genetic distance between populations along a river continuum would correlate with geographic distance, and there would be a downstream accumulation of diversity because of unidirectional gene flow. Some genetic studies have been conducted on North American cottonwoods and European poplars (e.g., Webber and Stettler 1981, Légionnet and Lefèvre 1996, Arens et al. 1998), but these researchers sampled populations across a broad geographical range, straddling many basins, or else they did not specifically consider the question at hand. Only Imbert and Lefèvre (2003) have looked at the genetic

structure along an entire river system, for the riparian poplar *Populus nigra* L. Their results lend mixed support to the hypothesis of hydrochorous seed dispersal: Gene flow was higher in the upper, steeper reaches of the river, but there was no evidence of diversity accumulating downstream.

During my field research, I observed many times that seeds falling on moving, more turbulent waters were quickly incorporated into the flow. On the other hand, those falling on the surface of pools, and mostly on backwaters, with little current speed, less turbulence, and reduced surface waves, would usually float on their pappus, and be very easily displaced by the wind. These seeds skated over the surface until reaching shore, where they accumulated in large numbers. Superposing a gradual stage recession to this wind-driven mechanism for lateral deposition results in the formation of bands with very high densities of seeds, which were observed along sandy shorelines in slow-flowing reaches of my study system. In the motion experiments with circulating chambers, I placed the seeds with their pappus on the exposed water surface, and they were rapidly incorporated into the flow. These observations, together with results of my seed flotation experiment, lend support to the proposed conceptual mechanism for "within-the-flow" versus "wind over the flow surface" dispersal of seeds with their pappus, depending on the turbulence of the flow.

In the cases of experiments 2 and 3, not all runs could be conducted simultaneously. This meant that seeds from the same original batch had to be used at different times, sometimes more than 4 weeks apart. In experiment 3, no care was taken to control for differences in germination vitality, as I was only interested in testing the effects of motion on germination, as compared with quiet water. The results of this experiment clearly showed how seed vitality decreased with time: contrary to expectation, the germination rates after 4 days under water were lower than those after 2 days. In this case, it was clear that the order in which the experiments were run had a more important effect on germination than the time of exposure under water, even though all tests were carried out at the same temperature. In the case of experiment 2, I attempted to minimize the effects of loss of vitality, by storing the seeds under controlled conditions between successive experimental runs. Still, all of the final results, obtained after a period at room temperature (e.g., those shown in Figures 5 and 6), strongly suggest that the

order in which the experiments were conducted had a fundamental effect, which overrode that of temperature. Germination rates were higher for bath temperatures of 10.0 and 15.0°C, followed by 12.5 and 20.0°C, and finally by 7.5 and 17.5°C. This is exactly the order in which the experiments were run. On the other hand, such effects are not really apparent in the partial results, after 4 days in the baths at controlled temperatures. The only way to control for the confounding effects of seed energy decay would be to conduct all temperature tests simultaneously.

References Cited

Arens, P., H. Coops, J. Jansen, and B. Vosman. 1998. Molecular genetic analysis of black poplar (*Populus nigra* L.) along Dutch rivers. *Molecular Ecology*, **7**, 11-18.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. In *Biology of* Populu*s and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 57-85.

Eckenwalder, J.E. 1996. Systematics and evolution of *Populus*. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 7-32.

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

Farmer, R.E., Jr., and F.T. Bonner. 1967. Germination and initial growth of eastern cottonwood, as influenced by moisture stress, temperature, and storage. *Botanical Gazette*, **128**, 211-215.

Hauer, F.R., and A.C. Benke. 1987. Influence of temperature and river hydrograph on blackfly growth rates in a subtropical blackwater river. *Journal of the North American Benthological Society*, **6**, 251-261.

Hauer, F.R., and V.H. Resh. 1996. Benthic Macroinvertebrates. pp. 339-370. In F.R. Hauer and G.A. Lamberti (eds). *Methods in Stream Ecology*. Academic Press. New York. p 674.

Hosner, J.F. 1957. Effects of water upon the seed germination of bottomland trees. *Forest Science*, **3**, 67-70.

Imbert, E., and F. Lefèvre. 2003. Dispersal and gene flow of *Populus nigra* (Salicaceae) along a dynamic river system. *Journal of Ecology*, **91**, 447-456.

Karrenberg, S., P.J. Edwards, and J. Kollmann. 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology*, **47**, 733-748.

Krasny, M.E., K.A. Vogt, and J.C. Zasada. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Holarctic Ecology*, **11**, 210-219.

Légionnet, A., and F. Lefèvre. 1996. Genetic variation of the riparian pioneer tree species *Populus nigra* L. I. Study of population structure based on isozymes. *Heredity*, **77**, 629-637.

Mahoney, J.M., and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment – An integrative model. *Wetlands*, **18**: 634-645.

Putnam, J.A. 1951. *Management of bottomland hardwoods*. Southern Forest Experimental Station, Occasional Paper N°16, New Orleans, Louisiana.

Rood, S.B., J.H. Braatne, and F.M.R. Hughes. 2003. Ecophysiology of riparian cottonwoods: Stream flow dependency, water relations, and restoration. *Tree Physiology*, **23**, 1113-1124.

Schreiner, E.J. 1974. *Populus* L. Poplar. In Seeds of woody plants in the United States. p. 645-655. C. S. Schopmeyer, tech. coord. U.S. Department of Agriculture, Agriculture Handbook 450. Washington, DC.

Weber, J.C., and R.F. Stettler. 1981. Isoenzyme variation among ten populations of *Populus trichocarpa* Torr. et Gray in the Pacific Northwest. *Silvae Genetica*, **30**, 82-87.

CHAPTER 5: COARSE SURFACE LAYER STRONGLY AFFECTS MOISTURE WITHIN

GRAVEL BARS: RESULTS FROM AN EVAPORATION EXPERIMENT

<u>Introduction</u>

As part of a comprehensive three-year study of the factors determining successful cottonwood establishment in a gravel-bed river, I dug a series of pits on gravel bars, at locations both with and without seedlings, after carefully removing the coarse surface layer (see Chapter 2). I consistently observed that the fine sediments located immediately under the coarse surface layer were still quite moist, independently of the sites' elevation in relation to the river stage, even after weeks or months with no rainfall. On the other hand, at those locations without a coarse surface layer, where the fine material reached the surface, the soil was usually very dry within only a couple of days after the last precipitation event, unless there was local capillary ascent from a shallow, alluvial water table. As this effect could have important implications for early establishment of riparian vegetation, I carried out an experiment to assess its magnitude.

Pristine floodplain corridors of alluvial rivers are among the most dynamic, complex, diverse, productive, as well as endangered ecosystems (Naiman and Décamps 1997, Tockner and Stanford 2002, Ward et al. 2002, Stanford et al. 2005). Woody plants are one of the primary controls on the biophysical complexity of river-floodplain ecosystems: Many of the processes that affect river corridor morphology and thus determine the structure and function of fluvial ecosystems, such as channel form, floodplain formation, habitat diversity and availability, particulate organic matter fluxes, bank stability, large woody débris dynamics, nutrient retention and transformation, water temperature, etc., are affected by floodplain forests located on, or upstream of, a given reach (Gregory et al. 1991, Décamps 1996, Bennett & Simon 2004). A good comprehension of riparian forest dynamics is thus a fundamental foundation for understanding the morphological and associated ecological pattern and process of river systems, and also in order to better manage fluvial systems, restore degraded river

corridors, and design and operate hydraulic projects in environmentally-friendly ways, based on ecological principles (Brierley et al. 1999, Montgomery and Bolton 2003).

