

**MULTI-SCALE IMPACTS OF INVASIVE PLANTS ON WATERSHED HYDROLOGY
AND RIPARIAN ECOLOGY—A SYNTHESIS**

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EXECUTIVE SUMMARY

Water resources in western North America have become increasingly limited due to landscape and river alteration, increased consumption and water pollution. Invasive species have the potential to strongly impact energy, nutrient, and hydrologic cycles in uplands and riparian areas, both negatively and positively. To date, research has addressed invasion mechanisms and chemical, biological and mechanical management for specific species. However, impacts on ecological services and process-based management of non-indigenous species have received much less attention. Consequently, there is a need to synthesize current information about the impacts of invasive plant species on watershed and river reach level ecosystem processes. We reviewed a diverse set of information sources to identify gaps in understanding, direct future research, and guide management. We conducted a comprehensive survey of information pertaining to watershed hydrology, riparian ecology, and invasive plant species through literature databases, information clearinghouses, and direct communications with managers, researchers, and environmental consultants. Through our search, we accomplished three functions. 1) We distinguished between observational, experimental, and conceptually-based information. 2) We assembled knowledgeable government, university, and private resource professionals at a round table discussion. 3) We identified critical research needs regarding the positive and negative impacts of invasive plants on watershed hydrology and riparian ecology.

We synthesized information via a four step process. First, we conducted an initial review, organization, and summarization of information gathered through a comprehensive survey of resources. Second, we created a searchable database detailing pertinent information such as citations, invasive species, habitat types, affected ecosystem processes, and methods for acquisition. Third, we facilitated a round-table discussion among managers, private consultants, and researchers regarding the current state of knowledge, research needs, and management priorities pertaining to the impacts of invasive plant species on multi-scale ecological functions. Fourth, we carried out a final synthesis of the knowledge and ideas generated. Our primary goal was to make available a useful summary of the current state of knowledge regarding the impacts of invasive plant species on watershed hydrology and riparian ecology to those who can put it to best use. Our customized database, literature review, annotated bibliography, and workshop products were organized around ecosystem processes operating at watershed and river reach scales. A synthesis of the most current information regarding the impacts of invasive plant species on multi-scale ecosystem function placed in the hands of managers, researchers, and the private sector will enhance information transfer, restoration success, and land management.

The comprehensive survey served as a guide for building the database structure, roundtable discussion topics, and literature review. The database included all resources surveyed during the creation of this synthesis report. At the time of submission it consisted of 200+ records and included such fields as citation, abstract, resource type, and environmental parameters. The database was designed to be searchable on any part of any field. The roundtable discussion group, interviews, and electronic communications indicated several main issues are at the forefront of efforts to understand and manage plant invasions. Most important of these issues was that the variable nature of plant invasions (type, intensity, and geography) does not lend itself to generalities. The discussions revolved around five main plant invasion topics re: 1) adverse, beneficial, and null effects, 2) environmental context, 3) management issues, 4) information needs, and 5) environmental resources and habitat.

Our literature review was organized around watershed function, water quality, riparian ecosystem function, processes, and traits. The premise of much work into the ecological and hydrological impacts of invasive species stemmed from the premise that species composition affects ecosystem processes (Gordon 1998; Tilman and others 1997; Vitousek 1990; Walker and Smith 1997). We found the primary impact of invasives on watershed function could be attributed to differences between native and invasive plant morphology, with lesser impacts due to differences in phenology and physiology. Water quality impacts due to invasives resulted from differences in litter composition between native and invasive species, as well as changes in amount of bareground. However, there are many drivers of increased bareground under invasives; therefore, these conclusions require further data for validation or rejection. While riparian zones are considered havens for invasive species (Masters and Sheley 2001; Stohlgren and others 1998), we found no studies that directly attributed changes in the drivers of riparian ecology to riparian invasives – namely floodplain geomorphology, flow magnitude, flow frequency, sediment regime, or nutrient cycling between stream and floodplain. Those studies that measured hydrologic, geomorphic, or nutrient parameters as they related to riparian invasives could not account for the effects regulated flow or upland landuse changes at the time of data collection. Thus, the vegetation, channel, and flow changes may be responses to changes in flow regime rather than impacts due to riparian invasives.

We suggest future work on this topic should take a watershed approach. The interdependence of environmental factors on hydrologic and ecological processes requires careful study design and a full exploration of alternate hypotheses. Without attention to the complexity of the system, findings from poorly designed studies may mislead management decisions.

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INTRODUCTION

Landuse change in Western North America due to human population expansion has altered water resources at many scales. The concomitant affects on ecosystem function range from slight to severe. Following natural or human disturbance, pioneer plant species colonize a site setting forth an array of successional processes. When invasive plant species establish in place of natives, the altered successional trajectories can change the physical and biological environment leading to changes in local and watershed scale hydrology and riparian ecology (Malanson 1993). The immediacy of the problem of invasive species has prompted multi-disciplinary action in many realms. University researchers have increased the depth of knowledge through rigorous, experimental, often theoretical, studies. Natural resource agency professionals have increased the breadth of knowledge through practical, field-based management. And, consultants in the private sector have explored new possibilities for understanding manipulated systems through restoration projects. Currently, the amount of information exchange among these three groups is low. Thus, there is a need to pull together information that quantifies the impacts of invasive species on watershed hydrology and riparian hydrology from these groups. We synthesized information on the impacts of invasive species on watershed hydrology and riparian ecology by involving scientists in, integrating information from, and tailoring deliverables to resource professionals in academia, natural resource management, and the private sector.

We chose one of two approaches to synthesizing information about the affects of invasive plants on watershed hydrology and riparian ecology in one of two ways. One possible approach was to assemble information about the effects of single species or complexes of species on the hydrology of uplands and riparian areas. A species-specific (or complex) approach would have narrowed the field of watershed and riparian processes for each given circumstance. However, Ehrenfeld (Ehrenfeld 2003) found that a single plant species can have varying effects on ecological processes such as nutrient cycling, decomposition, and hydrologic dynamics given different physical and compositional settings. Single-species ecology, as well as single factor ecology, has often failed to uncover discernable patterns and therefore has lacked applicability to management, restoration, and other practical endeavors. It was our professional opinion that a process-based approach would be useful to academicians, managers, and consultants. That an understanding of the driving mechanisms producing desired (or undesired) affects would more likely lead to solutions across the entire ecological range (Masters and Sheley 2001). We have synthesized knowledge gained from process-based studies on the negative and positive impacts of invasive plants on watershed hydrology and riparian ecology. Further we have differentiated between information based on observation, experiment, or review. This approach has allowed us to identify gaps in our understanding and to offer direction to future research, management, and restoration.

