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DISSERTATION

THE EFFECTS OF MOUNTAIN RESERVOIR OPERATIONS ON THE DISTRIBUTIONS AND DISPERSAL MECHANISMS OF RIPARIAN PLANTS, COLORADO FRONT RANGE

Submitted by

David M. Merritt

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 1999

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COLORADO STATE UNIVERSITY

June 29, 1999

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DAVID M. MERRITT ENTITLED THE EFFECTS OF MOUNTAIN RESERVOIR OPERATIONS ON THE DISTRIBUTIONS AND DISPERSAL MECHANISMS OF RIPARIAN PLANTS, COLORADO FRONT RANGE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

THE EFFECTS OF MOUNTAIN RESERVOIR OPERATIONS ON THE DISTRIBUTIONS AND DISPERSAL MECHANISMS OF RIPARIAN PLANTS, COLORADO FRONT RANGE

Many factors interact to determine the composition and successional dynamics of riparian plant communities. The colonization of newly created sites along river corridors and the addition of species into existing communities are limited by the dispersal of seeds, seed germination, and seedling survival. Water dispersal (hydrochory) is an important means of both short- and long-distance dispersal of seeds along riparian corridors. Interruptions in any phase of dispersal (primary or secondary dispersal or deposition) of a particular species are likely to influence the structure of plant populations. Dams affect dispersal of riparian plant propagules through: (1) modifying hydrologic regimes and hydraulics, affecting the dynamics of seed transport and deposition, (2) altering the temporal availability and suitability of streamside habitat through controlling river stage, and (3) imposing a barrier to the downstream movement of seeds and vegetative propagules. The purpose of this investigation was to develop an understanding of the influence of fluvial landforms and modified flow regimes on the dispersal and deposition of the seeds of riparian plants through a series of flume and field experiments.

Seeds were deposited non-randomly under all simulated flow regimes in flume experiments with the exception of the most rapid rate of drawdown (ramped hydrologic regime), which resulted in dispersal of seeds over a broad elevational gradient. Higher concentrations of seeds were deposited under stepped and gradually descending drawdowns, than under ascending and ramped hydrologic regimes. Early and late dispersing seeds were deposited in greater numbers than seeds released at intermediate times under descending and stepped regimes. Late dispersing species were favored under ascending flows and early dispersing species were favored under ramped regimes. Shape of the drawdown curve as well as timing of seed release determine the concentrations of seeds deposited along shorelines. Relative velocity (V/V_{mx}), which is an index of the strength of recirculating flow, explained a significant proportion (91%) of the variability in deposition of early dispersed seeds, indicating that seeds are deposited in the highest concentrations immediately below constrictions to flow, in zones of strong flow recirculation, and in slackwater areas adjacent to constrictions. Reynolds number, Froude number, and Weber number associated with flow fields at each fluvial feature explained as much as 75, 83, and 75 percent of the variability in seed deposition under the stepped regime, respectively.

Field measurements indicated that the seed density as well as species richness of the hydrochoric seed bank were depleted below reservoirs along two high gradient streams in Colorado, suggesting that reservoirs are effective traps for water-dispersed seeds. Hydrochoric species comprised from between 12 and 25 percent of riparian vegetation at these sites, whereas wind- and water-dispersed species comprised from 41 to 55 percent of the floras. Relationships between dispersal phenology, patterns of wind and water dispersal, and standing vegetation were quantified using a non-parametric measure of concordance (Kendall's *W*). The composition of wind-dispersed seed rain was found to vary as a function of local-scale factors such as site species composition. Species composition of hydrochoric seeds was less related to local- and reach-scale community composition upstream of reservoirs, but was highly related to standing vegetation below reservoirs. This suggests that seeds may be derived from sources throughout the watershed upstream from reservoirs, but that hydrochoric seeds are depleted and richness is 'reset' below dams. This fragmenting may have long-term implications for the structure of vegetation downstream from dams, and effects may become more evident with time since impoundment.

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"*It must be realised that every plant we find in any spot, or one of its ancestors, must somehow have contrived to get into the locality in which we observe it to be, and the question to be answered is: How did it arrive and establish itself there?*"

-Henry N. Ridley, 1930, *Dispersal of Plants Throughout the World*

CHAPTER 1

INTRODUCTION

The structure and composition of riparian vegetation are determined by a variety of physical and biological factors. Whereas the spatial configuration, characteristics, and temporal availability of habitat have a great bearing on the distribution of plants growing along watercourses, population structure and community composition are ultimately limited by the reproductive success of riparian plant species. Dispersal is a prerequisite of recruitment (Howe 1989). In many cases, the number of seeds produced by parent populations is not the limiting factor in successful regeneration of riparian plants (Bradley and Smith 1986, Walker *et al.* 1986, Friedman *et al.*1995). However, the efficient delivery of seeds to sites that are suitable for establishment and growth (safe-sites; *sensu* Harper 1977) may be a central factor in the maintenance of these populations. For many riparian species safe-sites are isolated to a narrow moist zone along stream margins. Interruptions in the processes that disperse and preferentially deposit seeds in these sites may have perceptible and even catastrophic effects on plant populations on time-scales approximating the life-span of the species.

The production of seeds in synchrony with times of maximum availability of suitable habitat is one evolutionary adaptation of importance to species lacking well developed seed dormancy. However, the timing of seed release (dispersal phenology) is only the first step in a complex process that precedes successful seedling establishment (Ribeiro 1991). Upon reaching maturity, dispersal of seeds and the final position of seeds on the landscape are determined by the characteristics of each of three dispersal phases: (1) primary dispersal, (2) secondary dispersal, and (3) seed deposition. Primary dispersal involves the dispersal of seeds from the parent plant to initial contact with the substrate. Whereas primary dispersal of wind-dispersed species (anemochores) may range from less than a meter to many kilometers (Ridley 1930, Van Der Pijl 1972), most gravity-dispersed species (barochores) are limited to very short dispersal distances from parent plants during primary dispersal (Van Der Pijl 1972). Secondary dispersal may occur by way of animals (zoochory), wind, or water (hydrochory) and may have a tremendous influence on the distributions of seeds across the landscape--the 'seed shadow' (Matlack 1989, Redbo-Torstensson and Telenius 1995). Deposition, the final phase for wind- and water-dispersed seeds, is influenced by landscape features (topography and surface roughness from rocks or vegetation) as well as the size and morphological characteristics of the seeds (Harper *et al.* 1970, Staniforth and Cavers 1976). The interruption or failure of any one of the three dispersal phases, through decoupling dispersal phenology from the timing of suitable habitat availability, interruption or loss of dispersal vectors which optimize transport and delivery of seeds to safe-sites, or modification in the processes that create and maintain safe-sites, may be the bottleneck which prevents effective dispersal and subsequent seedling establishment.

Many species of plants growing along rivers utilize river corridors for 'migration' (Sauer 1988), colonization (McBride and Strahan 1984, Johnson 1994), short and long distance dispersal and population maintenance (Staniforth and Cavers 1976, Johansson and Nilsson 1993), and invasion (Eggington and Robbins 1920, Graf 1978, Wilson 1980, Thébaud and Debussche 1991). In fact, access to water may greatly enhance the ability of plants to disperse long distances and to colonize or invade new habitats at rates exceeding those possible through other means of dispersal (Thébaud and Debussche 1991, Lonsdale 1993). Hydrologic regime--the timing, duration, and magnitude of flow--is thought to be the most important extrinsic factor determining the distance of dispersal and the final location of seeds deposited along the margins of rivers (Schneider and Sharitz 1988, Edwards *et al.* 1994). The velocity and direction of surface currents affect the distance and direction that waterborne seeds travel, as well as where they are ultimately deposited along shorelines (Schneider and Sharitz 1988, Nilsson *et al.* 1991b). The timing of flows in relation to timing of seed release affects the availability of habitat and for certain species (McBride and Strahan 1984). The volume of water in a stream influences the extent of floodplain inundation, which governs the extent of sources of, as well as sinks for, water-dispersed seeds (Kubitzki and Ziburski 1994, Nilsson *et al.* 1994, Hughes and Cass 1997).

The natural hydrologic regimes of a large proportion of rivers in the Northern Hemisphere have been significantly modified through land-use change, water diversion, and the construction of dams (Dynesius and Nilsson 1994). Dams affect streams through modifying daily and seasonal flows, fragmenting riparian corridors through blocking the movement of organisms, and preventing the downstream flow of mineral sediment and organic material along rivers (Ward and Stanford 1983, Williams and Wolman 1984, Andrews 1986). Regulation of streamflow typically alters the timing and magnitude of high flows, the shape and rate of the recession limb of the hydrograph, the flow duration, and the temporal availability and physical characteristics of habitat along dammed stream segments. Whereas studies have suggested that hydrochory is an important mechanism for a variety of aquatic and riparian plant species (Schneider and Sharitz 1988, Thébaud and Debussche 1991, Johansson and Nilsson 1993, Edwards *et al.* 1994), there have been no published studies documenting the effects of modified hydrologic regimes on the transport and deposition of water-dispersed seeds. Whereas natural lakes have been shown to be effective traps for water-dispersed propagules (Johansson and Nilsson 1993), and the fragmenting effect of dams on the upstream to downstream dissemination of propagules has been suggested by some authors (Nilsson *et al.* 1991a, Nilsson and Jansson 1995, Johansson *et al.* 1996), hydrochory above and below dams has not yet been quantitatively examined.

Through taking a quantitative approach to the process of water dispersal, the current work will provide an empirical basis for incorporating dispersal into predictive riparian vegetation models. Whereas many predictive vegetation models assume that dispersal is ubiquitous ('ubiquitous dispersal' *sensu* Hanson *et al.* 1990) and that physical conditions are the sole determinant of species composition along river margins, (Pearlstine *et al.* 1985), an incorporation of factors that influence dispersal and deposition of hydrochoric seeds across floodplains has the potential to lead to a refinement of these models. Through developing an understanding of how dams influence seed dispersal through influencing hydrologic regimes and physically blocking the flow of seeds, this work will provide information regarding how reservoir outflows could be modified or maintained to facilitate the regeneration of desired riparian plant species while inhibiting the establishment of undesired (i.e., invasive or adventitive) species.

Dams have the potential to affect hydrochory in three principal ways: (1) through modifying the hydrologic regime, dams affect stream hydraulics and the mechanics of seed transport and deposition, influencing how far seeds travel and where they are deposited along channel margins, (2) through modifying the volume of discharge and water surface elevation (stage) in the stream, dams affect the availability and suitability of streamside habitat for seed germination and establishment of riparian plants, and (3) dams may serve as a physical barrier to the downstream movement of plant disseminules, trapping and storing seeds in reservoirs and causing high rates of seed mortality. This dissertation consists of three chapters which address each of these dam-related effects on seed dispersal. Chapter 1 provides a general introduction to seed dispersal and flow regulation. Chapter 2 presents research aimed at addressing the first two potential impacts of dams listed above. In Chapter 2, the results of a series of flume experiments will be presented in which the hydraulic and hydrologic factors affecting where seeds are deposited along shorelines are quantified. The third potential impact of dams to seed dispersal will be examined in Chapter 3 through a series of field studies on upstream to downstream patterns of seed dispersal along two regulated streams in Colorado.

1.1 Dispersal Mechanisms

Dispersal is an important mechanism regulating the population biology of plants (Harper 1977). Dispersal of seeds or vegetative parts (diaspores) is the primary means by which populations of plants are sustained from one generation to the next, and is the sole means by which plant populations are able to shift positions in the landscape. Through dispersal, plant populations are able to migrate across the landscape in response to changes in climate or habitat to expand or shift their range (Sauer 1988). Dispersal operates at many levels from genetic to demographic, ultimately determining the potential species composition of plant communities. Dispersal facilitates exchanges of genetic material between spatially separated populations, increases the probability of survival through the avoidance of competition with parent plants and cohorts, and enables diaspores to reach and populate newly created habitat or to invade already occupied habitat.

For many species, habitat requirements during early life-history stages (germination and establishment) may differ from the requirements of adults (McLeod and McPherson 1973, Grubb 1977, Platt and Weis 1985). The unique set of site characteristics required by a particular species during early life-history stages has been referred to as the 'regeneration niche' (Grubb 1977). Many colonizing species cannot become established under a canopy of adults, thus seeds of these species must either remain in a seed bank until the parent canopy is no longer present, or seeds must be dispersed to more suitable sites ('escape hypothesis' *sensu* Janzen 1970). As a result, many colonizing species produce large quantities of small, often wind-dispersed seeds of low specific weight and possessing little or no dormancy, and disperse them widely (Howe and Smallwood 1982, Densmore and Zasada 1983, Braatne *et al.* 1996). In this way, parent plants are able to more efficiently 'sample' the environment for suitable sites for establishment. Because of the limited resources associated with the small size of the seeds of colonizing species, they must come into contact with suitable sites for germination shortly after release or perish (Moss 1938, Fenner *et al.* 1984). For example, many members of the willow family (Salicaceae) disperse seeds immediately after peak discharge, and continue to disperse seeds throughout a specific segment of the descending limb of the hydrograph (Braatne *et al.* 1996). Therefore the maximum number of seeds are available at a time when the availability of suitable germination sites (newly exposed, moist sand and gravel bars and stream margins) is also at its maximum (Fenner *et al.* 1984, McBride and Strahan 1984, Krasny *et al.* 1988, Skoglund 1990, Sacchi and Price 1992).

Species with specialized regeneration niches, such as those that colonize canopy gaps, those that colonize fallen logs, or floodplain species that must establish on newly deposited sediment, have a much higher probability of survival if they possess some mechanism of dispersal which enhances delivery of propagules to such sites ('directed dispersal' *sensu* Howe and Smallwood 1982). In many cases, dispersal has certain advantages over storage in a soil seed bank and waiting until habitat conditions become amenable to germination and growth (Grime and Hillier 1992). For example, colonizing species with no dormancy may be at an advantage in heterogeneous habitats with predictable temporal patterns of habitat availability. In contrast, well-developed dormancy may be advantageous in habitats in which the creation and availability of suitable safe establishment sites is more stochastic, such as in extremely arid areas or in areas prone to fire disturbance (Cook 1980). The selective advantages of dispersal-enhancing traits have led to many physiological and morphological adaptations which are often closely tied to the timing of habitat availability and the physical or biotic agents which disperse the seed.

1.2 Dispersal Phenology, Seed Morphology, and Patterns of Dispersal

Theoretically, seeds should be released and available to colonize sites at a time when habitat availability is at its maximum (Hamilton and May 1977). The timing of seed release, or dispersal phenology, is a function of the length of time from pollination to the production of fruit, which may vary within a population on a given year as well as between years according to the effects of climatic conditions on plant physiology (Krasny *et al.* 1988, Ribeiro 1991). Species that lack well-developed seed dormancy (such as many colonizing species) often do flower, produce seeds, and disperse over a specific interval of time in concurrence with the availability of habitat. In this way the seeds of these species are available when conditions (soil moisture, temperature, light availability) are better suited for germination than at other times during the growing season (Howe and Smallwood 1982, Ribeiro 1991, Kubitzki and Ziburski 1994). In seasonally available habitats, such as those associated with river margins, the timing of seed release (particularly of colonizing species) and the availability of habitat often occur in synchrony, thereby increasing the likelihood of successful seedling establishment (Bradley and Smith 1986, Johnson 1994, Braatne *et al.* 1996). Conversely, dispersal phenology may be timed to avoid less favorable conditions such as drought stress or inundation (Bliss and Zedler 1998). Even in species that are able to contribute seeds to a persistent seed bank, fruiting is often timed in synchrony with the availability or presence of the agent of dispersal (Stiles 1992, Kubitzki and Ziburski 1994). Examples include fruiting timed during songbird migration and seed maturity timed to the presence of abiotic dispersing agents such as rain-water (Redbo-Torstensson and Telenius 1995) or streamflow (Walker *et al.* 1986, Krasny *et al.* 1988, Johnson 1994). Once dispersed, the seeds of these species often persist in a seed bank until suitable conditions for germination and growth occur (Cook 1980, Van Der Valk 1981, Keddy and Reznicek 1982, 1986).

Variations in the timing of seed release of different species may have an important influence on the spatial distributions of plant populations. Even in cases in which the environment is relatively homogeneous or in which the species involved have wide ecological amplitudes, species-specific stands may be distributed in space according to the timing of seed dispersal rather than the spatial distributions of particular habitat types (McBride and Strahan 1984). Seeds dispersing when a seedbed is inundated are less likely to be deposited and germinate upon the site than seeds being released immediately following site exposure. For species with a short duration of seed viability, dispersal must be timed, and dispersal mechanisms sufficiently directed, so that some seeds reach suitable germination sites and become established before germination conditions deteriorate. Dispersal vectors then become the critical link between the parent plant and the suitable microsite.

Morphological adaptations of seeds to a variety of dispersal vectors (animals, insects, water, and wind) provide evidence supporting the theory that there is a selective advantage to possessing such traits. If the trait enhances the likelihood that at least some seeds will reach suitable microsites, the trait persists in the population (Platt and Weis 1985). However, some apparent adaptations to a particular dispersal mechanism may 'have no connection with the life-history of the plant' (Guppy 1906), may result from some physical constraint on seed size and shape as it is forming within the ovary (Harper *et al.* 1970), or may be pre-adaptations selected for some other purpose (Van Der Pijl 1972). In addition, the seeds of some species exhibit no apparent adaptations to any dispersal vector whatsoever (Guppy1906). The seeds of these species have been classified as barochores, or gravity dispersers, by some biologists (Van Der Pijl 1972). It is also important to note that many species inadvertently (i.e., through pre-adaptation, coincidence, or adaptation) utilize more than one means of dispersal. This generalist approach to dispersal may be advantageous as insurance in situations in which one of the dispersal agents is not present or is not functional at the time of seed release.

For many plant species selective pressures have resulted in intricate dispersal devices and tight interrelationships between seed morphology and dispersal agents ('dispersal spectra' *sensu* Hughes *et al.* 1994). Animal- or insect-dispersed seeds (zoochores) are often enclosed within an edible pericarp (fruit), have an edible appendage, or the seeds themselves are edible (i.e., nuts and acorns). Other adaptations to animal-dispersal include the attachment of an appendage to seeds that provides useful nest building material for birds or other animals (i.e., thistles *Breea* spp., *Cirsium* spp.), seeds with devices that adhere to fur or feathers, and seeds that must be consumed and exposed to digestive juices to break dormancy (Ridley 1930, Temple 1977). Patterns of deposition of animal-dispersed seeds vary greatly but typically follow either a scattered or clumped configuration (Howe 1989). Seeds dispersed by birds, bats, fish, and other small frugivores are typically scattered widely across the landscape, with the exception of the highly concentrated deposits of seeds in fecal deposits beneath roosts and perches (Losos 1993, Kubitzki and Ziburski 1994). Because bats defecate while feeding, bat-dispersed seeds are typically widely spaced, whereas bird-dispersed seeds are often deposited in concentrated areas under perches (Losos 1993). Dispersal of seeds by larger frugivores often results in a patchy, clumped pattern of seed deposition (Howe 1989). Therefore-animal dispersal results in a variety of spatial patterns in the distributions of species with different animal-dispersal vectors (i.e., 'bear gardens' of currant seedlings (*Ribes* spp.) in fecal deposits of bears, versus widely spaced raspberry (*Rubus* spp.) seedlings dispersed by songbirds (Willson 1992)). On average, the majority of animal-dispersed seeds are deposited within about 100 m of the parent plant, although dispersal of some seeds in excess of this distance is not uncommon (Bullock and Primack 1977).

Species that disperse seeds via wind (anemochores) often produce seeds of low specific weight (Ridley 1930). Many of these species also produce fruits with devices that decrease the fall velocity of the seeds (i.e., wings, plumes, or hair-like pappus), thereby increasing the length of time the seed is airborne and the distance that seeds may travel from their point of release (Augspurger and Franson 1987, Greene and Johnson 1992). Many pioneer species (i.e., species that colonize disturbed areas) are wind-dispersed (Van Der Pijl 1972, White 1979). Seeds that disperse via wind, although subject to the stochastic nature of varying wind speed and direction, typically fall within one or two times the canopy height of the parent plant (Harper 1977). The mean distance that seeds are dispersed by wind rarely exceeds 10 m for herbaceous plants (Harper 1977), but is likely to exceed 200 m given strong winds (Van Der Pijl 1972). The number and density of seeds deposited around the parent plant varies as a function of distance from the source, often following a right-skewed (leptokurtic) distribution, but seed densities may be extremely variable (Walker *et al.* 1986). The decrease in seeds as a function of distance from the source has been described as following a negative exponential or inverse power distribution (Okubo and Levin 1989). Secondary dispersal of wind-dispersed seeds, which often occurs via water- or secondary wind-dispersal, may result in much greater dispersal distances than are possible through wind-dispersal alone (Matlack 1989).

Species that utilize water as a means of dispersal (hydrochores) are often buoyant, have hydrophobic seed coats, and/or can germinate while floating or submerged (Ridley 1930, Edwards *et al.* 1994). Whereas many of these features may be pre-adaptations--air filled chambers, corky tissue in seed coats (air spaces between cells), and trapped air between the seed and seed coat or seeds and capsules--they all contribute to buoyancy in hydrochoric seeds (Guppy 1906, Ridley 1930, Edwards *et al.* 1994). Hydrophobic seed coats also increase the duration of buoyancy of seeds (Guppy 1906, Edwards *et al.* 1994). Duration of buoyancy may have a great influence on the distance seeds may travel as well as where seeds are deposited (Nilsson *et al.* 1991b, Danvind and Nilsson 1997). Although duration of buoyancy is an important determinant of the potential dispersal distance of seeds (Danvind and Nilsson 1997), seeds may travel great distances over a short period of time on particularly fast moving streams. Thus species with short float times may also be able to disperse widely during periods of high flow (Ridley 1930).

Seed coats with expanded wing-forming margins have higher surface area to volume ratios than seeds without wings. A high surface area to volume ratio may enhance the ability of the seed to remain on the surface of the water through the forces of surface tension (Thébaud and Debussche 1991, Edwards *et al.* 1994). In tranquil water, seeds that would otherwise sink (i.e., because seed density exceeds that of water) may remain on the water surface through surface tension alone given low specific weight or high surface area to volume ratios of the seed, seed coat, or fruit (Young *et al.* 1997). The movement of waterborne seeds is governed by stream hydraulics. Much as river-transported sediment is deposited according to the distribution of stream energy in the fluvial environment, seeds are likely deposited in a non-random fashion along channel margins. Seeds dependent upon surface tension to remain afloat may become submerged in very turbulent water. Conversely, buoyant seeds may become waterlogged and sink if retained for long periods of time in slow moving or stagnant water. The dispersal distance of submerged seeds is likely much shorter than seeds floating or suspended except under conditions of extremely turbulent flow.

In contrast to seed buoyancy in hydrochoric species, the seeds of other species that are typically found in wetlands or along river or pond shorelines may initially sink when dropped onto the surface of the water, but rise after a period of submergence, dispersing only after germination occurs (Ridley 1930). Wetland species included in the following genera all sink initially in water: *Carex, Juncus, Lysimachia, Mimulus,* and *Polygonum* (Waser *et al.* 1982, Danvind and Nilsson 1997). These seeds may rise to the water surface as they are breaking dormancy, because of swelling of the seed coat caused by the accumulation of CO_2 produced by respiration, or may float only after germination following the formation of CO_2 bubbles on leaf and stem surfaces caused by respiration of the cotyledon (Ridley 1930, Edwards *et al.* 1994). The movements of seeds and seedlings on the surface of the water then becomes a function of the velocity and direction of wind or water currents on the surface of the marsh, lake, or stream. It is in this way that shorelines become 'repositories' of high densities of seeds (Harper 1977).

Transport of submerged seeds as bedload may be important along alluvial streams that experience frequent mobilization and redistributions of sediment. Bedload transport of the heavy seeds of *Polygonum lapathifolium, P. pensylvanicum,* and *P. persicaria* not only deposits seeds in locations suitable for germination and establishment, but also facilitates seed coat abrasion, which may enhance seed germination (Lubke and Cavers 1969, Staniforth and Cavers 1976).

Seed deposition along shorelines is a function of seed morphology (Edwards *et al.* 1994, Redbo-Torstensson and Telenius 1995), bank roughness or the presence of obstructions to flow (Schneider and Sharitz 1988, Johansson and Nilsson 1993), as well as flow hydraulics and the shape of the hydrograph. Timing of peak flow and rate of drawdown have also been shown to affect survival following deposition along rivers (Fenner *et al.* 1985, Johnson 1994). Some investigators have theorized that appendages such as trichomes or perianth parts in various states of decay (Staniforth and Cavers 1976) or expanded wind-like seed-coat margins (Thébaud and Debussche 1991, Edwards *et al.* 1994) may be adaptive morphological features which enable seeds to catch and adhere to shorelines, enabling them to remain in sites that are suitable for germination and establishment. The fact that disproportionately higher percentages of wetland and riparian plant species possess adaptations to water dispersal than other vegetation types (Kalliola *et al.* 1991, Kubitzki and Ziburski 1994), and that species producing seeds of longer duration of buoyancy are more widespread along streams (Johansson *et al.* 1996), provides convincing evidence that there are selective advantages to utilizing water as a means of dispersal.

1.3 The Role of Hydrochory in Structuring Riparian Plant Communities

Although the structure and composition of riparian plant communities has been related to a variety of physical factors (elevation, hydrology, soil texture, soil chemistry, soil moisture) and biological factors (competition for water, light, nutrients, and space as well as herbivory, and disease), colonization of habitat patches is fundamentally limited by regeneration. The balance between successful regeneration and subsequent additions of individuals into the population, and the loss of individuals from the population through mortality, determines the population structure of riparian plant communities.

Vegetative spread through the dispersal of entire plants, or through the dissemination of rhizomes, stolons, tubers, and turions, plays an important role in maintaining localized populations, albeit of limited genetic variability. In cases where sexual reproduction is absent, populations of some species have been able to persist along watercourses through exclusively vegetative means of dispersal. Water dispersal of floating rhizome segments (*Ranunculus lingua*, Johansson and Nilsson 1993) or branch sections (*Salix* x *rubens* and *Salix fragilis*, Shafroth *et al.* 1994) was shown to be the exclusive means of regeneration and spread of the populations of these species along the Sävar River in Sweden and along low elevation rivers throughout Colorado, respectively.

Hydrochoric dispersal of floating rhizomes resulted in leptokurtic dispersal distributions (Johansson and Nilsson 1993), similar to those associated with wind- or animal-dispersed seeds.

Because persistent seed banks are not as well developed in riparian soils (Walker *et al.* 1986, Kalliola *et al.* 1991; but see Hughes and Cass 1997), as they have been shown to be along lakeshores and marshes (Keddy and Reznicek 1982, 1986, Van Der Valk 1981), sexual regeneration of riparian plants is dependent upon efficient dispersal of seeds to sites that are suitable for germination and survival of seedlings. For a variety of riparian species, streamflow provides an effective vehicle for the delivery of seeds to sites that are suitable for germination and establishment. The timing of seed release, the type of dispersal mechanism (wind, gravity, water, animal), channel and bed forms, and the timing and characteristics of the hydrologic regime all interact to determine the spatial and temporal distribution of propagules in the fluvial environment.

Water dispersal influences the population structure of riparian plant communities in three basic ways: (1) facilitating colonization and local population maintenance through delivering propagules to newly created or disturbed habitats, (2) maintaining species richness in plant communities along river margins through continually delivering propagules from upstream floras, and (3) providing a vehicle for long distance dispersal of seed hydrochores. Although none of these factors are mutually exclusive, each has a different role and consequently an unique influence on community structure; therefore, each will be discussed separately below.

1.3.1 Colonization and Local Population Maintenance

Whereas the frequency and magnitude vary from one stream to another, flow-related mechanical disturbance is a feature common to all streams. Mechanical disturbance often removes or buries existing vegetation and scours and re-deposits sediment, increasing habitat heterogeneity and making habitat available for colonization by riparian plants (Bradley and Smith 1984, Fenner *et al.* 1985, Kalliola and Puhakka 1988, Kalliola *et al.* 1991, Scott *et al.* 1996). As a consequence of the frequent disturbances associated with streams relative to surrounding landscapes, many species growing along streams have adaptations enabling them to rapidly colonize newly disturbed habitat patches (White 1979, Menges and Waller 1983). Colonization may occur through clonal growth or resprouting from a perennial root system, dispersal of vegetative parts or whole plants, or by sexual means through seed dissemination. Whereas some researchers have unequivocally stated that environment is the principal bottleneck that determines plant community structure (Kalliola and Puhakka 1988, Tabacchi *et al.* 1990, Kalliola *et al.* 1991), examining riparian plant communities without regard for reproductive dynamics provides only a partial picture.

A large proportion (often exceeding 50 percent) of riparian species are wind- or water-dispersed (White 1979, Kalliola *et al.* 1991, Kubitzki and Ziburtski 1994), and many have the ability to rapidly colonize new patches once cleared, created, or exposed by declining water levels (Walker *et al.* 1986, Houle 1994, Johnson 1994). Many factors influence the rate and characteristics of colonization of new sites, such as the life-history traits of the colonizing species (Menges and Waller 1983, Walker *et al.* 1986), the timing of seed release in relation to flow (McBride and Strahan 1984, Schneider and Sharitz 1988), and biotic and abiotic factors governing seedling survival preceding establishment (Sacchi and Price 1992, Segelquist *et al.* 1993, Merritt 1997). Releasing seeds too early may result in seed death; releasing seeds too late may increase seedling mortality (Houle 1994).

The chance availability of seeds of one species over another at the time of colonization may determine long-term structure of the community in the patch (Diamond 1975, Levin 1976, Malanson and Butler 1991). If first arrival is in fact advantageous, seeds transported and deposited with fluvial sediments would arrive sooner and have the greatest advantage in colonizing new sites (Staniforth and Cavers 1976). Water-dispersed seeds (in suspension and on the surface), wind-dispersed seeds, and finally the heavy seeded zoochores, would arrive sequentially following initial site formation. Studies of colonization along river margins emphasize the importance of the arrival of seeds to new sites in determining the long-term vegetation composition and successional trajectory of the site (McBride and Strahan 1984, Kalliola *et al.* 1991). Differential timing of seed release was shown to be more important than habitat differences such as soil texture in determining the spatial distribution of colonizing species along river margins along a California stream (McBride and Strahan 1984). Several studies throughout the western United States and Canada indicate that the decoupling of hydrograph characteristics from the timing of the seed release of colonizing species has inhibited regeneration of important forest species along regulated streams (Fenner *et al.* 1985, Rood and Mahoney 1990, Johnson 1992). Because they disperse seed later in the season and over a longer period of time, certain exotic species, such as salt-cedar (*Tamarix* spp.), may be pre-adapted to benefit from regulated flow regimes (Everitt 1980).

Colonization depends on the arrival of propagules as water levels recede. The main role of hydrochory is to secondarily transport seeds from their initial locations and redistribute them to sites suitable for germination (Schneider and Sharitz 1988). Seeds transported by water are often deposited in high densities along lines corresponding to declining water levels (McBride and Strahan 1984, Kalliola *et al.* 1991, Rood *et al.* 1998; Plate 1.1), often on point bars or other low energy areas such as eddies (Nilsson *et al.* 1991b, Johnson 1994). Moist sites are often optimal for germination and growth, implying that water may deliver seeds in a directed fashion to suitable sites, increasing the probability of seedling survival (Schneider and Sharitz 1988, Edwards *et al.* 1994). In this way, hydrochory may influence inter- and intraspecific seedling competition by determining seedling density, species composition through determining which species reach and colonize the site first, and the distribution of seeds in relation to microsites along river margins.

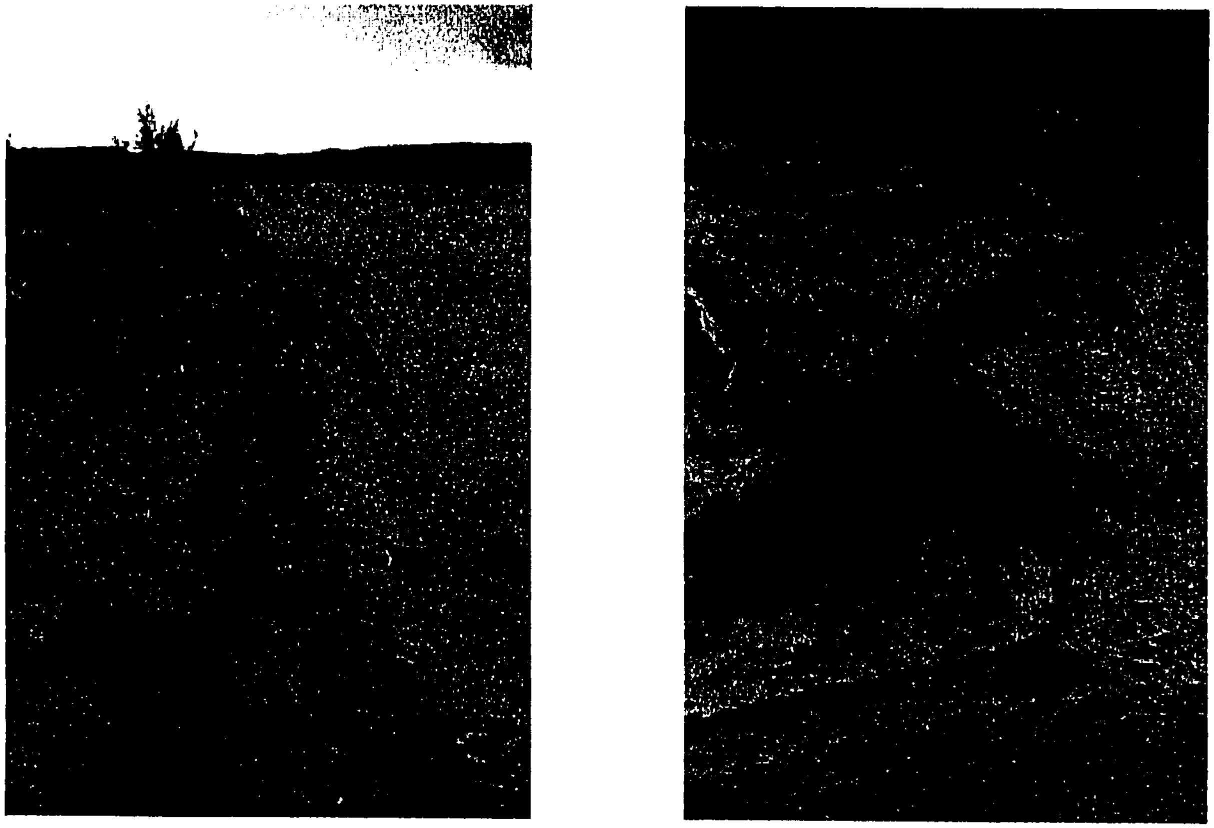


Plate 1.1. Linear bands of seedlings corresponding to lines of seeds deposited along shorelines during descending flows. Photos taken on the Yampa River, in northwestern Colorado. Book for scale.

1.3.2 Maintenance of Species Richness

A combination of local and regional factors governs plant species richness along river corridors. The loss of species from a community is often explained by local biotic controls such as competitive interactions, disease, and changes in habitat quality (Keddy 1992). However, additions of species to a local population are derived from a variety of sources ranging from *in situ* seed banks, local inter-patch seed sources, and speciation over long time-scales, as well as regional sources of propagules (Waser *et al.* 1982, Ricklefs 1987, Nilsson *et al.* 1994). Additions of species into existing riparian communities from regional sources may enhance species diversity in riparian patches through the 'mass effect', in which sufficient numbers of seeds are delivered to a site so that some germinate and may temporarily become established as transients (Shmida and Wilson 1985). The mass effect has been used to explain species richness in transition zones (i.e., ecotones) by acknowledging that non-self-maintaining populations may become established in these areas due to high influx of seeds. Through deriving seeds from sources throughout the watershed, hydrochory may be an important mechanism influencing species diversity along river margins (Malanson 1993, Nilsson *et al.* 1994).

Nilsson *et al.* (1994) have suggested that the potential plant species richness of river margins is limited by the species pool of the watershed. A 'river collector hypothesis' is suggested in which potential species richness in the hydrochoric 'seed bank' is thought to increase as a function of downstream distance, stream order, watershed area, or discharge. Although hydrochory was not measured, they noted an increase in species richness of riparian vegetation in a downstream direction moving from a species-rich region into a species-poor region. A subsequent decrease in richness along reaches downstream of the species-poor region provided evidence supporting the hypothesis that species transported over long distances via water influence species richness.