Riparian succession in gravel-bed rivers is usually initiated in the active part of the channel, when seedlings colonize bare river sediments exposed by the physical processes of erosion and sedimentation (Braatne et al. 1996, Stanford et al. 2005). The most critical phase in floodplain forest succession can be posited to be the early establishment of vegetation on the bare, exposed sediments of recently formed bars, as young seedlings need to survive the harsh conditions, involving frequent inundation, scouring by water and in some climates ice, and summertime desiccation (Mahoney and Rood 1998, Tabacchi et al. 1998, Stanford et al. 2005).

Cottonwoods, in the genus *Populus* (family Salicaceae), are important riparian trees in most of western North America, providing wildlife habitats and a host of values for humans (Braatne et al. 1996) . There is ample field evidence that damming and water abstractions have had deleterious effects on their floodplain forests, limiting recruitment (see reviews by Rood and Mahoney 1990, Braatne et al. 1996, and Rood et al. 2003). This has led to highly skewed age distributions of cottonwoods along many rivers in the Western US and Canada, with mostly old, remnant trees, but few young adults, saplings, and seedlings (Fenner et al. 1985, Bradley and Smith 1986, Rood et al. 1995, Rood and Mahoney 1995). Other poplar species in the same sections as those found in North America play the same ecological roles in riparian zones of Eurasia and Northern Africa (Eckenwalder 1996), so that similar impacts are probably occurring on many dammed and diverted rivers throughout the Northern Hemisphere (e.g., in Europe, Hughes and Rood 2003).

Successful establishment of cottonwoods is initially related to the availability of bare, moist sediment surfaces. Seedlings need a continued supply of water during their first growing season, in order not to desiccate (Braatne et al. 1996, Mahoney and Rood 1998, Rood et al. 2003). In areas where summers are typically dry, with little precipitation, the soil moisture within a bar generally comes from the river. This may occur either directly, as capillary ascent from the alluvial water-table (Mahoney and Rood 1998), or indirectly, as floodwater held within the matrix of fines after recession (see Chapter 2).

In many alluvial gravel-bed rivers, the bars consist of a framework of cobble and gravel particles, partially filled with a matrix of sand and silt. Such framework-supported mixtures of fines and gravels usually exhibit a bimodal sediment size distribution, whereby the sand, silt, large gravel, and cobbles make up most of a sediment sample, while the finer gravel sizes are under-represented (Church et al. 1987). Another ubiquitous feature of bars in gravel-bed rivers is the presence of a coarse surface layer composed of clean gravel and cobble overlaying the mixture of fines and gravel (Church et al. 1987). This has also been referred to as the 'winnowed layer' in the literature, an explicit reference to its possible formation by preferential removal of finer material. As depositional processes can also be involved (Andrews and Parker 1987), I will only use the more general term ('coarse surface layer') herein.

It should be expected on theoretical grounds that the presence of a coarse surface layer would decrease evaporation. Three conditions must be met for evaporation from a soil to occur and persist (Hillel 1998): First, a continuous supply of energy is required to change water-phase from liquid to gas. Second, vapor must be removed by advection or diffusion, so that a concentration gradient is maintained between the soil surface and the atmosphere. Third, there must be a continued supply of water to the evaporating surface from within the soil. The presence of a coarse surface layer of clean gravel and cobble can be expected to decrease evaporation from the soil surface by reducing both the amounts of energy and advection available. Solar radiation supply is reduced because the coarse particles shade the fines underlying them, reducing insolation (the amount of radiation energy received) at the wet, evaporating surface. The sensible heat flux towards the ground is decreased, because the open framework of the coarse layer has a low heat conductance, as the particles contact each other at a limited number of points and the interstitial spaces are filled with air. Advection at the evaporating surface is also reduced, because the coarse layer breaks the wind profile, sharply decreasing the removal of water vapor.

It has been known to man for thousands of years that placing a layer of stones over an agricultural field is a very effective mechanism for suppressing evaporation and increasing moisture in the underlying soils (Hillel 1998). Historians have reported the use of rock-mulch or lithic-mulch agriculture in places as disparate as present Israel and Italy,

the Atacama desert, Easter Island, and the Canary Islands, just to mention a few (Lightfoot 1994). Rock mulch also occurs naturally: Titus and del Moral (1998) report that seedling establishment on volcanically devastated sites around Mount St. Helens, USA, is influenced by the thickness of the tephra layer (fragments ejected by the eruption) acting as rock mulch, "which impedes evaporation from below and thus is capable of holding considerable moisture at lower depths".

In regions with dry summers, river gravel bars can be considered to be arid environments. Even though the moisture-protecting effect afforded by the coarse surface layer could be quite important in explaining seedling success in river floodplain environments (see Chapter 2), I have not been able to find any reference to it in the literature. Thus, the goal of this study was to quantify how the presence of a coarse surface layer of varying thickness affects water loss from the underlying mixture of fines and gravels, and the resulting soil moisture within the matrix of fines. In order to control for natural variation of depth to the water-table, vertical distance to the capillary fringe, and continuity of the fine matrix within the bar, I conducted an outdoor experiment simulating the conditions found on gravel-bars along the river environment.

The experiment consisted of a series of soil columns composed of two different mixtures of fines and gravel, which were covered with coarse surface layers of different thickness. They were exposed to the atmosphere - sun and wind, but not rainfall nor dew, for a period of almost two months. The working hypothesis governing the experiment was that a thicker coarse layer would result in decreased evaporation and enhanced soil moisture within the columns, and that the texture of the matrix material should have effects, as finer sediments are able to both hold and conduct more water by capillarity.

Methods

Experimental Design

I studied the effects that different thicknesses of the coarse surface layer have on evaporative water loss from a mixture of fines and gravels, and compared them with the case for homogeneous fine material without gravel, by constructing 40 soil columns that were placed in an outdoor location. I used a factorial design with two different materials

for the matrix - a finer and a coarser sand, and four different treatments: coarse surface layers of 0, 4, and 8 cm over the mixture of fines and gravels (hereafter referred to as '0 cm' treatment, '4 cm' treatment, etc.), and a treatment consisting of homogeneous matrix material from bottom to surface (referred to as the 'only fines' treatment). There were five replicates per combination of matrix material and treatment.

To control for uniformity of material yet provide similarity to riverine gravels, I obtained pit run sand, washed masonry sand, and 1½ inch rounded gravel from a local gravel pit mine. The finer matrix material used in the experiments was obtained by mixing pit run sand and washed masonry sand in a 50%-50% ratio by weight, while the washed masonry sand was used directly as the coarser matrix material. Both materials used for the sand matrix were previously sieved, discarding any particles larger than 1.40 mm. As the batches were prepared, five samples of each matrix material, weighing between 1500 and 2000 g each, were taken independently and were sieved in a Ro-Tap sieving machine, yielding the distribution of particle sizes given in Table 1 and shown in Figure 1.