There are many examples of watershed level hydrologic processes potentially impacted by invasive plants. We defined a watershed as the entire area draining water through a single outlet. Watersheds function to collect, store and release water (Black 1997). The collection of water as snow, rain and vapor is influenced by plant communities – the structure of individuals, communities and landscape mosaics, as well as their composition (Lambers and others 1998). Once collected, watersheds store water either on the surface, in soil, or in groundwater for various amounts of time. The effects of plant community composition and multi-scale structure on interception, evapotranspiration, and infiltration alter local storage of water and sediment. Further, timing and rate of snowmelt depends on the microclimate as it is influenced by

community composition and structure (among other environmental factors such as aspect and topography). The release of water occurs primarily as baseflow discharge and, to a lesser extent, surface runoff into streams and rivers. The rate and timing of discharge affects riparian and aquatic ecosystem dynamics from headwaters to deltas.

Riparian zones are susceptible to invasion by non-indigenous plant species (Masters and Sheley 2001). We define riparian areas as zones of seasonal to intermittent flooding along streams and rivers. Riparian zone functions include, flood attenuation, water purification, sediment buffering, groundwater recharge and habitat to incredible numbers of birds, mammals, amphibians, reptiles, invertebrates, and microbes. Riparian communities are characterized by highly diverse, disturbance dependent, early seral vegetation that reflect environmental heterogeneity vertically (from root zone to canopy), horizontally (from right to left bank), and longitudinally (from headwaters to deltas). Invasive species are often early seral species, also. Yet, their phenology, morphology, and niche requirements differ from native riparian species, and, therefore, may interact with the physical and biological environment differently. The likely result is a system with atypical character and function. Conversely, Stromberg (1998a) found that *Tamarix chinensis* played a significant role in trapping sediment in the absence or decline of native vegetation along the San Pedro River, Arizona. Thus, altered ecosystem services due to invasive plant species may have some benefit. Successional development in riparian habitats is fast, compared to their upland counterparts, and diverse. In riparian areas with invasive species, succession appears to have halted (Marlow 2002). The highly evolved, interdependent relationships between native riparian plant communities, upland and stream hydrology, and sediment transport provide the numerous functions attributed to riparian zones. The potential for invasive species to upset this interdependence has given resource managers cause for great concern.

The notion that plant community composition influences watershed and riparian zone functions has been a common one. It followed from this assumption that alterations to plant community composition by invasive plant species would have local and watershed scale affects. However, few studies offered direct support of the idea that invasive plant species altered watershed hydrology and riparian ecology. By synthesizing ideas from many studies, several potential mechanisms of impact presented themselves. 1) Decreases in soil binding ability of invasive plants relative to natives in upland and riparian communities could lead to hillslope and floodplain erosion degrading water quality, and riparian and aquatic habitat condition. 2) Replacement of native riparian vegetation with invasive species could alter hyporheic processes (transformations occurring due to interactions between groundwater and stream water) leading to degraded aquatic macroinvertebrate communities and loss of migratory songbird habitat. 3) Compositional shifts from native to invasive plant upland and riparian vegetation could alter fire frequency, increase habitat fragmentation, and degrade habitat quality for birds, mammals and amphibians, as well as aquatic vertebrates and invertebrates. 4) The phenological and morphological differences between natives and invasive species could alter microclimate, litter layer composition, soil properties, nutrient cycling, trophic cascades, and habitat quality, among many other environmental factors thereby altering watershed function and riparian vegetation dynamics.

We aimed to thoroughly develop the ideas above (and others) through a multidisciplinary search and to make the products available to researchers, managers, and private consultants. Our survey integrated literature reviews of academic, governmental, and private sector resources as

well as synergistic discussions with representatives from these areas. We limited the scope of our efforts to the central and northern portions of North America. Our objectives included:

- 1) Conduct a comprehensive survey of information regarding all aspects of watershed hydrology, riparian ecology, and invasive plant species in the focus area.
- 2) Develop a database compiling all current published and unpublished work involving invasive species, riparian systems, and watershed hydrology.
- 3) Conduct a workshop with researchers, managers, and consultants to discuss the future directions in the research and management of multi-scale ecological and hydrological impacts of invasive plants.
- 4) Draft a synthesis describing the current state of knowledge of impacts of invasive plant species on watershed hydrology and riparian ecology for communication among the scientific, management, and consulting communities through scientific and other publications.

GEOGRAPHIC SCOPE

Landuse change in Western North America due to human population expansion has altered water resources at many scales. Water issues in the western North America primarily focus on water quantity, while states east of the Mississippi River tend to focus on quality. Consequently, the water-related needs of land managers in the West differ from those in the East, as does the role of invasive plant species. For this reason, we will limit the scope of our efforts to the northwestern portion of North America (Oregon, Washington, Idaho, Montana, Wyoming, northern California, British Columbia, and Alberta). The Great Basin (Nevada, Utah, Arizona, and New Mexico) was targeted to lesser extents.

METHODS

Comprehensive Survey

We have conducted a comprehensive survey of information regarding the effects of invasive plant species on watershed hydrology and riparian ecology through literature and database searches, direct communications with managers and researchers, and a round table workshop. This initial review of literature, web sites, and reports of management agencies, research groups, professional societies, and non-governmental organizations was the basis for the organization of the database, the discussion points used in the roundtable discussion, and the scope of the literature review. Most published reviews on invasive species in upland and riparian areas have focused on distribution of invasive plants, the invasion process, and management, with few studies on the impacts of ecosystem processes. Therefore, our database, roundtable discussion, and literature review focused on physical and biological processes altered by compositional changes due to invasive plants.