Schneider and Sharitz (1988) demonstrated that hydrochory provided a link between spatially separated forests in lowland swamps in North Carolina. Increases in discharge through the swamp resulted in enhanced species richness of hydrochoric seeds as well as increased numbers of species not present in the standing vegetation on-site (Schneider and Sharitz 1988). Egginton and Robbins (1920) reported 81 species of weed seeds collected in water samples from irrigation ditches in Colorado. Wilson (1980) identified the seeds of 77 different species of plants in the water flowing through irrigation canals in Nebraska. Species richness of water-dispersed seeds was significantly higher (40 species) than the richness of standing vegetation (17 species) in a swamp connected to the Cache River in Illinois (Middleton 1995). Additionally, the total number of seeds captured by water-dispersed seed traps was eight-times higher than the number of seeds caught in wind-dispersed seed traps. Nilsson and Grelsson (1990) suggested that the high density of seeds (189,181 seeds/m^2) along drift lines deposited along the Vindel River in northern Sweden would increase species richness because 28% of the species in the seed flora were not present in the standing vegetation. Hughes and Cass (1997) determined that 26 of 40 species collected from flood-deposited debris along a Vermont stream were not present in the standing flora. All of the wind-dispersed seed rain measured on two river islands in Sweden was from adults present on the islands, whereas the seeds of ten species not present on the islands had been delivered by river water (Skoglund 1990). It was concluded that hydrochory was the primary means by which species richness on the islands could potentially increase. These studies suggest that water dispersal may enhance local species diversity (alpha diversity) through delivering sources of propagules from regional sources (beta diversity) to localized sites along river margins.

Habitat heterogeneity, spatial and temporal separation in the extent and degree of disturbance (Salo *et al.* 1986, Kalliola and Puhakka 1988, Kalliola *et al.* 1991, Friedman *et al.* 1996a), and the presence of a patchwork of both pre- and post-disturbance vegetation (Nilsson *et al.* 1991a, Nilsson and Jansson 1995) have been shown to be of great importance in maintaining species richness in riparian vegetation. More work is needed to ascertain the relative roles of physical and biological factors (such as seed dispersal) in maintaining species richness along river margins. The lack of definitive work in this area stems from the difficulty in collecting seeds, many of which are tiny, identifying seeds dispersed by various agents, and in isolating the relative contributions of seeds of different sources to community composition.

Because of the overt and aggressive nature of weed invasion, and the economic incentives to prevent its occurrence, several concentrated efforts have been undertaken to understand how weeds disperse, advance, and become dominant (Egginton and Robbins

1920, Kelley and Burns 1975, Wilson 1980, Radosevich *et al.* 1997). A few of these efforts have highlighted the richness of the water-dispersed seed bank, and the potential of this seed bank to result in a variety of weed communities in disturbed agricultural landscapes (Egginton and Robbins 1920, Wilson 1980). Understanding the strategies of highly specialized invaders may shed light on the more subtle roles of differential adaptations of different species to hydrochory and the role of these adaptations in maintaining populations and structuring communities.

1.3.3 Long-distance Dispersal and Invasion

There is little doubt that plants and animals utilize river margins as corridors for migration (Graf 1978, Sauer 1988, Tabacchi *et al.* 1990, Malanson 1993), but the degree to which the plants depend on flow to disperse their seeds during this migration is a matter of debate among ecologists. For many species, river margins may merely provide suitable habitat for germination, establishment, and growth (i.e., adequate moisture) rather than functioning as an active and necessary dispersal agent. The linear distribution of these species along river margins may simply be a reflection of population expansion into areas of suitable habitat. Certainly some species such as *Tamarix chinensis* that have sufficient means of disseminating their seeds by means other than water (i.e., wind), can spread rapidly even in an upstream direction (measured rate of 22 km/year) along watercourses where soil moisture is sufficient for germination and growth (Graf 1978). The results of the few studies that have examined relative roles of multiple dispersal pathways suggest that access to water may greatly enhance the abilities of certain species to extend their ranges.

On the Hérault River in France, hydrochory accounted for 95% of the range extension of *Fraxinus ornus* in the 65 years since its initial introduction to the region (Thébaud and Debussche 1991). Although primary dispersal of this species is via wind dispersal of winged samaras, secondary dispersal of seeds by water resulted in the rapid invasion of this species. Downstream invasion occurred at a rate of 970 m/year, resulting in a range extension of 65 km, whereas upstream invasion through wind dispersal occurred at a rate of less than 80 m/yr, resulting in the invasion of only 5 km of river margin. In comparing rates of wind versus water dispersal of an invasive wetland plant in Australia, Lonsdale (1993) concluded that wind alone could not account for the rates of spread of the adventitive *Mimosa pigra*. Based upon historic rates of spread, the aerial extent of *Mimosa pigra* was shown to have doubled every 1.2 years along watercourses, as compared to a doubling time of 6.7 years by wind dispersal throughout the rest of the region. These studies suggest that the ability to disperse by water enables hydrochoric species to have more extensive distributions than non-hydrochoric species, while at the same time enabling invasive species to spread more rapidly and widely than would be possible in the absence of water dispersal.

Whereas duration of buoyancy may be an important factor in determining the distance that a seed many float along a river, and subsequently the rate at which a species may invade, differences in seed buoyancy would be expected to result in differential distributions of species based on their floating ability. A strong correlation between the number of artificial seeds deposited in eddies and the duration of buoyancy of seeds of plants growing adjacent to eddies, led to the hypothesis that water dispersal and duration of buoyancy may interact to influence 'small-scale structuring of plant communities' along Swedish streams (Nilsson *et al.* 1991b). This was based on the assumption that the dispersal of seeds determines the distributions of adults, or that adult populations reflect the seed shadow (in some ways countering the ubiquitous dispersal hypothesis). Species with greater abilities to disperse long distances, for example common dandelion (*Taraxacum officionale*), are in fact more widespread throughout the world (Ridley 1930). To test the effect of duration of seed buoyancy on the distributions of riparian plants, Danvind and Nilsson (1997) measured the downstream limits of 17 alpine plant species and attempted to correlate the distributions of these species to the duration of buoyancy of their seeds. After finding no strong correlation, they concluded that other factors, such as habitat constraints, probably overshadowed the role of duration of buoyancy of seeds to the distributions of adults (Danvind and Nilsson 1997). They also noted that given sufficient time, species with a short duration of buoyancy could become established downstream in a 'stepwise fashion' one generation at a time. Thus, hydrologic regime, upstream to downstream connectivity, and the regeneration times of the species involved must be considered in examining the role of water dispersal along river corridors.

It has been asserted that hydrologic regime is the primary extrinsic factor controlling the dispersal of water-dispersed propagules (Schneider and Sharitz 1988, Edwards *et al.* 1994). It may be deduced that interruptions in natural hydrologic regimes, through river regulation, will have significant effects on the demographics and distributions of riparian plants utilizing hydrochory. Dams may also serve as a physical barrier to downstream dispersal. Johansson and Nilsson (1993) noted that the dispersal of floating rhizomes was effectively blocked from downstream movement by a large natural lake on the Sävar River in Sweden. If hydrochory is an important mechanism in the population biology of some plants, how might the widespread construction of dams on rivers throughout the world influence the populations of riparian plants and the communities they form? The loss or interruption of dispersal vectors has been shown to have significant consequences to certain species with particularly specialized dispersal mechanisms (Temple 1977, Bond and Slingsby 1984). In some cases, the loss of the dispersal vector has led to the population collapse of these specialized species (Temple 1977). Understanding the importance of dispersal vectors to the population biology of certain species has the potential to facilitate remediation for the loss or interruption of important flow-related dispersal vectors.

1.4 Effects of Dams on Streamflow Regime

River regulation and water diversion often result in significant changes in daily and seasonal distributions of streamflow (Petts 1984, Williams and Wolman 1984).

Natural streamflow regimes reflect the climate of a region, the geology of the watershed, and the characteristics of the drainage basin (drainage density, shape, slope, size; Dunne *et al.* 1991, Poff 1996). The hydrologic regimes of a vast majority of rivers have a seasonal flood component, such as snowmelt runoff or monsoonal rainfall, the characteristics of which are related to the morphometry, vegetation, and soil permeability of the basin (Carlston 1963, Murphey *et al.* 1977). Streamflow is the primary determinant of morphological (Leopold and Maddock 1953) and biological (Minshall 1988) characteristics of stream channels. Channel form and aquatic and riparian ecosystem functions are governed to a large degree by certain attributes of the hydrologic regime. Changes in the magnitude, frequency, and timing of streamflow influence the seasonal and spatial distributions of water, the characteristics of fluvial processes, and the frequency and magnitude of flow-related disturbance along streams, all of which result in changes in morphologic and biological attributes of these streams.

Among the most 'deliberate and widespread of human impacts' to natural flow regimes is the regulation of flows by dams (Dynesius and Nilsson 1994). River regulation modifies patterns of water and sediment discharge through time, often decreasing seasonal peaks, increasing base flows, increasing daily flow variability, and decreasing the supply of sediment to downstream river reaches. The effects of river regulation on discharge regimes are entirely dependent upon the operational objectives and the design specifications of the impoundment (Petts 1984). Rivers below dams managed for navigation may experience tremendous changes in seasonal flow variability, but experience very little change in daily flow fluctuations, whereas dams managed for hydroelectric power generation may cause substantial fluctuations in streamflow even over a period of a few hours. Outflows below dams managed for navigation and/or recreation are often released at a relatively stable rate throughout the year when compared to historic flows. This rate is achieved through releasing excess water in storage prior to periods of peak runoff (rain or snowmelt), detention of peak-flows during reservoir filling, and delayed release of an attenuated peak (Table 1.1). Reservoirs managed for flood control and hydroelectric power also decrease the magnitude and affect the timing of peak flow (typically delaying it), and increase base flows, increasing the flow duration downstream. Agricultural storage reservoirs typically attenuate seasonal peak flows, stabilizing or reducing base-flow or mid-growing season flow, and producing high-flows in late summer and autumn to meet agricultural demands downstream. This often produces a bimodal hydrograph with peaks in both the early and late growing season months, with interim periods of low flow.

Table 1.1. Dam management strategies and the most common effects on annual and daily downstream discharge.

Dam Management Strategy	**Seasonal Peak Flow**	**Seasonal Base Flow**	**Annual or Median Flow**	**Daily flow Variability**
Recreation/Navigation	decrease	increase	increase-no change	no change
Flood Control	decrease	increase	no change-increase	no change
Agricultural Storage	decrease	increase	increase	no change-increase
Hydroelectric Power	decrease	increase	no change	increase

In addition to modifying the timing and magnitude of peak flows and the magnitude and duration of low-flows, reservoir operations also affect the rate of change in flow during ascending and descending limbs of the hydrograph. Flows are often 'ramped' or 'stepped' up or down as a transition between high and low flows (Figure 1.1). Ramping involves a single rapid rise or decline in flow. Ramping between two desired or prescribed discharges may be so rapid that hydrographs take the form of a steep or nearly vertical rising or falling limb. Having been implicated in downstream degradation through accelerated rates of bank erosion (Schmidt and Graf 1990), fish mortality through abandonment in pools rapidly isolated from the main channel, and the mortality of seedlings of riparian plants (Rood and Mahoney 1990) and water-stress of adults (Tyree *et al.* 1994), ramping of flows is a less common practice today than it was in the recent past.

One common alternative to ramping is to conduct a stepped transition between high and low-flow. Stepped flows increase the length of time over which the transition from high to low flows occurs. A stepped flow hydrograph, as the name implies, involves a series of small vertical limbs (rapid drawdown) punctuated by nearly equal periods of time with no change in discharge (Figure 1.1). Stepped flows have been implemented to alleviate the previously mentioned physical and biological problems often encountered as a consequence of ramped flows. Given both the ramping or stepped transitions between flows and the modifications in the magnitude and variability of daily and seasonal flow regimes, dams influence every aspect of the hydrologic regimes of streams.

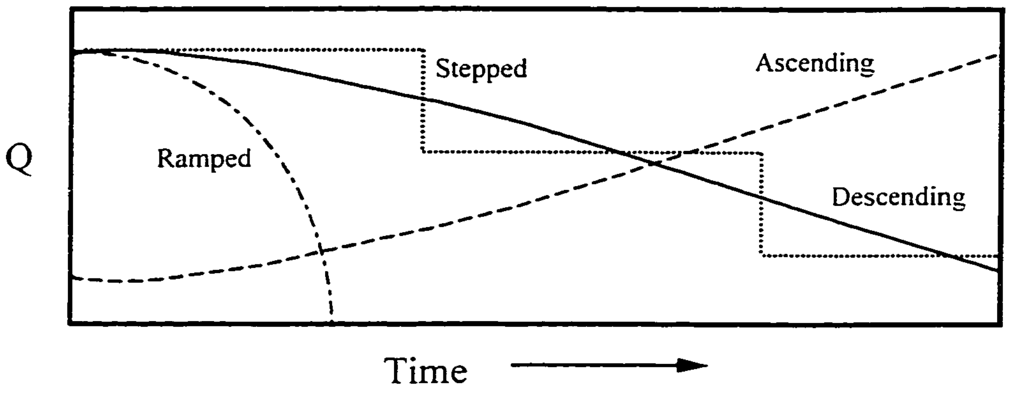


Figure 1.1. Schematic representation of natural (descending) and modified hydrologic regimes. Stepped and ramped flows are typical of outflows from dams managed for hydroelectric power, ascending flows are typical of agricultural storage reservoir outflows.

Because flow regime is the major factor governing channel form and the characteristics of aquatic and riparian ecological systems along watercourses, modifications in flow regime are likely to result in short as well as long-term changes in these systems. Whereas modified flow regimes cause changes in the spatial and temporal distribution of habitat across river bottoms, river damming may also cause other more subtle interruptions in key biotic processes, which may influence population and community level ecological processes along river corridors.

1.5 Study Objectives

The purpose of this study is to investigate the effects of dams on the upstream to downstream flow of hydrochoric seeds; to examine the interrelationships between dispersal phenology and spatial distributions of standing vegetation along rivers; and to examine the role of hydrologic regime in determining where seeds are deposited in relation to fluvial features. Flume studies, which investigate the relationships between the timing of seed release, the hydrograph characteristics, and fluvial landforms, are presented in Chapter 2. Flume studies were designed to test two research hypotheses:

> Hypothesis 2.1. Seeds will be retained and deposited in higher numbers along stream margins under natural snowmelt hydrologic regimes on the descending limb of the hydrograph than under each of three modified hydrologic regimes.

> Hypothesis 2.2. Seeds will be deposited non-randomly along river margins, depositing in higher concentrations in areas of reduced flow velocity such as in eddies, point bars, and pools.

Field investigations of the patterns of seed dispersal in relation to dispersal phenology, flow, and plant community composition above and below mountain reservoirs are presented in Chapter 3. These studies were designed to address the following three research hypotheses:

> Hypothesis 3.1. The number of hydrochoric seeds in the water column will be diminished below dams.

> Hypothesis 3.2. The species richness of hydrochoric seeds will be diminished below dams, and the composition of water-dispersed seeds will be a function of local sources of seeds below dams, and a function of regional sources above dams.

Hypothesis 3.3. Wind- and water-dispersed seeds will comprise a large proportion of the riparian flora (>50%) above and below dams, but species using hydrochory will occur closer to the channel below dams.

Hypothesis 3.4. Along free-flowing reaches, newly disturbed sites colonized by hydrochoric species or a combination of wind- and water-dispersed species will result in plant communities of higher species richness than sites colonized only by wind-dispersed species.

CHAPTER 2

AN EXPERIMENTAL STUDY OF RIPARIAN PLANT SEED DISPERSAL UNDER NATURAL AND MODIFIED HYDROLOGIC REGIMES

2.1 Introduction

Streamflow variability--the timing, duration, magnitude, and frequency of flows--exerts tremendous influence on stream ecosystems (Minshall 1988, Poff *et al.* 1997). The magnitude and frequency of flood-related disturbance (White 1979), the duration of inundation (Franz and Bazazz 1977, Auble *et al.* 1994), the depth of flow (Hosner 1960, Van Der Sman *et al.* 1993), and the fluvial processes associated with patterns of sediment and water discharge exert constraints upon, and provide opportunities for, aquatic and riparian biota. Whereas patterns of streamflow and disturbance determine the characteristics and suitability of riparian habitat, the ability of plants to colonize sites is largely constrained by the ability of plant propagules to disperse to suitable sites and to become established. The ability of plants colonize patches of newly available habitat or to invade previously occupied habitat is limited first by the ability of propagules to reach a site and second by the suitability of a particular site for germination and growth to maturity.

Although riparian plants exhibit adaptations to a variety of dispersal pathways (wind, gravity, ballistic, animal, and water), the stochastic nature of most dispersal pathways results in the delivery of a large proportion of the viable seeds released by a plant to sites that are not suitable for survival (Augspurger and Franson 1987, Augspurger and Kitajima 1992). In the context of plant population ecology, river margins and floodplains form a diverse patchwork of habitable and uninhabitable sites, some of which are submerged during some portion of the growing season during high flow, and are thereby unavailable to colonizers for some period of time (Kalliola *et al.* 1991). Furthermore, once sites are exposed after the recession of flows, edaphic conditions (soil moisture, depth to groundwater, nutrient availability) change rapidly, often resulting in a window of opportunity for pioneer species to colonize the site (Braatne *et al.* 1996). Whereas vegetative colonization through root suckering and rhizomatous growth and persistent soil seed banks may contribute to the colonization of new sites, the dispersal of seeds and vegetative propagules is the primary means by which plants are able to colonize suitable habitat patches, particularly along rivers (Kalliola *et al.* 1991).

Investigations of seed dispersal by water indicate that hydrochory is an important means of dispersal for many native aquatic and riparian plant species (Staniforth and Cavers 1976, Schneider and Sharitz 1988, Johansson and Nilsson 1993, Edwards *et al.* 1994), as well as for many introduced or adventitive riparian species (Egginton and Robbins 1920, Wilson 1980, Thébaud and Debussche 1991, Lonsdale 1993, Pysek and Prach 1993, 1994). Water dispersal may facilitate long-distance dispersal of seeds and increase the probability that seeds will reach sites that are suitable for germination and survival of seedlings (directed dispersal).

The portion of the research described in this chapter was designed to examine the relationships between hydrologic regime, flow regulation, stream channel morphology, and the patterns of dispersal and deposition of riparian plant seeds under experimental conditions in a flume. The purpose of this investigation is to develop an understanding of the mechanics of seed transport in relation to a variety of geomorphic features under 'natural' and 'modified' hydrologic regimes. The transport and dispersal of seeds under hydrologic regimes exhibiting a gradually descending drawdown, and a variety of modified hydrologic regimes, were examined using an experimental flume. It was hypothesized (Hypothesis 2.1) that more seeds would be retained and deposited under natural snowmelt hydrologic regimes on the descending limb of the hydrograph than under each of three modified hydrologic regimes: (1) stepped drawdown, (2) ramped drawdown, and (3) ascending flows. In addition, it was hypothesized (Hypothesis 2.2) that seeds would be deposited in greater numbers in areas of low flow velocity such as eddies, point bars, and pools (Nilsson *et al.* 1991b) rather than in higher energy sites such as areas of flow constriction, along cut-banks, along the lee sides of islands, and along stream margins on straight sections of channel. Replicated flume experiments were designed to test these two hypotheses, and to characterize and quantify the flow conditions most appropriate for the deposition of riparian plant seeds.

2.2 Methods

2.2.1 Flume Channel Design

A channel with fluvial features representative of high-gradient, pool-riffle streams was constructed in an experimental flume (20 m long and 1.8 m wide) located at the Engineering Research Center on the Foothills Campus of Colorado State University (Plate 2.1). The flume has a steel framework with walls and floor constructed of aluminum plates (thickness ~ 13 mm). The experimental channel was constructed from 3 m^3 of fill dirt consisting of a clay and gravel matrix. Fluvial features were structured to represent, in form and relative elevation, features typical of third and fourth order pool-riffle stream channels typical of mountainous regions throughout the world (Wohl, in review). Because the pool-riffle sequence is characteristic of both meandering and straight streams (Knighton 1998), a pool-riffle sequence was chosen for these experimental flume studies to increase the ability to make inferences from the results of this study to a wider variety of channel types.

Nine fluvial environments were represented in the flume: channel margin, constriction, cut bank, eddy, expansion, island, pool margin, point bar, and slackwater (Figure 2.1, Plate 2.1). The average channel width of the 9 m meandering segment of the channel was 0.96 m. Flow is conveyed through a 0.77 m-wide constriction, reducing the channel width by 20%, before entering a 1.2 m-wide eddy segment. Below the eddy, the channel again narrows by 48% flowing into a 0.62 m-wide flow constriction, and then abruptly widens to 1.8 m at the expansion and maintains this width through the pool segment. The channel splits into two flow paths around an island located below the pool

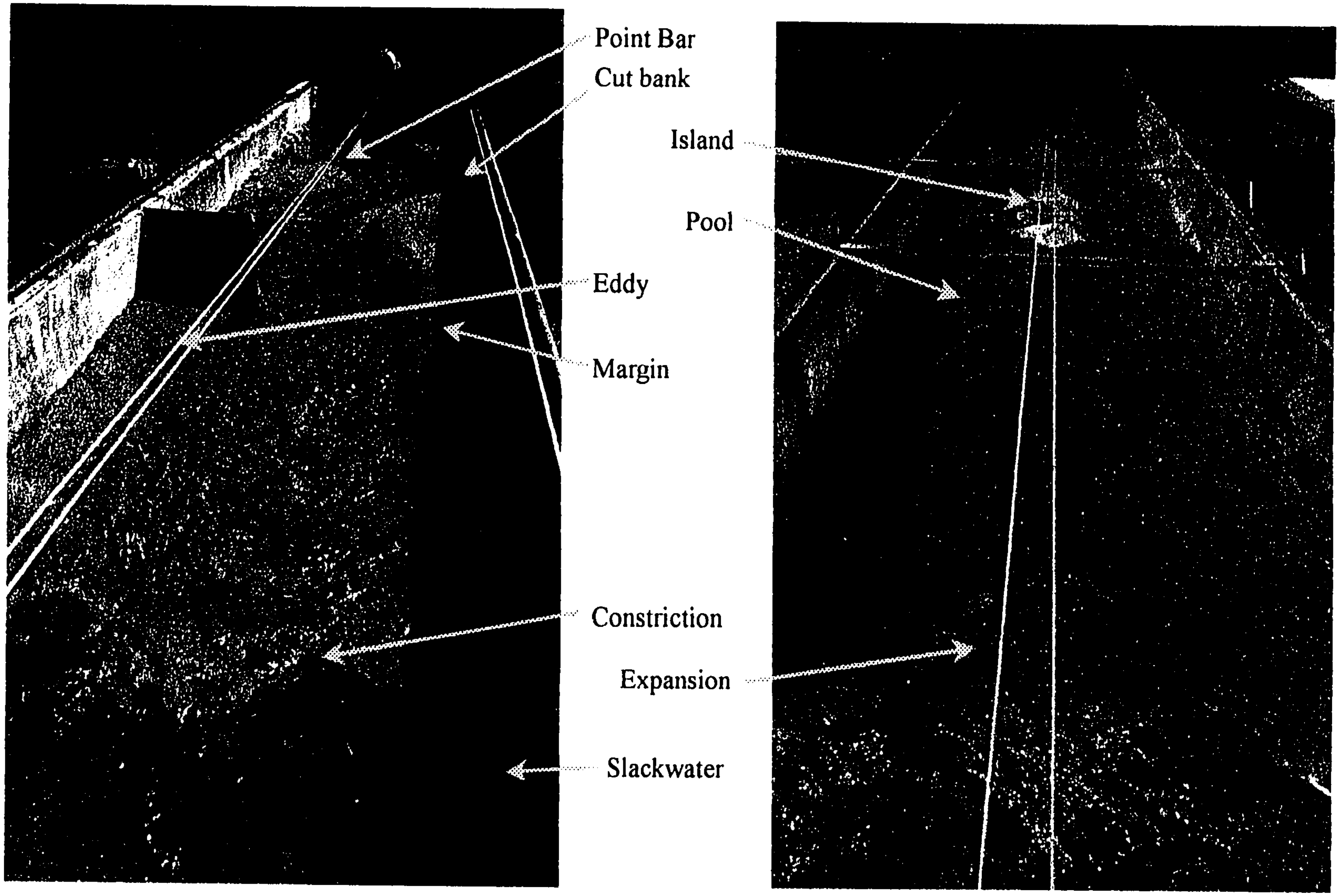


Plate 2.1. Experimental flume used in seed deposition experiments. Flow is from the top to bottom of the page on the left plate, and from bottom to top of page on the right plate.

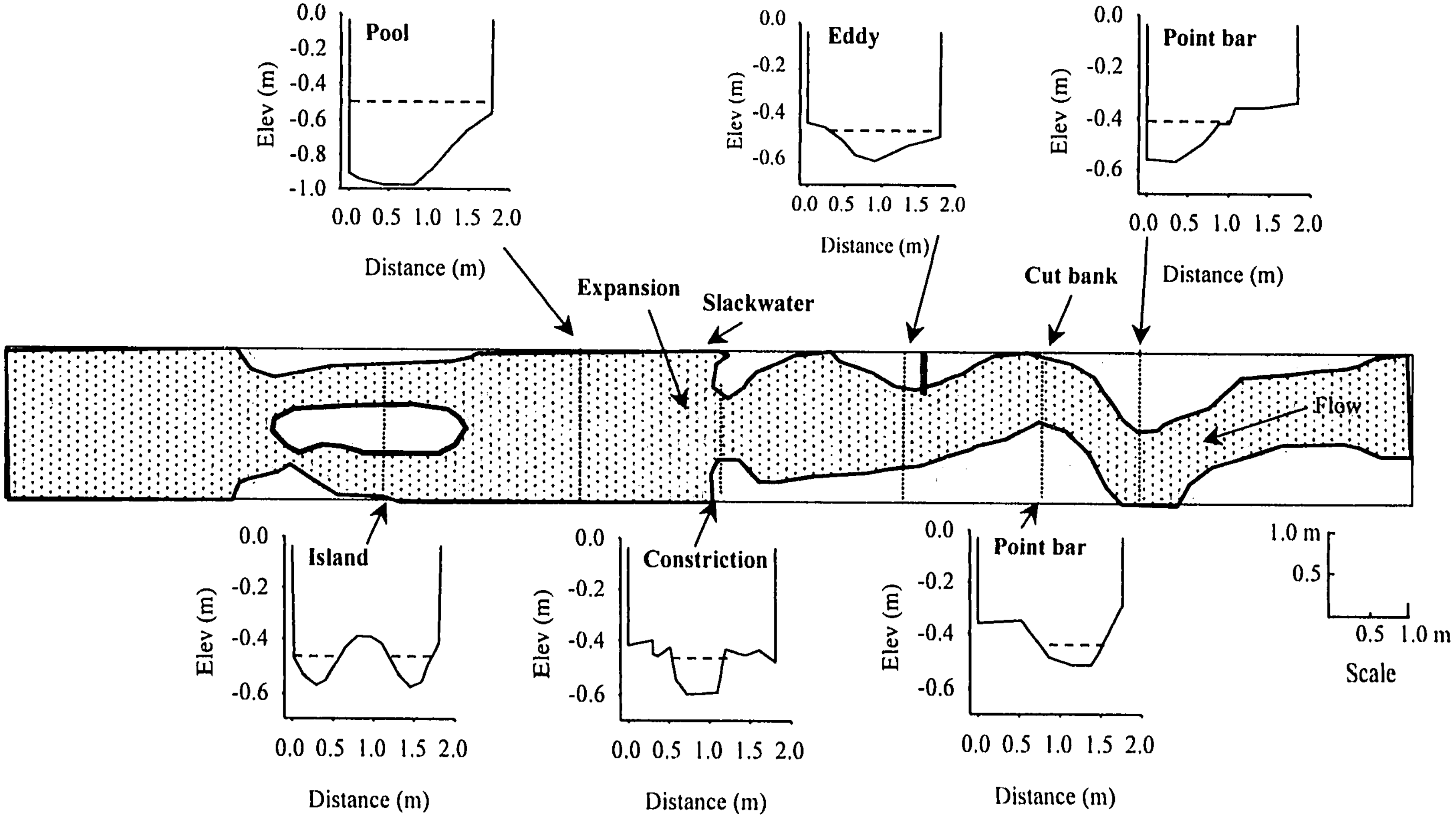


Figure 2.1. Experimental flume with fluvial features and cross-sections shown. Contour interval 0.03 m. Stippled areas are below the water surface for the flow illustrated here (0.030 m^3/s).

segment. The channel bed and all fluvial features were compacted mechanically and stabilized with a thin veneer of mortar cement (Manning coefficient of hydraulic roughness $n = 0.012$). A constant bedslope of 0.005 m/m was maintained for all flume trials.

The flume, although intended as a model of a natural stream channel, was not directly scaled from natural stream channel dimensions. The width of the flume channel was approximately 1:15 scale and the depth was scaled to approximately 1:5. The North Fork of the Cache La Poudre River (North Fork), a high gradient pool-riffle stream on the Front Range in Colorado which the flume channel was designed to represent, has width to depth ratios of 15, 25, and 53 at constrictions, pools, and through straight reaches, respectively. The flume channel had width to depth ratios of 7, 5, 9 for cross-sections in reaches of similar channel morphology to the North Fork.

2.2.2 Hydrologic Regimes and Seed Introduction

Water is supplied to the flume through a 0.10 m diameter high pressure PVC waterline which is supplied directly from a 0.91 m diameter main water line from Horsetooth Reservoir, in Fort Collins, Colorado. Maximum discharge available through the high pressure water line is 0.1 m^3/s. Discharge is controlled using a gate valve located on the 0.10 m water line at the upstream end of the flume. Flow is introduced to the flume through a T-section of PVC which extends vertically down into a 1.1 m deep head-gate section. Water enters the head-gate section through slot openings in the T-section and open pipe ends oriented perpendicular to the flume length and then flows through two layers of 0.2 cm mesh baffling before entering the main channel of the flume. Straight approach and exit sections (each 2 m in length) were established immediately below the head-gate and above the outlet of the flume to reduce turbulence prior to entering the experimental section and prior to exiting the flume through the flow measurement device. A 1.37 x 0.31 m (4.5 x 1 ft) cut-throat flume was installed immediately above the flume exit section to precisely measure discharge throughout each trial.

Four hydrologic regimes were routed through the flume and discharge was measured at the flume outflow in one-minute intervals over the course of each ten-minute trial. The 'natural' hyrologic regime was designed to be representative of the falling limb of the snowmelt hydrograph typical of mountain streams. Modified flow regimes were structured to represent the most common hydrologic patterns observed below dams managed for hydroelectric power and flood control (stepped and ramped hydrographs) and agricultural storage reservoirs (ascending late-season hydrographs; refer to Figure 1.1).

Ripe seeds of river birch (*Betula fontinalis* Sargent) were collected from mature individuals in the spring of 1998 for use in these experiments. River birch is a riparian shrub that grows along high elevation streams throughout the western U.S. River birch seeds are tiny (1.5 x 2 x 0.1 mm), flattened, winged nutlets that each weigh 1.6 x 10^{-4} g (mean of 200 seeds, standard error = 7.1 x 10^{-6} g). Seeds were introduced at one-minute intervals at the upstream end of the flume over the course of each hydrologic trial. Seeds were color-coded by applying a light mist of neon paint (red, green, and blue). Red coded seeds (Group A) were introduced in slugs of 330 seeds at one-minute intervals for the first three minutes of each trial, followed by green (Group B) for the next three minutes and then blue (Group C) for the final three minutes of each trial. A total of 2,970 seeds were introduced per trial. Seeds were color coded to emulate the natural occurrence of different riparian plants dispersing seeds over various segments of the hydrograph. Color coding also facilitated an evaluation of the residence times of seeds in various hydraulic environments and enabled quantification of the precise discharge, hydrograph characteristics, and hydraulics that were operating at the time of seed deposition. Experiments were initially designed to test the effects of seed density on patterns of transport and dispersal. The use of seeds of two specific weights were initially intended for this investigation. To simulate natural seeds that had lost their ability to float due to water-logging, color coded seeds were steeped in boiling water until they sank. Saturated seed trials were discontinued after three trials in which 100% of saturated seeds were deposited at the bottom of the entry slope of the pool.

Following each trial, seeds were counted in 0.5 m intervals along the entire length of the flume. Number of seeds on the right and left banks and in center of the channel was recorded. Because the terminal discharge during the ascending flow trials was high (0.030 m^3/s), seed deposition every 0.05 m along the channel was recorded using 8 mm video camera with a wide-angle to telephoto lense. A wheeled platform mounted over the flume enabled the measurement of seeds without disruption of the channel. Elevations of seed deposits were measured relative to a benchmark following each trial using a rod and level.

2.2.3 Hydraulic Measurements and Modeling

Direct measurements of water-surface elevations, flow velocity, and water depth were taken at three discharges--0.005, 0.014, and 0.030 m^3/s--along 16 cross-sections (100 points/discharge). Holding discharge constant, water-surface elevation was measured over the length of the flume at 1 m intervals at each of these discharges. Depth (D) and 0.6 x *D* velocity were measured along 16 cross-sections placed along the length of the flume at each of the three discharges. Flow velocity was measured using a Marsh-McBirney Model 2000 electromagnetic one-dimensional current meter, which measures both upstream and downstream flow.

A detailed digital-elevation map (DEM) of the channel was constructed from x, y, and z measurements placed at a concentration of 8 points per square meter (365 points total) using a Topcon laser elevation-distance meter (EDM). Points were placed along cross-sections at <1 m intervals along the length of the flume. Water-surface elevations and flow hydraulics were modeled using the HEC-RAS step-backwater model (HEC 1996) calibrated to measured water surface elevations and discharges. This model facilitated the calculation of water-surface elevations and cross-sectional average hydraulic characteristics for the seed-depositing discharges throughout the flume.

To understand how velocity of the fluid field at each of the fluvial features relates to flow in the main channel, a ratio of the average velocity of the fluid field associated with the fluvial feature (V) to the maximum velocity measured at the cross-section (V_{mx}) was calculated. Relative velocity (V/V_{mx}) is a measure unique to this study. V/V_{mx} provides a measure of the strength of recirculating flow through comparing the strength of flow along stream margins to the downstream component of flow. In addition, Reynolds number, Froude number, and the Weber number were calculated for each measurement station. These variables were calculated to characterize and quantify the flow conditions of the fluid fields associated with each of the fluvial features.

Reynolds number (Re) is a dimensionless variable which is derived from both the properties of water and the hydraulic properties of the channel. *Re* is a ratio of inertial to viscous forces in a fluid and serves as a criterion to distinguish between laminar ($Re < 500$) and turbulent ($Re > 2500$) flow in open channels (Knighton 1998). Flows with Reynolds numbers between 500 and 2500 are considered transitional flow. Reynolds number is:

Eq. 2.1 $$Re = \rho VD/\mu$$

where *Re* is the Reynolds number (dimensionless), *V* is the average velocity of the fluid in the vertical profile (0.6 x D) in m/s, *D* is the depth of flow in m, ρ is the density of water in kg/m^3, and μ is the dynamic viscosity of water in Ns/m^2.

Froude number (Fr) is another important dimensionless hydraulic variable that describes the flow regime in an open channel (Young *et al.* 1997). The flow regime is considered critical when $Fr = 1$, subcritical when $Fr < 1$, and supercritical when $Fr > 1$. Subcritical flow, also referred to as tranquil flow, typically occurs at lower flow velocities. *Fr* is a ratio of inertial to gravitational forces:

Eq. 2.2 $$Fr = V/\sqrt{(gD)}$$

where *Fr* is the Froude number (dimensionless), *V* is the average velocity of the fluid in the vertical profile (0.6 x D) in m/s, g is acceleration due to gravity (m/s^2), and D is the depth of flow in m.

The Weber number (We) is a dimensionless variable which characterizes the relationship between inertial forces and the surface tension of a fluid (Young *et al.* 1997). Because seeds typically float on the surface of the water, or are held on the water surface by surface tension, the balance of the forces conveying the seed downstream and the forces holding the seed on the surface were of interest. The Weber number is:

Eq. 2.3 $$We = \rho V^2 D / \sigma$$

where We is the Weber number (dimensionless), ρ is the density of water in kg/m^3, V is the average velocity of the fluid in the vertical profile (0.6 x D) in m/s, D is the depth of flow in m, σ is the surface tension of water in N/m.

Spatial coordinates and associated hydraulic measurement positions were entered into a spatial database (ARC/Info; ESRI 1998) and the inverse distance weighting method was used to interpolate a grid coverage for each of the parameters within the wetted channel at each of the three discharges measured. Inverse distance weighting uses neighboring points (eight nearest neighbors in this case) to calculate the values for grid cells in which the value of the parameter is unknown. This method resulted in twelve raster grids each with a cell size of 0.018 m. Hydraulic characteristics of each of the nine fluvial features were determined by calculating the average values of each of the hydraulic variables at each of the fluvial features through an overlay procedure in ARC/Info GRID (ESRI 1998).