Table 1. Particle size distributions and fractions per size class according to the Wentworth size classification for the two types of matrix material used in the experiments. Values are the means (± standard deviation) in percent of total weight, for samples of size n = 5.

	Finer Matrix Material		Coarser Matrix Material	
Retained in 1.00 mm sieve	0.0 (± 0.03)	7.2 (± 1.15) Coarse sand	2.1 (± 0.71)	16.8 (± 2.38) Coarse sand
Retained in 840 µm sieve	0.5 (± 0.10)		1.5 (± 0.36)	
Retained in 500 µm sieve	6.7 (± 1.04)		13.2 (± 1.36)	
Retained in 355 µm sieve	10.9 (± 0.51)	29.9 (± 1.50) Medium sand	22.8 (± 0.82)	57.2 (± 1.28) Medium sand
Retained in 250 µm sieve	19.0 (± 1.02)		34.4 (± 1.43)	
Retained in 125 µm sieve	40.2 (± 5.17)	Fine sand	22.4 (± 1.48)	Fine sand
Retained in 63 µm sieve	16.5 (± 5.11)	Very fine sand	2.9 (± 0.23)	Very fine sand
Passing the 63 µm sieve	6.1 (± 1.05)	Silt	0.7 (± 0.09)	Silt

In order to cover the natural range of grain size variation, as it relates to riparian vegetation establishment, the finer and coarser matrix materials for the experiments were chosen in order to broadly simulate the ranges of particle sizes found at bar locations with and without cottonwood seedlings of the year on my field study site: the Nyack Floodplain, Middle Fork of the Flathead River, Montana, USA. During the summers of 2006 and 2007, 52 matched pairs of 25 cm-deep pits were excavated on six different gravel bars along the reach. The paired pits were always close to each other, had similar surface texture, and were located at the same elevation, but one had cottonwood seedlings while the other did not (see Chapter 2 for more detail). Their mean particle size distributions are shown on Figure 1. The 0.20 mm median size of the finer experimental material matches the average river material at locations with seedlings. On the other hand, the coarser experimental material was more homogeneous than that found at the study sites without cottonwood seedlings; it has less grains both from the coarser and finer fractions, even though the median sizes are very similar (0.32 mm for the coarser experimental material versus 0.33 mm for the river material at sites without seedlings).
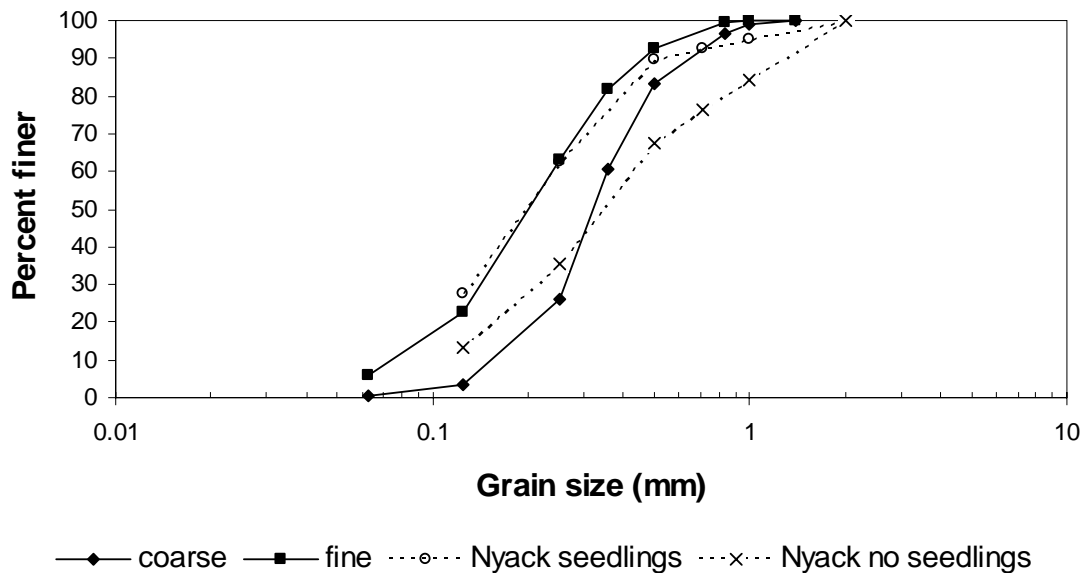

Figure 1. Mean grain size distributions for both matrix materials (n=5), and for a series of pits excavated on the Nyack Floodplain, Middle Fork of the Flathead River, Montana, USA, at locations with and without cottonwood seedlings of the year (n=21).

The median particle size for the finer matrix material (0.20 mm) is not much smaller than that for the coarser material (0.32 mm), but the finer material has a much larger proportion of very fine sand and silt (22.6 versus 3.6 %), which should result in a higher water retention capacity, lower hydraulic conductivity, and higher sorptivity (Hillel 1998).

Both theoretical calculations and field measurements indicate that the matrix can constitute between 22 and 32 percent of the total weight of a gravel-bed sample (Church et al. 1987). Using the mid-point of this range, I initially attempted to construct mixtures with 27% fines and 73% gravel, but in some cases this resulted in matrix-supported mixtures, where the gravel particles were not always in contact with each other due to excess of fines. Thus, I ended up using 25% fine material and 75% gravel, which always resulted in framework-supported mixtures of fines and gravels, as found in all pits excavated in the field. The soil columns were built in heavy-plastic round bags, with a diameter of 25.4 cm and 34 cm in height. In order to ensure homogeneity and matrix continuity within the soil column, the mixtures were built by layers, successively adding 750.0 (± 2.0) g of gravel and then 250.0 (± 0.05) g of oven-dried, fine material. After the final layer of fines was added, further fine material was added or some gravel subtracted, until the resulting soil surface was at the desired height, and approximately showed an areal composition of 50% gravel and 50% fines. Considering this extra material, the mixtures had a final composition of 26.5% fines (± 0.52% standard deviation, n = 30). This latter step was done to ensure that the area of the fine, evaporating surface was similar between treatments and replicates. Of course, the replicates for the 'only fines' treatment, with homogeneous matrix material, did not include any gravel, so that their upper (evaporating) surface always consisted of 100% fines.

In order to minimize differences between replicates and treatments, the gravel particles used for the coarse surface layer were visually selected from the 1½ inch gravel batch, so that only rounder particles in a narrow range of sizes were used. Two hundred such particles were randomly sampled and their major and minor axes were measured with a caliper. The mean length of the major axis was 30.9 mm, with a standard deviation of 3.7 mm and a range from 25 to 40 mm. For the minor axis, the mean was 21.2 mm,

with a standard deviation of 3.1 mm and a range from 16 to 33 mm. The ratio (major axis/minor axis) had a mean value of 1.48, with a standard deviation of 0.18 and a range from 1.12 to 2.06.