Bibliographic Database

We used Microsoft Access to develop a searchable database of resources surveyed. We included common bibliographic fields such as citation (CBE Name, Year), abstract, research notes, and keywords. We customized the database by adding fields listing the geography, habitat, and invasive species to provide a concise summary of the information related to invasive species and the context of each study. The information for each citation was evaluated based the sector (e.g. academic, government, private), resource type (e.g. peer-reviewed vs. report) and

study type (e.g. observational, experimental, review). We added fields for these information aspects, as well. We further tailored the database to reflect hydrologic functions and processes, and ecologic functions, processes, and traits addressed in each citation. The database will be housed at the Center for Invasive Plant Management at Montana State University (<http://www.weedcenter.org/>).

Roundtable Discussion

We gathered input from water and weed scientists representing research institutions, government agencies, nonprofit organizations, and the private sector through interviews, electronic discussion groups, and a roundtable discussion. In each forum, we inquired about the current knowledge and research needs pertaining to the impacts of invasive plant species on watershed hydrology and riparian ecology. Currently, the amount of information exchange among these three groups is low. The discussion was conducted during the Society for Range Management annual meeting in Vancouver, British Columbia, in 2005. After a brief presentation of the types of information available and examples of perceptions based on assumption, inference, and data-based conclusions, participants discussed “what we know,” “what we assume,” “what we need to know,” and “how do we get the word out.” Interviews were conducted with additional scientists who were unable to attend the conference due to the logistics and expense of traveling internationally. And, an inquiry was posted on the Society for Ecological Restoration invasive plant listserv. In all, 40 scientists were contacted. Nine researchers, seven government land managers, two nonprofit organizations, and three private consultants significantly contributed to the roundtable discussion or interviews. Scientists’ input represented British Columbia, Saskatchewan, Washington, Oregon, Montana, Idaho, California, Utah, Colorado, Nevada, Arizona, and New Mexico.

Discussion points addressed in the interviews, roundtable discussion, and listserv were generated based on findings from the comprehensive survey. They included:

- Good scientific thought tells us to expect impacts on processes such as erosion, trophic cascades, nutrient cycling, soil development in uplands, soil development in riparian areas, litter dynamics, and succession. Where has this been confirmed or refuted by observation, experimental investigation, or inference?
- We know that environmental parameters such as forage quality, biodiversity, aerial cover, rooting zone exploited, fire recurrence interval, and vegetation community vertical and spatial structure change when species composition changes. Do these changes differ (if they do) due to invasions compared to the compositional changes associated with succession? If so, how?
- What specific relationships between hydrology and invasive species presence have been documented? Examples might include peak runoff timing, runoff quantity, water quality in streams, floodplain turnover (geomorphology), etc.
- How much of what we know is transferable to different vegetation communities, moisture regimes, soil types, disturbance types, or disturbance frequency?
- How do we distinguish between invasive plant species as a vector versus invasives as a symptom? Are they the cause or result?
- What are the critical gaps toward which research emphases should be placed?

Literature Review

Our review of existing literature included grey, white, and peer-reviewed literature and recent and ongoing field projects dealing with invasive plant impacts on watershed hydrology and riparian ecology in natural areas. Professional journals from disciplines such as botany, hydrology, vegetation ecology, invasive species biology, riparian ecology, water resources, conservation biology, agriculture, weed science, entomology, and landscape ecology as well as those with regional emphases established the scope of science-based findings on watershed hydrology and riparian ecology. Electronic sources, government agency reports, conference proceedings, and project reports to non-governmental agencies citing impacts were also reviewed. Examples of governmental publications included Water Resources Investigations, General Technical Reports, and Northern Prairie Publications (USGS). Completed and ongoing field projects contributed information on the most up-to-date approaches and assumptions on the topic. Sources of ongoing projects involved resource professionals, research groups, and granting agencies (e.g. Rocky Mountain Research Station (USFS), The Invasive Species Initiative (The Nature Conservancy and UC Davis), and USDA National Research Initiative).

We have focused this review geographically to include the northwestern United States and southwestern Canada. While we have concentrated on Washington, Oregon, Idaho, Montana, Wyoming, and California, Great Basin and the Colorado Plateau states have been given some attention because of their vast information on invasives common to the Northwest (e.g. *Juniperus* spp., *Tamarix* spp., *Bromus* spp., *Centaurea* spp.)

Watershed hydrology has been defined here as the study of water movement, its quantity, and quality. We have included studies into the responses of upland ecosystem processes and traits where they relate to water quantity and quality in surface and subsurface environments. We have organized this information by watershed function (collection, storage, and release) and applicable components of the water cycle (interception, infiltration, percolation, evapotranspiration, and runoff) because they have facilitated taking a process-based approach.

Due to the fact that there has been controversy over the premise that vegetation can alter upland or riparian hydrology, we give this point significant attention with emphasis on invasive vegetation. To this end, we have investigated studies targeting changes to ecosystem traits (e.g. soil properties, landcover, soil properties, fire cycles) and ecosystem processes (e.g. erosion, nutrient cycling) potentially related to upland water movement, quantity, or quality.

Riparian functions included in this review were water purification, sediment trapping, flood attenuation, groundwater recharge. We have focused our literature review of the impacts of invasives on riparian ecosystem processes on sediment and flow regimes because of the tight interdependence between these processes and riparian structure, species composition, and function. For this reason, riparian habitat quality and hydrologic connection between floodplain and river have been carefully reviewed. Lesser attention was placed on the impacts to nutrient cycling, productivity, succession, and decomposition because they were often incorporated into habitat quality and floodplain connectivity. Lastly, stream water quality literature was assessed, although to a lesser degree, to complete the series of hydrologic links between upland, riparian, and aquatic resources.

We have examined the available literature where the impacts of invasives were related to hydrologic processes and ecology in upland, riparian, and aquatic environments. We have searched databases including Web of Science, EBSCOHost, Google Scholar, and Rocky Mountain Research Station (Treesearch). Literature was also obtained through conventional searches of bibliographies of papers and reports.