2.2.4 Data Analysis

Seed deposition data were first analyzed by pooling the color-coded seeds deposited after each trial and analyzing total numbers of seeds deposited in each hydraulic environment (fluvial feature). Seed count data were normalized by dividing the number of seeds by the shoreline distance occupied by the fluvial feature, which yielded number of seeds per meter of shoreline. A square-root transformation was applied to the count data prior to statistical treatment to more closely comply with the assumptions of normality and homogeneity of variance in the intended statistical tests. Two-way repeated measures analysis of variance (ANOVA) was used to compare the four flow regimes (REGIME), the eight fluvial features (FF) and to test for interactions. In the analysis, repetitions (RUNS) were nested within *REGIME* as a random effect and *FF* was the repeated measure. Pairwise differences in mean numbers of seeds between flow regime and between fluvial features within a particular flow regime were tested using a hand-calculated Tukey's adjustment and a significance level of $p < 0.05$. Whereas the seed count data were transformed prior to statistical treatment, the non-transformed normalized values of the data are presented in graphical form.

Linear regression was used to determine the strengths and directions of the linear relationships between number of seeds deposited at a particular fluvial feature and each of the hydraulic variables. For cases in which a curvilinear relationship was apparent, a quadratic term was entered into the regression equation. Dependent variables included total number of seeds, number of seeds of Group A, Group B, and Group C; independent variables included V, V_{mx}, V/V_{mx}, Re, Fr, and We. A pooled data-set including all flow regimes was first analyzed to discern general hydraulic trends from those associated with a particular hydrologic regime. Seed deposition data for each flow regime were analyzed individually.

2.3 Results

2.3.1 Total Numbers of Seeds Deposited

Flow ranged from 0.002 to 0.036 m^3/s for all seed release trials (Figure 2.2). Less than 20% of seeds introduced during each trial were deposited within the flume. Ample seeds were available to all fluvial features regardless of position within the flume, indicating that the source of seeds was not a factor limiting deposition of seeds to any feature. Three saturated-seed trials with descending flow regimes resulted in the deposition of 100% of the seeds on the channel bed immediately above the pool and in the bottom of the pool. It was concluded that saturated seeds, while potentially viable, were not effective dispersal units in these flume trials. However, saturated seeds have been shown to be important dispersal units on sandbed streams (Staniforth and Cavers 1976). In addition, some riparian and wetland hydrochores that do not float while dormant, do float and disperse following sub-aqueous germination. Because many of these considerations were beyond the scope of this study, saturated-seed trials were discontinued after three initial trials.

Twelve flume runs (four hydrologic regimes replicated three times) were conducted using air-dried, color-coded seeds. There were statistically significant differences in the numbers of seeds deposited under each of the four flow regimes as well

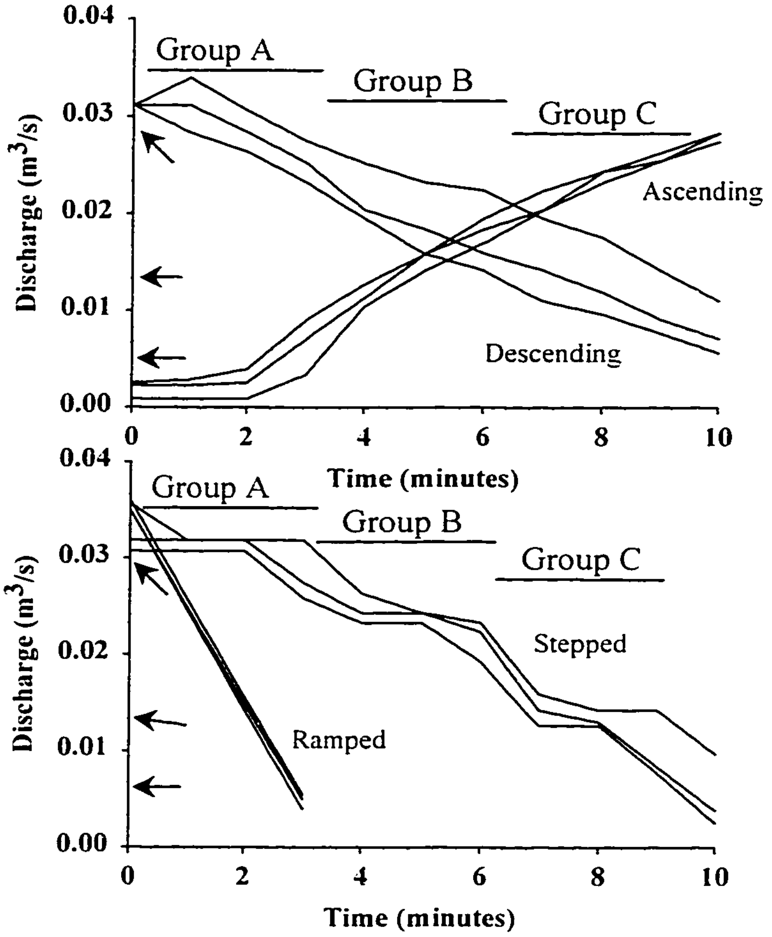


Figure 2.2. Hydrographs measured from flume trials. Period of seed release of Groups A, B, and C indicated by horizontal bars. Hydraulic measurements were taken at each of the discharges indicated by the arrows.

as between each of the nine fluvial features (Table 2.1, Figure 2.3). The interaction between flow regime and fluvial feature was also highly significant, indicating that there is differential deposition of seeds on fluvial features as a function of flow regime. Contrary to Hypothesis 2.1, the 'natural hydrologic regime' did not result in maximum seed deposition (Figure 2.3). The stepped flow regime retained most seeds (mean 524 seeds/trial), followed by the descending (natural) flow regime (mean 295 seeds/trial), ramped (mean 58 seeds/trial), and ascending (mean 49 seeds/trial) flow regimes. Whereas many seeds were deposited in areas of low flow energy (pool, eddy, slackwater, and expansion), some seeds were also deposited along cutbanks and at the constriction, which were the highest energy areas in the flume.

Table 2.1. ANOVA table for two-way repeated measures analysis on total number of seeds deposited.

Source	df	F	*p*-value
Flow Regime (FR)	3	28.5	0.0001
Fluvial Feature (FF)	8	12.7	0.0001
FR * FF	24	2.3	0.0044

Pairwise comparisons indicated that under ascending flow regimes significantly greater numbers of seeds were deposited at the expansion than were deposited along any other fluvial feature (Figure 2.4). Although the average number of seeds deposited was highest at the flow expansion under the ascending flow regime, there were no significant differences between the slackwater, expansion, eddy, and pool margin. The constriction, expansion, pool margin, eddy, and slackwater collected higher numbers of seeds than other features under the ramped flow regime, but these differences were not statistically significant. The eddy, expansion, and slackwater collected the greatest number of

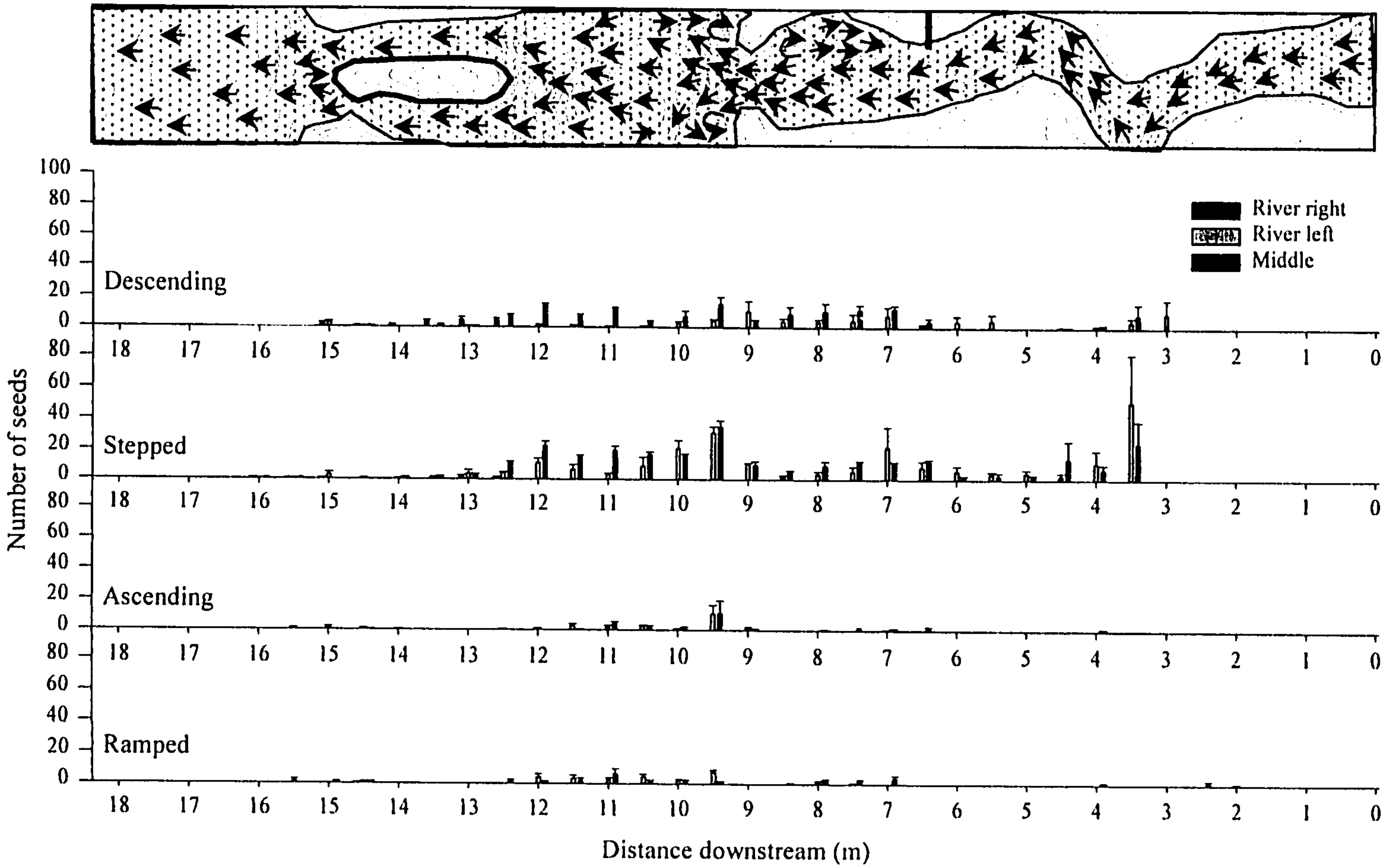


Figure 2.3. Top frame: Contour map of flume showing measured water surface (stippled) at a discharge of 0.030 m^3/s. Velocity vectors are indicated by arrows. Bottom frame: Plots showing numbers of seeds deposited on right and left channel margins and in the center of the channel measured at 0.5 m intervals. Mean and standard error of three replicates of each flow regime.

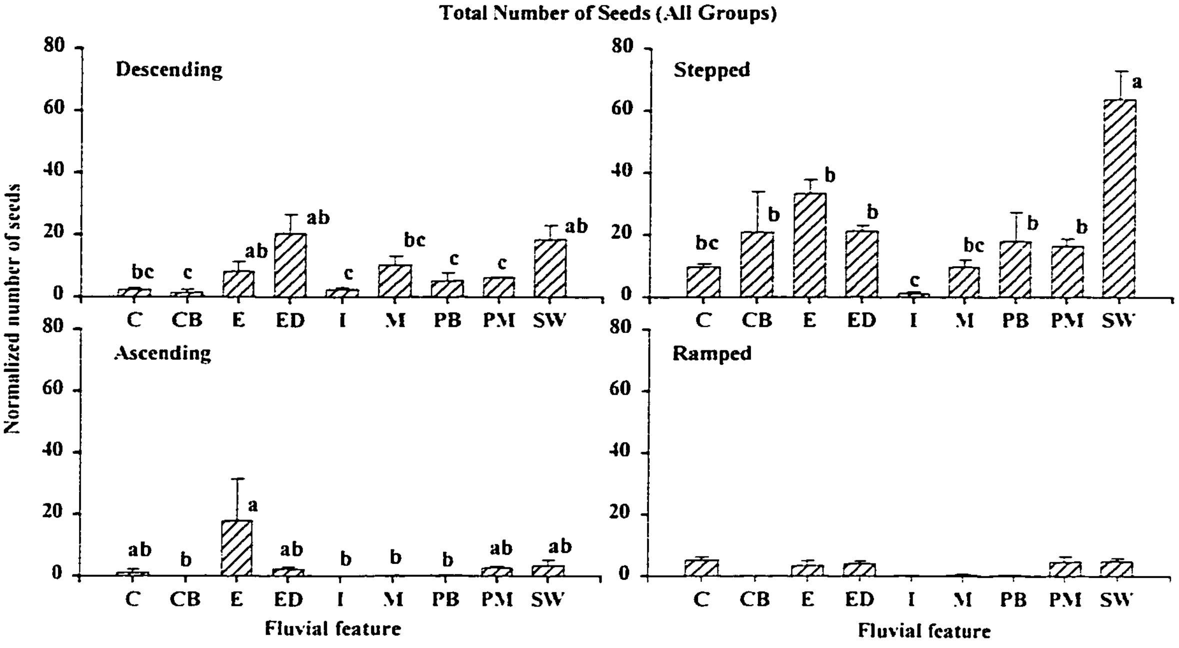


Figure 2.4. Summary of seed deposition results under four hydrologic regimes for all groups of seeds. Fluvial features indicated are: C--constriction, CB--cutbank, E--expansion, ED--eddy, I--island, M--channel margin, PB--point bar, PM--pool margin, and SW--slackwater. Mean and standard error of the mean for three repetitions for each flow regime. Means not sharing a letter are significantly different (Tukey adjustment, $p < 0.05$).

seeds under the natural (descending) flow regime, followed by the channel margin, pool margin, and point bar listed in order of decreasing order of numbers of seeds. This provides strong support for Hypothesis 2.2. The slackwater captured significantly greater numbers of seeds over all other fluvial features under the stepped flow regime. The cutbank, eddy, and expansion captured significantly greater numbers of seeds than were deposited on the island or constriction under the stepped flow regime.

2.3.2 Timing of Dispersal in Relation to Flow Regime

Seeds of the earliest dispersed seeds (Group A) were deposited in greater numbers than later dispersed seeds (Groups B and C) under all regimes with the exception of the ascending flow regime (Figures 2.5, 2.6, and 2.7). Under this regime, later dispersing seeds (Groups B and C) were deposited in greater numbers than seeds of Group A. These seeds were deposited at high elevations along channel margins. A majority of the early dispersing seeds of Group A were flushed completely through the flume under the ascending hydrologic regime, whereas the later dispersed seeds were recirculated and retained in the eddy and in other areas of flow separation and low or negative velocities such as those associated with the expansion and other channel irregularities. Seeds resided in these cells of recirculation until flow was terminated, at which time they were deposited at relatively high elevations on the shoreline. In test runs prior to formal flume experiments, seeds were retained and recirculated in the eddy and at the flow expansion for a duration of 22 minutes before flows were terminated.

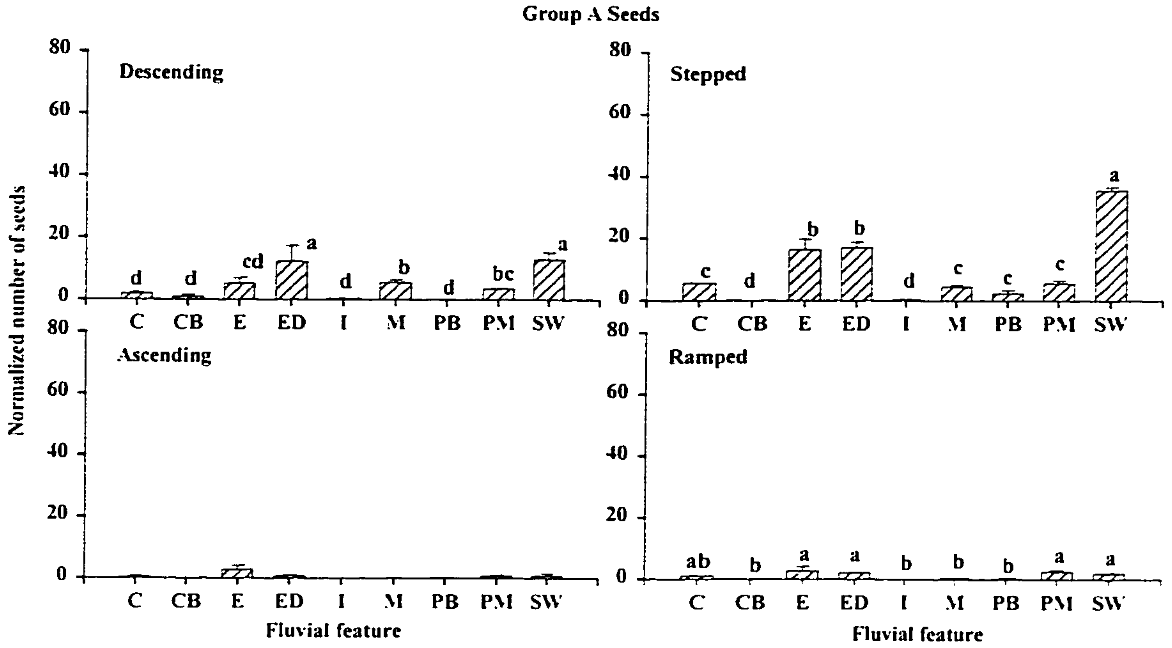


Figure 2.5. Summary of seed deposition (Group A) results under four hydrologic regimes. Fluvial features indicated are: C--constriction, CB--cutbank, E--expansion, ED--eddy, I--island, M--channel margin, PB--point bar, PM--pool margin, and SW--slackwater. Mean and standard error of the mean for three repetitions for each flow regime. Means not sharing a letter are significantly different (Tukey adjustment, $p < 0.05$).

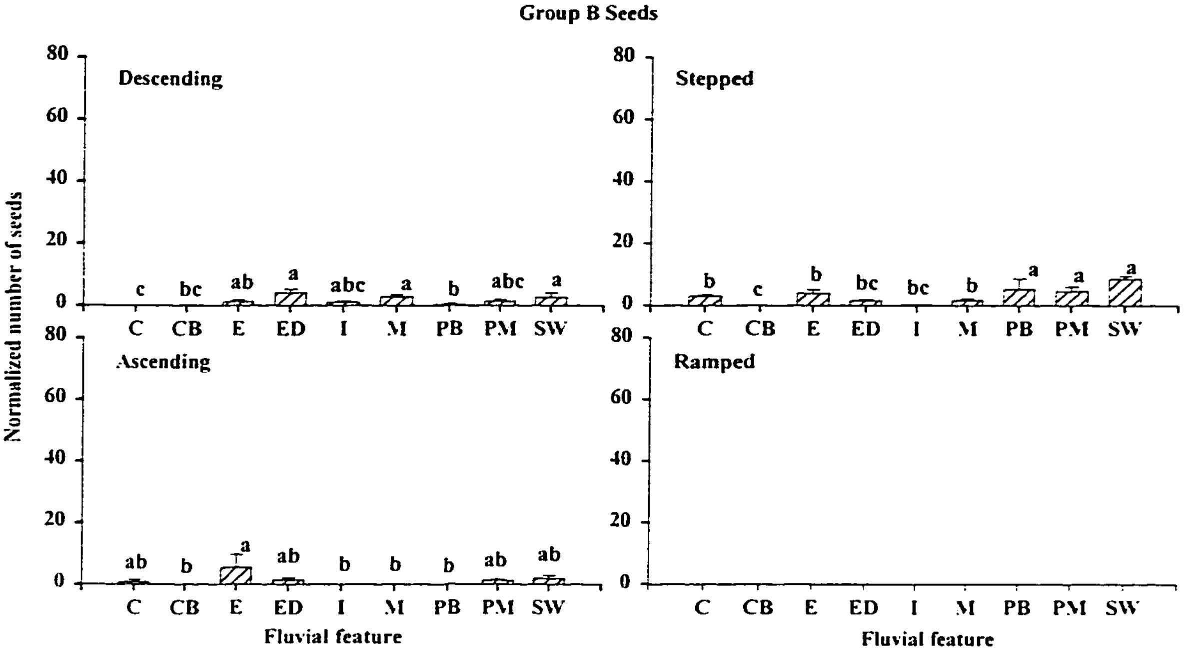


Figure 2.6. Summary of seed deposition (Group B) results under four hydrologic regimes. Fluvial features indicated are: C--constriction, CB--cutbank, E--expansion, ED--eddy, I--island, M--channel margin, PB--point bar, PM--pool margin, and SW--slackwater. Mean and standard error of the mean for three repetitions for each flow regime. Means not sharing a letter are significantly different (Tukey adjustment, $p < 0.05$).

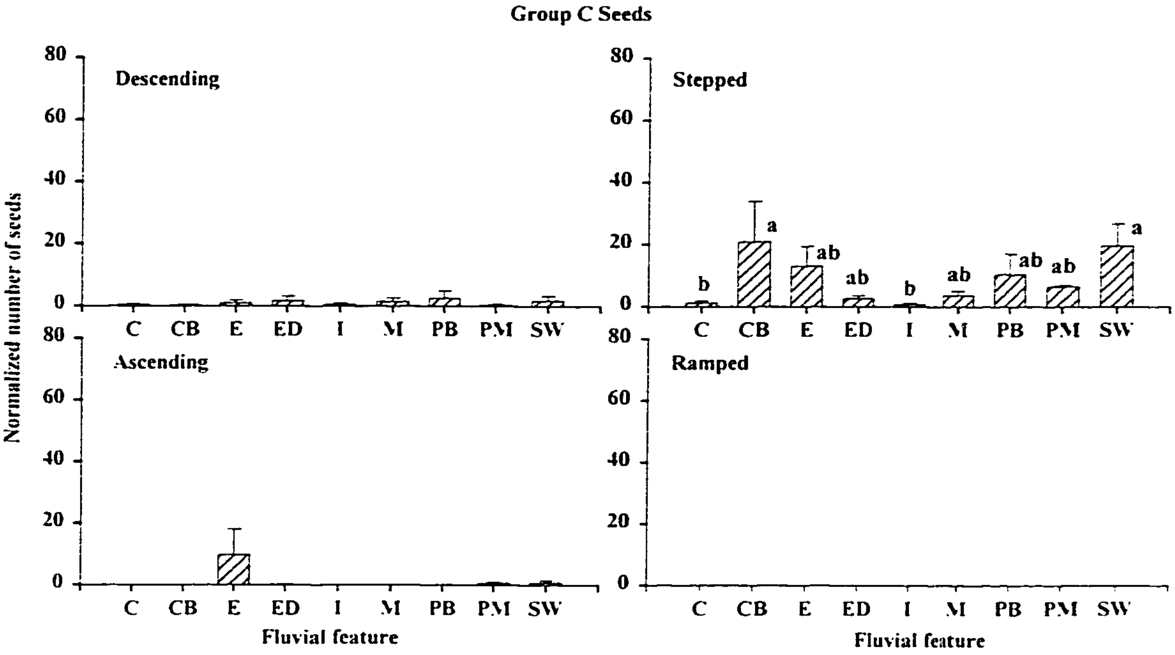


Figure 2.7. Summary of seed deposition (Group C) results under four hydrologic regimes. Fluvial features indicated are: C--constriction, CB--cutbank, E--expansion, ED--eddy, I--island, M--channel margin, PB--point bar, PM--pool margin, and SW--slackwater. Mean and standard error of the mean for three repetitions for each flow regime. Means not sharing a letter are significantly different (Tukey adjustment, $p < 0.05$).

In lab experiments in which the duration of buoyancy of river birch seeds was tested, it was found that 59% of seeds exposed to water remained floating after 11 days (200 seeds; Merritt, unpublished data). The percentage of seeds floating after 11 days dropped to 9% when samples were agitated, suggesting that surface tension may be an important factor in keeping river birch seeds on the water surface. Because zones of recirculation are areas of rather tranquil flow, a combination of buoyancy and surface tension serves to keep the seeds on the water surface in these areas. Thus seeds may recirculate in eddies for weeks under steady flow of sufficient magnitude for zones of recirculation to be maintained. These seeds may thus be available to downstream areas over a duration of time potentially longer than the period of seed release from parent plants.

Under descending and stepped flow regimes, seeds were generally deposited in bands along the shoreline at elevations slightly lower than the stage at the time of seed release. Due to retention of the seeds of Group A in zones of recirculation, the seeds of this group were more abundant and were deposited over a wider range of shoreline elevations than either of the two groups of later dispersed seeds. Because flow was high over the duration of release of Group A, zones of recirculation were well developed and were consequently very efficient at diverting, retaining, and recirculating seeds. Seeds of Group A were retained in these zones until flows were insufficient to maintain strong zones of recirculation, at which time seeds were either deposited along shorelines or re-entrained by flow in the main channel and deposited downstream. Nearly 80% of the seeds of Group A deposited during the descending hydrologic regime were deposited in the slackwater, the eddy, and at the expansion (Figure 2.5). Eighty-six percent of the seeds of Group A deposited by the stepped flow regime were deposited on the slackwater, the eddy, and at the expansion, providing strong support for Hypothesis 2.2.

Under descending and stepped flow regimes, many seeds of Group C were deposited on the point bars, but few seeds of Group A or B were deposited on point bars during these trials (Figures 2.5, 2.6, and 2.7). At high flows during the release of Group A, well-developed crescent-shaped eddies formed along the downstream extent of both point bars. These crescent-shaped zones of recirculation were very efficient at trapping and depositing seeds at higher flows (>0.028 m^3/s). At intermediate flows (0.012 - 0.026 m^3/s) during the period of time when the seeds of Group B were available, these crescent-shaped zones of recirculation were unstable and not well formed. The zone was characterized by irregular bursting associated with shedding vortices. As a consequence, these features were not efficient at trapping and depositing seeds at intermediate flows. At lower flows, flow over the apex of the point bars was only a few mm deep. Seeds being released during this period of time (Group C under all flows except ascending) often became trapped on the sloping tips of point bars as water levels gradually receded (Figure 2.7).

At intermediate discharges during the descending and stepped regimes, zones of recirculation beneath flow constrictions were well developed. Because the release of seeds of Group B occurred during this segment of the hydrograph, many seeds of Group B were detained in the eddy and at the flow expansion. These seeds were mixed with the seeds of Group A while recirculating in the eddy, and seeds of both groups were deposited simultaneously at the eddy and below the expansion, as well as along the pool margins. Below discharges of 0.010 m^3/s, the zone of recirculation associated with the eddy dissipated and a majority of the flow through the eddy portion of channel was in a downstream direction. As a consequence, most of the deposited seeds of Group C were found in the pool and downstream of the expansion during the descending and stepped flows (Figure 2.7).

During the ramped flow regime only 2.0% of the seeds released were deposited along the channel. Although flow was sufficient during the initial 1.5 min of the ramped flow to produce flow separation below constrictions, the rate of change in flow was so great that zones of recirculation never became well developed. As a consequence, very few seeds (19%) deposited during this trial were detained by these features during the ramped flow regime (Figure 2.4). Most of the seeds (81% of the total deposited) were deposited below the eddy at the constriction, expansion, and along the pool margins under ramped flows. The most conspicuous pattern of seed deposition during the ramped flow regime was the wide elevational band of deposition. Seeds were stranded at elevations ranging from the top of the rocks forming the constriction to the low-lying stream margins near the expansion, a range in elevation of 22 cm. This random pattern of deposition is strikingly different from the non-random shoreline zonation of seed deposition exhibited by the descending and stepped regimes.

Nearly all of the seeds of Group A that were deposited during the ascending flow regime were deposited at the expansion and the eddy (Figure 2.5). These three features captured 70% of the seeds of Group A captured during the ramped flow regime, with the remaining 30% being deposited in the pool margin and slackwater. There were significant differences in the number of seeds of Group A deposited between flow regime, fluvial feature and the interaction between flow regime and fluvial feature (Table 2.2).

Table 2.2. ANOVA table for two-way repeated measures analysis on number of seeds of Group A deposited.

Source	**df**	**F**	***p*-value**
Flow Regime (FR)	3	85.5	0.0001
Fluvial Feature (FF)	8	42.9	0.0001
FR * FF	24	7.1	0.0001

Seeds of Group B were deposited in the greatest numbers under stepped and descending flow regimes (Figure 2.6). Seeds of Group B deposited during the stepped flow regime were found at intermediate elevations, below the stage during which they were released. Seventy-five percent of these seeds were deposited in the slackwater, along pool margins, and on the point bars. Seeds of Group B were deposited over a wider range of elevations during the descending hydrologic regime. A large proportion (85%) of these seeds were deposited in the eddy, slackwater, and along pool and channel margins. There were significant differences in the number of seeds deposited by each of the four flow regimes, on each of the nine fluvial features, and the interaction between these two variables (Table 2.3).

Table 2.3. ANOVA table for two-way repeated measures analysis on number of seeds of Group B deposited.

Source	**df**	**F**	***p*-value**
Flow Regime (FR)	3	8.9	0.0062
Fluvial Feature (FF)	8	10.2	0.0001
FR * FF	24	2.8	0.0005

As with Group A and B, a larger proportion of seeds of Group C released was deposited during the stepped and descending hydrologic regimes than was deposited during ramped or ascending hydrologic regimes. The contrast between stepped and descending flow regimes was much greater for seeds of Group C than for any other group (Figure 2.7). These differences in numbers of seeds deposited between hydrologic regime were statistically significant (Table 2.4). Under the stepped hydrologic regime, 82% of the total number of seeds deposited were deposited in the slackwater, on the cutbank, at the expansion, and on the point bar. The slackwater, point bar, expansion, and eddy captured 71% of seeds during the descending flow. The expansion, pool margin, and slackwater caught nearly 100% of the seeds of Group C under the ascending flow regime.

Table 2.4. ANOVA table for two-way repeated measures analysis on number of seeds of Group C deposited.

Source	**df**	**F**	***p*-value**
Flow Regime (FR)	3	13.8	0.0016
Fluvial Feature (FF)	8	2.5	0.0222
FR * FF	24	1.6	0.0656

2.3.3 Hydraulics of Channel Features

Hydraulic attributes of the fluvial features were calculated from direct measurements of velocity taken at three steady discharges (0.005, 0.010, 0.030 m^3/s) at points throughout the flume. At the lowest discharge (0.005 m^3/s), average velocity in the flow fields at each of the fluvial features ranged from a low of 0.01 m/s at the expansion to a high of 0.42 m/s at the point bar. Average velocity ranged from -0.02 m/s (expansion) to 0.34 m/s (cutbank) at a discharge of 0.010 m^3/s, and ranged from 0.00 m/s (slackwater) to 0.37 m/s (cutbanks) at the highest discharge (0.030 m^3/s). Maximum velocity at a cross-section was lowest at the expansion at a discharge of 0.005 m^3/s, and lowest along the pool margins at 0.010 m^3/s and 0.030 m^3/s. Maximum velocity was highest at the point bar at a discharge of 0.002 m^3/s and highest at the constriction at both 0.010 m^3/s and 0.030 m^3/s. Froude numbers (Fr) were subcritical at all fluvial features and ranged from 0.04 at the expansion to 0.73 at the point bar at the lowest discharge measured (0.005 m^3/s). *Fr* was much more variable at higher discharges, ranging from 0.00 in the slackwater during both intermediate (0.010 m^3/s) and high (0.030 m^3/s) discharges to 0.47 and 0.49 at the cutbanks during these two discharges, respectively. Flow was turbulent at all locations at all discharges in the flume, with the exception of the slackwater. Flow was relatively tranquil at the expansion, eddy and at the island at the lowest discharge. Reynolds number (Re) ranged from 3,100 at the expansion to 12,500 at the point bar at this discharge. As expected, *Re* was highest at the constriction, cut banks, and point bars and lowest along the pool margins, expansion, eddy, and at the island for all flow regimes. The Weber number (We) ranged from 6 to 156, at the pool margin and at the point bar, respectively, under the low flow regime. At higher discharges, *We* fell to 0 in the slackwater and rose to 174 at the cutbank at 0.010 m^3/s, and to 299 at the constriction at a discharge of 0.030 m^3/s. In general, the island, pool margins, and expansion had low *We*, indicating that the influence of surface tension is high relative to inertial forces of the stream in these areas. *We* was highest at cutbanks, constrictions, and point bars.

Although neither described a large proportion of the variability in numbers of seeds deposited using the pooled data-set, the best hydraulic descriptors were average velocity in the flow field (V) and relative velocity (V/V_{mx}; Table 2.5). Flow velocity, V/V_{mx}, and Fr were the best determinants of the numbers of seeds of Group A deposited (Figure 2.8). None of the hydraulic variables described more than 10% of the variability

Table 2.5. R^2 for linear and quadratic (italic text) regression equations relating total number of seeds (all groups pooled) and seeds of Group A, B, and C deposited, to several hydraulic variables: velocity (V) is average velocity in the fluid field along the section of stream where the seeds were deposited: V_{mx} is the maximum velocity measured at the cross-section nearest the reach: V/V_{mx} is the ratio of average fluid field velocity to max velocity at the cross-section--relative velocity: Froude, Reynolds, and Weber numbers are dimensionless parameters describing hydraulic conditions of the fluid field (see text). P-values from F-test < 0.05 are indicated by *; those <0.005 are indicated by **.