Before adding the coarse surface layer, the bags containing the mixtures of fines and gravels were placed in buckets, and the vertical distances from the soil surface to the rim of the buckets were measured, to ensure that all replicates within a given treatment would be comparable in terms of insolation and wind environment. Then, water was slowly added to each bag, until its level matched the matrix surface (or the sand surface for the case of the 'only fines' treatment). Water filling was done over a period of three days, to allow for air bubbling, thus ensuring full saturation of the soil columns. The bags were then punctured at their base, covered to avoid evaporative losses, and let to rest for 48 hours, to allow excess water to drain gravitationally. Then, the holes at the base were sealed with tape, a coarse surface layer of the desired thickness (0, 4, or 8 cm) was placed on top of the mixture of fines and gravel, the bags were placed in the buckets, the upper part of the space between the bags and the bucket walls was filled with Styrofoam for insulation, and finally gravel (of the same caliber as that used for the coarse surface layer) was laid on top of the Styrofoam, around the bags, level with that atop the soil column.

The buckets, complete with their bag containing the wet soil column, the Styrofoam, and the gravel, were weighed to the nearest tenth of a gram, in order to compute the net amount of water at the beginning of the experiment and the initial bucket weight. They were then placed randomly, in a rectangular arrangement of five by eight buckets, surrounded by white-painted fiberboard of the same height, lined on its inside with 1-inch thick Styrofoam board, for insulation. The site was located on the grounds of the Flathead Lake Biological Station, Polson, Montana, USA, a short distance from the lake shore. The array of buckets was fenced, in order to avoid disturbances by people or animals, which could alter the experiment weights. The 40 buckets with their soil columns were exposed to the atmosphere for 58 days, between August 29 and October 25, 2008. In order to allow only for progressive drying, the gravel columns were covered with a tarp on rainy days and at nights, to avoid rainfall and dew water inputs. The mean characteristics of the soil columns for each of the eight treatments are given in Table 2.

Table 2. Characteristics of the soil columns for all combinations of matrix material and treatment. Each value is the mean of five replicates (± standard deviation).

Treatment	Gravel weight (g)	Matrix fines weight (g)	Initial water weight (g)	Initial average water content (g/g)	Surface to bucket rim distance (mm)
Finer matrix material					
0 cm coarse layer	10656.4 (± 25.9)	3790.1 (± 26.5)	993.3 (± 7.2)	0.262 (± 0.002)	9.2 (± 0.8)
4 cm coarse layer	9737.5 (± 25.2)	3512.5 (± 28.9)	885.9 (± 13.8)	0.252 (± 0.004)	40.8 (± 1.1)
8 cm coarse layer	8420.3 (± 89.2)	3075.2 (± 80.4)	806.0 (± 7.1)	0.262 (± 0.008)	79.6 (± 1.1)
Only matrix material	n/a	10574.0 (± 151.6)	2239.5 (± 41.4)	0.212 (± 0.006)	10.0 (± 1.2)
Coarser matrix material					
0 cm coarse layer	10673.3 (± 12.2)	3700.7 (± 33.3)	919.4 (± 15.1)	0.248 (± 0.005)	9.2 (± 1.3)
4 cm coarse layer	9442.6 (± 112.4)	3492.4 (± 50.2)	865.8 (± 17.5)	0.248 (± 0.006)	40.2 (± 1.8)
8 cm coarse layer	8259.8 (± 56.3)	3000.0 (± 0.0)	789.3 (± 19.8)	0.263 (± 0.007)	79.8 (± 1.3)
Only matrix material	n/a	10060.0 (± 204.1)	1993.5 (± 22.5)	0.198 (± 0.005)	10.2 (± 1.6)

It is clear that the standard deviations are in all cases much smaller than the corresponding means, indicating that the five replicates for each one of the eight possible combinations of matrix material and treatment were very similar to each other in all respects.

Measurements and Analyses

After the initial weighing, the buckets were re-weighed at specific time intervals, totalling seven occasions over a 58 day total experiment duration. This was done on a Mettler PK-36 Deltarange balance, which can weigh up to 30 kg with a precision of 0.1 g. Weights were rounded off to the nearest gram when recording. As the initial bucket weights were known, all differences were assumed to correspond to water losses by evaporation at the soil column surfaces, so that the remaining water weight could be computed. The spatially averaged soil moisture (gravimetric water content in g/g, on a dry basis) in each column was computed for each date by dividing the water weight by the known dry weight of fines in the matrix, i.e., by assuming that all water in the bags is held within the matrix material. This should be a very good assumption, considering the

large size difference between the gravel and the fines in the mixture. After each weighing session, the buckets were randomly placed back in the outdoor array.

After checking for normality and equality of variances, statistical analyses of variance of the soil moisture data were carried out using a General Linear Model (GLM) with repeated measures, in SPSS version 16.0 (SPSS, Inc.) This is essentially a two-factor ANOVA in which the same measurement is made several times on each subject, with matrix material and treatment as between-subject factors, and the repeated measurements on eight different occasions during the experiment as within-subject factors. For significant models, post-hoc pairwise comparisons were carried out using both Tukey's honestly significant difference (HSD) test and Tamhane's T2 test.

Results

The results from this evaporation experiment are presented as temporal variation of two different, inter-related variables: cumulative water loss (in g) and spatially averaged gravimetric water content (in g/g), for the soil columns.

Water Loss

The average cumulative water loss at the end of the experiment ranged from less than 200 g to more than 1800 g of water per soil column, depending on the combination of matrix material and treatment (Figure 2).

The water losses through time looked very similar for both matrix materials when there was a 4 or 8 cm thick coarse surface layer present. In the '0 cm' treatment, where the mixture of fines and gravel reached the top of the soil column, the finer matrix material showed a much faster water loss (for example, 598.4 g after 11 days, versus only 358.4 g for the coarser matrix material). This resulted in a final loss which was 33.7% higher for the finer than for the coarser matrix material. For the case of the coarser matrix material, the presence of an 8 cm thick surface layer of clean gravel reduced final water loss by a factor of 3, with respect to the case where the mixture of fines and gravels reaches all the way to the surface. The treatment with a 4 cm thick surface layer saw a decreased water loss of 31.9%, as compared with the '0 cm' treatment.

Figure 2. Cumulative water loss over the duration of the experiment, for each matrix material and the four different treatments. Each value is the mean (± standard deviation) of five replicates. Vertical scale is the same for both plots.

These differences are larger for the finer matrix material: the 8 cm thick layer reduces water loss by a factor of 3.8, and the 4 cm thick layer by 48.7%, with respect to the case without coarse surface layer.

Shapiro-Wilks tests for normality were carried out for each one of the 56 combinations of matrix material, treatment, and measurement date. I used a significance level $\alpha = 0.10$, as recommended by Helsel and Hirsch (1992) for small sample sizes, in order to increase power to detect non-normality. In all cases, the null hypothesis that the data are normally distributed was not rejected. I used Levene's test to check for equality of error variances; for all of the measurement dates, I rejected the null hypothesis that the error variance of the cumulative water losses was equal across the different groups. Because the required assumptions for analysis of variance were not met in the case of the water loss data, and there is no equivalent non-parametric test to the two-factor ANOVA with repeated measures, I decided to carry out the analysis of variance only on the soil moisture data, which mostly passed the normality and equality of variances tests. Also, as

discussed below, soil moisture is the derived variable of interest when investigating vegetation establishment.