We had intended to evaluate each study on the basis used for conclusion (assumption, inference, data based, etc.). This endeavor proved to be ineffectual early in the review process. In lieu of evaluating study designs and conclusions, we have categorized studies according to scientific approach. The variety of approaches researchers, managers, and practitioners has taken to detect, describe, and quantify the impacts of invasives on watershed hydrology and riparian ecology has produced a wide range of perceptions. We have structured our notation after Ehrenfeld (2003). In each bibliography entry the following codes were added: O – observational studies in which environmental parameters were measured under adjacent or nearby communities dominated by invasive and noninvasive plants; F – experimental field study where community composition was manipulated through removal or addition of target species; G – experimental greenhouse study where plant composition and environmental conditions were controlled in pots or mesocosms; R – review papers where the results of several studies were synthesized; C – conceptual papers where select studies were used to construct a framework for current understanding and future investigation.

We have created an annotated bibliography of all literature reviewed using EndNote 9.0. This product was placed with the Center for Invasive Plant Management, Montana State University (<http://www.weedcenter.org/>).

RESULTS

Comprehensive Survey

The comprehensive survey served as an initial review to identify the scope of our synthesis on the impacts of invasive plants on watershed hydrology and riparian ecology. We found much information on weed management, species distributions, and changes in plant community composition. We found very little direct evidence to support claims that invasives impact ecological processes. These findings served as a guide for building the database structure, roundtable discussion topics, and literature review.

Our initial intentions were to evaluate the basis used for conclusion (assumption, inference, data based, etc.) for each reviewed study. However, we found that this level of assessment required detailed communication with the authors regarding experimental design. This endeavor proved to be ineffectual early in the review process. Instead, we chose to categorize studies according to scientific approach following Ehrenfeld (2003). The variety of approaches researchers, managers, and practitioners has taken to detect, describe, and quantify the impacts of invasives on watershed hydrology and riparian ecology has produced a wide range of perceptions.

Bibliographic Database

The database included all resources surveyed during the creation of this synthesis report. At the time of submission it consisted of 200+ records. The database was placed with the Center for Invasive Plant Management at Montana State University (<http://www.weedcenter.org/>). It was designed to be a dynamic resource, such that records may be added and updated as new resources become available. The database was designed to be searchable on any part of any field. Keywords in the citation, abstract, resource type, or environmental fields would be used to run a search (Figure 1). The returned records can be printed or exported into a tab-delimited text file that can be input into other database or bibliographic programs.

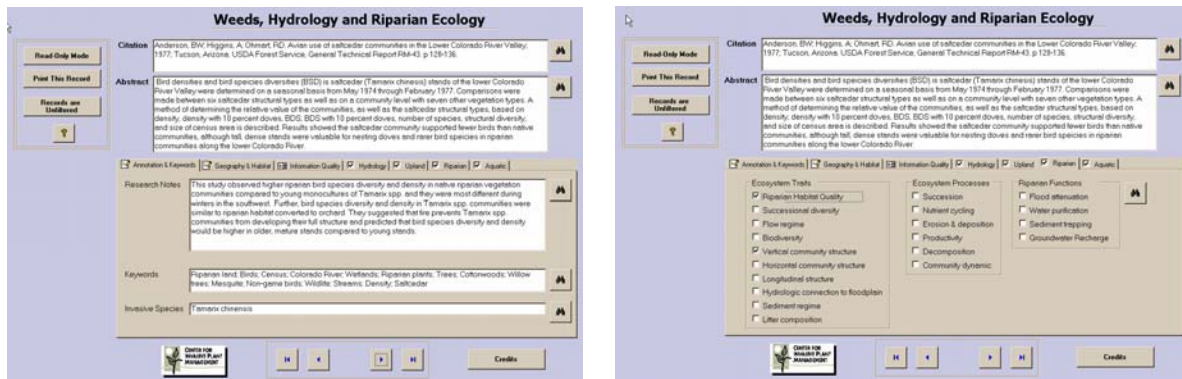


Figure 1. The Weeds, Hydrology, and Riparian Ecology bibliographic database contains information quality and environmental fields in addition to common bibliographic fields. It is searchable on any part of any field. For access contact the Center for Invasive Plant Management at Montana State University (<http://www.weedcenter.org/>).

Interdisciplinary Discussions

The roundtable discussion group, interviews, and electronic communications indicated several main issues are at the forefront of efforts to understand and manage plant invasions. The variable nature of plant invasions (type, intensity, and geography) does not lend itself to generalities. The impacts of invasive plant species depend on the environmental context of the location. This also poses difficulties for land managers who, armed with scant information, must rely on generalities to make resource decisions. Gathering information on the impacts to natural resources of plant invasions requires an understanding of convoluted histories, interactions, and environmental settings. This section outlines the main points posed during discussions. These main points are addressed in detail in the following section, **Literature Review**.

Adverse, Beneficial, or Null Effects

- The general belief is that invasives alter diversity and community structure in adverse ways. However, there is contradictory data that supports and refutes this belief.
- There may be functional redundancy between natives and invasives in such a way that there are no adverse impacts to a site.

Environmental Context

- The ecological impacts on one system do not necessarily transfer to "our" systems. And yet we often manage land based on the knowledge gained in other places-sometimes similar and sometimes not.
- Soil properties respond to changes in plant community traits.
- Mechanisms for impacts of invasives are not studied. Most are based on conjecture and good scientific thought. A common approach is to measure changes in parameters attributed to a process or mechanism. For example, comparing streamflow measurements in areas infested with *Tamarix* spp.

- compared to those with native shrubs lends insight into the hydrologic impacts of *Tamarix* spp. but does not measure it directly.
- Competition studies measure the response of different species to changes in dominant abundance but are not able to document the specific processes operating to produce the observed responses.
 - Ecological impacts must be viewed at varying scales to be assessed properly. For example, the impact of invasives at the scale of a gravel bar does not indicate impacts on a watershed scale.
 - In California rangelands, researchers are testing the hypotheses that the impacts of invasives on native cool season bunch grasses are driven by soil properties, topography (slope and aspect), precipitation, and Mediterranean climate.
 - In arid, steep landscapes with shallow soil, species composition is less important than vegetative cover.