POOLED REGIME

	Velocity (m/s)	Froude number	Reynolds number	Weber number	V_{mx}	V/V_{mx}
Total seeds	0.05*	0.03	0.02	0.08*	0.002	0.06*
Group A	0.30**	0.28**	_0.25**_	0.11**	0.05*	0.34**
Group B	0.09**	0.08**	0.02	0.10**	0.01	0.06*
Group C	0.01	0.00	0.07*	0.06*	0.09*	0.02

DESCENDING REGIME

	Velocity (m/s)	Froude number	Reynolds number	Weber number	V_{mx}	V/ V_{mx}
Total seeds	0.01	_0.41**_	0.00	0.02	0.04	0.02
Group A	0.60**	_0.62**_	_0.59**_	_0.46**_	_0.44**_	_0.74**_
Group B	_0.39**_	_0.39**_	0.00	_0.23*_	0.03	0.00
Group C	0.02	0.03	0.00	0.01	0.01	0.00

ASCENDING REGIME

	Velocity (m/s)	Froude number	Reynolds number	Weber number	V_{mx}	V/ V_{mx}
Total seeds	0.29**	0.28**	0.02	0.17*	0.06	0.22*
Group A	0.30**	0.28**	0.08	0.14*	0.05	0.24*
Group B	0.32**	0.31**	0.03	0.19*	0.08	0.23*
Group C	0.16**	0.15**	0.02	0.12	0.1	0.09

STEPPED REGIME

	Velocity (m/s)	Froude number	Reynolds number	Weber number	V_{mx}	V/ V_{mx}
Total seeds	0.00	_0.12_	0.03	0.00	_0.23*_	_0.27*_
Group A	_0.81**_	_0.83**_	_0.75**_	_0.75**_	_0.57**_	_0.91**_
Group B	0.04	_0.26*_	0.00	0.04	_0.12_	_0.25*_
Group C	0.02	0.02	0.03	0.02	0.01	0.09

RAMPED REGIME

	Velocity (m/s)	Froude number	Reynolds number	Weber number	V_{mx}	V/ V_{mx}
Total seeds	_0.34*_	_0.32*_	_0.14_	0.23*	0.11	_0.30*_
Group A	_0.60**_	0.32**	0.29**	0.37**	0.26*	0.53**
Group B	_0.30*_	0.18*	0.07	0.19*	0.13	0.19*
Group C	0.11	0.09	0.01	0.09	0.05	0.04

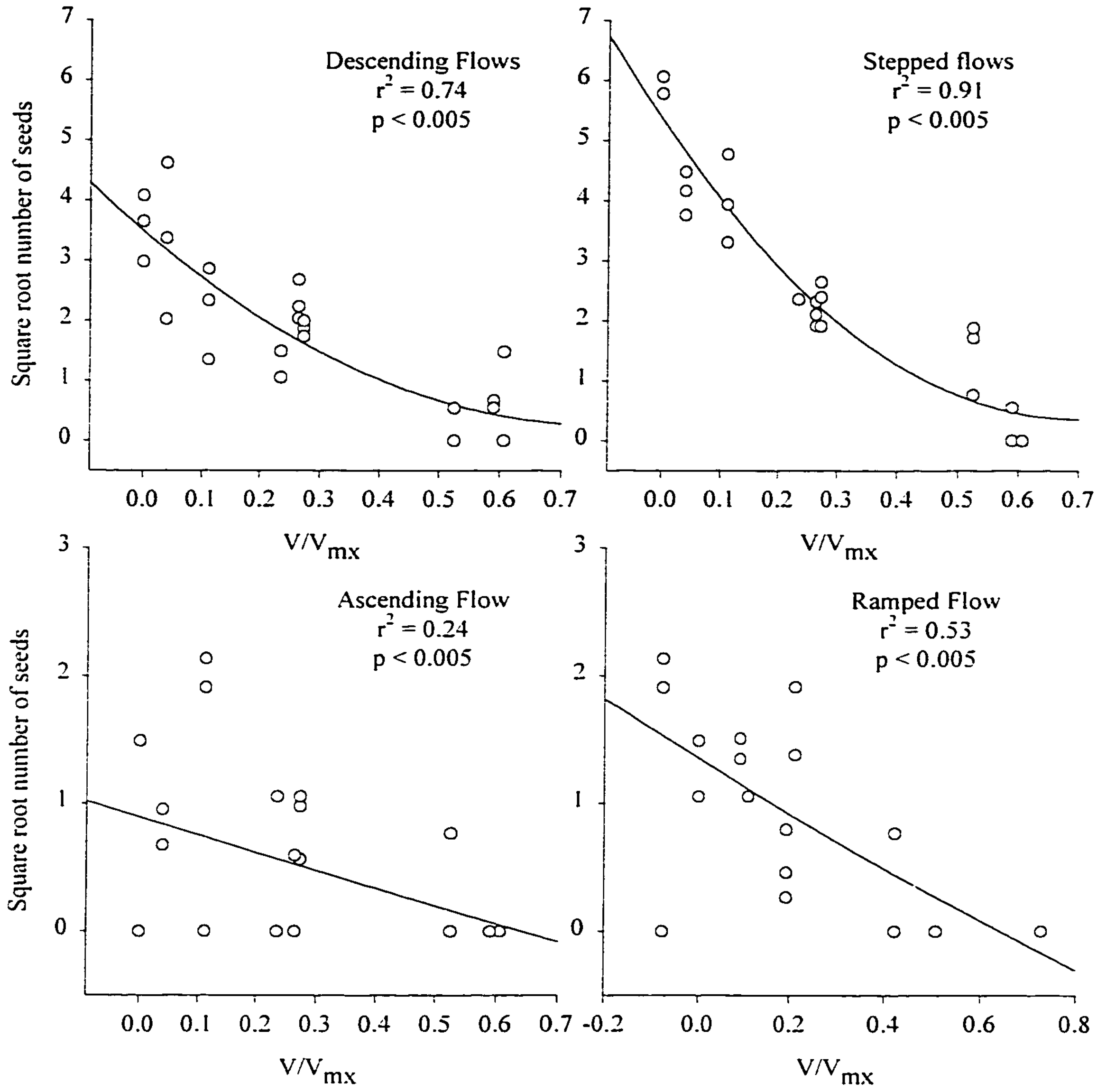


Figure 2.8. Number of seeds deposited (square root transformed) on each of eight fluvial features (see text) versus relative velocity (V/V_{mx}) for four discharges in a flume.

in numbers of seeds of Group B and C deposited using the pooled data-set. The only general trend from the pooled analyses was that the seeds of early dispersing seeds tend to become deposited in areas of lower flow velocity. This provides support for Hypothesis 2.1.

An examination of each hydrologic regime separately yielded stronger relationships between flow hydraulics and seed deposition than were evident from analysis of the pooled data-set (refer to Table 2.5). Under descending flows, total numbers of seeds and seeds of Group A and B were deposited in the areas with the lowest *Fr*. V/V_{mx} explained greater than 70% of the variability in total seed deposition of early dispersed Group A (Figure 2.8) under the descending flow regime. More seeds of Group A were deposited in areas where the ratio of average to maximum velocity was lower, such as at the expansion where upstream flow occurs along stream margins in contrast to a high-velocity downstream jet immediately below the constriction. There was a significant inverse relationship between relative velocity and seed deposition for Groups A and B under descending and stepped flow regimes (Figure 2.8). However, V/V_{mx} was not a significant determinant of seed deposition of Group B. This is likely due to the fact that areas of flow separation were not as well formed during lower flows (<0.026 m^3/s) during the release of Group B. None of the hydraulic variables explained the deposition of the seeds of Group C for the descending flow regime (Table 2.5).

Under ascending flow regimes, velocity of the flow field at each of the fluvial features and *Fr* best described seed deposition of total numbers of seeds and seeds of all groups analyzed separately. The inverse relationships between velocity and the numbers of seeds of the latest dispersing seeds (Group C), and *Fr* and Group C, were greater under the ascending flow regime than under any of the other flow regimes. This is attributed to the fact that discharge was greater when the seeds of Group C were being released than under any other flow regime. As a consequence, areas of flow separation were better developed at the time of release of Group A during this flow regime, and were likely to have been more efficient seed-traps.

Analysis of seed deposition data from the stepped flow regimes resulted in the strongest relationships between hydraulic patterns and seed deposition measured in these experiments. Whereas velocity, *Fr*, and V/V_{mx} explained modest proportions of seed deposition data in analyses of total numbers of seeds deposited, these variables explained from 81 to 91 percent of the variability in the numbers of seeds of Group A deposited under stepped flows (Figures 2.9, 2.10, and 2.11). In addition, *Re* and *We* explained 75 percent of the variability in numbers of seeds of Group A deposited in these trials. Therefore, numbers of seeds of early dispersing groups deposited may be adequately predicted using any of these hydraulic measures under a stepped flow and descending regime. Predictive ability diminishes for later dispersing groups, but two of the hydraulic measures (Fr and V/V_{mx}) nonetheless explain 25 percent of the variability in the deposition of Group B. A majority of the seeds were deposited along pool margins under ascending regimes. The areas where the few additional seeds were deposited was in the eddy and the channel margins below the island (Figure 2.3). These areas of slow velocity and V/V_{mx} and low *Fr*, although much less efficient seed traps than the same sites under stepped and descending flow regimes, were places where seed deposition was maximized.

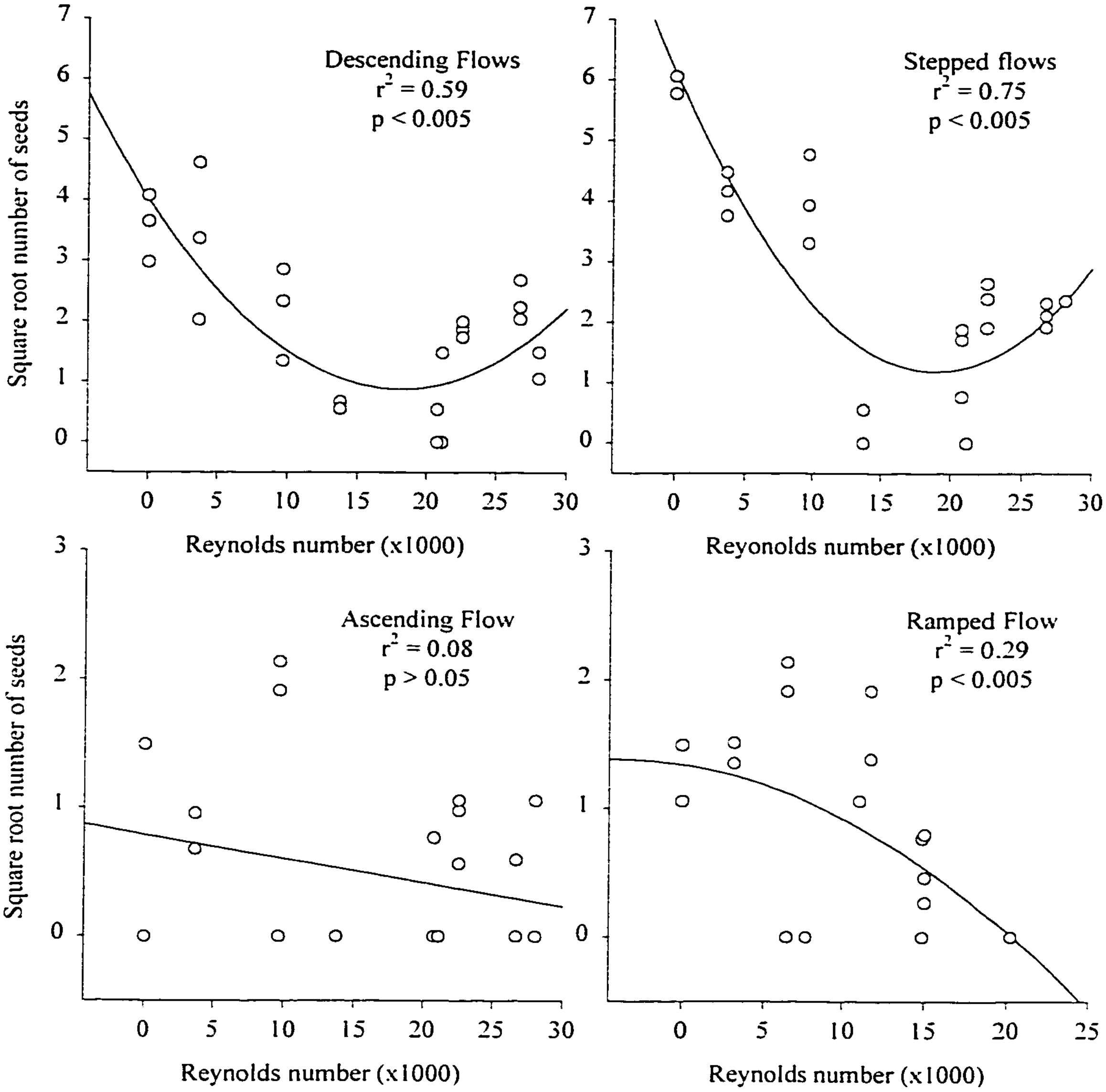


Figure 2.9. Number of seeds deposited (square root transformed) on each of eight fluvial features (see text) versus Reynolds number for four discharges in a flume.

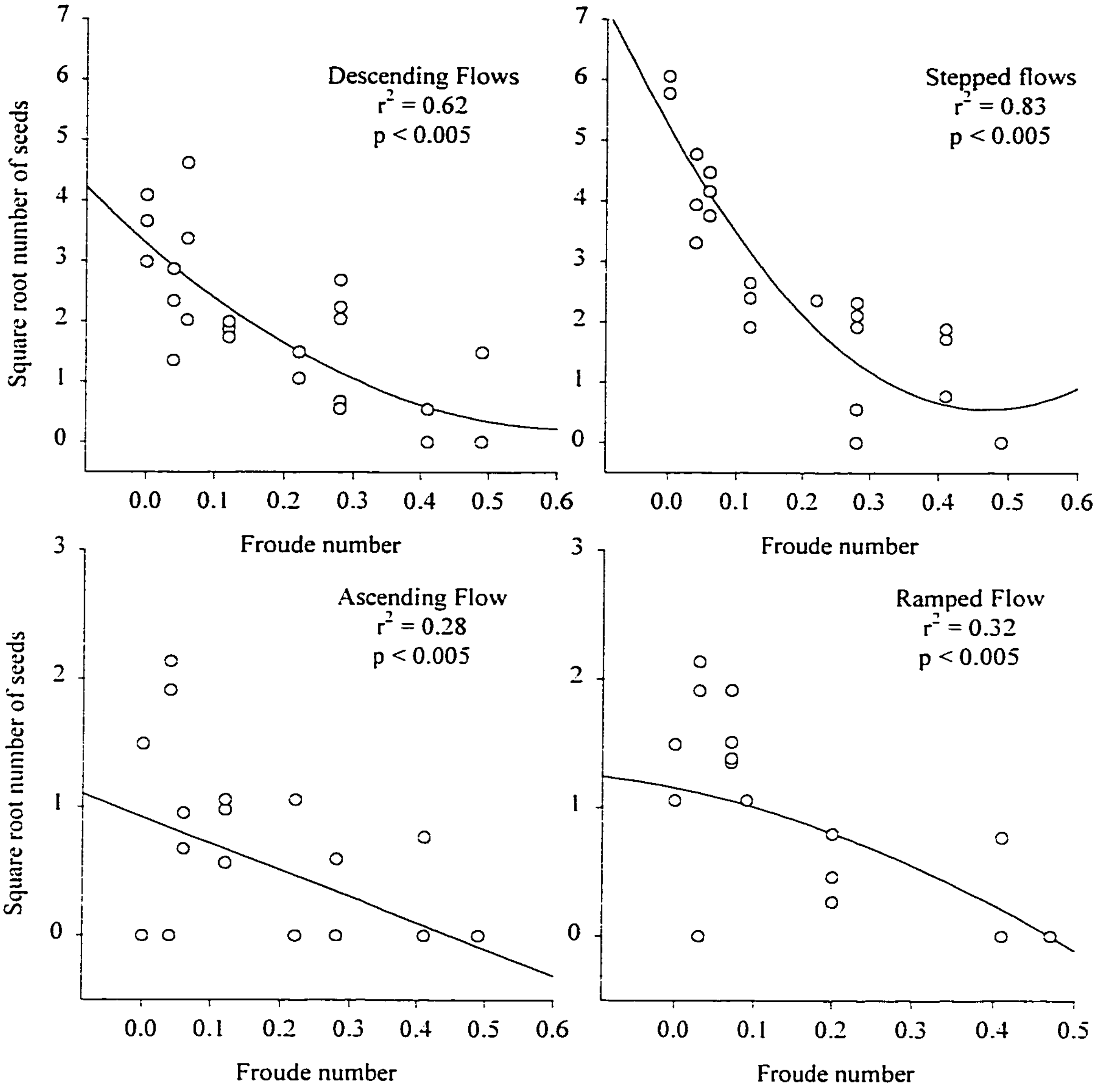


Figure 2.10. Number of seeds deposited (square root transformed) on each of eight fluvial features (see text) versus Froude number for four discharges in a flume.

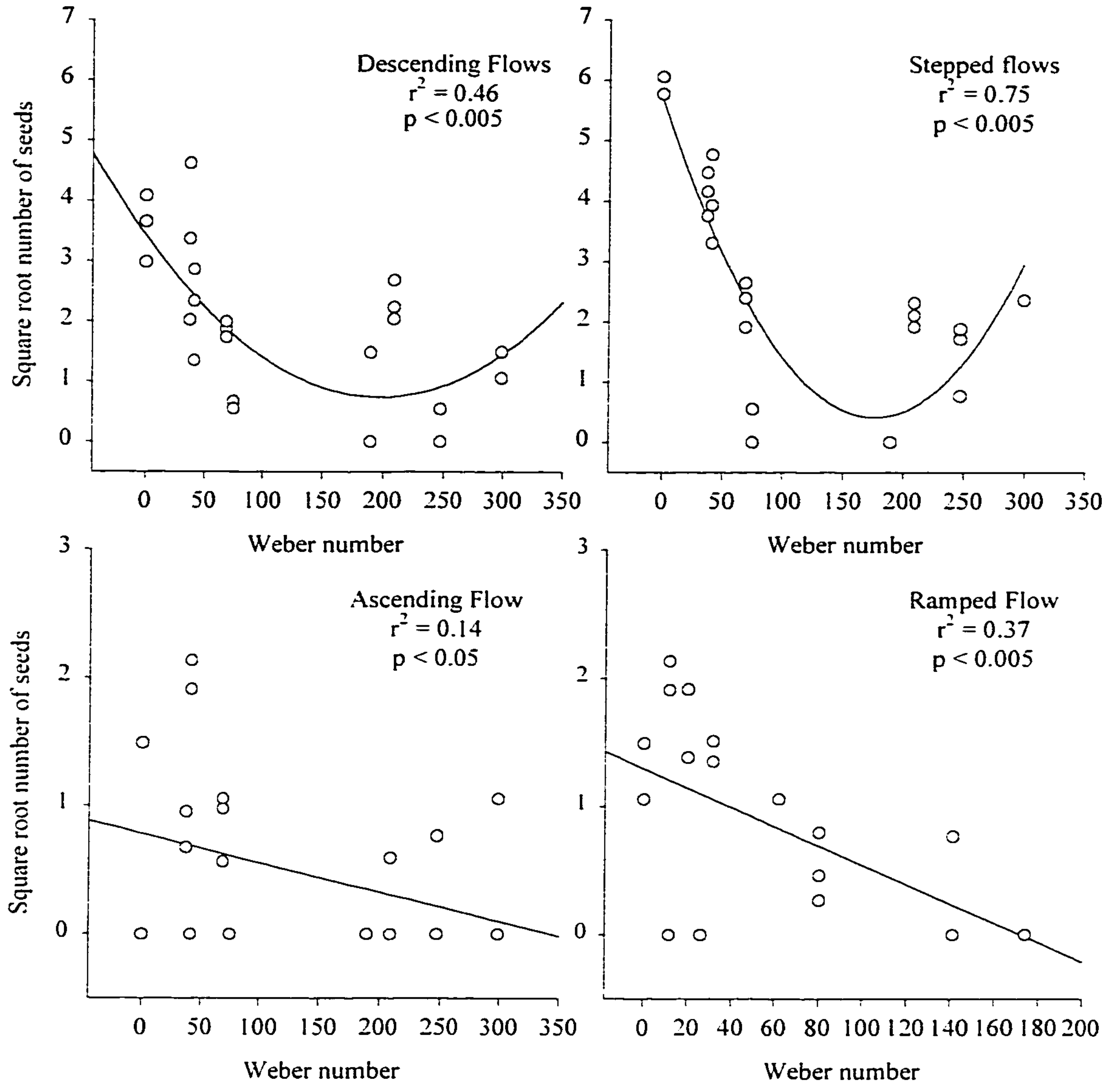


Figure 2.11. Number of seeds deposited (square root transformed) on each of eight fluvial features (see text) versus Weber number for four discharges in a flume.

The eddy was much less effective than the expansion at capturing seeds under the ascending flow regime.

Ramped flow regimes resulted in very few seeds being deposited on any feature in the flume. Nonetheless, the areas of seed deposition under the ramped flow regime were at the eddy and below the expansion. As a consequence, the lower V, V/V_{mx}, and Fr associated with these features explained a large proportion of the numbers of seeds deposited. Because flow separation was best developed at both the eddy and the expansion at high velocities, seeds released at the highest flows in the ramped regime (Group A) were best predicted by hydraulic measures. Sixty percent of the variability in the deposition of the seeds of Group A was explained by flow velocity. Velocity explained 30 and 14 percent of the numbers of Groups B and C deposited, respectively. The relationship between Fr and total numbers of seeds deposited was curvilinear. Greater numbers of seeds were deposited at intermediate Fr (~0.20), and numbers of seeds deposited diminished at lower (0.00) and higher (~0.50) Fr. Waves produced by bursting and the shedding of vortices (Yalin 1992) also contributed to anomalous seed deposition in high energy areas. These wave-producing hydraulic factors were observed to deposit seeds slightly above the water surface even in the highest energy fluvial environments in the flume (i.e., cut banks and constrictions). These results suggest that there are two scales of hydraulic factors governing seed deposition: (1) macro-scale hydraulics such as eddies and expansions which detain and recirculate seeds, depositing them once flows begin to recede, and (2) micro-scale hydraulics such as small waves produced by bursting phenomenon at higher flows and hydraulics caused by channel micro-topography and bedform irregularities that are only influential at lower flows. Discharge and the timing of seed release interact to determine where and in what numbers seeds of various groups will be deposited under any given flow regime.

Average velocity in the flow field (V/V_{mx}) was the most significant hydraulic variable describing seed deposition under both ramped and ascending flow regimes. The coefficient of determination (r^2) ranged from 0.20 (Group C) to 0.39 (Group B) under the ascending flow regime ($p < 0.05$). *Fr* and *We* were also significant explanatory variables for total number and for all individual groups under the ascending flow regime. From 26 (Group C) to 48 (Group A) percent of seed deposition was explained by velocity (V) under the ramped flow release.

2.4 Discussion

Flume experiments of water dispersal under natural and a variety of modified flow regimes indicate that waterborne plant seeds disperse and are deposited in a non-random fashion along the margins of swift-flowing streams. Whereas wind-dispersed seeds are subject to the stochastic nature of turbulent wind currents of varying direction and velocity, water-dispersed seeds are consistently deposited in specific hydraulic environments, albeit in different concentrations, under a variety of flow regimes. Furthermore, water-dispersed seeds have the potential to travel distances far in excess of those achieved by wind-dispersed seeds alone.

Whereas investigations of wind dispersing seeds have shown that a large proportion of wind-dispersed seeds fall within a diameter approximately two to three times the canopy height of the parent plant (inverse-square dispersal curve; Harper 1977), the results of this study suggest that the potential for long-distance seed dispersal by water is in excess of 200 times the distance possible by wind dispersal alone, generating log-linear decay curves (Figure 2.12).

In flume experiments under simulated natural hydrologic regimes, 4% of the 2,970 seeds released per trial were retained in the 18-m long experimental section. Under stepped, ascending, and ramped flow regimes 17.6%, 1.6%, and 2.0% of the seeds introduced were deposited along the 18 m experimental section. Based on these rates of deposition, seeds released into stepped, descending, ascending, and ramped flow regimes have the potential to disperse great distances downstream (extrapolated distances were 1 km, 3 km, 9 km, and 10 km, respectively). These calculations are based upon the assumption that each segment of stream experiences similar hydrologic conditions to those occurring along the experimental flume segment. This would not be the case under ramped flow conditions. Under ramped conditions, seeds would likely be flushed downstream and deposited at a wide range of elevations along stream margins. Under conditions in which numbers of seeds are not a limiting factor, dispersal distance could exceed 24 km/day at the average surface velocity measured in the experimental flume. Thus water dispersal provides hydrochores with a tremendous potential for dispersing seeds along watercourses in distances exceeding those possible by wind dispersal alone.

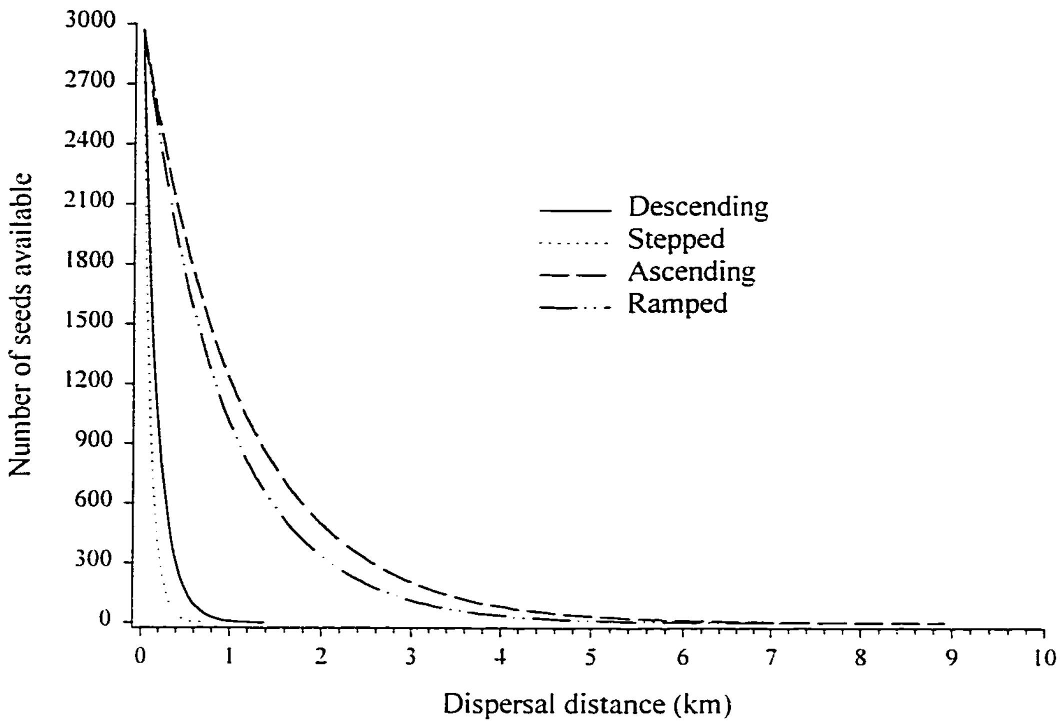


Figure 2.12. Log-linear curves showing the distance downstream that seeds could travel at the rate of seed retention that occurred through the 18 m section of flume.

Other investigations have shown similar patterns of long-distance dispersal for water dispersing species. Populations of the exotic species *Fraxinus ornus* L. invaded downstream along river margins at a rate of nearly 1 km per year along the Hérault and Vis Rivers in France (Thébaud and Debussche 1991). The population of this species was able to achieve a downstream range of 61 km by water dispersal of seeds, while invading less than 1 km in an upstream direction through wind dispersal over the 65 years since the species was introduced. Analytical models of wind dispersal and field measurements indicated that the introduced *Mimosa pigra* L. invaded wetland margins in Australia by means of water dispersal (Lonsdale 1993). Water dispersal enabled this species to invade shorelines at a rate four times the maximum rate of spread possible through wind dispersal alone (Lonsdale 1993). Both of these investigations indicate that dispersal of seeds by water is central to the rapid rate of spread of these species along watercourses.

The final location of water-dispersed seeds along riparian corridors is a function of a variety of physical and biological factors: (1) the structure of the hydrologic regime during seed release and transport --timing and magnitude of peak flow and the rate and direction of change in discharge with time, (2) the phenology (timing) of seed release, and (3) channel morphology and the hydraulic attributes of the fluvial features represented.

2.4.1 Hydrologic Regime

Whereas the phenology of seed release is a largely independent biological (intrinsic) factor, flume experiments support the hypothesis that hydrologic regime is the most important extrinsic factor influencing the dispersal distance and deposition of seeds along river margins. In contrast to Hypothesis 2.1, the stepped flow regime resulted in the highest number of seeds deposited. However, the natural descending hydrologic regime did result in significantly greater numbers of seeds deposited than either the ramped or ascending regimes, suggesting that certain managed flows inhibit seed deposition (Hypothesis 2.1). Patterns of seed dispersal were also more predictable under stepped and descending flows, in contrast to the indeterminate nature of seed deposition under ascending and ramped flows (Figures 2.8-2.11). In support for Hypothesis 2.2, most seeds are deposited in areas of reduced velocity (eddies, expansions, and slackwaters). Deposition in these areas is a function of the relative velocity (V/V_{mx}), which explained as much as 91% of the variability in seed deposition.

Whereas the quality and textural and chemical characteristics of habitat are determined by the history of flooding and disturbance of a site, the exposure of the site to the shear stresses exerted by the flowing water of the stream, and the type of sediment transported by the channel, the availability of the habitat to dispersing seeds is entirely reliant upon river stage and rate of change in discharge at the time of seed release. Even habitats that are exposed during the period of seed release are unlikely to capture and retain available seeds under ascending flow conditions (Figure 2.5). Likewise, habitat that is exposed abruptly during a rapidly descending, ramped draw-down is unlikely to retain many seeds because of the flushing effect of flows during a steep recession limb. A gradual or stepped hydrologic regime provides the optimal hydraulic conditions for seed deposition.

Delayed seasonal peak flow, a modification associated with flood detention reservoirs, results in the deposition of early dispersing seeds adapted to colonization of habitats that are exposed during the recession limb of the hydrograph, at positions higher on the floodplain than they would be deposited under unregulated conditions. Deposition of seeds in these sites decreases the likelihood of germination and survival of seedlings (Ribeiro 1991, Braatne *et al.* 1996). Habitats that are submerged when species are dispersing are unavailable as potential colonization sites. The timing of flows and phenology of floodplain species influence the temporal availability of habitat resulting in distinct spatial patterns of established plant communities.

McBride and Strahan (1984) highlighted the importance of dispersal phenology in relation to flows along an alluvial stream in California by demonstrating that although low elevation sandbed sites were suitable to cottonwood seed germination and survival, these surfaces were submerged when cottonwood were dispersing seeds. As these sites were exposed by receding water levels, they were colonized by willow, which began to disperse seed after cottonwood dispersal had ended. Although the lower habitat would have been suitable for cottonwood establishment, and the higher habitat could have supported willows, these habitats were either submerged and unavailable at the time of seed release, or the surfaces were desiccated by the time seeds were available, respectively. This balance between dispersal phenology and hydrologic patterns resulted in distinctive bands of these species parallel to the river channel (see Plate 2.2). These segregated bands of vegetation had previously been attributed to differences in substrate texture of the various habitats (McBride and Strahan 1984).

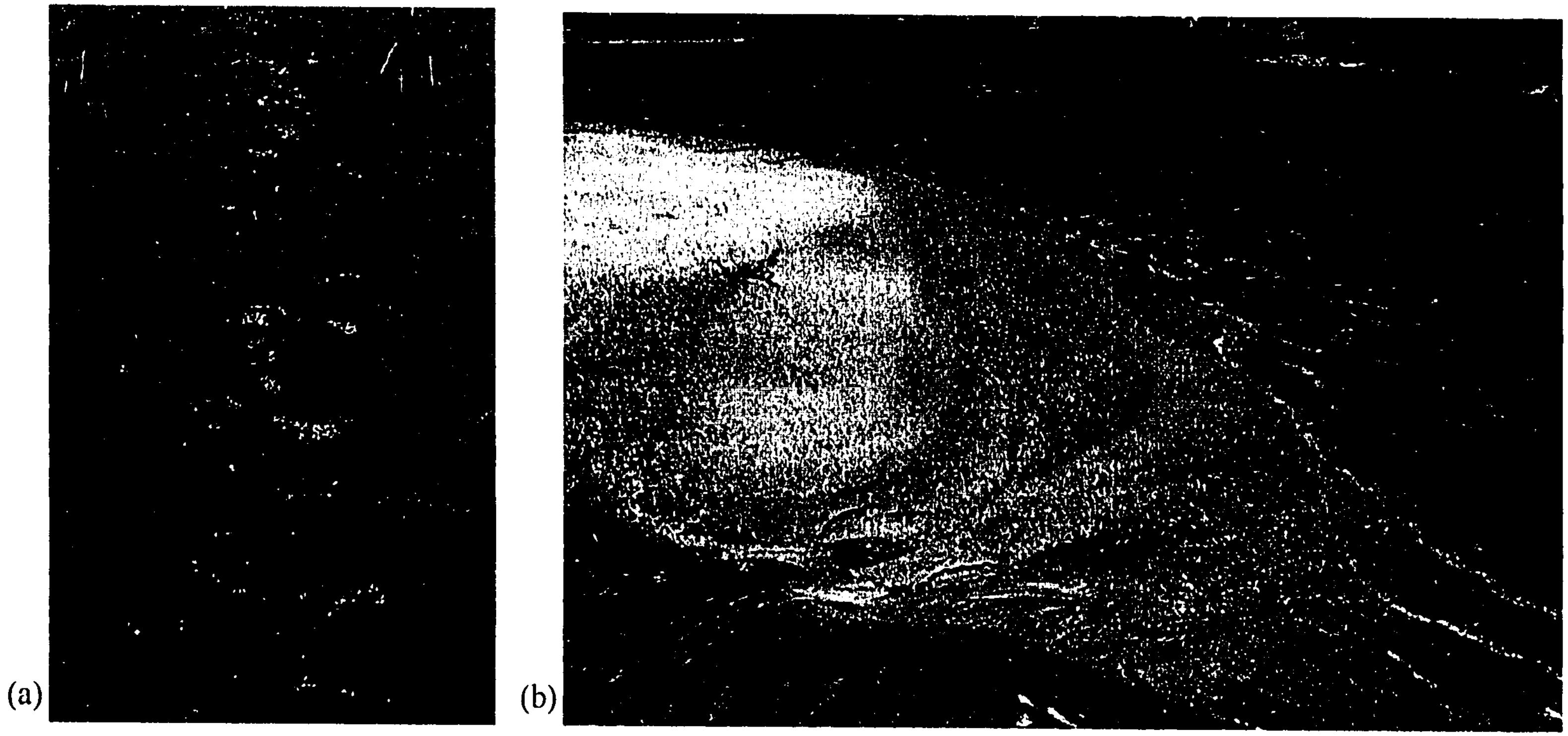


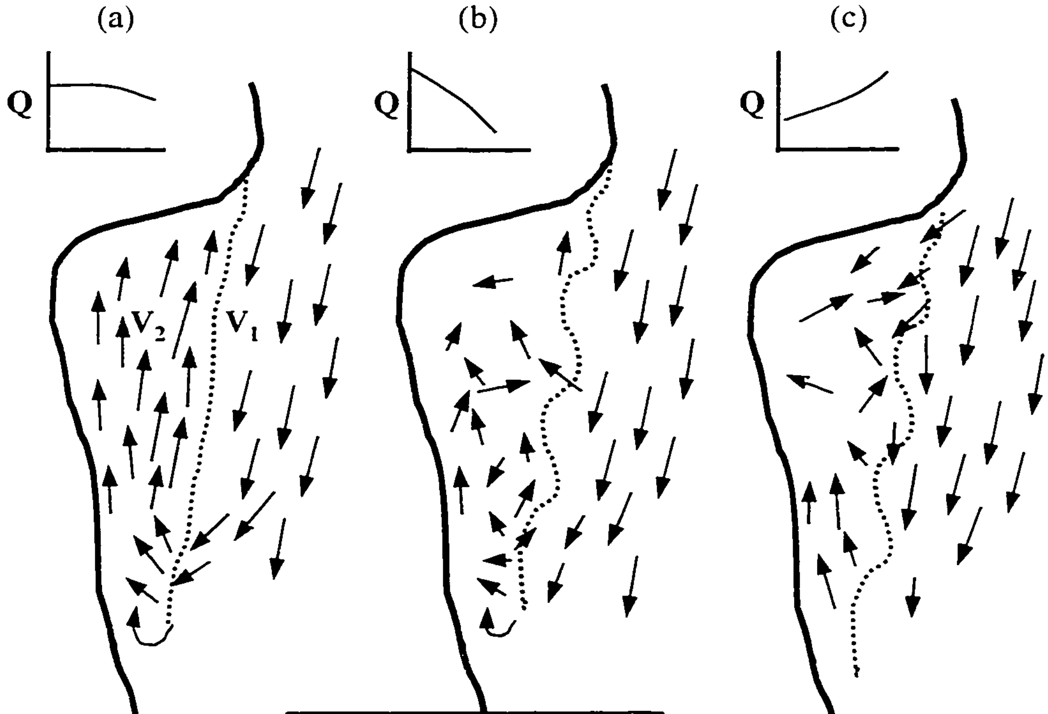
Plate 2.2. (a) Wind dispersed seeds, secondarily transported by water and deposited in suitable 'safe-sites'; (b) bands of seedlings of species dispersing over different periods of time during the recessional limb of the hydrograph.

Understanding the relationships between the timing of seed release and probabilities of deposition under various hydrologic regimes may facilitate the restoration of certain attributes of hydrologic regimes, at the appropriate times, so that successful regeneration of desired species is enhanced. Synchronizing exposure of suitable habitat. hydrographs of the appropriate rate of drawdown, and providing conditions suitable for deposition with the timing of seed availability for a species of concern could be a very cost-effective way to maintain or restore populations of certain species of riparian plants. Conversely, such an understanding of the relationships between timing of seed release. flow regime, and the nature of the fluvial environment may facilitate the manipulation of flows that inhibit deposition of the seeds of undesirable species such as invasive exotics.

2.4.2 Channel Morphology and Flow Hydraulics

It is not surprising that higher concentrations of seeds were recorded in areas of reduced flow velocity such as in eddies. expansions. and slackwaters. Areas of recirculating flow have been recognized by geomorphologists as important controls on the deposition of mineral sediment in natural stream channels (Schmidt 1990. Cluer 1997). Biologists have also recognized that flow patterns may influence where seeds are deposited along rivers and along reservoir margins (Nilsson *et al.* 1991b, Rood *et al.* 1998). Nilsson *et al.* (1991b) observed that buoyant wooden cubes used to simulate seeds were deposited in greater numbers in ‘eddies downstream from rapids and along some outer curves of slow glides’ following their release on the Sävar River in Sweden. In these flume experiments, eddies captured a large portion of seeds under naturally descending and stepped flow regimes, but were significantly less effective at retaining seeds during ramped and ascending flows. Given sufficient magnitude of discharge to initiate flow separation below constrictions, gradually changing or steady flow conditions enable zones of recirculation to become established and to become relatively stable. Although there is some pulsation and irregularity in the zone of flow separation even under steady flow conditions (Rubin and McDonald 1995), observations in the flume suggest that this instability is amplified under rapidly changing or ascending flow conditions (Figure 2.13). This instability in the zone of flow separation was observed to affect the numbers of seeds trapped and retained in eddies.