Wilcoxon-Mann-Whitney tests were used to look at differences in water loss between treatments, across the two different matrix materials. For the two treatments with a coarse surface layer (8 or 4 cm thick), the null hypothesis that the water loss data for the finer and the coarser matrix material come from the same population was not rejected, for all measurement times. In other words, when there is a coarse surface layer, there is no effect of the matrix material on soil evaporation. For the two treatments with fines reaching the top of the soil column, water losses were significantly different when comparing the finer and the coarser matrix material (p = 0.008 at all measurement times, except for the 'only fines' treatment, where p = 0.016 at the third measurement date, and there were no significant differences for the first and second dates; all of these are exact significance levels).

Soil Moisture

The mean gravimetric water content also showed clear differences between matrix materials and treatments (Figure 3.) Shapiro-Wilks tests for normality were conducted on the soil moisture data for each one of the 64 possible combinations of matrix material, treatment, and measurement date: In all cases but one (coarser matrix material with 0 cm

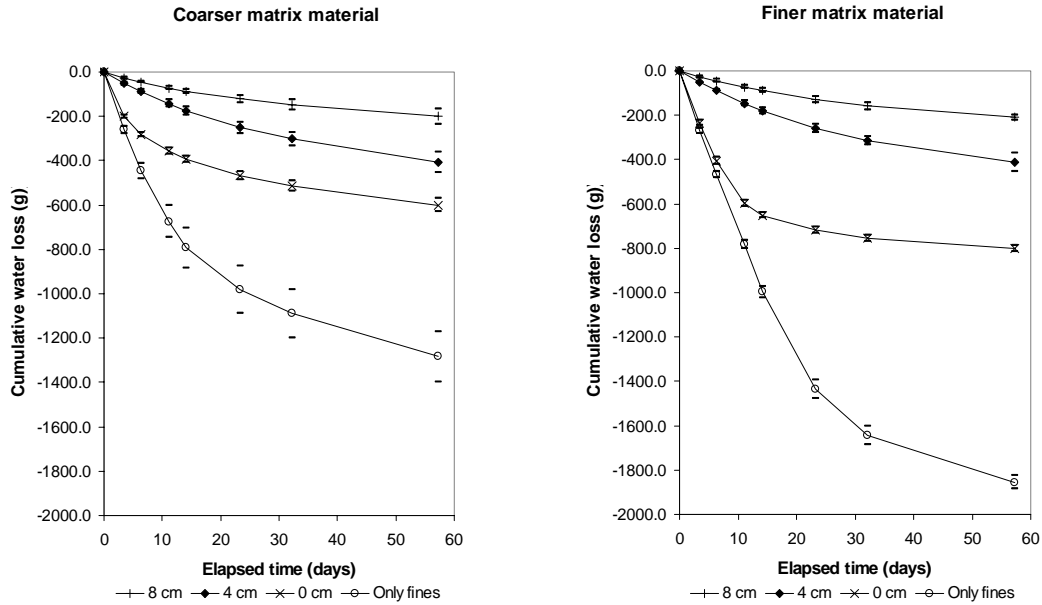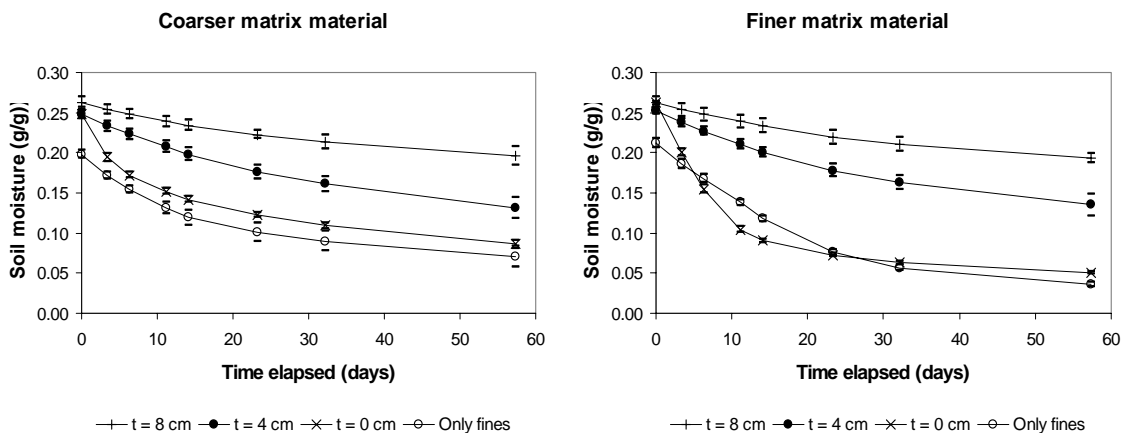Figure 3. Gravimetric water content (soil moisture) over the duration of the experiment, for each matrix material and the four different treatments. Each value is the mean (± standard deviation) of five replicates. Vertical scale is the same for both plots.

126

thick surface layer, for the second measurement date, which had p = 0.007), the null hypothesis that the data are normally distributed was not rejected at a significance level α = 0.10. Using Levene's test for the equality of error variances, I found that for all of the measurement dates, the null hypothesis that the error variance of the soil moisture data is equal across the different groups was not rejected at a significance level α = 0.05. On the fifth, sixth, and eighth (final) measurement dates, p was in the range 0.05-0.10.

The GLM with repeated measures was highly significant (p<0.0001). All multivariate tests, tests of within-subject effects, and tests of between-subject effects indicated that all of the model factors (matrix material, treatment, and measurement date) as well as all of their possible 2 and 3-way interactions were significant with p<0.0001. The post-hoc overall pairwise comparisons between treatments were all significant with p<0.0001, for both Tukey's HSD and Tamhane's T2 tests. The only exception was Tamhane's T2 test comparing the 'only fines' with the '0 cm' treatments, where p was 0.195.

In order to look at pairwise comparisons of soil moisture between treatments, but across the two different matrix materials, I used exact Wilcoxon-Mann-Whitney tests. As was the case for the water loss data, mean moistures were not significantly different between the finer and the coarser material for the '8 cm' and '4 cm' treatments, throughout the duration of the experiment. On the other hand, in the case of the '0 cm' treatment, only for the first re-weighing date (3.4 days after beginning the experiment) were the means not significantly different; afterwards, moisture decreased faster and to lower values, in the case of the finer matrix material. For the 'only fines' treatment, mean moistures were significantly different between the coarser and the finer matrix material for six of the eight measurement dates.

Discussion

The soil columns were dismantled 82 days after the beginning of the experiment, a period during which no water at all was added to them. By then, the soil was dry in both treatments with fines to the surface (the '0 cm' and 'only fines' treatments); on the other hand, in all replicates with a coarse surface layer (the '4 cm' and '8 cm' treatments), the

upper surface of the matrix was still moist, almost wet, and this was the case for both matrix materials. These differences are clearly shown in my data: The soil water content, as averaged over the columns, is significantly larger for the two treatments with a coarse surface layer, by a factor of up to 5.3 times (comparing the '8 cm' and the 'only fines' treatments, in the case of the finer matrix material). Even the thinner, 4 cm coarse layer results in large increases in soil moisture, by a factor of up to 3.7 times (when comparing the '4 cm' versus the 'only fines' treatment, for the finer matrix material).