Management Issues

- Ecological impacts are based on the values of the managing entity.
- In Texas, *Pennisetum ciliare* (buffelgrass), a nonnative bunch grass, was planted in the early 1940s to reduce erosion. Since that time wildlife has been displaced. As a result, land owners are finding it difficult to change their business foci from ranching to outfitting on these lands.
- Nonprofits are taking proactive approaches to conserving natural areas. By using lessons learned by others, they focus on preventing invasion and removing invasives where they potentially impact resources.

Information Needs

- Land use change and invasive plant infestations occur faster than knowledge can be gained. Partly, because we learn from these changes. Partly, because the actions we take today may not have an effect for decades to come.
- The bottom line is "the bottom line." Land managers will take action to maximize profits and minimize short term debt. Researchers will research topics which funding agencies solicit. Restorationists will restore based on the values of the clients. And, these values may be driven by aesthetics, forage quality, recreational tourism, or ecosystem function.
- There is a need to increased funding for inventory and monitoring to find out what we are dealing with and how to deal with it.
- In Montana, the NRCS has set invasives and water quality as their highest priorities. They are targeting landowners as this is a gap in the current efforts to reduce the expansion of invasives.

Resources and Habitat

- In the Southwest, riparian sites restored to native plant communities use the same amount of water as salt cedar.

- Hunter and others (1988) in the Southwest found that bug and bird biodiversity decreases in plant communities dominated by salt cedar.
- The southwest willow fly catcher uses salt cedar as nesting habitat when more suitable habitat is not available.

Literature Review

The premise of much work into the ecological and hydrological impacts of invasive species stems from the premise that species composition affects ecosystem processes (Gordon 1998; Tilman and others 1997; Vitousek 1990; Walker and Smith 1997). “If an introduced species can in and of itself alter ecosystem-level processes such as primary or secondary productivity, hydrology, nutrient cycling, soil development, or disturbance frequency, then clearly the properties of individual species can control the functioning of whole ecosystems” (Vitousek 1990).

Invading plant morphology, phenology, and physiology different from upland natives may alter how water is collected, stored, and released in a watershed. In riparian areas, these compositional changes may alter riparian functions (flood attenuation, water purification, and sediment trapping); modify riparian habitat quality, and change the hydrologic connection between stream and floodplain. Aquatic systems may be influenced indirectly by impacts to upland and riparian systems by altered inputs of woody debris, organic matter, and nutrients as well as changes in flow regime (flood timing, magnitude, frequency, duration) (Poff and others 1997).

Few studies offer direct support of the idea that invasive plant species alter watershed hydrology and riparian ecology. By synthesizing ideas from many studies, several potential mechanisms of impact present themselves. 1) Decreases in soil binding ability of invasive plants relative to natives in upland and riparian communities can lead to hillslope and floodplain erosion degrading water quality, and riparian and aquatic habitat condition (e.g. Winward 2000). 2) Replacement of native riparian vegetation with invasive species can alter hyporheic processes (transformations occurring due to interactions between groundwater and stream water) leading to degraded aquatic macroinvertebrate communities and loss of migratory songbird habitat (Ehrenfeld 2004). 3) Compositional shifts from native to invasive plant upland and riparian vegetation can alter fire frequency, increase habitat fragmentation, and degrade habitat quality for birds, mammals and amphibians, as well as aquatic vertebrates and invertebrates (e.g. Whisenant 1990). 4) The phenological and morphological differences between natives and invasive species can alter microclimate, litter layer composition, soil properties, nutrient cycling, trophic cascades, and habitat quality, among many other environmental factors thereby altering watershed function and riparian vegetation dynamics.

Invasives may play a valuable, null, or detrimental ecological role in the communities they enter. Most invasions do not alter large-scale ecosystem properties and processes. Those that do have received the majority of the research and management attention (Vitousek 1990). This leads to the conception that all invasive species will alter large scale ecosystem processes. Williams (Williams 1997) poses a conceptual model of the varying ecological roles—detrimental and beneficial—nonindigenous species may take. In short, on a gradient from natural to impacted to anthropic systems, nonindigenous species (some invasive) may have differing levels of ecological value. He hypothesized that in natural systems if a nonindigenous species fills the same niche as a native, its ecological value would be low. Conversely, the same species in an

anthropic or reclaimed site may fill an unoccupied niche and provide a valuable function such as soil stabilization.

Motivated by demands for greater water supply, there is substantial experimental and observational data to support the premise that vegetation structure has an influence on watershed hydrology. These data date back to 1909 (Bates 1911) and have been reviewed periodically (Bosch and Hewlett 1982; Brown and others 2005; Hibbert 1967). Bosch and Hewlett (1982) conducted a review of 95 paired watershed studies aimed at quantifying changes in water yield due to forest landcover conversion to grassland/bareground – 37 occurred in the focus area of this review. They surmised that every 10% in watershed area converted from forest or shrubland to grassland generated a corresponding increase in annual stream flow. Further, they found that areas with high precipitation demonstrated stronger annual runoff responses to vegetation conversion than regions of lower precipitation. These data demonstrate that there can be an impact of upland vegetation on watershed hydrology. However, invasive plant species have many different morphologies and occur in many different climates. The effect of invasive plant species on watershed hydrology may need to be determined through empirical studies in the location in question.

There is a strong, cyclic interaction between riparian plant community composition and structure and fluvial geomorphology. River geomorphology influences vegetation composition and structure. In turn, vegetation influences the formation and destruction of riverine landforms (Hupp and Osterkamp 1996). In arid regions subsurface water and oxygen gradients have strong controls on riparian vegetation composition and structure (e.g. Stromberg and others 1996), in humid regions flood frequency, magnitude and duration appear to be dominant controls (e.g. Hupp and Osterkamp 1996). Further, Mahoney and Rood (1998) observed flood timing and rate of water table decline as controlling factors in the establishment of woody riparian vegetation in western North America. Thus, any process or impact that affects floodplain topography or flow regime (magnitude, frequency, duration, timing, and rate of change) will have a geomorphic impact on a riparian ecosystem – including changes in vegetation composition and structure. Depending on the type and density of cover, water use rates, resistance to flowing waters (roughness), and how strongly individuals and stands are rooted, vegetation will exert varying degrees of influence on floodplain hydrogeomorphology. If an invasive species causes a change in composition in a riparian community, there may be a response in the physical processes of river and floodplain and a corresponding ecological response along the impacted reach (Gurnell and Gregory 1995).