Because seed retention and deposition are functions of stream hydraulics, and the stability of seed-retaining features such as zones of recirculation increases under gradually changing flow conditions, more seeds were deposited under stepped flows. Under stepped flow regimes the boundary between the downstream component of flow and the recirculating flow (the eddy fence) is able to become very well developed, thereby detaining and recirculating seeds (Figure 2.13). During intermittent periods of drawdown, recirculating seeds are deposited along shorelines. Because these zones of recirculation are formed below constrictions to flow, expansions and eddies are areas of concentrated seed deposition. Whereas instability of the eddy fence under conditions of steady flow has been shown to result from vortex shedding at the point of flow separation (Rubin and McDonald 1995), this instability becomes magnified under rapidly changing flow conditions (Figure 2.13). Under these conditions, the deformation and collision of dissipating vortices in the wake of the separation point cause the eddy fence



Q (m^3/s)	V_1 (m/s)	V_2 (m/s)
0.005	0.26	-0.02
0.010	0.68	-0.06
0.030	1.15	-0.07

Figure 2.13. Schematic diagram of flow separation beneath a constriction under various hydrologic regimes (inset graphs). Under steady or gradually descending flows (frame a) the eddy fence (dotted line) is well formed, stable, and the recirculating cell is very efficient at detaining seeds. Under rapidly descending or ramped flows (frame b) the eddy fence does not form completely or stabilize. This less-stable recirculation cell is less efficient than that shown in (frame a) at capturing and retaining seeds. Similarly, under ascending flows (frame c) eddy fence formation and stabilization is inhibited by bursting, leading to a less-efficient recirculation cell. The strength of the cell of recirculation at three levels of steady discharge (0.005, 0.010, and 0.030 m^3/s) are indicated by the velocity of the downstream component of flow (V_1) and the velocity of upstream flow in the zone of recirculation (V_2; inset table).

to undulate (Rubin and McDonald 1995). The exacerbation of vortex shedding under rapidly changing conditions resulted in a less stable eddy fence and less efficient seed-trapping ability of these features under ramped flow regimes (Figure 2.13). The eddy was also less stable during ascending flows, but the expansion still exhibited strong zones of recirculation and was therefore more efficient than the eddy at detaining seeds under this flow regime.

Under rapidly changing conditions, recirculation cells only partially form, leading to less retention of entrained material, and thus greater downstream movement of seeds. Under gradually changing (quasi-steady) flow conditions, areas of flow separation and recirculation are very effective at capturing and retaining material in transport. The velocity of the recirculating flows in the eddy increased fourfold, from -0.02 m/s to -0.08 m/s, over the range of discharges measured (Figure 2.13). With increasing strength, eddies become increasingly more effective at trapping and retaining material from the main channel. It became evident during test runs of the flume that many seeds are retained in eddies under steady flow conditions but that very little seed deposition occurs along the banks in these areas. Descending flows are required for deposition of seeds along eddy margins. If flow recession occurs too rapidly, seeds are merely reintegrated into the main current and delivered to downstream reaches. Under steady flow conditions, more seeds are deposited in high-energy areas above the water level through the lapping of waves against channel side-walls than in zones of recirculation. Eddies are very transient features under a varied flow regime, and become even more so under rapidly changing conditions (Schmidt 1990).

Areas of strong flow reversal, characterized by low V/V_{mx}, are efficient systems for detaining and recirculating seeds. These experiments provided strong support for Hypothesis 2.2. Eddies, slackwaters, and expansions (areas with the lowest V/V_{mx} values) are areas of high seed deposition under descending and stepped flow regimes. Although seed deposition is almost entirely random with respect to fluvial features under ramped flow regimes, flow expansions remain areas of flow recirculation even under ascending flow regimes. As a consequence, these areas had the highest seed deposition under ascending flows.

Seed deposition on point bars occurs over a range of discharges, and occurs at different locations under intermediate versus low discharges. When flows are of sufficient magnitude, crescent-shaped zones of recirculation form on the downstream faces of point bars. These areas are very efficient seed traps, and under descending flow regimes are areas of concentrated seed deposition. At lower discharges, shallow flow over the apices of point bars traps floating seeds. Along meandering alluvial streams, the fresh sediment deposited by point bar flooding provides key seedbed sites for colonizing species such as cottonwood and willow (Bradley and Smith 1986, Scott *et al.* 1996). During high magnitude flows, when most of these depositional zones of point bars are submerged, seeds may be deposited in areas of asymmetric cross-sectional form (such as cutbanks) or areas where there is a confinement of flow (such as at constrictions) by waves produced by bursting or macroturbulent flow (*sensu* Yalin 1992). During low magnitude flows, small-scale channel features may influence flow to a higher degree than when they are drowned-out at higher flows. These small-scale hydraulic features may influence where seeds are deposited at lower flows by trapping them and pushing them up onto shorelines. In the flume, one such feature, a hydraulic jump, occurred only at flows below 0.007 m^3/s. When present, this hydraulic jump prevented the downstream passage of seeds and essentially drove them onto channel margins. Any seedlings resulting from such small-scale features are likely to be scoured by subsequent high flows because of their low position on the floodplain.

Other small-scale channel features that obstruct flow and reduce flow velocity also have an influence on patterns of seed and sediment deposition. Schneider and Sharitz (1988) noted that fewer tupelo (*Nyssa aquatica* L.) and cypress (*Taxodium distichum* L.) seeds were captured at increased water depths in South Carolina swamps. They attributed this to increased surface velocities and decreased availability of emergent substrates that could trap seeds. Although the habitat provided by open-sites was perfectly suitable for germination of these species, seeds were preferentially deposited in areas where emergent obstacles such as tree trunks, logs, branches, cypress knees, and stumps were present. Other roughness elements along shorelines of streams, such as the stems of herbaceous plants, also decrease flow velocity and provide surfaces for wet seeds to adhere to, likely resulting in higher concentrations of water-deposited seeds in these areas. In contrast, Nilsson *et al.* (1991b) found a strong negative correlation between percent cover of shoreline vegetation and the deposition of wooden cubes used to simulate seeds.

Areas of low velocity and shear stress such as eddies and flow expansions, are also areas where finer stream-transported sediment fractions are deposited. These finer textural classes of mineral sediment create seedbeds of higher water-holding capacity than areas exposed to higher shear stress, thus providing 'safe-sites' for some species that are particularly vulnerable to drought stress in early stages of growth. Many species of riparian plants are vulnerable to desiccation during germination and seedling stages. The seeds of many of these mesophytic species, such as willows and cottonwood, have very short periods of seed viability, slow initial root growth rates, and experience high mortality under dry soil conditions (Moss 1938, Fenner *et al.* 1984). The finer sediments that are deposited in the eddies, areas of flow expansion, and pool margins, where most seeds are deposited, may also provide drought intolerant species safe-sites for germination and growth. Because willows (Salicaceae) have a very short period of seed viability, sexual reproduction is successful only when conditions are favorable during the period of seed dispersal (Krasny *et al.* 1988). The preferential delivery of water-dispersed seeds to such sites increases the likelihood of successful regeneration.

2.4.3 Ecological Significance of Hydrochory

Dispersal away from parent plants has many advantages to seedlings by allowing them to: (1) avoid competition with parent plants, (2) colonize newly disturbed habitats, and (3) locate microhabitats suitable for establishment and growth (Howe and Smallwood 1982). Running water, although a relatively unidirectional vector, offers tremendous potential for long distance dispersal of seeds. In certain situations, this puts plants with seeds capable of dispersing via water at a certain advantage over those without such traits. Under conditions of changing climate, migration of plants along rivers has been referred to as 'crucial' to the persistence of some riparian plant species (Sauer 1988). Under steady climatic regimes, the advantages of long-distance dispersal are likely to have diminishing returns once a certain threshold distance from the point of release is attained, and the disseminule itself departs the climatically constrained boundaries of the range of its population. Because reproducing adults typically occur in areas suitable for survival of the species, seeds dispersed shorter distances from the parent plant may have higher probabilities of survival--the Jansen-Connell effect (Howe 1989). In contrast, a species that has recently been introduced to a region suited to its survival may be greatly advantaged by long-distance dispersal via stream corridors (Turner and Karpiscak 1980, Thébaud and Debussche 1991, Lonsdale 1993). In many cases, particularly for colonizing species, dispersal away from the parent plant is necessary because adults and seedlings have different habitat requirements (McLeod and McPherson 1973). Seedlings of many colonizing riparian species require full sunlight and moist seedbeds, and are poor competitors, all conditions that do not pervade in stands of adults.

Flood-related disturbance is an important process that exerts tremendous influence on species composition of riparian vegetation along river corridors (Salo *et al.* 1986, Walker *et al.* 1986, Roberts and Ludwig 1991, Friedman *et al.* 1996b, Scott *et al.* 1996, White 1979). Flooding produces scouring and deposition, which may remove or cover existing vegetation with sediment, typically opening new sites for colonization (Kalliola and Puhakka 1988). Whereas plants nearby may recolonize the site by asexual means (Krasny *et al.* 1988) or local dispersal of seeds to the site, colonization of freshly disturbed sites often occurs by way of seed dispersal (Walker *et al.* 1986, Skoglund 1990). Seeds deposited onto these sites by water have the advantage of moist seedbeds, higher quality of sunlight, and reduced competition (Menges and Waller 1983, Salo *et al.* 1986).

The non-random nature of dispersal by running water may yield certain advantages to seedlings if the sites where seeds are congregated provide higher quality habitat than sites where seeds are deposited at random. In this investigation, the highest concentrations of seeds were deposited in eddies, areas of flow expansion, slackwater areas, and pool margins. In addition to being areas where seeds are deposited, these areas exhibit several qualities conducive to the germination of seeds and to the survival of seedlings. Fine mineral sediment and organic material are deposited in areas of reduced flow velocity such as eddies and along pool margins. These fine grained deposits offer soils of higher water retention capacity and higher nutrient status than the coarse grained deposits associated with areas of higher flow velocity, affording plants better growing conditions for seedlings and adults (Brinson *et al.* 1983). Additionally, shear stress exerted by flowing water on the bed and banks is lower in eddies, expansions, slackwaters, and pool margins, offering seedlings some degree of protection against removal or damage from scouring flows. Whereas areas of low flow velocity offer certain advantages to establishing seedlings, there are certain disadvantages to the presence of congregations of seeds and subsequently seedlings into these areas.

Competitive interactions between seedlings, as well as competitive interactions between adults and seedlings, are likely to be more intense in these areas. Plants dispersed by animals in fecal clumps, although deposited in much higher concentrations than are likely by water dispersal, usually produce no more than one adult per clump due to interspecific competition and self-thinning of seedlings (Howe 1989).

2.4.4 Implications for Dam Management

Full restoration of historic hydrologic regimes below impoundments is often impractical or impossible, although there are some recent exceptions (i.e., removal of mainstem dams on the Columbia and Snake Rivers). Recognition of the role of high magnitude flows to ecological and physical features along watercourses has resulted in the implementation of prescribed flood releases as a flow management strategy for dams in the western United States. These prescriptive floods typically focus on a particular magnitude of flood that is not necessarily timed to accommodate ecological processes. Other restorative measures include the establishment of minimum instream flows to maintain channel morphology, fish and invertebrate habitat, or to provide uniform water table levels to accommodate riparian vegetation. These measures are usually taken to address a specific issue or species, and to restore individual mechanisms that do not severely interrupt the operational protocol of the impoundment.

The results of this work suggest that flows could be modified for a specific segment of the hydrograph to maximize efficient seed delivery and deposition, and ultimately the regeneration of species which rely on or benefit from hydrochory to disperse their seeds to suitable sites. Adjusting the timing of late-season high flows to accommodate the natural regenerative process of a particular species of interest could provide a greater return for the cost than other forms of remediation over large areas (i.e., manually planting seedlings or broadcasting seed; Barrow 1992, Friedman *et al.* 1995). Relatively simple measurements of the dispersal phenologies of target species at a site, an understanding of the regeneration niche of the species, and knowledge of historic hydrologic patterns of a site, could provide a sound ecological framework for restoring flows over a specific segment of the annual hydrograph to maintain or enhance the reproductive success of certain species.

This work has provided some insight into the relative influences of a variety of typical hydrologic modifications to patterns of dispersal along pool-rifle streams. The timing, magnitude, direction, and rate of change in discharge must all be considered when designing ecologically based flow release schedules.

CHAPTER 3

PRIMARY AND SECONDARY DISPERSAL AND COLONIZATION IN NATURAL STREAM CHANNELS

3.1 Introduction

To understand how the mechanics of seed dispersal relate to seed transport and deposition, vegetative colonization of river margins, and to patterns of plant community organization along free-flowing and regulated reaches of natural stream channels, a series of field studies was initiated in 1997 and completed in 1998. Field sampling involved collection of wind- and water-dispersed seeds, measurement of standing vegetation, and measurement of hydrology and hydraulics on two regulated streams in Colorado. Field experimentation was also conducted to understand the importance of dispersal to the colonization of bare stream margins under natural flow conditions.

The primary objectives of this research were to: (1) document the phenology of seed release in relation to historic and current hydrologic regimes along mountain streams, (2) measure water-dispersed seeds at sites located above and below impoundments to examine local and longitudinal patterns of hydrochory on free-flowing and regulated reaches of mountain streams, (3) examine the spatial distribution of standing vegetation in relation to patterns of seed dispersal and seed dispersal mechanisms, and (4) determine the relative importance of hydrochory versus wind dispersal in colonizing disturbed stream margins.

It was hypothesized (Hypothesis 3.1) that the numbers of seeds in the hydrochoric seed bank would be diminished below dams, effectively causing a seed shadow analogous to the 'silt shadow' commonly observed below dams. Furthermore, it was hypothesized (Hypothesis 3.2) that species richness and composition of the hydrochoric seed bank would reflect the regional species pool, increasing as a function of distance downstream along free-flowing reaches, but would be more closely related to local sources of seeds below impoundments. It was hypothesized (Hypothesis 3.3) that wind- and water-dispersed species would comprise a large proportion (>50%) of the riparian flora and that the distributions of hydrochoric species would reflect reductions in the frequency and extent of floodplain inundation below dams through occurring closer to the channel. Furthermore, it was hypothesized (Hypothesis 3.4) that newly disturbed sites colonized by hydrochoric seed sources would result in plant communities of higher species richness than plant communities colonized solely by wind-dispersed seeds, and that sites colonized by both wind- and water-dispersed species would exhibit even greater species richness along unregulated reaches.

3.1.1 Study Sites

The systems chosen for this study are two high-gradient, laterally stable mountain streams located in the Front Range of north-central Colorado. The North Fork of the Cache La Poudre River (North Fork) and South Boulder Creek are fourth-order tributaries of the Cache La Poudre River and Boulder Creek, respectively, both of which are tributaries of the South Platte River (Figure 3.1). Both streams flow through similar geologic formations; deep canyons composed of Precambrian metamorphic and igneous

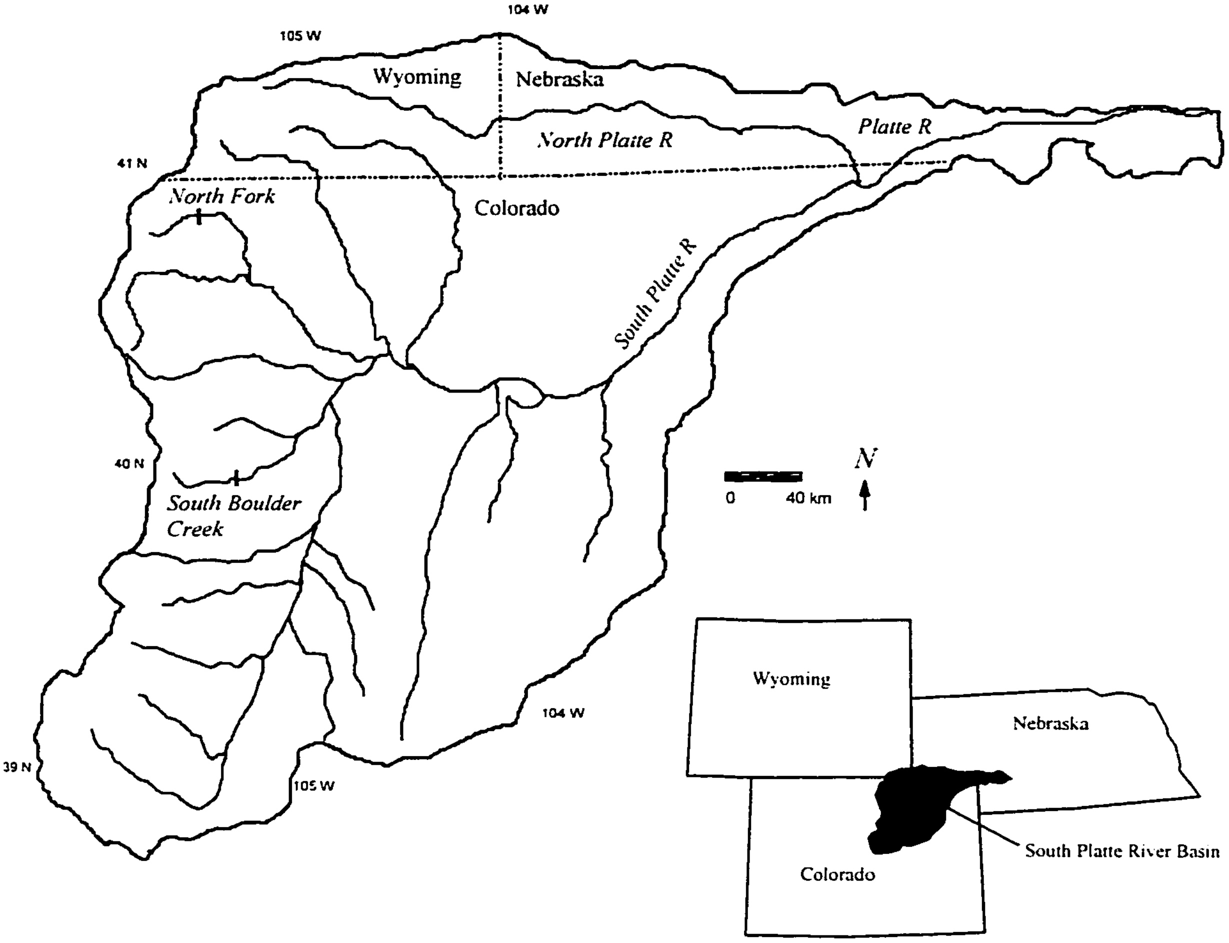


Figure 3.1. South Platte River Basin location map indicating positions of the study areas on the North Fork of the Cache La Poudre River (North Fork) and South Boulder Creek.

bedrock (Tweto 1979). The streams flow through physiographically similar areas classified as foothills and lower montane forest (Paddock 1959) in the Southern Rocky Mountain Ecoregion (*sensu* Bailey 1995). The North Fork and South Boulder Creek receive 43 and 53 cm of precipitation annually (N.O.A.A. 1998).

These two fourth-order mountain streams were chosen for the investigation of seed dispersal because they exhibit: (1) significant seasonal stream-flow variability which is driven primarily by an annual cycle of snowmelt runoff; (2) channels that are laterally confined by bedrock and are thus relatively geometrically stable on the time-scale of the life-spans of most riparian plants; (3) physiographic and elevational similarities; (4) reservoirs managed for agricultural/municipal water supplies, and (5) a lack of significant land-use impacts such as roads paralleling the channels, grazing, logging, or other significant human influences not related to regulated streamflow.

3.1.2 North Fork of the Cache La Poudre River

The North Fork study area is located approximately 40 km northwest of the City of Fort Collins, Colorado. The North Fork is a tributary of the Cache La Poudre River which flows into the South Platte River near Greeley, Colorado (Figure 3.1). The North Fork flows through a valley composed of Silverplume granite, biotitic gneiss, schist, and migmatite (Tweto 1979). The valley of the North Fork is approximately 160 m deep and ranges from 100 to 500 m in width through the study reach which is 8.9 km in length, including the 3.5 km-long Halligan Reservoir. Average precipitation, measured at the nearest weather station located in Red Feather Lakes, approximately 18 km southwest of the study area, was 43 cm for the period 1941–1990 (N.O.A.A. 1998). The watershed area of the North Fork above the study area is 904 km^2. Average streamflow measured at the nearest U.S. Geological Survey streamflow gages (North Fork of the Cache La Poudre at/near Livermore, CO U.S.G.S. gage numbers 06751490 and 06751500), was 1.3 m^3/s for the period of record (1929-31, 1947-65, and 1986-1996). Annual peak discharge (of daily averages) for the same period of record was 17 m^3/s. Peak flow typically occurs on 2 June. All hydrologic data available for the North Fork postdate the filling of Halligan Reservoir.

The Halligan Dam was built in 1909-10 to provide agricultural and municipal water storage for Fort Collins and the surrounding area. Halligan Dam is an arched cyclopean masonry dam spanning 107 m between exposed granite bedrock valley walls. The dam is 29 m high from the base of the foundation to the dam crest which sits at an elevation above mean sea level of 1,940 m. A 33.5 m long spillway is located in the center of the dam and sits at 1,937 m in elevation. Halligan Reservoir has a maximum storage capacity of 7.90×10^6 m^3 (6,400 acre-ft). The dam and reservoir are owned and operated by the North Poudre Irrigation Company.

3.1.3 South Boulder Creek

The study area on South Boulder Creek is located 11 km southwest of Boulder, Colorado. South Boulder Creek flows through deep valleys (~200 m) comprised of Boulder Creek Granite with exposures of bitotic gneiss, schist, and migmatite (Tweto 1979). The valley through which South Boulder Creek flows is very narrow (<250 - 450 m) throughout the length of the study reach. The study reach is 11.6 km long (including the 4.4 km reservoir) and drops from an elevation of 2,440 m to 2053 m (0.03 m/m) from the upstream to the downstream study sites. Average annual precipitation, measured at a meteorological station at Gross Dam, is 53 cm (N.O.A.A. 1998). The drainage basin area of South Boulder Creek above the study site is 282 km^2. Average discharge, measured at the South Boulder Creek near Eldorado Springs U.S. Geological Survey streamflow gage (no. 06729500), is 1.8 m^3/s for the period 1904-1995. Average annual peak flow, which typically occurs on 18 June, is 8.6 m^3/s for the period of record.

The construction of Gross Dam was completed on South Boulder Creek in 1954. As a part of an extensive water supply system, Denver Water Board diverts Colorado River water east across the Continental Divide through the Moffat Tunnel, into South Boulder Creek, through which it is delivered to Gross Reservoir for storage. Water is released from Gross Reservoir to meet downstream demands through the South Boulder Creek Diversion Canal, which is located 8.0 km downstream of Gross Dam. Gross Dam is a gravity arch concrete dam that is 103 m high from the streambed to the crest. The dam spans 320 m across the valley through which it is constructed abutting exposed granite on either side. The top of the dam spillway sits at an elevation of 2,220 m above mean sea level. Storage capacity of Gross Dam is $5.16 \times 10^7 m^3$ (41,811 acre-feet). Because Denver Water Board has junior water rights, storage and diversion typically occur during the high flow periods (May–July). This results in attenuated peak flows in the spring and higher flows in the late summer months below the dam.

3.2 Methods

3.2.1 Site Establishment and Cross-sections

Six study cross-sections were established on the North Fork and five cross-sections were established on South Boulder Creek. Difficult access to reaches upstream from the reservoir on South Boulder Creek inhibited installation of a third upstream cross-section. Cross-sections were established immediately above and below each reservoir and additional cross-sections were established at 1 km intervals upstream and downstream from these sites, respectively. Each study cross-section was oriented perpendicular to the stream channel and endpoints were permanently marked with rebar posts.

Staff gages were installed at each cross-section to monitor water levels on sampling dates and to develop stage-discharge relationships at each site. Wind-dispersed seeds, water-dispersed seeds, stage, discharge, and vertical velocity profiles were measured weekly from May-August on the North Fork in 1997 and on South Boulder Creek in 1998. Field measurements of discharge were not necessary during the 1998 water year as discharge data were available from the Denver Water Board for gaging stations located upstream and downstream of Gross Reservoir.

3.2.2 Phenology: Primary Dispersal

Aerial seed traps consisted of wooden platforms (16.0 x 15.5 cm) mounted horizontally 0.5 m above the ground on rebar posts. These platforms were coated with Tanglefoot™ insect trap, which is a weather-proof, sticky coating. Two traps were installed at each of the sampling cross-sections on the North Fork in 1997, one on either side of the river, within the zone of annual flooding. Traps were emptied approximately once weekly and recoated with Tanglefoot™. Seeds were counted, sorted, and identified to species. When capsules, catkins, or other dispersal units containing more than one seed were collected, the unit was opened and seeds were counted individually. Sample species richness, composition, and seed-rain density (seeds/m^2) were determined for all samples.

Observations and detailed field notes were taken documenting the dispersal phenologies of selected species in the field. This was accomplished by observing the initiation of seed or fruit maturity in the field, collecting seeds of dispersing species, and recording the date of the termination of dispersal. Seeds were collected as they matured and catalogued in a seed bank, which was later used to assist in identification of seeds collected.

3.2.3 Transport: Secondary Dispersal

Water-dispersed seeds were measured in the thalweg of each cross-section from three levels in the water column: surface, in suspension (at 0.6 x the depth at the thalweg), and on the channel bed. Seeds floating on the surface and in suspension were sampled using specially designed seines constructed of polyester precision mesh fabric (mesh size 0.25 mm) sown to a framework of brass rings to form an expanded entrance. Water flowed through the seine material trapping waterborne material in a removable, PVC sampling container located at the bottom of the sampler. The expanded entrance (orifice size 120.4 cm^2) was effective in increasing hydraulic efficiency of the sampler, thereby preventing backflow that could otherwise result in the loss of waterborne seeds. Seeds were sampled from the bed of the stream with a Helley-Smith bedload sampler (orifice size 58.1 cm^2, mesh size 0.25 mm; Edwards and Glysson 1988). At each site, all samples were collected simultaneously by affixing the surface and suspended samplers to the rigid handle of the bedload sampler and allowing water to flow through the traps for a period of 10 minutes.

In a laboratory, samples were air dried and weighed. Seeds were sorted from the samples using a dissecting microscope. Seeds were counted and identified to species when possible, to genus or family otherwise. Total numbers of seeds, species richness, and species composition were recorded for each sample as well as for each sample site (by pooling surface, suspended, and bedload samples). Several resources were utilized in identification of seeds: a catalogued seed bank from field specimens, seed keys and seed identification manuals (U.S.D.A. 1952, Delorit 1970, Montgomery 1978), local and regional floras (Cronquist *et al.* 1994, Weber and Wittmann 1996), and the extensive resources at the Seed Laboratory located on the campus of Colorado State University.

Vertical velocity profiles were taken at 10 cm vertical increments at each sampling location at the time of measurement with a Marsh-McBirney electromagnetic velocity meter. Depth of flow at the sampling point was also recorded. Flow data were then used to calculate the volume of water sampled at each level of the profile (surface, suspended, bed) to normalize seed count data to unit volume (seeds/m^3).

3.2.4 Vegetation Sampling and Dispersal Mechanisms

Vegetation was sampled in 178 plots (75 upstream and 103 downstream of Halligan Reservoir) on the North Fork and in 153 plots (83 upstream and 70 downstream of Gross Reservoir) on South Boulder Creek. Plots were located along transects at each of the seed sampling cross-sections as well as at additional transects placed at 0.5 km intervals between seed-sampling cross-sections. Transects extended across the channel from perennially inundated areas to areas away from the channel and beyond the extent of riparian vegetation. Percent cover of all vascular plant species present was recorded in each plot. All species nomenclature follows Weber and Wittmann (1996). Percent cover was estimated using a six-level cover-class scale to ensure repeatability and to reduce error associated with ocular estimation. Sampling plots were rectangular and sized 1 m^2 for sampling herbaceous vegetation. Plot dimensions were increased to 4 m^2 for sampling of shrub and tree species. Vegetation surveys were conducted in July and August in both sampling years (1997 and 1998).

Elevation above the channel, distance from the channel, soil moisture, and soil texture were measured from each of the 331 plots at the time of each vegetation survey. Elevation was measured above the level of the active channel as determined in the field by botanical and geomorphic evidence (Sigafoos 1961, Osterkamp and Hedman 1977). Horizontal distance from the active channel boundary was also measured. Soil moisture was estimated in the field at the time of sampling by assigning samples to one of five moisture classes: (1) Xeric - very dry to touch, typically crumbly soil, rarely inundated; (2) Sub-mesic - dry to touch, moisture near wilting point, cohesion of finer textured soils, inundated occasionally; (3) Mesic - moist to touch, plant available moisture, inundated annually on average; (4) Wet/Saturated - wet to touch, signs of anaerobiosis in the rooting zone, inundated annually; (5) Inundated - submerged for a long portion of the growing season.

Soil texture was recorded in the field and assigned to one of seven texture classes: (1) Clay - cohesive soils, sticky when wet, grains ranging from 2.4 x 10^{-4} to 2.0 x 10^{-3} mm in diameter; (2) Silt - somewhat cohesive soils when wet, not sticky when wet, grains ranging from 2.0 x 10^{-3} - 5.0 x 10^{-2} mm in diameter; (3) Fine sand - low cohesivity soils when wet, grains ranging from 5.0 x 10^{-2} - 2.0 x 10^{-1} mm in diameter; (4) Medium sand - grains ranging from 2.0 x 10^{-1} - 4.0 x 10^{-1} mm in diameter; (5) Coarse sand - grains ranging from 4.0 x 10^{-1} - 3.0 mm in diameter; (6) Pebbles - grains ranging from 3.0 - 16.0 mm; (7) Cobbles - grains greater than 16.0 mm in diameter. All size-classes within a plot were recorded. Diameter values are general definitions of the visually classified substrates; no sieve analyses were performed.

All plant species were categorized by longevity, origin, life-form, and primary dispersal mechanism. Origin indicates whether a plant is adventitive (i.e., introduced) or native as listed in Weber and Wittmann (1992). Longevity, or life-span, was classified as annual, biennial, or perennial. Life-form categories included forbs, graminoids (Cyperaceae, Juncaceae, Poaceae), shrubs, and trees. Dispersal mechanisms were classified as anemochoric (wind dispersed), barochoric (gravity dispersed or possessing no apparent dispersal mechanism), hydrochoric (water dispersed), zoochoric (animal dispersed). Morphological seed traits and published verifications of dispersal mechanisms of a particular species were used in classifying a species to one of the dispersal modes (Ridley 1930, Van Der Pijl 1972). Species utilizing more than one means of dispersal were classified according to their primary dispersal mode (Appendix 1).

3.2.5 Seed Dispersal and Seedling Establishment

Seed exclosure experiments were conducted on the North Fork along a 1 km reach upstream of Halligan Reservoir in May 1998. The purpose of these experiments was to determine the relative importance of wind and water dispersal in colonizing disturbed patches along unregulated streams. Experimental plots were established at three types of fluvial features: channel margins along riffles, islands, and pool margins. Two replicates of each fluvial feature were chosen at random along this 1 km reach. At each fluvial feature, three plots 30 x 30 cm in size separated by a 20 cm buffer between plots, were marked with metal pins within areas of relatively homogeneous vegetation cover. Percent cover of all species within the plots was recorded at this time using the methods outlined above.

The area within each plot, and a distance 20 cm outside of each plot, were disturbed by mechanically removing all above-ground vegetation, agitating the soil, and removing as much root biomass as possible. Screen material was installed over the anemochoric exclosure (Treatment 1) prior to inundation of the plots in May 1998 to exclude wind-transported seeds from reaching these plots. Upon flooding of the plots, screen was installed in the hydrochoric exclosure (Treatment 2) which was designed to prevent water-dispersed seeds from reaching plots during the period of inundation. A third control plot was unscreened for the duration of the experiment and was therefore open to colonization from both anemochoric and hydrochoric seeds. Upon recession of water levels, the screen material was again removed from Treatment 2 and replaced on Treatment 1, to exclude wind-dispersed seeds from these plots for the remainder of the growing season. In August 1997, each plot was revisited and species composition and percent cover were measured.

3.2.6 Data Analysis

Initiation of seed release, duration of peak of seed release, and end of seed release were determined for all wind-dispersed species and plotted (by family) in relation to the average historic hydrograph and the hydrographs measured in 1997. To determine where in the water column seeds are transported, seeds gathered from all sample dates were pooled and plotted by level for the North Fork and for South Boulder Creek. To test Hypothesis 1, spatial and temporal patterns of water dispersal of seeds were compared using a two-way repeated measures analysis of variance (ANOVA). The binary variable *DAM* (upstream or downstream of dam) and Julian date (TIME) were fixed effects in the model, and distance downstream (DSDIST) nested within *DAM* was defined as a random effect. The three-way interaction *TIME*DSDIST(DAM)* was used as an estimate of error. Response variables included seed density and species richness. Seed density was $\log_{10}$ transformed and richness data were square-root transformed prior to statistical treatment to more closely comply with the assumptions of normality and homogeneity of variance. Plots of studentized residuals versus predicted values verified compliance with these assumptions. F-tests were performed to compare means of the response variables by *TIME* and *DAM*, and to test for an interaction between these two variables. Pairwise comparisons were performed using Tukey's adjustment to test the null hypothesis of no difference between the means. These analyses were performed on both the seed data collected in 1997 on the North Fork and on the data from 1998 collected on South Boulder Creek.

Hypothesis 2 was tested by determining the relationship between wind- and water-dispersed seeds measured at a site over the entire season and local (at the scale of the cross-section) versus reach-scale sources of seeds from standing vegetation. Vegetation data from each cross-section (local-scale) and reaches above each cross-section (reach-scale) were summarized by first determining the total cover of each species (COV) in all plots, the relative frequency (F) of each species in all plots, and calculating an importance value (I) for each species by taking the product of these two values.

Eq. 3.1 $$I = F * COV$$

where I is the importance value assigned to each vascular plant species, F is the relative frequency of each vascular plant species (number of plots species recorded in/number of plots), and COV is the total cover of species of interest in all plots at the location.

At each sample the concordance between species composition of wind-dispersed seeds (seeds/$m^2$of each species present), water-dispersed seeds (seeds/m^3 of each species present), and standing vegetation (importance value of each species) was determined using Kendall's tau (τ) and Kendall's coefficient of concordance (W). τ and W provide measures of strength of the relationship among the ranks of two or multiple variables, respectively. W provides a single measure that describes the overall relationship among three or more variables of interest. τ or W of 0 represents no agreement among the variables, whereas τ or W of 1 represents a perfect agreement. τ may also be negative in cases of negative association between the two variables. In calculating τ and W, the appropriate adjustments were made in cases of tied ranks (Gibbons 1993). Because wind-dispersed seeds were not measured in 1998, τ was used to test for concordance between standing vegetation and hydrochoric seeds on South Boulder Creek. For comparative purposes, τ was measured to relate standing vegetation (at each of the two spatial scales) to water-dispersed seeds on the North Fork as well.

Presence-absence data for each dispersal type were analyzed using logistic regression to: (1) determine the strength of the relationships between abiotic factors and the probability of the presence of a particular dispersal mechanism and (2) to determine whether the relationship between abiotic factors and dispersal type differed between vegetation located upstream and downstream from the dam. Spearman rank correlation analysis indicated that there was collinearity between the measured environmental variables (Table 3.1). As a result, logistic models were fitted as a function of distance from the active channel boundary (DIST).

Table 3.1. Spearman rank correlation coefficients and significance of linear relationships between distance and other measured environmental variables measured in 178 vegetation plots on the North Fork of the Cache La Poudre River and in 153 plots sampled on South Boulder Creek. Null hypothesis: no linear relationship between ranks of the variables.

North Fork			**South Boulder Creek**		
Variable	*Distance*	p-**value**	**Variable**	*Distance*	p-**value**
Elevation	0.70	0.0001	Elevation	0.89	0.0001
Texture	-0.12	0.0370	Texture	0.03	0.7449
Moisture	-0.63	0.0001	Moisture	-0.66	0.0001

Logistic regression models were fitted by dispersal type for each stream. A dummy variable (DAM) was used to generate separate functions above and below each reservoir. An interaction term (DAM*DIST) was included in the equation to evaluate the fit of the two functions for each dispersal type. In other words, significance of the interaction term indicates that probability of the dispersal type as a function of distance from the channel is different upstream from reservoirs than below. The ratio of the deviance to the model degrees of freedom was used to evaluate the model fit. A low ratio of deviance to degrees of freedom (i.e., <1) is an indication of good model fit (Hosmer and Lemeshow 1989).