I obtained large differences in water loss and soil moisture, even though my experimental design was very restrictive in terms of water availability: The soil columns were initially filled with water at saturation, but were then allowed to drain gravitationally for 48 hours. It is usually assumed in agricultural practice that draining a soil for two days will result in moisture at field capacity, except when there is clay present. In this case, with sands ranging from medium to very fine, and some silt, I am reasonably certain that all water that could have drained by gravity did so during this 48-hr period. Thus, only the volume of water held by capillarity, in the pores of a 34-cm tall soil column, was available for evaporation during the 58 day long experiment, carried out in late summer and early fall. Still, the final moisture values were very high when a coarse surface layer was present.

Evaporation from the soil is a process that occurs in two distinct phases, separated by a sharp transition (Philip 1957, Stewart and Broadbridge 1999): In the initial stage, the soil surface is wet enough for water to be supplied at a rate sufficient to meet atmospheric demand. In this phase, evaporation is weather-controlled, i.e., its rate is limited by external meteorological conditions, such as radiation, wind speed, air humidity, etc. Soil surface conditions such as reflectivity and the presence of a mulch will influence evaporation but there is no effect of the soil profile. After a few hours or days under normal conditions, the soil will become too dry to maintain the atmospherically-set evaporativity (the potential evaporation rate). This is the second, soil profile-controlled stage of evaporation, where the rate is limited by the ability of the soil profile to deliver moisture to the evaporating surface.

In this case, there were significant differences in moisture between matrix materials only for those treatments in which the fines reached the top of the columns. On

the other hand, I observed no significant difference between the two matrix materials, over the 58 day duration of the experiment, when a coarse surface layer was present. This indicates that the presence of a coarse surface layer delays the occurrence of the profile-controlled phase of the evaporation process, from a few days to a few months. In other words, because of the reduced radiation, advection, and ground heat flux, the atmosphere-controlled phase of evaporation lasts much longer; this is why there are no differences in water loss or soil moisture attributable to the two different matrix materials. Of course, it is important to note that in these cases, the 'atmosphere' that is felt by the evaporating surface is indeed very different from that only 4 or 8 cm above it, at the actual top of the column.

It is well known that finer soils can hold more water against gravity by capillarity (Hillel 1998). On the other hand, towards the end of my experiment, the finer matrix material consistently showed significantly lower moistures for all treatments without a coarse surface layer. How can this be explained? Even though it can initially hold more water against gravity, the finer material also has a higher sorptivity (a measure of capillary absorption) than the coarser one, because of its smaller pores. This allows moisture to move up the soil column more easily than for a coarser sand. As the atmosphere dried the soil surface and evaporation progressed from the first, weather-controlled stage, to the second, profile-controlled stage, water was drawn from the lower part of the soil columns at a faster rate for the finer material, resulting in the observed lower water contents. Note that if a shallow water-table were present, as can happen under actual river bars, a finer matrix material would cause a higher capillary fringe and a faster rate of upward water flux, resulting in higher soil moisture contents within the bar.

As should be expected, the water losses are much higher for those treatments involving only homogenous matrix material, without gravel. This is due in large part to the fact that the spatially-averaged porosity (over the whole column), and thus the initial water content, are much larger, but can also be explained by the larger evaporating surface. Comparing results for the finer and the coarser material, the water losses are very similar for a few days at the beginning of the experiment, when evaporation is still controlled by atmospheric conditions, but then diverge (means are not significantly different for the first two weighing dates, on days four and seven, but are significantly

different for all subsequent times). After evaporation becomes profile-controlled, losses are much higher for the finer matrix material than for the coarser. Final water loss for the finer matrix material is 44.6% larger than it is for the coarser material, in the case of the 'only fines' treatment.

It is important to note that the total amount of water present in the soil column, which is directly related to the cumulative water loss, is not the most relevant variable from a plant's perspective. Instead, what really matters is how moist the soil is, i.e., how much water mass there is per unit mass of dry soil (the gravimetric water content on a dry basis), as this determines the soil-water matric potential against which the roots must work in order to extract moisture.

Most literature on vegetation establishment on gravel bars, and specifically that on cottonwoods (reviewed in Braatne et al. 1996 and Rood et al. 2003), has stressed the importance of moisture availability on seedling success. The currently accepted model for cottonwood establishment (the 'Recruitment Box', Mahoney and Rood 1998) is based on the fact that cottonwood seedlings are obligate phreatophytes, i.e., that their growing roots must continuously tap either the alluvial water table or the capillary fringe (the tension-saturated zone immediately above the groundwater). My results suggest that a ubiquitous feature of gravel-bed rivers, the presence of a coarse surface layer, can strongly affect water content within bars, maintaining high levels of soil moisture for weeks or months, even when there is no underlying water table. It should be noted that my experiments are a limiting case; there would be even more water available to the soil in a natural river setting: rainfall and dew inputs could add moisture, the flood recession would result in a more gradual draining of the soil within the bar, and the presence of a continuous matrix of fines would allow for continued soil water replenishment from the alluvial water table, by capillary rise, at least over a certain vertical range of elevations.

I suggest that the occurrence of a coarse surface layer has such important effects on soil moisture, that it should be incorporated into any model for vegetation establishment specifically developed for gravel-bed rivers. As a corollary, I think that establishment models developed for sand-bed streams should not be applicable to the case of gravel-bed rivers.

Many of my observations in the field support these ideas; for example, I have found that seedlings can establish successfully at much higher elevations with respect to river stage on gravel bars than on sand deposits. Indeed, I have observed extensive mortality of seedling bands on sand bars, even close to shore, as the shallow water table and the adjacent capillary fringe recede, allowing the sand to be dried by the atmosphere's evaporative capacity. Also, at many locations on my study reach, I have observed single lines of cottonwood seedlings and saplings, established along the downstream edges of clean gravel sheets deposited on older, finer bar surfaces. In such cases, there is no establishment whatsoever upstream of the line, on the clean gravel, or downstream of it, on the bar sand; it only happens at the intersection between the new gravel deposit and the fine surface. The most probable explanation for such localized success is that the gravel sheet acts as rock mulch, conserving moisture under it; seedlings cannot establish on the clean gravel nor the dry bar surface, but conditions are adequate along the narrow zone where the gravel sheet and the fine surface intersect. This example indicates that the moisture-enhancing benefits of the coarse surface layer cannot be used by the vegetation if the layer of clean gravel is too thick, as this would impede initial establishment because of light limitations. Thus, there should be a trade-off for seedling establishment with respect to the thickness of the coarse surface layer, between increased moisture for growth on one hand, but decreased light for initial seed establishment on the other.