Determining the role of an invading plant species in a given environment requires knowledge of the existing plant community composition, structure, and function; morphology, physiology, and phenology of existing and invading species; current and historic conditions; landuse history; and management objectives. Invasions are only part of a convoluted set of impacts to ecosystems (Hobbs 2000). The vectors which introduce invasive plant species often alter the environment in several ways. For example, some of the direct impacts of historic grazing densities on California grasslands included the introduction of invasives, removal of natives, increased bare ground, and soil compaction. These environmental impacts can lead to changes in microhabitat, soil moisture content, runoff rates, and timing of peak runoff. The combination of grazing, fire regime alteration, invasives, and other land uses result in vegetation community structure and composition (Vankat and Major 1978). It is folly to attribute ecosystem process, trait, or function changes to one vector when several act in concert.

Our literature review focused on watershed function, water quality, and riparian ecology, with lesser attention given to aquatic ecology. We reviewed 275 sources (Table 1). Of these, 44% were observational, 33% were reviews, 10% were experimental, 10% were conceptual, 5% were greenhouse studies.

Table 1. The references for watershed functions, water quality, riparian ecology, and aquatic ecology indicate that the impacts of invasive plants do not lend themselves to generalities.

Topic	% References
<i>Watershed Function</i>	
<u>Collection</u>	<1%
<u>Storage</u>	3%
<u>Release</u>	6%
<i>Water Quality</i>	10%
<i>Riparian Ecology</i>	
<u>Ecosystem Function</u>	
<u>Sediment Trapping</u>	15%
<u>Flood Attenuation</u>	9%
<u>Water Purification</u>	9%
<u>Ecosystem Traits</u>	
<u>Habitat Quality</u>	28%
<u>Successional Diversity</u>	19%
<i>Aquatic Ecology</i>	6%

Watershed Function

We have organized information regarding the current understanding of the affects of invasive plants on watershed hydrology by watershed function. Watersheds function to collect, store, and release water as well as to provide pathways for chemical transformations and conditions for a variety of habitats the processes of the water cycle (Figure 2) (Black 1997). Because these factors are spatially and temporally variable within and among watersheds, no two watersheds are identical in structure, function, or response to impacts such as invasive plants.

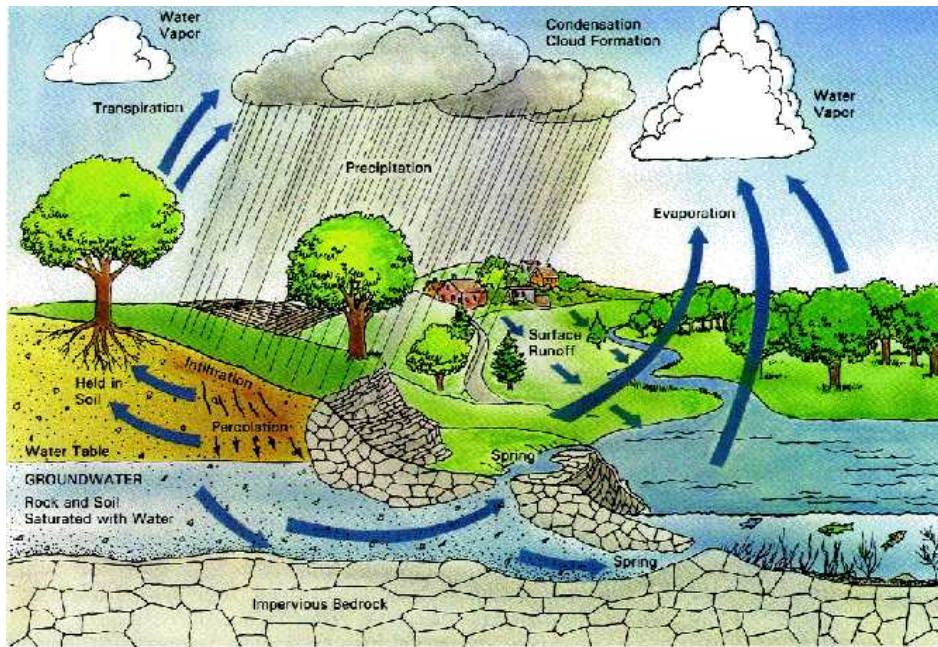


Figure 2. The hydrologic cycle.

Watersheds respond physically and chemically to precipitation events. The physical response is to hydrologically attenuate the extremes of storm runoff through the integration of its collection, storage, and release functions. That is, the time over which a point in a watershed responds to a rain event is a characteristic trait of that point. Some watersheds are “flashy” while others respond slowly over a longer periods of time. The integration of watershed functions depends on climate, geology, topography, and land use as well as their organization across the area draining to a given location (Black 1997). The chemical response of a watershed to a precipitation event is to flush excess soluble and suspended solids from the system. Excess sediment, nutrients, or pollutants are deposited at and moved between storage sites along a flowpath (surface and subsurface) until completely removed from the system (Black 1997). The degree of attenuation and flushing can be impacted by changes in watershed characteristics that alter collection, storage, and release of water. The remainder of this section will address the impacts of land cover change from native communities to those dominated by invasive plants on watershed hydrologic function.

Invasives can alter components of the water cycle by their morphology, phenology, or physiology (Ehrenfeld 2003). However, once water moves past the root zone, vegetation has little or no affect on the water movement. Further, if invasives have morphology, phenology, or physiology different from natives, the impact of plant biology can be great. Erhenfeld (2003) summarized literature regarding the impacts of invasives on soil ecology and found that morphological differences were primarily responsible for impacts to soil hydrology. However, invasives which have phenological differences such as leaf out dates, timing of peak photosynthesis rates, and growing season length may alter peak runoff timing (Walker and Smith 1997). Furthermore, physiological strategies such as nitrogen fixation (Vitousek 1986), salt uptake (Harper and others 1996), and water use efficiency (Ehrenfeld 2003) can alter surface and subsurface water quality.