To test Hypothesis 4, mean species richness within and between treatments and fluvial features was compared using two-way factorial analysis of covariance (ANCOVA) with fluvial feature and treatment as classification variables. Initial species richness prior to treatment was entered into the model as a covariate. In cases of significant effects, Tukey's test was used to conduct pairwise comparison tests.

With the exception of calculations of Kendall's coefficient of concordance (W), SAS was used for all statistical procedures (Proc CORR, GENMOD, GLM, and MIXED; SAS Institute 1996). Calculations of W were performed using SPSS (SPSS Inc. 1994).

3.3 Results

3.3.1 Phenology: Primary Dispersal

A total of 209 aerial seeds representing 15 species and 6 different families were measured on the North Fork in 1997. Poaceae, Betulaceae, and Asteraceae were the families most represented in the aerial seed rain (Table 3.2). *Bromus japonicus*, *Phalaris arundinaceae*, *Agrostis gigantea* were the most abundant grasses represented in the seed rain, comprising 14, 8, and 8 percent of all the seeds captured, respectively. Although the birch family was represented by both *Alnus tenuifolia* and *Betula fontinalis*, *B. fontinalis* was by far the most abundant of the two species in the seed rain, comprising 34 percent of all seeds caught. Although *B. fontinalis* disperses its seeds in the fall and continues to disperse throughout the winter months, monitoring of seed traps was terminated at the end of August. As a consequence, only the first portion of the annual seed release of *B. fontinalis* was measured. *Tragopogon dubius* and an unknown species were the most abundant Asteraceae represented, comprising 12 percent of all seeds caught. The only early dispersing species represented in the seed rain were members of the willow family (Salicaceae), and seeds of *Salix* spp. and *Populus* spp. comprised 11 percent of all seeds recorded.

Table 3.2. Summary of wind dispersed seeds caught in seed traps placed at each cross-section on the North Fork Cache La Poudre River in 1997.

Family Common Name	Family Scientific Name	Number of Species	Proportion Total Number of Seeds	Maximum Seed Density (seeds/m^2)	Timing of Maximum Release
Sunflower	Asteraceae	2	0.125	1492	late August
Birch	Betulaceae	2	0.338	1976	late August
Cypress	Cupressaceae	1	0.003	40	mid-July
Grass	Poaceae	7	0.400	1008	late August
Knotweed	Polygonaceae	1	0.016	161	late August
Willow	Salicaceae	2	0.118	524	mid-July

The phenologic adaptations of riparian species to the historic average hydrologic regime were characteristic of the life-history traits of the species measured (Figure 3.2). Colonizing species, such as the willows, released seeds over a three-week period in synchrony with the descending limb of the hydrograph. During this period, seeds deposited along shorelines were delivered through both primary (wind) and secondary (water) dispersal processes.

Two major peaks were observed in the temporal distribution of the aerial seed rain, one in early summer (~June 15) and the other in late summer (~July 15) through autumn. The early peak was driven largely by the willows, the later peak by members of

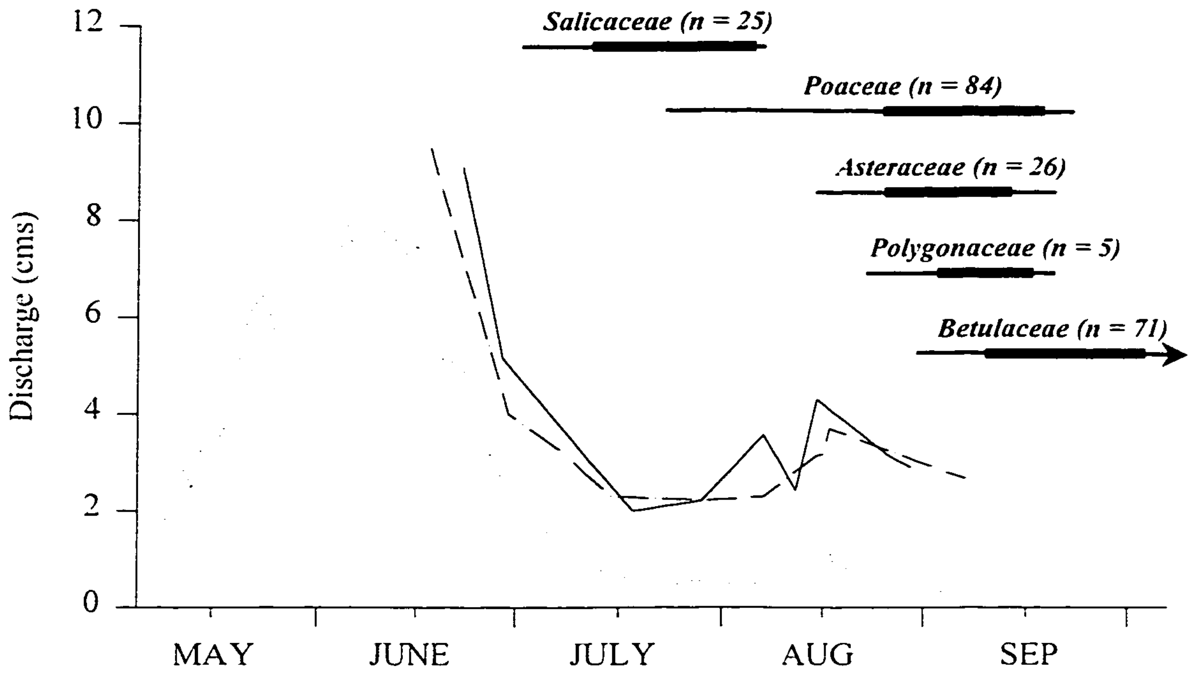


Figure 3.2. Phenology of seed release in relation to historic flows and flow the year of seed measurement on the North Fork Cache La Poudre River (North Fork). Historic flows (dotted line) are daily average flows measured at the North Fork Cache La Poudre near Livermore U.S. Geological Survey gage (1929-31, 1947-65, and 1986-1996). Flows above (solid) and below (dash-dot) Halligan Reservoir were measured in 1997 at the sampling cross-sections. Phenology data are based on initial to final capture dates (solid line) of 209 seeds of 15 species measured with aerial seed traps and period of maximum seed release (thick line).

Poaceae and Asteraceae. Betulaceae formed another peak later in the fall. Median species richness of all 70 samples was 0. Median richness of samples in which seeds were recorded (24 samples) was 1. Maximum richness was recorded on two dates, July 22 and August 1, and consisted of three species.

3.3.2 Transport: Secondary Dispersal

A total of 343 hydrochoric seeds representing 16 families were collected on the North Fork in 1997. Two-hundred seventy seven hydrochoric seeds representing 16 families were collected on South Boulder Creek in 1998 (Table 3.3).

Table 3.3. Summary table of seeds collected in hydrochoric seed traps at sites located upstream and downstream of reservoirs. Values are total numbers of seeds pooled over the season by site.

River/Location	Number of Seeds	Average Number of Seeds Per Cross-section	Number of Sampling Dates
North Fork			
Upstream	203	67.7	8
Downstream	140	46.7	8
South Boulder Creek			
Upstream	189	94.5	9
Downstream	88	29.3	9

Almost 80 percent (78.5 percent) of hydrochoric samples from the North Fork contained seeds. Of these samples, the median number of seeds, density of seeds and species richness of the samples were 7 seeds, 0.59 seeds/m^3, and 3 species, respectively. The median number of seeds, density of seeds, and species richness of all of the samples were 3 seeds, 0.38 seeds/m^3, and 2 species, respectively. The maximum number of seeds, density of seeds and species richness of the samples were 98 seeds, 45.8 seeds/m^3 of water, and 12 species, respectively. These values emphasize the extreme variability in density and species composition of hydrochoric seeds.

Over 90 percent of the hydrochoric samples collected on South Boulder Creek contained seeds. Median number, density, and richness of these samples were 5 seeds, 0.37 seeds/m^3, and 2 species, respectively. Median number, density, and richness of all samples were 3 seeds, 0.26 seeds/m^3, and 2 species, respectively. Maximum number, density, and richness were 39 seeds, 3.0 seeds/m^3, and 10 species, respectively.

Willows (*Salix* spp.) were the most abundant species in the hydrochoric samples upstream from the reservoir on the North Fork and both upstream and downstream on South Boulder Creek (Table 3.3). Two other members of Salicaceae, *Populus angustifolia* and *P. deltoides*, were also represented in the hydrochoric samples, but were less abundant than were the several species of willow represented as *Salix* spp.: *S. amygdaloides*, *S. bebbiana*, *S. drummondiana*, *S. exigua*, *S. lucida* subsp. *caudata*, *S. lucida* subsp. *lasiandra*. Although seeds of each of these species were collected from adult plants in the field, the seeds of these species were indistinguishable from one another and were therefore categorized as *Salix* spp. Willow seeds were present in the hydrochoric samples from 23 June through 8 July, and 22 May to 17 July in the North Fork and South Boulder Creek samples, respectively.

Other well-represented families in the hydrochoric seed bank included Poaceae, Betulaceae, and Asteraceae. The most abundant grasses included two native species *Glyceria striata* and *Elymus trachycaulus*, as well as a variety of adventitive species such as *Agrostis gigantea*, *Anisantha tectorum*, *Bromus japonicus*, and *Phalaroides arundinacea*. Of the three species in Betulaceae recorded in the vegetation surveys, *Betula fontinalis* and *Alnus incana* subsp. *tenuifolia* were the only two represented in the hydrochoric samples. The other species in this family present in the vegetation on South

Boulder Creek, *Corylus corulata*, produces animal-dispersed nuts (filberts). *B. fontinalis* and *A. incana* subsp. *tenuifolia* were abundant in the hydrochoric samples in early June and again in late August. This bimodal distribution of seeds of these species represents (1) remobilization and secondary dispersal of seeds initially deposited on the floodplain the previous year and (2) wind-dispersed seeds deposited on the water surface during the year of seed production, beginning in late August.

A majority (56 percent) of the seeds sampled on the North Fork were transported on the surface of the stream, whereas 17 and 28 percent were transported in suspension and on the bed of the stream, respectively (Figure 3.3). Most of the seeds collected on South Boulder Creek were transported in suspension (48 percent), whereas 31 and 21 percent were measured from the surface and bed of the stream, respectively.

Seasonal and temporal trends in total numbers of seeds and species richness of samples are shown in Figure 3.4. Two distinct peaks in total seed number, one in late June and the other in mid-August, are evident on the surface plot of the North Fork data. Three distinct peaks are evident on the plot of South Boulder Creek data; one in early-June, one in mid-July, and one in late-August. It is likely that an early peak occurred on the North Fork but was not recorded due to the late initial sampling date of 10 June in 1997. The seed content of these three peaks indicate that there is an early peak in secondarily transported seeds re-entrained during spring runoff, a second peak which is composed almost exclusively of members of the willow family, and a third peak late in the season corresponding to the late summer dispersers. A fourth peak likely occurs in August in conjunction with the maturity and dispersal of the seeds of *B. fontinalis* and *A. incana* subsp. *tenuifolia.*

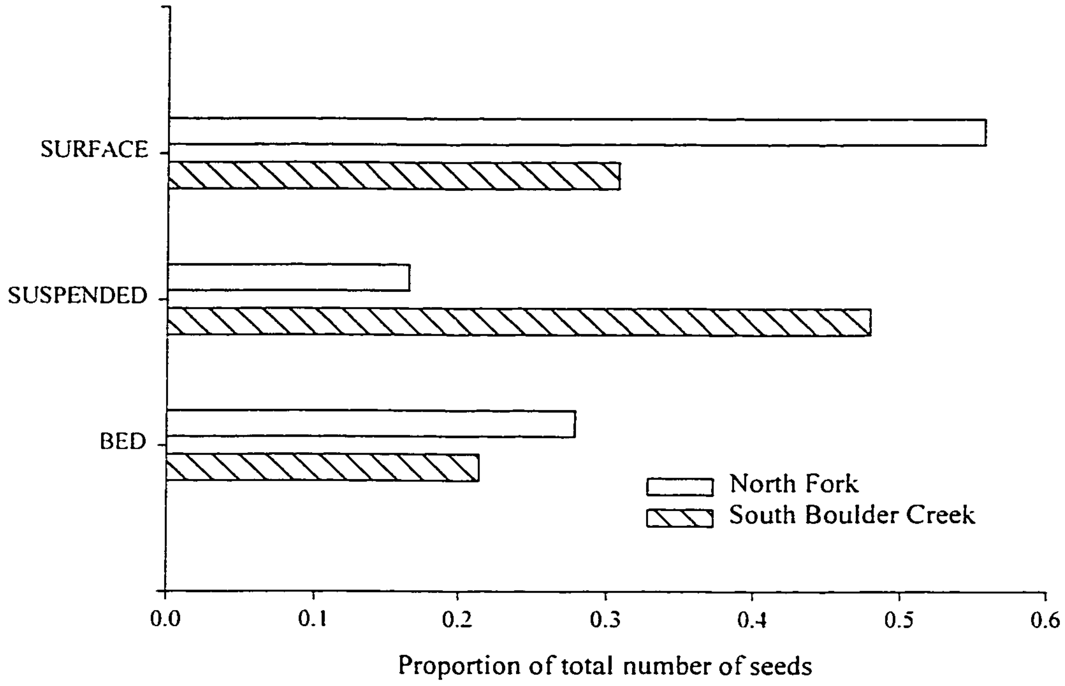


Figure 3.3. Relative proportions of total number of seeds caught in hydrochoric seed traps in 1997 on North Fork of the Cache La Poudre River and in 1998 on South Boulder Creek by level in the water column. Seeds were collected from the surface, in suspension (0.6 x the depth of flow in the thalweg), and on the bed of the stream. Proportions represent 620 seeds. 343 and 277, collected on the North Fork and South Boulder Creek, respectively.

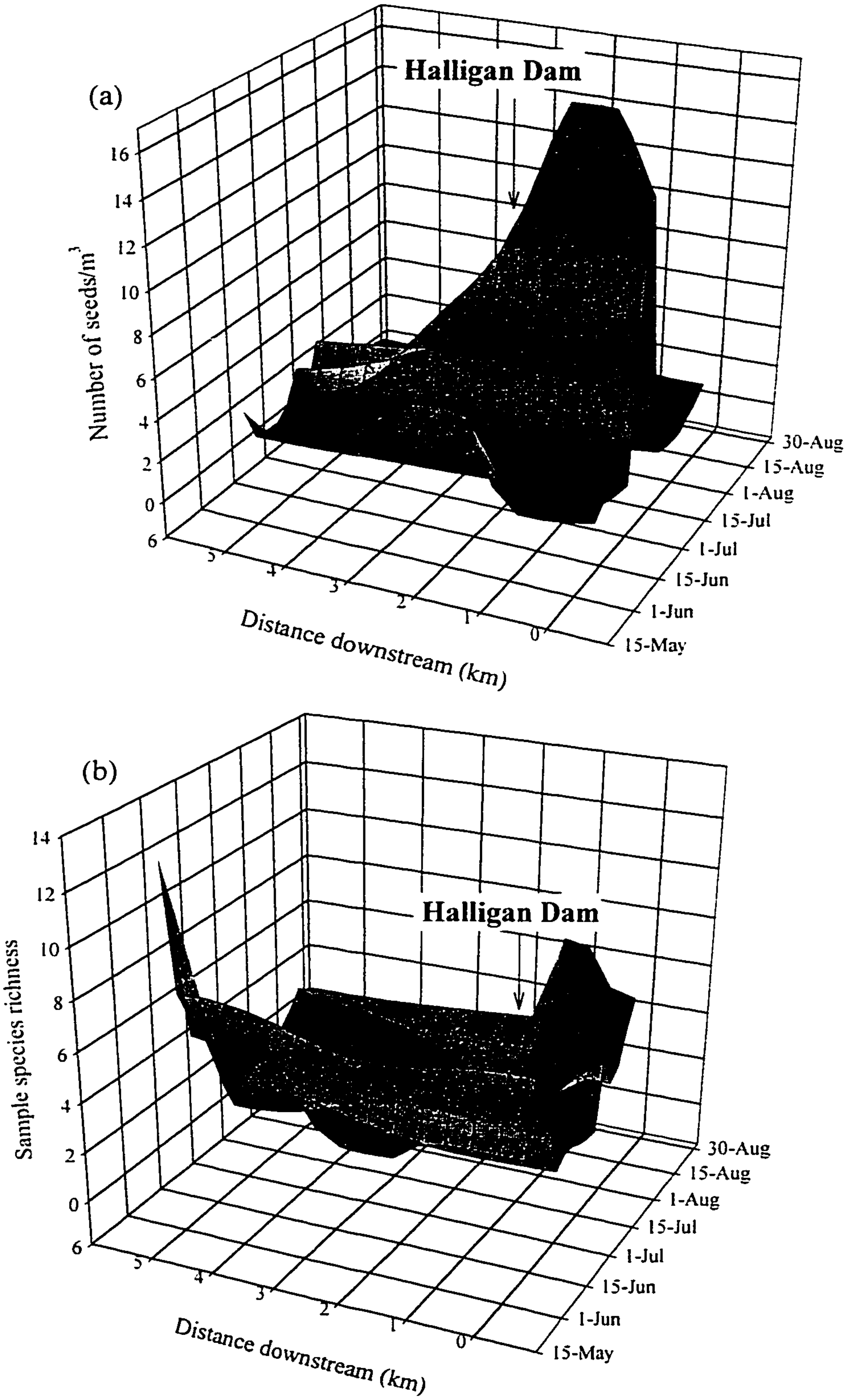


Figure 3.4. Interpolated surface plots of hydrochoric seed density (a) and species richness (b) from the North Fork of the Cache La Poudre River above and below Halligan Reservoir.

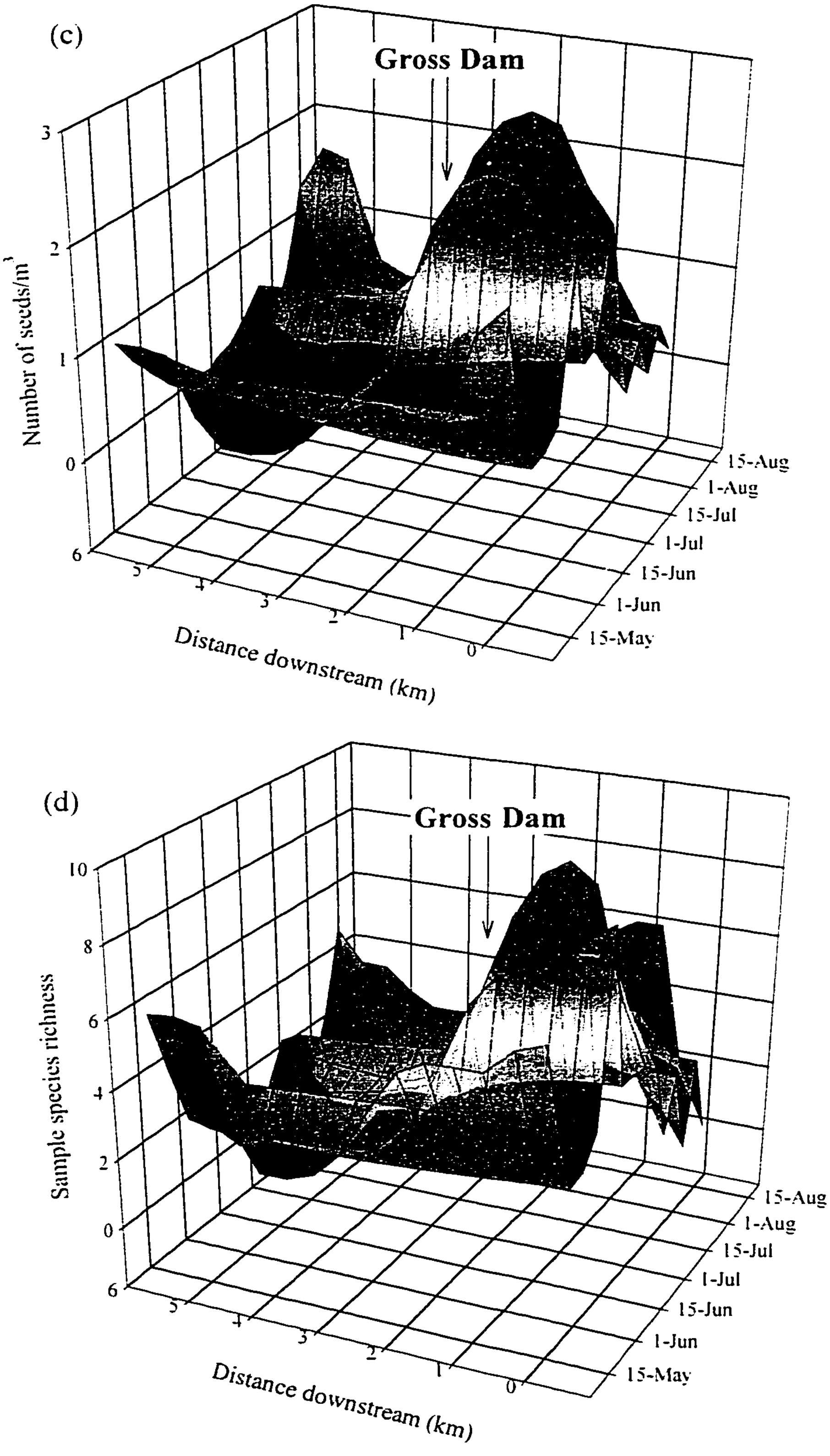


Figure 3.4 (*Continued*). Interpolated surface plots of hydrochoric seed density (c) and species richness (d) from South Boulder Creek above and below Gross Reservoir.

Table 3.4. Hydrochoric seeds collected on the North Fork of the Cache La Poudre in 1997 (343 seeds) and on South Boulder Creek in 1998 (277 seeds). Seeds collected upstream and downstream of reservoirs on the two streams are summarized by family. Values are the proportion of all seeds collected represented by species in the corresponding family.

Family		**North Fork**		**South Boulder Creek**	
Common Name	**Scientific Name**	**Upstream**	**Downstream**	**Upstream**	**Downstream**
Maple	Aceraceae	0.01	<0.01	0.06	<0.01
Parsley	Apiaceae	<0.01	<0.01	0.01	0.10
Sunflower	Asteraeae	<0.01	<0.01	<0.01	0.02
Birch	Betulaceae	0.08	0.31	0.09	0.15
Borage	Boraginaceae	<0.01	0.01	<0.01	<0.01
Mustard	Brassicaceae	0.02	0.02	0.05	0.02
Goosefoot	Chenopodiaceae	0.01	0.01	0.01	0.02
Cypress	Cupressaceae	<0.01	0.01	<0.01	<0.01
Sedge	Cyperaceae	0.04	0.06	0.05	0.03
Pea	Fabaceae	<0.01	0.01	0.01	<0.01
Currant	Grossulariaceae	<0.01	<0.01	<0.01	0.01
Mint	Lamiaceae	<0.01	0.01	0.01	<0.01
Evening-Primrose	Onagraceae	<0.01	<0.01	0.02	<0.01
Pine	Pinaceae	<0.01	<0.01	0.02	0.01
Grass	Poaceae	0.09	0.28	0.05	0.14
Knotweed	Polygonaceae	<0.01	0.04	0.01	0.01
Buttercup	Ranunculaceae	<0.01	0.01	0.01	<0.01
Rose	Rosaceae	0.02	0.01	0.01	0.01
Willow	Salicaceae	0.70	0.16	0.52	0.38
Figwort	Scrophulariaceae	<0.01	0.01	<0.01	<0.01
Valerian	Verbenaceae	<0.01	0.01	<0.01	<0.01
Unknown	Unknown	0.04	0.04	0.10	0.10

Seed density declined downstream of the reservoirs on both the North Fork and on South Boulder Creek (see arrows in Figure 3.4 and see Figure 3.5). The gradual downward trend shown in the interpolated surface of the North Fork data is slightly misleading. The decline in seed numbers begins at the first cross-section below the reservoir. The interpolated surface was used because it provides a more interpretable plot that the alternative (scatter plot). On both streams, this abrupt decline in seed numbers occurred during the period of maximum seed release (see wind dispersal section above). This was also the period of the highest seed densities recorded on both streams, which was 8 July and 17 July on the North Fork and on South Boulder Creek, respectively. Seed density was reduced by 94 percent (6.5 to 0.4 seeds/m^3) from above to below the reservoir on the North Fork and by 70 percent (3.0 to 0.9 seeds/m^3) on these dates in 1997 and 1998, respectively.

F-tests from two-way repeated measures ANOVA indicated that there were significant differences in mean seed density both through time and above and below impoundments (Figure 3.6). Seed density was lower below impoundments on both streams, but due to high variance in seed density on the North Fork, this difference was statistically significant only on South Boulder Creek (DAM effect, F = 23.2, df = 3, and p-value = 0.0171 and F = 0.15, df = 5, and p-value = 0.7172 for South Boulder Creek and the North Fork, respectively; Figure 3.6). TIME effects were insignificant for seed density data on the North Fork (F = 1.53, df = 17, p-value = 0.2264) but the interaction (DAM*TIME) was significant (F = 3.42, df = 17, p-value 0.0213). Density decreased through time below the reservoir on the North Fork, but varied widely (Figure 3.6a). Seed density varied significantly by *TIME*, and the interaction between *DAM* and *TIME* was significant, on South Boulder Creek (Figure 3.6b). Seed density was higher from 15 June through 15 July upstream from the reservoir on South Boulder Creek.

Distinct spatial and temporal differences in species richness were evident in comparisons between the North Fork and South Boulder Creek. Richness varied significantly through time on the North Fork (TIME effect: F = 3.63, df = 17, p-value = 0.0168) but neither *DAM* nor the *DAM*TIME* interaction were significant at the $p < 0.05$ level. Species richness was actually slightly higher (3.5 species) below than above (2.7 species) average over the season on the North Fork, but these differences were not significant at $p < 0.05$ (Figures 3.5 and 3.6c). This higher species richness was attributed

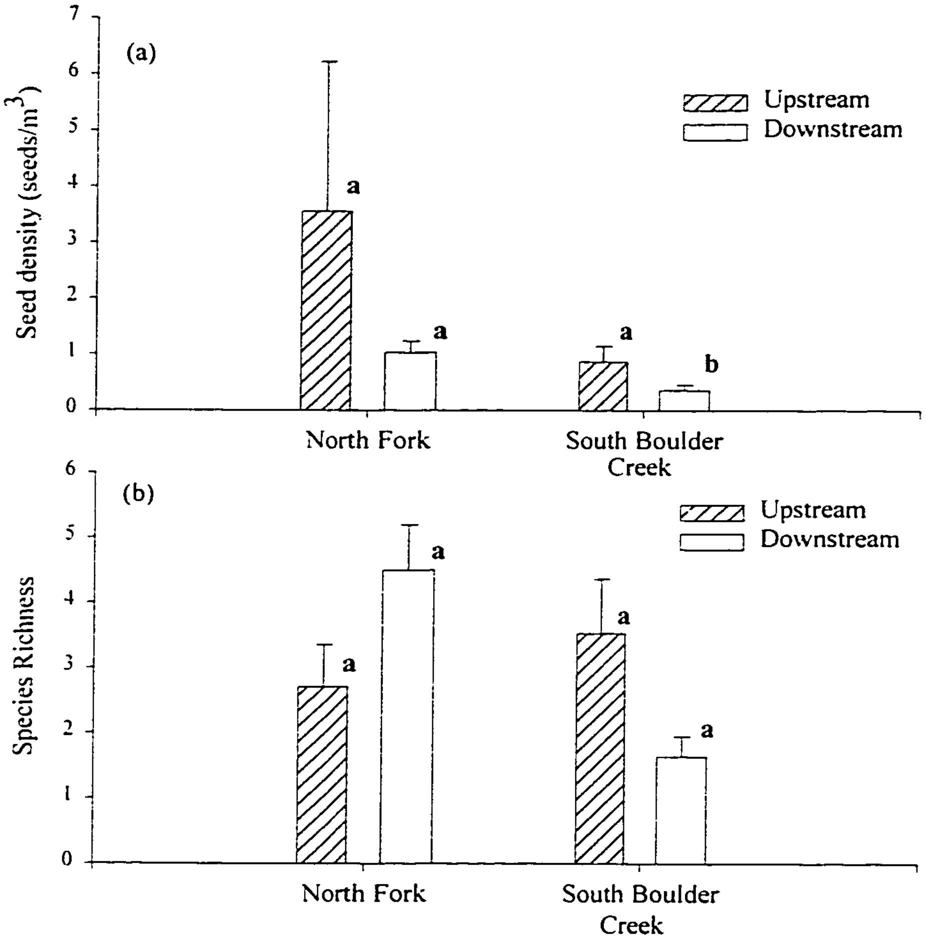


Figure 3.5. Comparisons of (a) seed density and (b) species richness of hydrochoric seed samples from 343 seeds caught on North Fork of the Cache La Poudre River in 1997 and 277 seeds trapped on South Boulder Creek in 1998. Different letters indicate statistically significant difference between means (Tukey's test, $p < 0.05$). Comparisons were made separately for each stream.

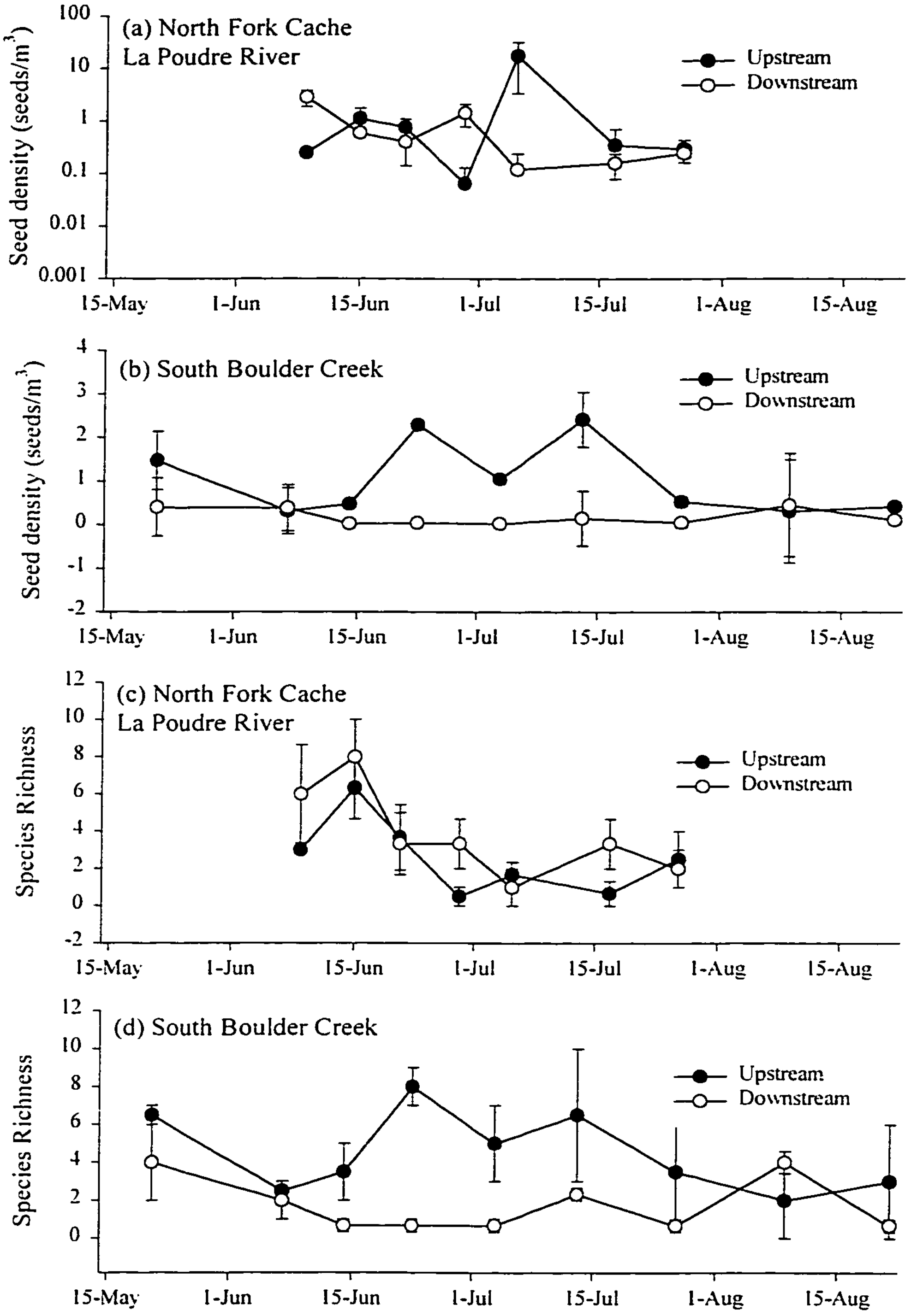


Figure 3.6. Seed density and species richness through time and in relation to dams. Hydrochoric seed samples from 343 seeds caught on North Fork of the Cache La Poudre River in 1997 and 277 seeds trapped on South Boulder Creek in 1998. Note $\log_{10}$ scale in frame a.

to a single sample taken from the cross-section furthest downstream on (10 June) which had a species richness of 12. Whereas species richness was higher during the June 15 - July 15 portion of the summer on South Boulder Creek, and was lower below the reservoir than above, neither *TIME* (F = 1.70, df = 22, p-value = 0.1549), *DAM* (F = 7.20, df = 3, p-value = 0.0748) nor their interaction (F = 2.13, df = 22, p-value = 0.0767) were significantly different ($p < 0.05$; Figure 3.6d). Therefore seed density decreased at one site but species richness did not decrease significantly at either site.

3.3.3 Vegetation Sampling and Dispersal Mechanisms of Riparian Plants

One-hundred fifty-seven vascular plant species were sampled on the North Fork and 150 species were sampled on South Boulder Creek. A complete list of the life-history traits (longevity, origin, life-form, and primary dispersal mechanism) is presented in the Appendix. Frequency of occurrence and total cover of each species are also presented in the Appendix for plots sampled above and below reservoirs on both streams. Life-history traits were quite similar between streams as well as above and below reservoirs on the two streams (Table 3.5). Over 75 percent of the species sampled at all locations were native perennials. About the same number of graminoid and tree species occurred at all locations, but the North Fork had more forb species and fewer shrubs than South Boulder Creek. Fifty-three and 41 percent of all species were either anemochorous or hydrochorous on the North Fork and South Boulder Creek, respectively, and these values varied little when comparing upstream to downstream floras. Hydrochoric species were more abundant in the North Fork flora than in the South Boulder Creek flora.

Table 3.5. Life-history traits of all vascular plant species sampled in vegetation plots on the North Fork of the Cache La Poudre River and South Boulder Creek upstream and downstream of reservoirs. See text for full explanation of terminology. Numbers indicate the proportion of all species measured at the locations indicated exhibiting the trait.

Life-history Trait		**North Fork**		**South Boulder Creek**	
		Upstream	**Downstream**	**Upstream**	**Downstream**
Longevity	Annual	0.14	0.14	0.04	0.07
	Biennial	0.04	0.04	0.02	0.05
	Perennial	0.82	0.82	0.94	0.89
Origin	Native	0.75	0.76	0.86	0.78
	Adventitive	0.25	0.24	0.14	0.22
Life-form	Graminoid	0.26	0.28	0.26	0.30
	Forb	0.55	0.53	0.44	0.42
	Shrub	0.15	0.15	0.23	0.20
	Tree	0.04	0.03	0.07	0.08
Dispersal Mechanism	Anemochore	0.32	0.30	0.29	0.30
	Barochore	0.31	0.26	0.36	0.30
	Hydrochore	0.21	0.25	0.12	0.18
	Zoochore	0.16	0.19	0.22	0.22

Concordance analysis indicated that there is much variability in the relationship between the composition of hydrochoric seeds in transport and the composition of the potential sources of those seeds (i.e., standing vegetation at the cross-section and above the cross-section). Lack of strong measures of association could suggest that seeds measured in transport originated from other sources, such as vegetation growing along reaches further upstream in the watershed or secondary wind dispersal. There were strong and significant associations between local- as well as reach-scale vegetation and hydrochoric seeds at stations sampled upstream and downstream from the reservoir on the North Fork (Table 3.6). Hydrochoric seed composition was most strongly associated with local- and reach-scale vegetation at the cross-section located immediately below the reservoir (3 km), suggesting that hydrochoric seeds may be a function of local rather than regional seed sources below reservoirs. These patterns were even more evident on South

Boulder Creek. Average τ (τ_{avg}) on South Boulder Creek was 0.20 upstream of the reservoir whereas below the reservoir average τ was greater than twice as strong (τ_{avg} = 0.42). Although the strength of the difference in associations upstream and downstream is not as strong on the North Fork (τ_{avg} was 0.16 upstream, and 0.24 downstream of Halligan Dam), the direction of the pattern is consistent between streams.