Conclusions

My experimental results and field observations clearly show that the presence of a coarse surface layer over a mixture of fines and gravels, as is typically found in gravel-bed rivers, can have a very strong effect in maintaining high soil moisture levels within the underlying fine matrix, for periods of weeks or even months without any water input. Such effects are realized even when there is no alluvial water table from which water could be drawn by capillarity. I suggest that this rock mulching effect could be fundamental in allowing successful establishment of seedlings of cottonwoods (and other riparian plants). Thus, establishment models developed for sand-bed streams should not

be expected to perform well in gravel-bed rivers. Thickness of the coarse surface layer should be expected to enhance seedling success, because of increased effects on moisture, but decrease initial seed establishment, because of light limitations.

References Cited

Andrews, E.D., and G. Parker. 1987. Formation of a coarse surface layer as the response to gravel mobility. In *Sediment Transport in Gravel-Bed Rivers*. Edited by C.R. Thorne, J.C. Bathurst, and R.D Hey. John Wiley and Sons, Chichester. Pp. 269-299.

Bennett, S.J., and A. Simon. 2004. *Riparian Vegetation and Fluvial Geomorphology*. Water Science and Application series N°8, American Geophysical Union, Washington, DC.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 57-85.

Bradley, C.E., and D.G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany*, **64**, 1433-1442.

Brierley, G.J., T. Cohen, K. Fryirs and A. Brooks. 1999. Post-European changes to the fluvial geomorphology of Bega catchment, Australia: Implications for river ecology. *Freshwater Biology*, **41**, 839-848.

Church, M.A., D.G. McLean, and J.F. Wolcott. 1987. River bed gravels: Sampling and Analysis. In *Sediment Transport in Gravel-Bed Rivers*. Edited by C.R. Thorne, J.C. Bathurst, and R.D Hey. John Wiley and Sons, Chichester. Pp. 43-88.

Décamps, H. 1996. The renewal of floodplain forests along rivers: a landscape perspective. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **26**, 35-59.

Eckenwalder, J.E. 1996. Systematics and evolution of *Populus*. In *Biology of* Populus *and its Implications for Management and Conservation*. Part I, Chapter 3. Edited by R.F. Stettler, H.D. Bradshaw, P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa. Pp. 7-32.

Fenner, P., W.W. Brady, and D.R. Patton. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. *Journal of Range Management*, **38**, 135-138.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience*, **41**, 540-551.

Helsel, D.R., and R.M. Hirsch. 1992. *Statistical Methods in Water Resources*. Studies in Environmental Science 49, Elsevier, Amsterdam. 530 pages.

Hillel. 1998. *Environmental Soil Physics*. Academic Press. San Diego.

Hughes, F.M.R., and S.B. Rood. 2003. Allocation of river flows for restoration of floodplain forest ecosystems: A review of approaches and their applicability in Europe. *Environmental Management*, **32**, 12-33.

Lightfoot, D.R. 1994. Morphology and ecology of lithic-mulch agriculture. *Geographical Review*, **84**, 172-185.

Mahoney, J.M., and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment – An integrative model. *Wetlands*, **18**, 634-645.

Montgomery, D.R. and S.M. Bolton. 2003. Hydrogeomorphic variability and river restoration. Pages 39-80 in R.C. Wissmar and P.A. Bisson, editors. *Strategies for Restoring River Ecosystems: Sources of Variability and Uncertainty in Natural and Managed Systems*. American Fisheries Society, Bethesda, Maryland.

Naiman, R.J., and H. Décamps. 1997. The ecology of interfaces – riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621-658.

Philip, J.R. 1957. Evaporation and moisture and heat fields in the soil. *Journal of Meteorology*, **14** 354–366.

Rood, S.B., and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. *Environmental Management*, **14**, 451-464.

Rood, S.B., J.M. Mahoney, D.E. Reid, and L. Zilm. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. *Canadian Journal of Botany*, **73**, 120-1260.

Rood, S.B., and J.M. Mahoney. 1995. River damming and riparian cottonwoods along the Marias River, Montana. *Rivers*, **5**, 195-207.

Rood, S.B., J.H. Braatne, and F.M.R. Hughes. 2003. Ecophysiology of riparian cottonwoods: Stream flow dependency, water relations, and restoration. *Tree Physiology*, **23**, 1113-1124.

Stanford, J.A., M.S. Lorang, and F.R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **29**, 123-136.

Stewart, J.M., and P. Broadbridge. 1999. Calculation of humidity during evaporation from soil. *Advances in Water Resources*, **22**, 495-505.

Tabacchi, E., D.L. Correll, F.R. Hauer, G. Pinay, A.M. Planty-Tabacchi, and R.C. Wissmar. 1998. Development, maintenance and role of riparian vegetation in the river landscape. *Freshwater Biology*, **40**, 497- 516.

Titus, J.H., and R. del Moral. 1998. Seedling establishment in different microsites on Mount St. Helens, Washington, USA. *Plant Ecology*, **134**, 13-26.

Tockner, K., and J.A. Stanford. 2002. Riverine flood plains: Present state and future trends. *Environmental Conservation*, **29**, 308-330.

Ward, J.V., K. Tockner, D.B. Arscott, and Claret. 2002. Riverine landscape diversity. *Freshwater Biology*, **47**, 517-539.

CHAPTER 6: CONCLUSIONS

On the Underwater Germination of Cottonwood Seeds

Seeds of *Populus trichocarpa* germinate under water, and the seedlings are perfectly able to grow immersed. Both the proportion of seeds undergoing successful underwater germination and the speed at which it occurs have a positive functional dependence on water temperature and time of immersion. At higher temperatures and longer durations under water, germination rates are higher, and the seedlings grow faster. This joint effect of water temperature and immersion time is clearly exposed when one considers germination rate as a function of cumulative degree-days.

My results suggest that the probability of success of an ungerminated seed deposited by the river at a suitable location depends on previous conditions, such as how much time it was in the flow, under which water temperatures. These findings are ecologically relevant: cottonwood seeds falling in snowmelt waters and transported downstream by the flow will have their germination delayed until they reach more favorable temperatures. According to the motion experiments, even if germination did start while the seeds are being washed downstream, it would not cause any detrimental effects, at least in the first few days.

These findings raise the prospect of long-distance hydrochorous seed dispersal in *P. trichocarpa* (and maybe in other riparian *Populus* and Salicaceae in general), in the downstream direction, along the longitudinal axis of a river.

I have documented a series of temperature and motion effects on underwater germination of *P. trichocarpa*. The scant literature available on this topic, as well as some of my own observations with a willow species, suggests that these effects occur across most, if not all riparian Salicaceae. I believe that this overlooked life history trait is a fundamental mechanism employed by these species in seed dispersal, and an important characteristic of the regeneration niche of riparian salicaceous trees. Such specific adaptations suggest that cottonwoods in particular, and other riparian Salicaceae in general, must rely predominantly on hydrochory for dispersal of their seed.

The mean settling velocity of cottonwood seeds in quiet water at 21°C was 1.83 cm/s for the 448 seeds that I tested. I found highly significant, albeit small differences in settling velocities, as a function of hydration times. Speeds were higher for hydration times between 2 and 8 hours, and decreased for shorter or longer durations under water.