Water Collection (Interception, Infiltration, Stemflow, and Percolation)

The collection watershed function involves the precipitation, snowmelt, and runoff components of the water cycle (Figure 2). Interception, infiltration, stemflow, and percolation are the specific hydrologic processes potentially affected by changes in upland plant communities. The definitions used in this review follow Dunne and Leopold (1978). Interception is that portion of precipitation caught by vegetation and other surfaces that evaporates before entering the soil. Water can move through the canopy prior to entering the soil via stemflow (running down stems or trunks) or throughfall (falling through the spaces between leaves, twigs, and branches). Infiltration is the process of water entering the soil surface and held as soil moisture. Lastly, percolation is the process of water moving vertically or laterally through the soil environment into groundwater or streams.

Forest and shrub cover have greater capacities for rainfall interception and higher leaf area index leading to higher water loss due to evapotranspiration than herbaceous vegetation (Zhang and others 2001). Juniper invasion of grasslands and sagebrush steppe in the Great Basin were observed by Eddleman and Miller (1992) to increase interception, leading to increased evaporation and sublimation and a corresponding loss of up to 50% soil moisture and stream water yield.

Water Storage

The storage function depends on recharge into groundwater and subsurface soil in addition to geologic flow properties. Recharge in arid and semiarid environments was shown to depend on soil and vegetation properties (Gee and others 1994). As water drains through the root zone it may be affected by vegetation where native xeric shrubs have been replaced by shallow-rooted species, often annual grasses and forbs (Link and others 1990; Seyfried and others 2005). These changes reduce soil water levels and evapotranspiration leading to increased water release in streams, rivers, and lakes (Ludwig and others 2005).

Eucalyptus spp. have invaded many types of ecosystems in California, especially grassland systems. While no data have been published for *Eucalyptus* spp. in California grasslands, Van Lill (1980) observed a dramatic decrease in runoff from watersheds with grassland vegetation converted to *Eucalyptus grandis* plantations in South Africa. *Eucalyptus* spp. have much deeper roots than native grass species and extract water from deeper in the soil profile.

Particularly in arid and semiarid environments, the soil depth from which vegetation extracts moisture will have more or less impact on watershed storage. California native grasses (e.g. *Nasella pulchra*) use deeper soil water than invasives in the *Avena* and *Bromus* genera. This may be due to the shallow root systems and early senescence of these groups of invasives. Conversely, *Centaurea solstitialis* (yellow starthistle) is a deep rooted, late-season annual that has invaded northwest grasslands and riparian zones. Borman (1992) observed differences in water use depth between *C. solstitialis*, perennial native grasses, and invasive annual grasses in southwestern Oregon. Invasive annual grasses and *C. solstitialis* use soil water earlier in the growing season than perennial native grasses (*Agropyron spicatum*, *Festuca idahoensis*). Zaveleta (2007) observed an increase in soil moisture where *C. solstitialis* was removed. In communities where annual grasses and forbs dominate, the remaining deep soil water may result in earlier and larger peak runoff rates in streams, as demonstrated where forest landcover has been converted to grassland (Brown and others 2005). The remaining deep water can flow through the vadose (moist soil) zone or groundwater to streams and rivers. This can alter watershed release and timing through larger peak flows that come earlier in the season.

However, data reviewed by Brown and others (2005) also showed that the hydrologic response is less in arid and semi-arid climates.

Invasives able to use water at different times of the season or at greater soil depths may impact water collection, storage, or release. Winters in the Great Basin are cold and wet. Snow melt is the dominant source of recharge. *Bromus tectorum* breaks dormancy earlier than native grasses and shrubs due to its ability to germinate and begin root elongation at low temperatures (Harris and Wilson 1970). This can deplete soil moisture effectively reducing groundwater recharge (storage) and stream discharge (release).

Water Release

Water release involves water loss due to evaporation as well as surface runoff and groundwater discharge into streams, rivers, and lakes. Water loss in the form of evaporation from rock, soil, and leaf surfaces and evapotranspiration from photosynthesis can account for tremendous amounts of water released from a system (Zhang and others 2001). Surface runoff includes water in ephemeral, intermittent, and perennial streams as well as transient rills, gulleys, and washes. Because the three watershed functions we are addressing here do not have distinct boundaries, much of the literature reviewed that involves water release related to upland communities has been summarized above. Lastly, evaporative water loss from upland invasive plants has been integrated with interception and impacts on water storage due to morphological, phenological, or physiological adaptations.

There are very few studies of the impacts of upland invasive plants on stream flow, and most of these occurred in South Africa. The primary process responsible for water release impacts is evapotranspiration, and interception to a lesser degree. In South Africa, Van Lill and others (1980) carried out a field experiment where they collected 12 years of stream flow data prior to experimentally planting two watersheds – one in *Eucalyptus grandis* and another in *Pinus patula*. A third was maintained in native vegetation. After three years, the *Eucalyptus grandis* watershed streamflow declined to one-third of the pre-planting average. After another five years, streamflow reached equilibrium at half the pre-planting water yield. Le Maitre and others (2004) quantified the impacts of *Acacia cyclops*, *Prosopis* spp., *Acacia* spp., *Solanum mauritanum*, and *Pinus* spp. to surface water runoff in streams and rivers in the Vaal River watershed (South Africa). By mapping species density and applying a water use model based on vegetation age, they found that invasive riparian and upland shrubs and trees in the Vaal River watershed consumed about 75% of the mean annual runoff. Without direct approaches such as these examples, attributing changes in water yield to invasives is mere conjecture.

Tamarix spp. have invaded waterways from northern Mexico to central Montana and from central California to central Kansas. Distributions of *Tamarix* spp. has been temporally and spatially correlated with river regulation (e.g. Friedman and others 2005). *Tamarix* spp. can contribute to increased water loss due to deep roots which access water tables (Zavaleta 2000). However, this is true of other common riparian woody species (e.g. *Populus* spp., *Salix* spp., *Prosopis* spp.). Sala and others (1996) found that *Tamarix* spp. transpire at rates similar to native phreatophytes such as *Pluchea sericea*, *Prosopis pubescens*, and *Salix exigua* in the southwest. That *Tamarix* spp. patches grow at greater densities than do native communities results in higher stand leaf area index and higher transpiration rates. It also inhabits greater proportions of riparian zones than native stands. The impact of *Tamarix* spp. on stream flows is measurable in some cases (Sala and others 1996). Most, if not all, studies on the effects of *Tamarix* spp. on hydrology and fluvial geomorphology have taken place in the southwest where

the river systems are flashy. It is unknown if the same responses will occur in the greater northwest under different climatic and hydrologic conditions.