Table 3.6. Results of concordance analyses between the composition of standing vegetation and the composition of hydrochoric samples from the North Fork of the Cache La Poudre River. Kendall's tau (τ), a measure indicating the strength of the association between the ranks of two variables, is presented for (1) tests of concordance between water dispersed seeds and local vegetation and (2) tests of water dispersed seeds and vegetation sampled upstream of the cross-sections (reach). $\tau = 0$ indicates no association, $\tau = 1$ indicates a perfect association between the two variables. Upstream and downstream refer to position in relation to impoundments.

		North Fork				**South Boulder Creek**			
		(1) Local		**(2) Reach**		**(1) Local**		**(2) Reach**	
	Distance Downstream (km)	**τ**	***p*-value**	**τ**	***p*-value**	**τ**	***p*-value**	**τ**	***p*-value**
Upstream	0	0.29	*	0.29	*	0.05	ns	--	--
	1	0.23	ns	0.20	ns	0.35	**	0.18	ns
	2	-0.05	ns	0.27	*	--	--	--	--
Downstream	3	0.36	**	0.34	**	0.48	***	--	--
	5	0.18	ns	0.33	**	0.27	*	0.47	***
	6	0.18	ns	0.25	*	0.52	****	0.28	*

ns = non-significant at $\alpha = 0.05$. * $p < 0.05$. ** $p < 0.01$. ***$p < 0.001$. ****$p < 0.0001$. -- indicates no available information.

Tests for association between local- and reach-scale vegetation and both wind- and water-dispersed seeds exhibited similar variability to the tests above. Kendall's coefficient of concordance (W_a) ranged from 0.04 to 0.27 in tests using local vegetation, and from 0.03 to 0.56 using reach-scale vegetation. Again, average concordance was higher below Halligan Reservoir when compared to average concordance above the reservoir at both the local (upstream $W_a = 0.13$ and downstream $W_a = 0.16$) and reach (upstream $W_a = 0.22$ and downstream $W_a = 0.32$) scales. This may indicate that seeds are supplied from sources throughout the watershed upstream from impoundments, but are derived primarily from local sources below them. These general patterns are obscured by the conflicting W_a from the cross-section immediately above the reservoir (2 km) which showed significant concordance at both the local- ($W_a = 0.22$) and reach- ($W_a = 0.52$) scales (Table 3.7).

Table 3.7. Results of concordance analyses between the composition of standing vegetation, the composition of the seed rain, and the composition of hydrochoric samples from the North Fork of the Cache La Poudre River. Kendall's coefficient of concordance (W_a) is presented for (1) tests of concordance between wind- and water-dispersed seeds and local vegetation and (2) tests of wind- and water-dispersed seeds and vegetation sampled upstream of the cross-sections (reach). $W_a = 0$ indicates no association, $W_a = 1$ indicates a perfect association between the three variables. Upstream and downstream refer to position in relation to reservoirs.

North Fork		**(1) Local**		**(2) Reach**	
Distance Downstream (km)		W_a	*p*-value	W_a	*p*-value
Upstream	0	0.07	0.0260	0.07	0.0260
	1	0.09	0.0110	0.08	0.0200
	2	0.22	0.0001	0.52	0.0001
Downstream	3	0.18	0.0001	0.03	0.2920
	5	0.27	0.0001	0.56	0.0001
	6	0.04	0.1130	0.38	0.0001

Logistic regression resulted in very distinct spatial patterns of distributions of hydrochoric and zoochoric species (Figure 3.7). Parameter estimates and regression diagnostics indicate that the distribution of hydrochoric and zoochoric species is a function of distance from the active stream channel on both free-flowing and regulated reaches; the probability of hydrochory is greatest near the channel whereas the probability of zoochory increases with distance from the channel (Table 3.8). In general, barochory increases with distance from the active channel, but this response was only significant for South Boulder Creek. The wide spatial distributions of anemochores and barochores with respect to distance from the active channel are reflected by insignificant

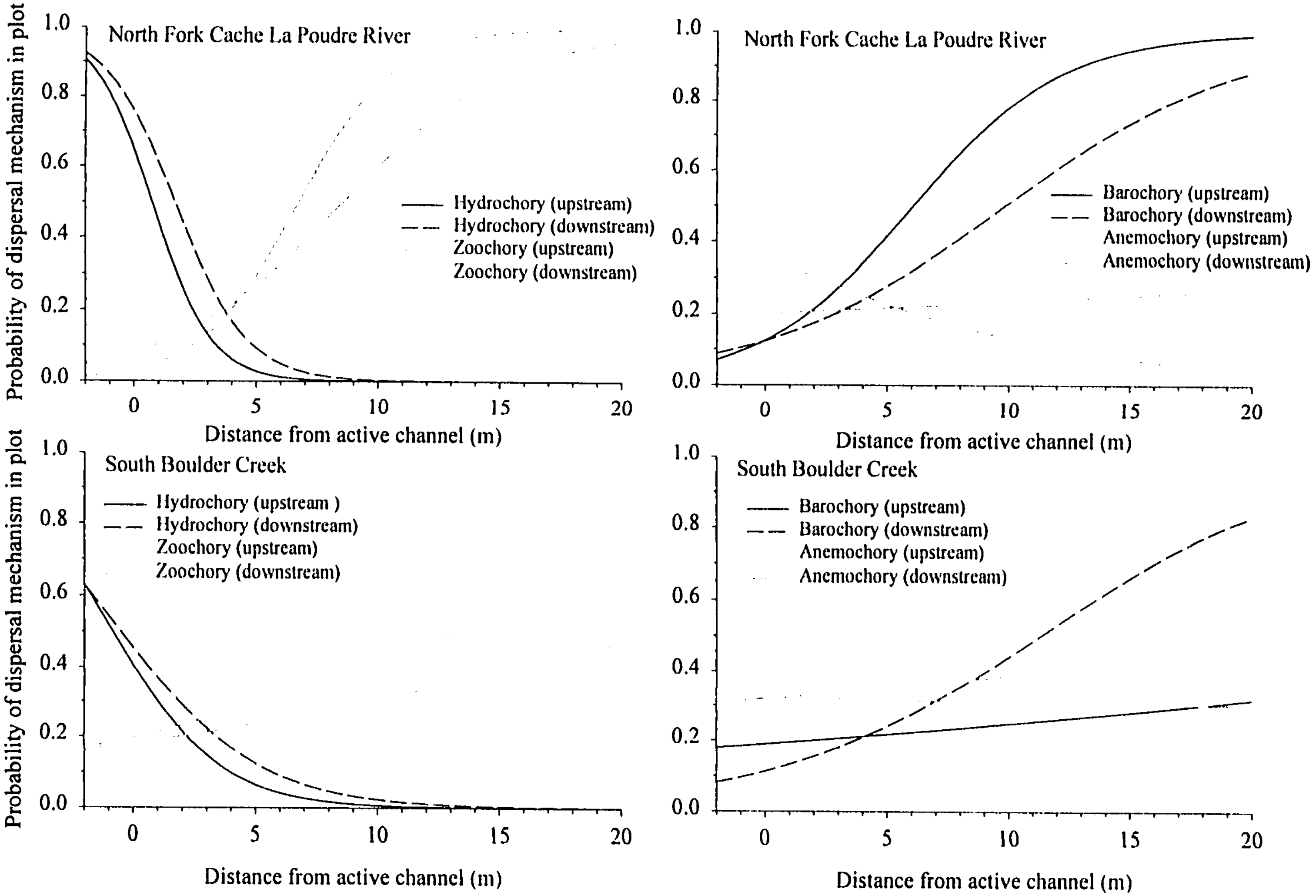


Figure 3.7. Logistic regression models of dispersal mechanisms as a function of distance from the active stream channel from data collected on the North Fork of the Cache La Poudre River (178 vegetation plots) and South Boulder Creek (153 vegetation plots). One-hundred fifty seven vascular plant species were classified as wind (anemochore), gravity (barochore), water (hydrochore), or animal (zoochore) dispersed and presence and absence data were modeled separately upstream and downstream of reservoirs.

DIST terms in the fitted models. Factors other than distance from the active channel may account for the distributions of species possessing these dispersal mechanisms along mountain stream channels. In contrast, hydrochores and zoochores are non-randomly distributed along the distance gradient. Distance may represent a moisture and elevation gradient as well, as suggested by collinearity between these variables (see Table 3.1).

Table 3.8. Parameter estimates from logistic regression analyses from riparian vegetation sampled on the North Fork Cache La Poudre River and South Boulder Creek. Dispersal mechanisms (anemochory, barochory, hydrochory, and zoochory) were fitted as a function of distance from the active stream channel (DIST). Models also contained a dummy variable *DAM* (above = 0, below = 1) and the interaction between *DIST* and *DAM*. Deviance (D) divided by model degrees of freedom (df) provides an indication of model fit; *D/df* near 1 suggests that the model is an acceptable fit.

Site	Dispersal Mechanism	Intercept (β_0)	*p*-value	DIST (β_1)	*p*-value	DAM (β_2)	*p*-value	DIST*DAM (β_3)	*p*-value	D/df
North Fork										
	Anemochory	-1.67	****	0.15	ns	1.11	**	-0.28	*	1.12
	Barochory	-1.95	****	0.14	ns	0.01	ns	0.18	ns	0.95
	Hydrochory	1.15	****	-0.69	****	-0.54	ns	-0.15	ns	1.12
	Zoochory	-2.41	****	0.28	***	-0.96	ns	0.22	ns	0.73
South Boulder Creek										
	Anemochory	-0.75	**	-0.01	ns	-0.01	ns	0.04	ns	1.29
	Barochory	-2.06	****	0.18	*	0.61	ns	-0.15	ns	0.97
	Hydrochory	-0.18	ns	-0.35	**	-0.20	ns	-0.10	ns	0.94
	Zoochory	-1.52	****	0.07	ns	0.12	ns	0.03	ns	1.11

ns = non-significant at $\alpha = 0.05$. * $p < 0.05$. ** $p < 0.01$. ***$p < 0.001$. ****$p < 0.0001$.

Significance of the interaction term provides a measure of how the probability of encountering a dispersal type as a function of distance from the stream differs above and below reservoirs. In other words, if the *p*-value of the interaction is significant, the two functions (upstream and downstream) for a particular dispersal type are significantly different (Figure 3.7). This test of upstream to downstream similarities was significant only for anemochores on the North Fork (Table 3.8). The probability of anemochory decreases as a function of distance from the channel along unregulated reaches of the North Fork, but does not vary significantly with distance from the channel downstream from the dam. Although average distances of vegetation plots containing each of the dispersal types were not formally compared (i.e., using ANOVA), comparative statistics are presented in Table 3.9.

Table 3.9. Mean distance +/- standard error of the mean from the active channel (m) of four dispersal types (anemochory, barochory, hydrochory, and zoochory) upstream and downstream of reservoirs.

	Dispersal Mechanism	**North Fork** Distance (m)	**South Boulder Creek** Distance (m)
Upstream	Anemochory	1.67 +/- 0.26	4.63 +/- 0.56
	Barochory	2.97 +/- 0.39	4.72 +/- 0.64
	Hydrochory	0.91 +/- 0.14	1.67 +/- 0.73
	Zoochory	3.99 +/- 0.53	5.30 +/- 0.60
Downstream	Anemochory	2.89 +/- 0.42	2.47 +/- 0.44
	Barochory	2.92 +/- 0.48	3.91 +/- 0.72
	Hydrochory	1.23 +/- 0.16	1.33 +/- 0.35
	Zoochory	3.69 +/- 0.45	2.97 +/- 0.47

In general, zoochores occur at the furthest distances from the channel on both streams. In addition, zoochores occur closer to the channel below reservoirs and further from the channel along undammed reaches. Hydrochores occur nearer the channel below the dam on South Boulder Creek but at slightly greater distances from the channel on the North Fork. Average distance from the active channel of plots containing barochores is slightly greater above when compared to below reservoirs. Patterns of zoochores and barochores are consistent above and below dams; patterns of anemochores and hydrochores are less clear.

3.3.4 Seed Dispersal and Seedling Establishment

A total of 17 species were recorded in the 18 plots sampled as a part of the colonization exclosure. Prior to the removal of vegetation and installation of treatments, species richness was significantly higher at riffle margins and on islands (average richness 4.5 and 4.5, respectively) than along pool margins (average species richness 3.2). Results of one-way ANOVA comparing mean initial species richness on fluvial feature were significant ($F = 15.4$, $df = 2$, $p = 0.0002$). After removing all vegetation from plots, applying treatments, allowing plots to become revegetated through colonization, and re-measuring species richness in all plots, species richness was not significantly different in any of the treatment combinations ($F = 0.91$, $df = 2$, $p = 0.4218$).

After introducing initial richness into the ANOVA model as a covariate, and comparing mean final species richness between the factors (fluvial feature and treatment), there were no significant differences between either fluvial feature or treatment (ANCOVA, $F = 0.50$, $df = 9$, $p = 0.8409$). Although every attempt was made to control for external effects, re-colonization of plots through vegetative means was a major source of 'noise' in this experiment.

Many species capable of vegetative growth from perennial root systems were present in the plots: *Carex nebrascensis, C. lanuginosa, Eleocharis palustris, Juncus confusus, Phalaroides arundinacea,* and *Scirpus microcarpus* were the most common of these species in the experimental plots. Another factor that was not accounted for was the colonization of plots by spore-bearing species. The spores of *Equisetum arvense* (field horsetail) were able to penetrate the exclosure screen and take advantage of the initially bare ground in the treatment plots. As a consequence this species was responsible for the measured increases in species richness in many of the plots regardless of exclosure treatment.

Although these experiments did not provide support for Hypothesis 4, this does not indicate that hydrochory is not an important dispersal pathway for colonizing species along river margins. These results demonstrate the potential importance of vegetative reproduction in colonizing margins that either are not scoured to a depth sufficient for the removal of root-systems or deposited upon to a depth sufficient to bury existing roots.

3.4 Discussion and Synthesis

Developing an understanding of seed dispersal is essential to understanding the dynamics of populations of plants and the development of plant communities along streams (Okubo and Levin 1989). Whereas until recently much of the work published on the importance of hydrochory has been largely based upon observational studies examining individual populations of plants, the current investigation presents a quantification of the hydrologic and hydraulic factors governing the transport and deposition of seeds of multiple species along rivers. In addition this work provides insight into hydrologic regimes most conducive to the deposition of seeds along river margins (Hypothesis 2.1), and relates spatial distributions of riparian plants to the dispersal traits of individual species along rivers subjected to regulation for different lengths of time (50-100 years).

3.4.1 Stream Hydrology and Hydraulics

Experimental work presented in Chapter 2 provided support for Hypothesis 2.2 which was based in part on the observations of Nilsson *et al.* (1991b); that seeds are deposited along river margins in areas of reduced flow velocity, such as in meander bends and eddys. In flume experiments, 91% of the variability in the deposition of seeds was explained by the relative velocity of the flow field associated with a particular fluvial feature (Figure 2.8). In other words, seeds are not only deposited non-randomly in areas where flow velocity is lower, but are detained and deposited preferentially in areas where well-developed flow separation and recirculation cells are formed. The level of development of these cells of recirculation is partially dependent upon the shape of the hydrograph during flow recession. During simulations of natural snowmelt hydrographs (descending flows), eddies were the areas of highest seed deposition for early and 'mid-season' dispersers, whereas point bars became important sites of deposition for later dispersing species (Figures 2.4- 2.7). Under stepped hydrologic regimes, which are typical of the outflows from reservoirs, very well developed zones of recirculation were shown to form during intermittently steady periods of flow. The combination of steady flow, stabilization of zones of recirculation, and detention of seeds in these zones, followed by short but steep drawdown curves, provided all of the conditions necessary for optimal seed deposition. In addition, 'mid-season' dispersing seeds were deposited in higher numbers on point bars and pool margins than in eddies or areas of flow expansion. Therefore, the synchronization of hydrologic conditions conducive to the deposition of seeds on a particular fluvial feature could be managed to accommodate species that disperse over a specific interval during the growing season. In this way, the directional nature of hydrochory could be utilized to re-synchronize the dispersal phenologies of certain species with suitable safe-sites for successful regeneration of these species.

At higher flows, large-scale hydraulics govern where seeds are detained and deposited. At lower flows small scale-hydraulics become increasingly important. Macro-turbulence and wave formation resulted in seed deposition in high-energy areas at the highest flows in the flume, whereas small-scale hydraulics such as hydraulic jumps and turbulence associated with roughness elements became important factors at lower flows. Future studies should incorporate varied levels of boundary roughness as a factor in seed deposition experiments. Both Schneider and Sharitz (1988) and Nilsson *et al.* (1991b) concluded that obstructions to flow and standing vegetation had diminishing importance in determining where seeds were deposited at increasingly higher discharges. This is due to the fact that the roughness elements became drowned-out (submerged) at higher flows. In fact, Nilsson *et al.* (1991b) found a negative correlation between roughness and the deposition of wooden cubes along the Sävar River in Sweden. Incorporating roughness elements into flume experiments such as those presented here may provide valuable insight into the interactions between large and small scale hydraulics and the importance of these factors in determining where and in what densities seeds are deposited along stream margins.

3.4.2 Patterns of Seed Dispersal on Regulated Streams

In this study, the synchrony between the timing of seed release in small-seeded, colonizing species such as *Salix* spp. and the availability of suitable microsites along undammed stream reaches were documented through field measurements of wind- and water-dispersed seeds (Figure 3.2). Fall release of *Betula fontinalis* and *Alnus incana* subsp. *tenuifolia* and secondary dispersal by water in the spring were also recorded. Similar patterns of fall dispersal have been shown to be advantageous for other early successional riparian species (Staniforth and Cavers 1976, Densmore and Zasada 1983, Matlack 1989, Thébaud and Debussche 1991). Each of the autumn-dispersed riparian species in these studies requires a period of low temperature (cold stratification) prior to breaking dormancy. *Betula* spp. may also remain dormant for several years prior to germination (Houle 1994). Thus seeds may be dispersed across the floodplain by wind the year of seed production, stratify during overwintering, and germinate after secondary dispersal by spring floods the following season.

Whereas the flume experiments provided strong evidence that certain types of hydrologic regimes prevent the directed dispersal of seeds to suitable safe-sites, field experiments provided evidence that dams also serve as a physical barrier to the downstream movement of seeds (Figure 3.5). These results provide support for Hypothesis 3.1, that reservoirs, as well as natural lakes along rivers (Nilsson *et al.* 1991a), may serve as effective seed-traps, blocking the downstream movement of propagules (Johansson and Nilsson 1993, Nilsson and Jansson 1995). The difference in seasonal trends of dispersing hydrochores also provides field evidence that dams may serve to desynchronize the availability of habitat from the availability of seeds (Figure 3.6b and d).

Field data did not provide strong support for the 'river collector hypothesis' suggested by Nilsson *et al.* (1994) in which rivers act as collectors of seeds and the number of species in the drift are hypothesized to increase as a function of downstream distance (Hypothesis 3.2). This may be attributed to the relatively small scale at which this investigation was focused. Because study reaches extended approximately 3 km above and below each reservoir, and due to the fact that there were no major tributaries to contribute seeds to the study streams through these reaches, the ability to detect the accumulation of seeds as a function of distance downstream was limited. The distance downstream required for seed density and seed species richness to recover below dams was also unclear. On the North Fork there was no recovery in seed density downstream from the reservoir within the study reach at any time during the growing season. On South Boulder Creek, seed density showed little recovery early in the season but seed density recovered to upstream levels within 3 km below the dam during the fall months. Species richness, which had a curvilinear relationship to seed density on the North Fork ($r^2 = 0.46$, $p < 0.05$) and on South Boulder Creek ($r^2 = 0.87$, $p < 0.05$), showed similar patterns. On the North Fork species richness recovered to higher than upstream values early in the season, but showed no recovery later in the season. Richness of the South Boulder Creek water-dispersed seeds showed no recovery in the middle of the growing season, but rapid recovery within about 3 km early and late in the season (Figure 3.4).

Lower concordance between local and reach-scale standing vegetation and hydrochoric seeds sampled upstream from reservoirs suggests that hydrochoric seeds may have been supplied from sources further upstream in the watershed, providing indirect support for Hypothesis 3.2; the 'river collector hypothesis' of Nilsson *et al.* (1994). This also suggests that future studies of hydrochory should focus on larger stream segments, so that an understanding of the basin-scale controls on the hydrochoric seed bank may be developed.

Concordance analysis suggested that water-transported seeds were related more strongly to local- and reach-scale vegetation below impoundments when compared to Kendall's τ values above impoundments. On both streams the relationship between standing vegetation and hydrochoric seed composition was strongest immediately below reservoirs, suggesting that hydrochoric seeds are derived primarily from local seed sources below impoundments. This suggests that dams may fragment streams in terms of the longitudinal interactions between populations via seed dispersal (Nilsson and Jansson 1995). This is likely not as important for early dispersing, colonizing species such as *Salix* spp. which may have the ability to disperse seeds over long distances by wind, as well as dispersing seeds by water during periods of high flow when dam spillways are operational. Spillways may allow the passage of seeds transported on the water surface unless they become trapped along shorelines within the reservoir. Dam-caused fragmentation may be a more important factor for later successional species that lack wind dispersal and disperse later in the growing season after spillways are no longer flowing.

Analyses of the distributions of standing vegetation in relation to a variety of life-history traits indicated that hydrochoric species comprise from 12 to 25 percent of the species occurring along these two mountain stream channels. Wind- and water-dispersed species comprised from 41-55% of the riparian floras, providing support for Hypothesis 3.3. Hydrochoric species were from 4 to 6% more abundant below reservoirs than above them. Exlpanations for these patterns are unclear. Distinctions in the spatial distributions of hydrochoric and zoochoric species along mountain streams indicated that the probability of hydrochory increases near the active stream channel and that animal-dispersed species are more probable at greater distances from the active channel. Probability curves indicate that the probability of hydrochory increases steeply within about 5 m of the active stream channel (Figure 3.7). Growth in these locations is beneficial in that these areas closer to the stream are flooded more frequently than areas further from the stream, providing these species with access to the stream for dispersal of propagules. It is also likely that hydrochores occur within the frequently flooded zones along stream margins because their seeds were delivered there by water. Although hydrochores did occur closer to the stream channel downstream from the reservoir on South Boulder Creek on average, they occurred slightly further from the channel downstream of Halligan Dam on the North Fork (Table 3.9). It is reasonable to hypothesize that because of decreased frequency of flooding below reservoirs, it would be beneficial for hydrochoric species to grow in closer proximity to the channel, but there was little evidence to support this (Hypothesis 3.3). Conversely, because of decreased peak flows downstream of reservoirs, hydrochores are unable to be transported as far from the low-flow channel. Therefore hydrochores may be confined to areas nearer the active channel by dispersal rather than habitat limitations. Johansson *et al.* (1996) found that species producing ‘long-floating’ seeds were more common in river bank vegetation (located near the active channel) than short-floating species along ten streams in Sweden.

In theory, such a pattern of hydrochores occurring closer to the stream channel would become more evident with increasing time elapsed since impoundment along dammed streams. Although Halligan Dam on the North Fork is nearly half a century older than Gross Dam on South Boulder Creek, the logistic models do not suggest that hydrochoric species occur significantly closer to the channel below the older dam than they do below the more recently installed dam. The probability curves for animal-dispersed species do however indicate that animal-dispersed species have higher probabilities of occurring closer to the channel below the dam on the North Fork than along undammed reaches of the North Fork or on South Boulder Creek.

Animal-dispersed species with heavier seeds are often associated with later successional communities. Heavy-seeded animal-dispersed species have been shown to be of little importance in early and mid-successional riparian forests (Weaver 1960, Johnson *et al.* 1976). In a morphometric study of 58 temperate woody species, Cornelissen (1999) demonstrated that smaller, often wind-dispersed seeds are typically produced by small statured, fast-growing, shade-intolerant species typical of primary successional habitats, whereas species that produce larger seeds are typically slower growing, shade tolerant, later successional species. Shade tolerance was also associated with larger seeds in a study of temperate woody species (Hewitt 1998), and shade intolerance with smaller, more readily dispersed seeds. As a consequence, heavy seeded species often do not occur in close proximity to stream channels where disturbance is more intense and more frequent (Weaver 1960, Johnson *et al.* 1976, White 1979, Hupp 1992). Once disturbance is removed or reduced following regulation, heavier seeded species may slowly invade stream margins, displacing shade intolerant species. This pattern is evident in comparing the distributions of zoochoric species upstream and downstream of Halligan Dam on the North Fork (Figure 3.7).

Seed exclosure experiments did not provide support for the hypothesis that water dispersal enhances potential species richness of a site (Hypothesis 3.4). Because vegetative reproduction was the primary means of recolonization of newly disturbed sites, the relative roles of wind and water dispersal remain unclear. It is likely that colonization of sites by vegetative means is important during low magnitude and relatively frequent flooding. However, high magnitude, less frequent disturbances are likely to completely remove fine-grained deposits during the rising limb of the hydrograph, resulting in the removal of roots and vegetative plant parts as well. The re-formation of these fine-grained deposits during the falling limb of the hydrograph (Cluer 1997) would provide suitable sites for primary colonization following large floods. Primary succession of these sites would, by definition, then require the influx of propagules from elsewhere. Under such circumstances, a similar experiment to the one performed here would be likely to yield more definitive results. Alternatively, the complete removal of roots and rhizome pieces through complete excavation or application of herbicides would provide the necessary conditions to develop a better understanding of the relative importance of wind and water dispersal in colonizing such sites.

Interruptions in the mechanisms of water dispersal through modification of flows during portions of the season when seeds of these species are being dispersed, limits the spectrum of possible sources of propagules to a site to the standing vegetation, aerial seed rain, and the seed bank (Hughes and Cass 1997). Modifying the timing of habitat availability may result in the establishment of entirely different communities on a site depending on what species are available when the site is exposed (Diamond 1975, McBride and Strahan 1984). The assumption that patterns of establishment of species along stream margins may be adequately determined by the physical characteristics of a site has been referred to as the assumption of 'ubiquitous dispersal' (Hanson *et al.* 1990). Under this assumption it is assumed that if a site provides suitable habitat conditions for the germination and establishment of a certain species, then the species will occur there. But if the site is unavailable at the time when this species is dispersing, if another species arrives first, or if the distance between the suitable site and parent exceeds the potential dispersal distance of the seeds, this assumption becomes invalid. The inclusion of information regarding the method of dispersal of individual species and the timing of dispersal, as well as information regarding the types of flows that deposit seeds most effectively, may lead to a refinement of our ability to develop ecologically sound flow strategies below reservoirs that enhance the continued regeneration of desirable riparian species.

CHAPTER 4

CONCLUSIONS

The ecological and evolutionary importance of water-dispersal to riparian and aquatic plants has been demonstrated in studies on a variety of streams throughout the world. In tropical (Kalliola *et al.* 1991, Kubitzki and Ziburski 1994), humid (Schneider and Sharitz 1988, Edwards *et al.* 1994), sub-humid (Thébaud and Debussche 1991), semi-arid (Waser *et al.* 1982), temperate (Staniforth and Cavers 1976), and boreal (Johansson and Nilsson 1993, Nilsson and Jansson 1995) streams, hydrochory has been shown to be the primary means of dispersal for most aquatic and many riparian species. Although flowing water is a unidirectional vector (i.e., downstream) for seed dispersal, rivers provide an important means for long-distance, perhaps 'directed dispersal', for certain species of riparian plants (Staniforth and Cavers 1976, Schneider and Sharitz 1988, Thébaud and Debussche 1991, Johansson and Nilsson 1993). The current study has demonstrated that reservoirs influence both the transport and deposition phases of hydrochory through: (1) modifying hydrologic processes which influence the availability, suitability, and transience of physical habitat along stream margins, (2) influencing the mechanics of seed delivery to suitable habitats, and (3) serving as a physical barrier to the downstream flow of seeds.

In contrast to the hypothesis that seeds would be retained and deposited in higher numbers under natural snowmelt hydrologic regimes than under each of three modified hydrologic regimes (Hypothesis 2.1), the highest concentrations of seeds were deposited under stepped flow regimes. However, descending flows did result in significantly higher seed deposition than either of the other two modified hydrologic regimes (ascending and ramped flows). This not only provides partial support for Hypothesis 2.1, but provides an interesting contrast between 'natural' flow regimes and stepped flows observed below reservoirs. Intermittent periods of steady flow during stepped flow regimes enable flow separation cells to become well formed and relatively stable. These cells of recirculation become important hydraulic features, detaining, recirculating, and ultimately depositing hydrochoric seeds. Intermittent periods of rapid drawdown (vertical steps in the stepped regime) facilitate the deposition of recirculating seeds along shorelines. Under these conditions seeds are deposited in higher concentrations than under gradually descending flows modeled after snowmelt hydrographs. Under unsteady flows recirculation cells do not become fully developed and areas such as flow expansions below channel constrictions become more important depositional sites for hydrochoric seeds.

With the exception of the ramped flow regime, seeds were deposited non-randomly along river margins under both regulated and snowmelt flow regimes, providing strong evidence in support of Hypothesis 2.2. Seeds were deposited in significantly higher numbers in areas of strong recirculation such as in eddies, below point bars, and in slackwaters adjacent to downstream jets. This non-random pattern of dispersal provides an example of directed dispersal of seeds to sites with conditions that increase the probability of germination and long-term survival of seedlings. Zones of recirculation are characterized by finer grained substrates with higher water-holding capacities, higher nutrient status, and are areas that are protected from scouring flows.

Field investigations of the patterns of seed dispersal in relation to dispersal phenology, flow, and plant community composition above and below mountain reservoirs provided support for Hypothesis 3.1; that the number of hydrochoric seeds in the water column would be diminished below dams. Reservoirs were shown to serve as effective seed-traps modifying not only the number of hydrochoric seeds moving downstream, but also species richness and species composition of hydrochoric seeds. The composition of water-dispersed seeds was most highly associated (Kendall's τ) with local species composition immediately below reservoirs, providing support for Hypothesis 3.2. Low values of τ at cross-sections upstream from reservoirs may suggest that hydrochoric seeds are derived from local-, reach-, and basin-scale sources of seeds, but are derived primarily from local sources immediately below impoundments.

Wind- and water-dispersed seeds comprised a large proportion of the riparian flora (41 to 55 percent) above and below dams, providing support for Hypothesis 3.3. Whereas hydrochores were more abundant closer (<3 m) to the active channel, and zoochores typically occurred at distances further (>5 m) from the channel, the distributions of hydrochores and zoochores as a function of distance from the active channel were not significantly different above and below reservoirs.

Experiments designed to determine the relative importance of wind- and water-dispersed seeds in colonizing mechanically disturbed sites did not provide strong support for Hypothesis 3.4. Whereas species richness in standing vegetation was significantly higher on eddy deposits and islands when compared to pool margins prior to application of treatments, richness was neither significantly different between fluvial features or between plots receiving only wind- or only water-dispersed seeds following exclosure treatments. Clonal rather than sexual reproduction was the most important means of recolonization in these experimental plots; however, mechanical disturbance did provide opportunities for a single spore-bearing species (*Equisetum arvense*) to become established through a combination of wind- and water-dispersal.

As most hydrochoric seeds are deposited in eddys, on bars, pool margins, and microtopographic features along river margins during the descending limb of the hydrograph (Nilsson *et al.* 1991b), the shape of the hydrograph, the timing of peak flows, and the magnitude of flows, the number of peaks, and the geomorphic setting are all important factors for hydrochoric species. Interruptions in these key factors may lead to long-term shifts in community composition and vegetation structure in riparian ecosystems (Nilsson *et al.* 1991a, Johansson and Nilsson 1993, Nilsson *et al.* 1994, Nilsson *et al.* 1997).

This study has taken a quantitative approach to the study of hydrochory in an attempt to test several hypotheses concerning hydrochory and to provide further insight for future studies. Whereas many hypotheses have been developed throughout the last decade concerning the role of hydrochory in structuring plant communities along river corridors, few studies have considered more than a single species. Furthermore, no study to date has examined the effects of river regulation on hydrochory, or the fragmenting effects of dams on upstream to downstream flow of seeds. Future studies should examine hydrochory from a multi-species perspective, consider examining hydrochory at multiple scales from that of a fluvial feature to that of the watershed, and experiments should be designed that provide documentation of the relative roles of wind, water, and riparian seed banks in colonizing river margins.

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APPENDIX

LIST OF VASCULAR PLANT SPECIES SAMPLED ON THE NORTH FORK OF THE CACHE LA POUDRE RIVER AND SOUTH BOULDER CREEK: LIFE-HISTORY TRAITS AND PERCENT COVER AND FREQUENCY ABOVE AND BELOW DAMS.

Appendix Table. List of vascular plant species sampled on the North Fork Cache La Poudre River (NF) and South Boulder Creek (SBC). Species are arranged by family, which is indicated by the first four letters of the family name. Under life-history trait O is origin (native or exotic), L is longevity (annual, biennial, or perennial), LF is life-form (forb, graminoid, shrub, or tree), and D is dispersal mechanism (anemochory, barochory, hydrochory, or zoochory). Upstream and downstream indicate vegetation sampling location in relation to dams. %Cov and Freq are total percent cover (sum of cover in all plots) and frequency (plots species in which specie occurs divided by total number of plots).