The Role of the Coarse Surface Layer

My experimental results and field observations clearly show that the presence of a coarse surface layer over a mixture of fines and gravels, as is typically found in gravel-bed rivers, can have a very strong effect in maintaining high soil moisture levels within the underlying fine matrix, for periods of weeks or even months without any water input. Such effects are realized even when there is no alluvial water table from which water could be drawn by capillarity. I suggest that this rock mulching effect could be fundamental in allowing successful establishment of seedlings of cottonwoods (and other riparian plants) in gravel bars. Thus, establishment models developed for sand-bed streams, which cannot account for this effect, should not be expected to perform well in gravel-bed rivers. A thicker coarse surface layer should be expected to enhance seedling success, because of increased effects on moisture, but decrease initial seed establishment, because of light limitations.

On Timing of Seed Dispersal and its Measurement

I found that *P. trichocarpa* at my study floodplain have a pronounced peak in the temporal distribution of seed dispersal. The distribution is highly skewed, with a vast majority of seeds released in the first few days of the dispersal period, and a long tail to the right. Integrating the temporal distribution of seed rain, I obtained an average of 1842 seeds/m^2 over the 5-week long period of seed dispersal. The single highest measurement was 372 seeds/d/m^2, and the maximum mean across sites for any given sampling period was 160 seeds/d/m^2. The tight and highly significant correlation between seed rain measured at closely-located pairs of traps indicates that the proposed methodology is an effective way of quantitatively measuring the rain of falling cottonwood seeds.

Cottonwood Establishment at the Bar Scale

I found that the proportion of finer material in the root zone, within the matrix, and the thickness of the coarse surface layer are important controlling variables that explain 0+ seedling presence-absence and growth at the within-bar scale. On the other hand, the vertical distance to water seems to play no role. Also, simple comparisons between the length of roots and the depth to water at the end of the growth season indicate that it is impossible, even for the fastest growing seedlings, to maintain contact with the receding water table or capillary fringe during the growing season. Thus, I suggest that cottonwood seedlings growing on gravel bars are facultative instead of obligate phreatophytes, at the very least for their first year of life.

All excavated plants were seedlings, as were most of the cottonwoods of the year that I observed colonizing recently formed bars. Clonal recruitment was only observed at a few previously colonized bars, where flood training and sediment accretion had covered most of the original plants.

The distribution of the particle sizes of the matrix material, within the root zone, controls establishment success because it determines water holding capacity by capillarity. The presence of a coarse surface layer of clean gravel has contrasting effects: On one hand, it acts as mulch, maintaining soil moisture in the underlying fines, but if it is too thick, it impedes establishment. My field measurements and the literature indicate that both controlling variables are spatially variable at very short scales, so that bars must be considered patchy environments in regards to their suitability for establishment.

Over the three growth seasons, I always found many more bars without any establishment than bars with bands or patches of successfully recruited cottonwoods. This was so, even though all of the bars were similar in landscape position, elevational range, surface texture, and floodwater recession rates. This indicates that currently accepted models for cottonwood establishment, which are based only on elevation with respect to stage and on recession rates (and how these are timed in comparison with seed release) are not describing all of the variability in presence-absence of successfully established 0+ seedlings. Actually, such models seem to be much better at explaining where the

seedlings will not be able to establish (i.e., those areas falling outside of the recruitment box), than the actual probability of establishment within the band.

<div align="center">Cottonwood Establishment at the Reach Scale</div>

The Recruitment Box Model, which is the current paradigm for cottonwood establishment, predicts that cottonwood seedlings will recruit on clearly delimited elevational bands. It is based on the assumptions that: (i) cottonwood seedlings are obligate phreatophytes, (ii) the groundwater under river bars is horizontal (or very close to it) and connected to the river stage, and (iii) the capillary fringe is parallel to the water table. None of these assumptions hold for my study reach, but I still observed and documented the formation of very clearly delimited bands of cottonwood seedlings, as has been mentioned recurrently in the literature. On the other hand, in some years and at some locations, cottonwoods established in patches that covered entire bars, instead of forming recruitment bands.

Based on my observations of seeds and germinants in the drift, on experimental results confirming that cottonwood seeds germinate, establish and grow under water, and on comparisons of seedling establishment limits with flow profiles, I am proposing the River Seeding Concept of cottonwood establishment in gravel-bed rivers. This conceptual model posits that hydrochory is the primary establishment mechanism creating recruitment bands and patches of seedlings. Wind-dispersed seeds fall on the water, are incorporated into the drift, and are deposited by receding floodwaters along shallow shorelines where underwater establishment occurs. This process can only occur during the period of availability of seeds within the drift.

This period is much shorter than expected. Its beginning coincides with the start of seed dispersal. Its end, which is reflected in the lower limit for establishment, broadly corresponds to the abrupt decrease that occurs just after the peak in seed dispersal. In other words, the long tail to the right in the temporal distribution of seed release does not affect at all the lower limit of cottonwood establishment.

The occurrence of recruitment patches, covering bars from the ridge-top down, instead of bands surrounding them, is easily explained with this conceptual model: In

years for which the seed release starts while the flood stage is still above the bar ridges, the river will be able to sow entire bars. If seeds become available in the drift after bar ridges are above flood stage, then bars will be formed.

According to this reach-scale model, all bars in a reach would exhibit recruitment bands or patches, in years where the timing of the flood peak and that of the peak in seed release overlap. The limitations to establishment imposed by the need for fine matrix material and by the thickness of the coarse surface layer will determine which bars get actually colonized.

Implications for Conservation of Riparian Cottonwoods

In the most general aspects, the management implications of the River Seeding Concept (RSC) are quite similar to those derived from the Recruitment Box Model (RBM): Floods are needed with sufficient magnitude, appropriate timing, and adequate rates of recession, in order to ensure successful recruitment of cottonwoods.

On the other hand, because the RSC focuses on hydrochory as the main establishment mechanism, seeds can only establish where dropped by the flow. This tenet introduces two important practical differences with the predictions from the RBM, and thus with management recommendations for regulated rivers. First, if there is no flood, or if the flood is not synchronized with the period of seed availability in the drift, seedlings will only establish in a very narrow band, at a low elevation. Second, the riverbed area over which potential recruitment can occur in any given year will be that uncovered by the flow during the period of seed availability in the drift. Thus, the total range in stage draw-down during seed availability will determine the area available for recruitment. In regulated rivers, this requirement would call for the release of large artificial floods, with steep recession limbs during seed availability, in order to maximize establishment.

This suggests that there could be a trade-off regarding the role of the rate of recession. According to the RSC, a faster rate of recession would be needed during the few days of seed availability, in order to obtain initial establishment over a wider area. The RBM, on the other hand, proposes that slower recession rates result in a higher rate of success for the established seedlings, because this ensures water availability. Natural

floods have their steepest recession rates shortly after the peak, and the slope of the hydrograph is much flatter afterwards. Thus, it would seem that the best management strategy for regulated rivers, in order to maximize both coverage and success, would be to mimic natural floods, with steep recession rates during seed availability, and flatter rates thereafter.

The findings about the important roles played by fine material and the thickness of the coarse surface layer suggest that the upstream presence of a dam can affect cottonwood recruitment at least in two additional ways. First, by retaining most of the fines carried by the river, because of sediment trapping in the reservoir, and second, by causing deposition of thick layers of coarse sediments, if there is an unnaturally large stage draw-down at the end of the flood.