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
		O	L	LF	D	%Cov	Freq	%Cov	Freq	%Cov	Freq	%Cov	Freq
Acer	*Acer glabrum* Torrey Mountain maple	n	p	s	a	15.5	0.03	0.0	0.00	330.0	0.12	62.5	0.01
Alis	*Paronychia jamesii* Torrey & Gray Nailwort	n	p	f	b	0.0	0.04	0.0	0.00	0.0	0.00	0.0	0.00
Alis	*Cerastium fontanum* Baumgartner Common mouse ear	a	a	f	b	0.0	0.01	0.0	0.00	1.0	0.02	0.0	0.01
Alis	*Cerastium nutans* Rafinesque var. brachypodium Engelmann Mouse ear	n	a	f	b	0.0	0.00	0.0	0.00	0.5	0.01	0.0	0.00
Anac	*Rhus aromatica* Aitin subsp. trilobata (Nuttall) Weber Skunkbrush	n	p	s	z	20.0	0.04	0.0	0.01	0.0	0.00	0.0	0.00
Anac	*Toxicodendron rydbergii* (Small) Greene	n	p	s	z	15.5	0.03	0.0	0.00	0.0	0.00	2.5	0.04
Apia	*Cicuta douglasii* (de Candolle) Coulter & Rose Water hemlock	n	p	f	h	0.0	0.01	7.6	0.12	0.0	0.00	0.0	0.00
Apia	*Heracleum sphondylium* L. subsp. *montanum* (Schleicher) Briquet	n	p	f	a	0.5	0.03	57.5	0.06	25.0	0.07	253.5	0.21
Apia	*Osmorhiza depauperata* Philippi	n	p	f	?	0.0	0.00	0.0	0.00	0.0	0.00	17.5	0.04
Apoc	*Apocynum androsaemifolium* L. Spreading dogbane	n	p	f	a	67.5	0.04	280.5	0.08	81.5	0.10	0.0	0.00
Apoc	*Apocynum cannabinum* L. Indian hemp	a	p	f	a	0.0	0.00	0.0	0.00	15.0	0.01	33.5	0.13
Aspa	*Asparagus officinalis* L. Asparagus	a	p	f	b	0.0	0.00	0.0	0.00	0.0	0.00	0.5	0.01
Aste	*Achillia lanulosa* Nutall Yarrow	n	p	f	a	1.0	0.07	18.0	0.04	22.5	0.14	16.0	0.16
Aste	*Ambrosia tomentosa* Nutall Ragweed	n	p	f	a	0.0	0.01	2.5	0.01	0.0	0.00	0.0	0.00
Aste	*Ambrosia trifida* L. Giant ragweed	a	a	f	a	0.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Aste	*Antennaria parviflora* Nutall Pussytoes	n	p	f	a	0.0	0.00	0.0	0.00	1.0	0.02	0.0	0.00
Aste	*Arctium minus* (Hill) Bernhardi Burdock	a	a	f	z	0.0	0.00	0.5	0.01	0.0	0.00	0.0	0.00
Aste	*Artemesia biennis* Willdenow Biennial sage	a	b	f	a	1.0	0.03	0.0	0.00	0.0	0.00	0.0	0.01
Aste	*Artemesia frigida* Willdenow Silver sage	n	p	f	a	3.0	0.07	3.0	0.03	0.0	0.01	2.5	0.01
Aste	*Artemesia ludoviciana* Nuttall	n	p	f	a	3.5	0.05	0.0	0.02	7.5	0.18	1.5	0.06
Aste	*Aster lanceolatus* Willdenow subsp. *hesperius* (Gray) Semple & Chmielewski	n	p	f	a	0.0	0.05	54.1	0.10	0.5	0.04	0.0	0.00
Aste	*Breea arvensis* (l.) Lessing Canada thistle	a	p	f	a	0.0	0.00	120.5	0.07	0.0	0.00	0.0	0.00
Aste	*Cirsium flodmanii* (Rydberg) Arthur Thistle	n	p	f	a	0.0	0.01	2.5	0.01	0.0	0.00	0.0	0.00
Aste	*Cirsium vulgare* (Savi) Tenore Bull thistle	a	b	f	a	0.0	0.00	0.0	0.00	0.0	0.00	17.5	0.04
Aste	*Cirsum* spp.	–	–	–	–	15.5	0.07	134.1	0.23	6.1	0.11	0.0	0.01
Aste	*Conyza canadensis* (L.)	a	a	f	a	1.0	0.03	0.5	0.03	0.0	0.00	0.0	0.00

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
	Cronquist Horseweed												
Aste	*Erigeron coulteri* Porter	n	p	f	a	0.0	0.00	0.0	0.00	0.0	0.00	6.0	0.09
Aste	*Erigeron pumilis* Nutall	n	p	f	a	0.0	0.03	0.0	0.01	0.5	0.02	0.0	0.00
Aste	*Gaillardia aristata* Pursh blanketflower	n	p	f	b	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.01
Aste	*Gnaphalium* spp.	–	–	–	–	0.0	0.00	0.0	0.00	0.0	0.01	0.0	0.00
Aste	*Grindelia squarrosa* (Pursh) Dunal Gumweed	a	b	f	a	0.0	0.01	0.0	0.00	0.0	0.00	2.5	0.01
Aste	*Heliomeris multiflora* Nutall	n	p	f	b	0.0	0.00	0.0	0.00	0.0	0.00	15.0	0.01
Aste	*Heterotheca villosa* (Pursh) Shinners	n	p	f	a	56.0	0.11	2.5	0.02	0.0	0.00	4.0	0.06
Aste	*Lactuca serriola* L. Prickly lettuce	a	a	f	a	0.0	0.03	0.0	0.00	0.0	0.00	0.0	0.01
Aste	*Rudbeckia ampla* Nelson Golden-glow	n	p	f	b	0.0	0.00	0.0	0.00	1.0	0.02	20.5	0.06
Aste	*Rudbeckia hiruta* L. Black-eyed Susan	n	p	f	b	0.5	0.04	0.0	0.00	0.0	0.01	0.0	0.00
Aste	*Solidago canadensis* L. Goldenrod	n	p	f	a	0.0	0.00	0.0	0.00	0.5	0.02	93.5	0.09
Aste	*Solidago gigantea* Aiton Goldenrod	n	p	f	a	2.5	0.01	20.5	0.04	0.0	0.00	10.0	0.07
Aste	*Solidago missouriensis* Nuttall Goldenrod	n	p	f	a	0.5	0.01	0.0	0.01	0.0	0.00	2.5	0.01
Aste	*Solidago nana* Nutt. Goldenrod	n	p	f	a	0.0	0.00	0.0	0.00	0.5	0.01	0.0	0.00
Aste	*Taraxacum officinale* G.H. Weber Common dandelion	a	p	f	a	0.0	0.01	3.0	0.03	0.5	0.05	0.0	0.00
Aste	*Tragopogon dubius* Scopoli subsp. *major* (Jacquin) Vollmann Oysterplant	a	b	f	a	0.0	0.00	0.0	0.01	0.0	0.00	0.0	0.00
Aste	*Virgulus falcatus* (Lindley) Reveal & Keener Aster	n	p	f	a	0.0	0.00	0.5	0.02	0.0	0.00	0.0	0.00
Berb	*Mahonia repens* (Lindley) Don Oregon-Grape	n	p	s	z	0.0	0.00	0.0	0.00	0.0	0.00	45.5	0.06
Betu	*Alnus incana* (L.) subsp. *tenuifolia* (Nutall) Breitung Alder	–	–	–	–	0.0	0.00	0.0	0.02	5.5	0.07	155.5	0.07
Betu	*Alnus incana* (L.) subsp. *tenuifolia* (Nutall) Breitung Alder sapling-adult	n	p	s	h	411.0	0.17	1775.5	0.42	107.5	0.05	325.0	0.06
Betu	*Betula fontinalis* Sargent River birch seedling	–	–	–	–	0.0	0.01	0.0	0.00	88.5	0.04	0.0	0.00
Betu	*Betula fontinalis* Sargent River birch sapling-adult	n	p	s	a	485.0	0.13	275.0	0.09	1126.0	0.23	212.5	0.06
Betu	*Corylus cornuta* Marshall Hazelnut	n	p	s	z	0.0	0.00	0.0	0.00	0.0	0.00	175.0	0.03
Bora	*Cynoglossum officionale* L. Hound's tongue	a	b	f	z	0.0	0.00	0.0	0.00	0.0	0.00	11.5	0.10
Bora	*Hackelia floribunda* (Lehmann) Johnston stickseed	n	b	f	z	0.0	0.00	0.5	0.01	0.0	0.00	0.0	0.00
Bora	*Lappula squarrosa*(Retzius) Dumortier Stickseed	a	a	f	z	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Bora	*Mertensia ciliata* (James) G. Don	n	p	f	b	0.0	0.00	0.0	0.00	1.0	0.04	2.5	0.01
Bras	*Camelina microcarpa* Andrzejowski False flax	a	a	f	b	0.0	0.00	0.0	0.01	0.0	0.00	0.0	0.00
Bras	*Cardamine cordifolia* Gray Bittercress	n	a	f	b	0.0	0.00	0.0	0.00	15.5	0.02	0.0	0.00
Bras	*Descurania sophia* (L.) Webb	a	a	f	b	0.5	0.01	0.0	0.01	0.5	0.04	0.0	0.00
Bras	*Hesperis matronalis* L. Rocket	a	a	f	b	0.0	0.00	2.5	0.01	0.0	0.00	15.0	0.01
Bras	*Lesquerella montana* (Gray) Watson Bladderpod	n	a	f	b	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Bras	*Sisymbrium loeselii* L. Jim Hill mustard	a	a	f	b	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
Bras	*Descurania* spp.	–	–	–	–	0.0	0.00	0.0	0.00	0.5	0.01	0.0	0.00
Cact	*Opuntia fragilis* (Nuttall) Haworth Prickly pear	n	p	f	z	0.5	0.03	0.0	0.00	0.0	0.00	0.0	0.00
Camp	*Campanula rotundifolia* L. Common harebell	n	p	f	b	0.0	0.00	0.0	0.00	1.5	0.08	0.5	0.06
Cann	*Humulus lupulus* L. *americanus* (Nuttall) Love and Love Hops	n	p	f	b	0.0	0.00	17.5	0.02	0.0	0.00	0.0	0.00
Capp	*Cleome serrulata* Pursh Rocky mountain bee plant	n	a	f	b	0.0	0.00	0.5	0.01	0.0	0.00	0.0	0.00
Capr	*Symphoriocarpos occidentalis* Hooker Snowberry	n	p	s	z	101.0	0.12	160.5	0.07	17.5	0.02	7.5	0.06
Capr	*Viburnum edule* (Michaux) Rafinesque Bush-cranberry	n	p	s	z	0.0	0.00	0.0	0.00	16.0	0.06	0.0	0.00
Capr	*Linnea borealis* L. Twinflower	n	p	s	z	0.0	0.00	0.0	0.00	15.0	0.01	0.0	0.00
Chen	*Chenopodium berlandieri* Moquin	n	a	f	b	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Chen	*Chenopodium foliosum* (Moench) Ascherson	a	a	f	b	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Chen	*Chenopodium* spp.	–	–	–	–	0.0	0.01	0.0	0.01	0.0	0.00	0.0	0.00
Conv	*Maianthemum amplexicaule* (Nutall) Weber False Solomon's seal	n	p	f	z	0.0	0.00	0.0	0.00	9.0	0.08	0.0	0.00
Conv	*Maianthemum stellatum* (L.) Link False Solomon's seal	n	p	f	z	0.0	0.00	0.5	0.01	3.0	0.04	15.5	0.07
Conv	*Convolvulus arvensis* L. Creeping Jenny	a	p	f	b	0.0	0.00	0.5	0.01	0.0	0.00	0.0	0.00
Corn	*Swida sericea* (L.) Holub Red osier seedling	–	–	–	–	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.03
Corn	Swida sericea (L.) Holub Red osier sapling-adult	n	p	s	z	62.5	0.01	37.5	0.01	37.5	0.01	205.0	0.07
Cupr	*Juniperus communis* L. subsp *alpina* (Smith) Celakovsky Juniper	n	p	s	z	0.0	0.00	0.0	0.00	58.0	0.07	117.5	0.07
Cupr	*Sabina Scopulorum* (Sargent) Rydberg Rocky Mountain Juniper seedling	n	p	t	z	0.0	0.00	0.0	0.00	0.0	0.00	2.5	0.01
Cupr	Sabina Scopulorum (Sargent) Rydberg Rocky Mountain Juniper sapling-adult	n	p	t	z	0.0	0.00	176.5	0.13	0.0	0.00	53.5	0.06
Cype	*Carex athrostachya* Olney Sedge	n	p	g	b	1.5	0.05	0.0	0.00	0.0	0.00	0.0	0.00
Cype	*Carex emoryi* Dewey Sedge	n	p	g	h	0.0	0.00	963.5	0.18	0.0	0.00	0.0	0.00
Cype	*Carex lanuginosa* Michaux Woolly sedge	n	p	g	h	192.5	0.21	145.0	0.05	0.0	0.00	5.0	0.03
Cype	*Carex nebrascensis* Dewey Nebraska sedge	n	p	g	h	17.5	0.04	219.0	0.09	0.0	0.00	107.5	0.07
Cype	*Carex pensylvanica* Lamark subsp. *heliophila* (Mackenzie) Weber Sedge	n	p	g	b	0.0	0.00	0.0	0.00	21.0	0.08	18.0	0.07
Cype	*Carex scoparia* Schkuhr Sedge	n	p	g	h	0.0	0.00	62.5	0.01	0.0	0.00	0.0	0.00
Cype	*Carex* spp.	–	–	–	–	2.5	0.01	190.0	0.06	1.5	0.07	57.5	0.06
Cype	*Carex sprengelii* Dewey	n	p	g	h	15.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Cype	*Carex utriculata* Boott Sedge	n	p	g	h	0.0	0.00	37.5	0.01	2.5	0.01	65.0	0.03
Cype	*Carex vesicaria* L. Sedge	a	p	g	h	0.0	0.00	0.5	0.02	0.0	0.00	0.0	0.00
Cype	*Eleocharis palustris* (L.) Roemer & Schultes Spikerush	n	p	g	h	493.0	0.28	512.0	0.19	0.0	0.00	0.0	0.00
Cype	*Schoenoplectus lacustris* (L.) Palla subsp. acutus (Muhlenberg) Love & Love Three-square	n	p	g	h	0.0	0.00	0.0	0.01	0.0	0.00	0.0	0.00
Cype	*Scirpus microcarpus* Presl Bulrush	n	p	g	h	185.5	0.17	65.0	0.03	0.0	0.00	0.0	0.00

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
Elea	*Shepherdia canadensis* (L.) Nutall Buffaloberry	n	p	t	z	0.0	0.00	0.0	0.00	225.0	0.10	0.0	0.00
Equi	*Equisetum arvense* L. Field horsetail	n	p	f	h	134.1	0.41	70.0	0.24	365.1	0.31	271.5	0.37
Equi	*Hippochaete hyemalis* (L.) Bruhin subsp. *affinis* (A. Braun) Weber	n	p	f	a	3.0	0.04	38.0	0.06	0.0	0.00	6.0	0.06
Equi	*Hippochaete laevigata* (A. Braun) Farwell Scouring rush	n	p	f	a	0.0	0.00	0.0	0.00	0.0	0.01	0.0	0.00
Eric	*Arctostaphylos uva-ursi* (L.) Sprengel Kinnikinnick	n	p	s	z	0.0	0.00	0.0	0.00	0.0	0.00	17.5	0.04
Euph	*Tithymalus uralensis* (Fischer) Prokhanov Leafy spurge	a	p	f	b	3.0	0.05	0.0	0.00	0.0	0.00	0.0	0.00
Faba	*Glycyrrhiza lepidota* Pursh Wild licorice	n	p	f	z	143.0	0.08	37.5	0.01	0.0	0.00	0.0	0.00
Faba	*Lupine argenteus* Pursh. subsp. *ingratus* (Greene) Harmon	n	p	f	b	0.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Faba	*Medicago lupulina* L. Black medic	a	a	f	b	3.0	0.04	2.5	0.02	0.0	0.00	0.0	0.00
Faba	*Melilotus officionale* (L.) Pallas Sweetclover	a	p	f	b	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Faba	*Thermopsis divaricarpa* Nelson Golden Banner	n	b	f	b	9.0	0.09	3.5	0.04	0.0	0.00	0.0	0.00
Faba	*Trifolium pratense* L. Red clover	a	p	f	b	6.5	0.08	0.0	0.00	0.0	0.00	0.0	0.01
Faba	*Trifolium repens* L. Red clover	a	p	f	b	0.0	0.00	0.0	0.00	2.5	0.02	0.0	0.00
Gera	*Geranium caespitosum* James Geranium	n	p	f	b	0.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Gera	*Geranium richardsonii* Fischer & Trautvetter Geranium	n	p	f	b	3.0	0.07	3.0	0.03	1.5	0.04	11.5	0.19
Gros	*Ribers americanum* Miller Currant	n	p	s	z	0.0	0.00	0.0	0.00	0.5	0.01	0.0	0.00
Gros	*Ribes aureum* Pursh Golden Currant	n	p	s	z	1.0	0.04	3.0	0.03	0.0	0.00	0.0	0.00
Gros	*Ribes cereum* Douglas Gooseberry	n	p	s	z	0.0	0.00	18.0	0.03	0.0	0.00	58.0	0.07
Gros	*Ribes divaricatum* Douglas Gooseberry	n	p	s	z	3.0	0.03	5.5	0.03	0.0	0.00	0.0	0.00
Gros	*Ribes inerme* Rydberg Currant	n	p	s	z	0.0	0.01	20.5	0.10	3.5	0.04	17.5	0.03
Gros	*Ribes montigenum* McClatchie Gooseberry	n	p	s	z	0.5	0.03	5.0	0.03	38.5	0.08	38.0	0.03
Hell	*Delphinium nuttallianum* Pritzel Larkspur	n	p	f	b	0.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Hell	*Aconitum columbianum* Nutall Monkshood	n	p	f	b	0.0	0.00	0.0	0.00	1.5	0.04	0.0	0.00
Hell	*Actaea rubra* (Aiton) Willdenow subsp. arguta (Nutall) Hulten Baneberry	n	p	f	z	0.0	0.00	0.0	0.00	22.0	0.08	3.5	0.04
Hydr	*Jamesia americana* Torrey & Gray Waxflower	n	p	s	b	0.0	0.00	2.5	0.01	86.5	0.12	118.0	0.07
Hydr	*Hydrophyllum fendleri* (Gray) Heller Waterleaf	n	p	f	b	0.0	0.00	0.0	0.00	0.0	0.01	0.0	0.00
Junc	*Juncus arcticus* Willdenow subsp. *ater* (Rydberg) Hulte'n Rush	n	p	g	h	40.5	0.15	20.0	0.05	0.0	0.00	152.5	0.06
Junc	*Juncus bufonius* L. Toad rush	a	a	g	h	0.0	0.00	0.0	0.01	0.0	0.00	0.0	0.00
Junc	*Juncus confusus* Coville Rush	n	p	g	h	63.0	0.04	0.0	0.00	0.0	0.00	2.5	0.01
Junc	*Juncus nodosus* L. Rush	n	p	g	h	15.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Junc	*Juncus saximontanus* Nelson Rush	n	p	g	h	0.0	0.00	0.0	0.00	0.0	0.00	12.5	0.07
Junc	*Juncus tenuis* Willdenow Rush	n	p	g	h	19.0	0.08	3.0	0.02	37.5	0.01	2.5	0.03
Junc	*Luzula parviflora* (Ehrhart) Desvaux Woodrush	n	p	g	a	0.0	0.00	0.0	0.00	0.0	0.00	2.5	0.01
Lami	*Mentha arvensis* L. Fieldmint	n	p	f	h	53.5	0.19	387.6	0.52	3.0	0.02	15.0	0.01

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
Lami	*Monarda fistulosa* L. var. *menthifolia* (Graham) Fernald	n	p	f	b	0.0	0.00	2.5	0.01	0.0	0.00	1.0	0.03
Lami	*Scutellaria galericulata* L. subsp. *epilobifolia* (Hamilton) Jordal	n	p	f	h	20.5	0.07	26.5	0.10	0.0	0.00	0.0	0.01
Lami	*Stachys palustris* L. subsp. *pilosa* (Nuttall) Epling Hedge-nettle	n	p	f	h	2.5	0.01	7.0	0.09	0.0	0.00	0.0	0.00
Onag	*Chamerion denielsii* (Daniels) D. Love Fireweed	n	p	f	a	0.0	0.00	0.0	0.00	131.5	0.23	15.0	0.03
Onag	*Epilobium brachycarpum* Presl. Willowherb	n	a	f	a	0.0	0.00	0.5	0.01	0.0	0.00	0.0	0.00
Onag	*Epilobium ciliatum* Rafinesque Willowherb	n	p	f	a	0.5	0.04	6.5	0.06	3.5	0.08	43.0	0.07
Onag	*Epilobium glaberrimum* Barbey var. *fastigiatum* (Nutt.) Trel. ex Jeps.	?	p	f	a	0.0	0.00	0.5	0.01	0.0	0.00	0.0	0.00
Onag	*Oenothera coronopifolia* Evening-primrose	n	p	f	a	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Onag	*Oenothera villosa* Thunberg Evening-primrose	n	b	f	a	0.0	0.00	1.0	0.02	0.5	0.02	0.0	0.00
Pina	*Picea engelmannii* (Parry) Engelmann Engelmann Spruce seedling	–	–	–	–	0.0	0.00	0.0	0.00	2.5	0.04	7.5	0.06
Pina	*Picea engelmannii* (Parry) Engelmann Engelmann Spruce sapling-adult	n	p	t	a	0.0	0.00	0.0	0.00	147.5	0.07	62.5	0.01
Pina	*Picea pungens* Engelmann Colorado Blue Spruce sapling adult	n	p	t	a	0.0	0.00	0.0	0.00	116.0	0.07	50.0	0.09
Pina	*Pinus ponderosa* Douglas subsp. *scopulorum* (Watson) Weber Ponderosa pine	–	–	–	–	0.0	0.00	0.0	0.00	15.0	0.04	405.5	0.16
Pina	*Pinus ponderosa* Douglas subsp. *scopulorum* (Watson) Weber Ponderosa pine	n	p	t	a	0.0	0.01	62.5	0.01	330.0	0.07	350.0	0.09
Pina	*Pseudotsuga menziesii* (Mirbel) Franco Douglas-fir seedling	n	p	t	a	0.0	0.00	0.0	0.00	108.0	0.08	139.5	0.17
Pina	*Pseudotsuga menziesii* (Mirbel) Franco Douglas-fir sapling-adult	n	p	t	a	0.0	0.00	0.0	0.00	93.5	0.08	205.0	0.07
Plan	*Plantago major* L. Common plantain	a	p	f	b	4.0	0.09	11.0	0.09	0.0	0.00	0.0	0.00
Plan	*Plantago patagonica* Jacquin Woolly plaintain	n	a	f	b	0.5	0.04	0.0	0.00	0.0	0.00	0.0	0.00
Poac	*Achnatherum nelsonii* (Scribner) Barkworth Needlegrass	n	p	g	b	0.0	0.00	0.5	0.01	0.0	0.01	55.5	0.06
Poac	*Agrostis exarata* Trinius Bentgrass	a	p	g	h	0.0	0.00	0.0	0.00	0.0	0.00	3.5	0.06
Poac	*Agrostis gigantea* Roth Redtop	a	p	g	h	305.5	0.20	474.6	0.34	2.5	0.01	397.0	0.44
Poac	*Agrostis scabra* Willdenow Bentgrass	n	p	g	h	0.0	0.00	0.0	0.00	0.5	0.01	0.5	0.01
Poac	*Alopecurus aequalis* Sobolewski Foxtail	n	p	g	h	0.0	0.00	1.0	0.02	0.5	0.01	0.0	0.00
Poac	*Anisantha tectorum* (L.) Nevski Cheatgrass	a	a	g	z	169.0	0.13	83.0	0.05	0.0	0.01	0.5	0.01
Poac	*Beckmannia syzigachne* (Steudel) Fernald subsp. *baicalensis* (Kuznetsow) Koyama & Kuwano	n	p	g	h	1.0	0.03	17.5	0.03	0.0	0.00	0.0	0.00
Poac	*Bromopsis canadensis* (Michaux) Holub. Perennial brome	n	p	g	b	0.0	0.00	0.0	0.00	0.0	0.00	0.5	0.01
Poac	*Bromopsis inermis* (Leysser) Holub Smooth brome	a	p	g	b	617.0	0.29	0.0	0.01	0.0	0.00	128.5	0.09

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
Poac	*Bromopsis pubescens* (muhlenberg) Holub. Perennial brome	n	p	g	b	0.0	0.00	0.0	0.00	8.0	0.14	3.5	0.04
Poac	*Bromopsis pumpelliana* (Scribner) Holub. Perennial brome	n	p	g	b	0.0	0.00	0.0	0.00	0.0	0.05	0.0	0.00
Poac	*Bromus japonicus* Thunberg Brome	a	a	g	a	4.0	0.08	2.5	0.01	0.0	0.00	0.0	0.00
Poac	*Bromus racemosus* L. Brome	a	a	g	b	0.0	0.00	0.0	0.00	0.0	0.00	2.5	0.01
Poac	*Bromus* spp.	–	–	–	–	0.0	0.00	0.0	0.00	0.0	0.01	67.5	0.07
Poac	*Calamagrostis canadensis* (Michaux) P. Beauvois Canada reedgrass	n	p	g	a	0.0	0.00	0.0	0.00	108.5	0.11	427.0	0.34
Poac	*Chondrosum hirsutum* (Lagasca) Sweet Grama	n	p	g	a	5.5	0.05	2.5	0.01	0.0	0.00	0.0	0.00
Poac	*Critesion jubatum* (L.) Nevski Foxtail barley	n	p	g	b	0.0	0.00	0.0	0.01	0.0	0.00	0.0	0.00
Poac	*Dactylis glomerata* L. Orchardgrass	a	p	g	b	0.0	0.00	0.0	0.00	0.5	0.02	2.5	0.01
Poac	*Danthonia spicata* (L.) Beauvois Poverty oatgrass	n	a	g	b	0.0	0.00	0.0	0.00	0.0	0.00	3.0	0.06
Poac	*Elymus canadensis* L. Canada wild rye	n	p	g	b	20.5	0.05	7.5	0.03	0.0	0.00	0.0	0.00
Poac	*Elymus longifolius* (Smith) Gould Squirreltail	n	p	g	b	0.0	0.00	0.0	0.00	3.0	0.02	0.0	0.00
Poac	*Elymus* spp.	–	–	–	–	0.0	0.00	0.0	0.00	0.0	0.00	2.5	0.01
Poac	*Elymus trachycaulus* (Link) Gould Wild rye	n	p	g	b	4.5	0.08	8.5	0.06	15.5	0.02	15.0	0.01
Poac	*Elytrigia dasystachya* (hooker) Love & Love	n	p	g	b	0.0	0.00	0.0	0.00	17.5	0.02	0.0	0.00
Poac	*Elytrigia repens* (L.) Nevski Quackgrass	a	p	g	b	0.5	0.04	2.5	0.01	2.5	0.01	0.0	0.00
Poac	*Glyceria grandis* Watson Mannagrass	n	p	g	h	146.5	0.13	344.0	0.18	0.0	0.00	0.0	0.00
Poac	*Glyceria striata* (Lamarck) Hitchcock Mannagrass	n	p	g	h	15.0	0.01	13.5	0.12	0.0	0.02	13.5	0.11
Poac	*Hesperostipa comata* (Trinius & Ruprecht) Barkworth Needle and thread grass	n	p	g	b	3.5	0.04	2.5	0.02	0.0	0.00	0.5	0.01
Poac	*Koeleria macrantha* (Ledebour) Schultes Junegrass	n	p	g	b	0.0	0.00	0.0	0.00	0.0	0.00	17.5	0.03
Poac	*Leymus ambiguous* (Vasey and Scribner) Dewey Wild rye	a	p	g	b	0.5	0.01	0.0	0.00	0.5	0.01	0.0	0.00
Poac	*Leymus cinerius* (Scribner & Merrill) Love Giant wild rye	n	p	g	a	2.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Poac	*Muhlenbergia asperifolia* (Nees & Meyen) Parodi Muhly	n	p	g	b	3.0	0.04	0.0	0.01	0.0	0.00	0.0	0.00
Poac	*Muhlenbergia filiformis* (Thurber) Rydberg Muhly	n	p	g	b	0.0	0.00	0.0	0.00	0.0	0.01	0.0	0.00
Poac	*Nassella viridula* (Trinius) Barkworth Sleepygrass	n	p	g	b	38.0	0.04	15.0	0.01	0.0	0.00	0.0	0.00
Poac	*Oryzopsis asperifolia* Michaux Ricegrass	n	p	g	b	0.0	0.00	0.0	0.00	125.5	0.04	2.5	0.01
Poac	*Oryzopsis micrantha* (Trinius & Ruprecht) Thurber Ricegrass	n	p	g	b	0.0	0.00	0.0	0.00	0.0	0.00	18.0	0.04
Poac	*Pascopyrum smithii* (Rydberg) Love	n	p	g	b	61.0	0.11	40.0	0.03	3.5	0.05	0.0	0.00
Poac	*Phalaroides arundinacea* (L.) Rauschert Canarygrass	a	p	g	h	167.5	0.35	97.5	0.05	40.5	0.05	37.5	0.01
Poac	*Phleum pratense* L. Timothy	a	p	g	b	0.0	0.00	16.0	0.04	10.5	0.08	12.5	0.21
Poac	*Poa compressa* L. Canada bluegrass	n	p	g	b	2.5	0.04	0.0	0.00	0.0	0.00	15.5	0.03
Poac	*Poa nemoralis* L. subsp. *interior* (Rydberg) Butters &	n	p	g	b	0.0	0.00	0.0	0.00	3.0	0.02	0.0	0.00

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
	Abbe.												
Poac	*Poa pratensis* L. Kentucky bluegrass	a	p	g	b	168.0	0.33	492.5	0.34	19.1	0.27	67.0	0.20
Poac	*Poa secunda* Presl.	n	p	g	b	0.0	0.00	0.0	0.00	0.5	0.02	0.0	0.00
Poac	*Poa* spp.	–	–	–	–	5.5	0.05	15.0	0.01	0.0	0.02	0.0	0.00
Poac	*Sporobolus cryptandrus* (Torrey) Gray Dropseed	n	p	g	b	17.5	0.03	0.0	0.00	0.0	0.00	0.5	0.01
Poly	*Persicaria coccinea* (Muhlenberg) Greene Scarlet smartweed	n	p	f	h	0.0	0.00	403.5	0.11	0.0	0.00	0.0	0.00
Poly	*Persicaria lapathifolia* (L.) S. Gray Smartweed	a	p	f	h	0.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Poly	*Rumex* spp.	–	–	–	–	0.0	0.00	0.0	0.01	0.0	0.00	0.0	0.00
Poly	*Rumex aquaticus* L. subsp. *occidentalis* (Watson) Hulten	n	p	f	a	0.5	0.01	15.5	0.06	0.0	0.01	0.0	0.00
Poly	*Rumex crispus* L. Curly dock	a	p	f	a	0.0	0.03	2.5	0.08	0.0	0.00	0.5	0.01
Poly	*Rumex patientia* L.	?	p	f	a	0.0	0.00	2.5	0.01	0.0	0.00	0.0	0.00
Prim	*Dodecatheon pulchellum* (Rafinesque) Merrill	n	p	f	h	0.0	0.00	0.0	0.00	15.5	0.02	66.5	0.16
Prim	*Lysimachia cilliata* L. Loosestrife	n		f	b	17.5	0.03	108.5	0.10	0.0	0.00	0.0	0.00
Pyro	*Orthilla secunda* (L.) House One-sided wintergreen	n	p	f	?	0.0	0.00	0.0	0.00	38.0	0.06	0.0	0.00
Ranu	*Clematis ligusticifolia* Nutall Virgin's bower	n	p	f	a	32.5	0.05	320.5	0.19	0.0	0.00	0.0	0.00
Ranu	*Ranunculus glaberrimus* Hooker var. ellipticus Greene	n	p	f	h	6.0	0.08	0.0	0.00	0.0	0.00	0.0	0.00
Ranu	*Ranunculus macounii* Britton Buttercup	n	p	f	h	0.0	0.00	25.0	0.09	0.0	0.00	0.0	0.00
Ranu	*Ranunculus uncinatus* Don Buttercup	n	p	f	h	0.0	0.00	3.0	0.03	0.0	0.00	0.0	0.00
Ranu	*Thalictrum sparsiflorum* Turczaninov Meadowrue	n	p	f	h	0.0	0.00	0.0	0.00	0.0	0.01	0.0	0.00
Rosa	*Fragaria virginiana* Miller subsp. *glauca* (Watson) Staudt Strawberry	n	p	f	z	0.0	0.00	0.0	0.00	1.6	0.10	0.0	0.00
Rosa	*Geum aleppicum* Jacquin Yellow avens	n	p	f	b	0.0	0.00	0.0	0.00	1.0	0.06	0.0	0.00
Rosa	*Amelanchier alnifolia* Nutall Serviceberry	n	p	f	z	0.0	0.00	0.0	0.00	87.5	0.01	0.0	0.00
Rosa	*Amelanchier utahensis* Koehne Serviceberry	n	p	t	z	0.5	0.01	0.0	0.01	0.0	0.00	0.0	0.00
Rosa	*Cerasus pensylvanica* (L.*f.*) Loiseleur Pin cherry	n	p	t	z	0.0	0.00	0.0	0.00	0.0	0.00	6.0	0.06
Rosa	*Cercocarpus montanus* Rafinesque Mountain mahogany	n	a	f	b	0.0	0.00	0.5	0.01	0.0	0.00	62.5	0.01
Rosa	*Oreobatus deliciosus* James Raspberry	n	p	s	z	0.5	0.01	2.5	0.02	52.5	0.02	31.0	0.07
Rosa	*Padus virginiana* (L.) Miller subsp. *melanocarpa* Nelson (Weber) Choke cherry	n	p	s	z	169.0	0.17	563.0	0.24	82.0	0.11	20.5	0.06
Rosa	*Physocarpus monogynus* (Torrey) Coulter Ninebark	n	p	s	b	0.0	0.00	2.5	0.01	191.5	0.22	173.0	0.11
Rosa	*Physocarpus opulifolius* (L.) Maximovicz Ninebark	n	p	s	b	0.0	0.00	0.5	0.01	32.5	0.04	0.0	0.00
Rosa	*Potentilla norvegica* L. Norway cinquefoil	a	a	f	b	0.0	0.03	2.5	0.02	0.0	0.00	0.0	0.00
Rosa	*Potentilla platensis* Nutall Cinquefoil	n	p	s	b	0.0	0.00	0.0	0.00	1.0	0.02	0.0	0.00
Rosa	*Rosa woodsii* Lindley Woods rose	n	p	s	z	26.5	0.15	53.0	0.16	305.6	0.51	114.0	0.27
Rosa	*Rubus idaeus* L. subsp. *melanolasius* (Dieck) Focke Red raspberry	n		s	z	0.0	0.00	0.0	0.00	45.0	0.10	0.0	0.00

Family	Species	Life-history Trait				NF, upstream		NF, downstream		SBC, upstream		SBC, downstream	
Rubi	*Galium aparine* L. Bedstraw	a	a	f	z	0.0	0.01	0.5	0.01	0.0	0.00	62.5	0.01
Rubi	*Galium septentrionale* Roemer & Schultes Northern bedstraw	n	p	f	z	0.5	0.03	0.0	0.00	4.5	0.13	5.5	0.14
Rubi	*Galium trifidum* L. subsp. *subbiflorum* (Fernald & Wiegand) Puff Bedstraw	n	p	f	z	0.0	0.00	15.0	0.02	2.5	0.01	0.0	0.01
Sali	*Populus angustifolia* James Narrowleaf cottonwood sapling-adult	n	p	t	a	2.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Sali	*Populus deltoides* Marshall subsp. *monilifera* (Aiton) Eckenwalder Plains cottonwood seedling	–	–	–	–	0.0	0.01	0.0	0.01	0.0	0.00	0.0	0.00
Sali	*Populus deltoides* Marshall subsp. *monilifera* (Aiton) Eckenwalder Plains cottonwood sapling-adult	n	p	t	a	0.5	0.03	0.0	0.00	0.0	0.00	0.0	0.00
Sali	*Salix amygdaloides* Andersson Peach-leaved willow	n	p	t	a	3.5	0.05	0.0	0.00	0.0	0.00	0.0	0.00
Sali	*Salix bebbiana* Sargent Bebb willow	n	p	s	a	0.0	0.00	0.0	0.00	9.0	0.10	182.5	0.09
Sali	*Salix drummondiana* Barratt Blue willow	n	p	s	a	0.0	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Sali	*Salix exigua* Nuttall Sandbar willow seedling	–	–	–	–	9.5	0.11	5.0	0.02	0.0	0.00	0.0	0.00
Sali	*Salix exigua* Nuttall Sandbar willow sapling-adult	n	p	s	a	1442.0	0.45	309.5	0.13	0.0	0.00	98.0	0.10
Sali	*Salix geyeriana* Andersson	n	p	s	a	0.0	0.00	0.0	0.00	3.0	0.02	0.0	0.00
Sali	*Salix lucida* Muhlenberg subsp. *caudata* (Nuttall) Argus seedling	–	–	–	–	3.5	0.05	0.0	0.00	0.0	0.00	0.0	0.00
Sali	*Salix lucida* Muhlenberg subsp. *caudata* (Nuttall) Argus sapling-adult	n	p	s	a	38.0	0.13	1.0	0.03	102.5	0.02	0.0	0.00
Sali	*Salix lucida* Muhlenberg subsp. *lasiandra* (Bentham) Argus adult	n	p	s	a	0.0	0.00	0.0	0.00	121.0	0.08	0.0	0.00
Saxi	*Heuchera parvifolia* Nutall Alum root	n	p	f	b	0.0	0.00	0.0	0.00	18.0	0.04	0.0	0.00
Scro	*Limosella aquatica* L. Mudwort	n	a	f	z	0.0	0.00	0.0	0.01	0.0	0.00	0.0	0.00
Scro	*Linaria vulgaris* Miller Toadflax	a		f	a	2.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00
Scro	*Verbascum thapsus* L. Great Mullein	a	b	f	b	22.1	0.23	0.5	0.03	3.0	0.06	2.5	0.03
Scro	*Veronica americana* (Rafinesque) Schweinitz American brooklime	a	a	f	h	0.0	0.00	0.0	0.00	0.0	0.00	87.5	0.01
Scro	*Veronica catenata* Pennell	a	p	f	h	1.5	0.04	15.0	0.03	0.0	0.00	0.0	0.00
Scro	*Veronica perigrina* L. subsp. *xalapensis* (Humboldt, Bonpland, & Kunth) Pennell Purslane speedwell	a	a	f	a	0.0	0.00	0.0	0.04	0.0	0.00	0.0	0.00
Thal	*Thalictrum fendleri* Engelmann Meadow rue	n	p	f	b	117.5	0.05	89.0	0.21	0.0	0.00	18.0	0.04
Ulma	*Celtis reticulata* Torrey Hackberry	n	p	t	z	0.0	0.00	37.5	0.01	0.0	0.00	0.0	0.00
Urti	*Urtica gracilis* Aiton Nettle	n	p	f	a	0.0	0.00	25.0	0.05	37.5	0.02	0.0	0.00
Viol	*Viola rydbergii* Greene Violet	n	p	f	b	2.5	0.01	0.0	0.00	0.0	0.00	2.5	0.01
Viol	*Viola* spp.	–	–	–	–	0.0	0.00	1.1	0.07	0.0	0.00	0.0	0.00
Zann	*Zannichellia palustris* L. Horned pondweed	n	p	f	h	37.5	0.01	150.0	0.07	0.0	0.00	0.0	0.00