Many government and private water, weed control, and restoration programs spend millions of dollars to recoup water and habitat lost to invasive riparian species each year. Shafroth and others (2005) have reviewed the efforts to regain water and habitat resources lost due to *Tamarix* spp. invasions. They found that when *Tamarix* spp. was removed for “water salvage,” stream flow increases were lower than expected from evapotranspiration measurements conducted before *Tamarix* spp. removal. Explanations included measurement errors in streamflow, climatic variations within sites, and capture by groundwater pumping. However, Shafroth and others (2005) go on to point out that interactions between groundwater and evapotranspiration are poorly understood. It is possible that decreases in evapotranspiration are compensated by increases in groundwater storage. These changes would not be detectable in stream flow measurements.

Water Quality

Water quality is affected by all physical or biological substances or processes along a flowpath. Therefore, water quality is a function of upland and riparian environments. In this section, we address impacts due to upland invasions on water quality, while those due to riparian invasions will be discussed below in *Riparian Ecology*. Water quality refers to the suitability of water in soil, geologic layers, or on the ground surface to support life. There are few studies directed at the impacts of invasives to water quality. We included those studies which document altered upland erosion and nutrient cycling because the flow of water from place to place carries soluble and suspended solids (Viney and others 2000). The result can be leached source areas, concentrated sinks, or polluted streams, rivers, lakes, and oceans (Burt 2001; Smith and others 2003).

Many research, control, and management studies involving invasives list increased erosion as an impact. The premise is that the invasion increases bareground at the surface or decreases soil stability or both. Weed ecologists pose many mechanisms to explain these observations. Allelopathy has been observed to inhibit productivity of other species (Ehrenfeld 2006). Several studies show invasives to be more competitive than some natives for space, light, water, or nutrients. Timing of resource use by invasives renders conditions unsuitable for native species (e.g. Ludwig and others 2004; Shainsky and Radosovich 1992). However, erosive responses to bareground depend on soil type and structure, amount and intensity of rainfall, slope, and antecedent moisture conditions (e.g. Kirkby and others 2002). If physical crusting occurs, infiltration is reduced and erosion rates increase. For example, *Centaurea maculosa* was reported to increase erosion rates by displacing native bunch grasses in Montana. Increased sediment loss and higher runoff rates were found from areas dominated by *C. maculosa* compared to native bunch grasses. These areas had a larger fraction of bareground (Lacey and others 1989) due to lower basal cover and crusting of soil in infested sites (Olson 1999). Where restoration efforts have used invasives to quickly stabilize disturbed ground, erosion is reduced by the presents of invasives (Jones and others 1997; Ludwig and others 2005). In flat settings, if soils are medium or light textured (loam to sandy), bareground can increase infiltration rates compared to vegetated areas. This technique is practiced by agriculturalists when farmed fields are rotated between fallow and crop.

If plant composition can alter soil nutrient cycling, there may be an impact on water quality of streams and rivers in their catchments. Wedin and Tilman (1990) demonstrated that nitrogen mineralization and soil N availability varied under five different grass species. Smith and others

(2003) showed that change in landcover altered nutrient loading in runoff leading to hypoxia in the Gulf of Mexico. In the Appalachians, Bolstad (1997) found that land cover had a higher impact on stream water quality during storm flow compared to base flow. During storm flow, stream nitrate, ammonia, turbidity, and coliform bacteria increased in areas converted from forest to agriculture. Land conversion from forest to grass, or grass to pasture can alter nutrient and sediment export from uplands into riparian zones and streams. This has been demonstrated in the Appalachians (Scott and others 2002) and New Zealand (Niyogi and others 2007).

In a review of the effects of invasive plants on soil nutrient cycling, Ehrenfeld (2003) found that compared to the natives displaced, invasives tend to have:

- higher standing crop biomass
- higher net primary productivity
- faster growing rates
- higher shoot-root ratio
- produce easily decomposed litter
- have more extractable N
- increased rates on N mineralization (nitrification)
- non-N-fixing invasives can alter N fixation rates indirectly by affecting other N fixers associated with displaced native plants
- altered nutrient flux timing and distribution

Even with these carefully made generalizations, it is difficult to predict impacts to nutrient cycling for a given location-even for the same species. For example, *Bromus tectorum* increased rates of N mineralization and nitrification in cool deserts (Bolton and others 1990) but decreased them in warm, arid grasslands (Evans and others 2001). *Eucalyptus globulus* in the Berkeley Hills of California produced thick litter layers that immobilized N and released it slowly (Robles and Chapin III 1995). Conversely, annual grasslands of California (*Bromus*, *Avena*, and *Lolium*) have thin, easily decomposed litter that significantly increased N in soil stores (Robles and Chapin III 1995). Canon and others documented that *Salsola tragus* mobilized soil P by releasing oxalic acid from its litter. *Stipa pulchra* was able to take up newly available P. *Halogeton glomeratus* may have a similar affect on soil P levels because it produces high concentrations of oxalic acid (Whitson and others 1996). Also, Harper and others (1996) observed *Halogeton glomeratus* to possibly salinize soil by absorbing salts from the soil and depositing them at the soil surface in leaf litter. Increases in soil nutrients not immobilized by biota may leach into ground and surface waters.

Christian and Wilson (1999) found that *Agropyron cristatum* had less dense root biomass than dominant native grasses. This led to a decrease in soil organic matter and 25% less total carbon than native prairie soil in the Northern Great Plains. Soils under spotted knapweed were depleted in potassium, nitrogen and phosphorus by 44-88% compared to those under a grass overstory (Harvey and Nowierski 1989). Conversely, Sperber and others (2003) found no consistent differences in soil physical properties when comparing soil under *Centaurea maculosa* to that under Montana native grasses.

Riparian Ecology

The dynamic nature of riparian systems is rooted in their dependence on fluvial disturbances which vary in magnitude and frequency. Flow regime incorporates magnitude, frequency, duration, timing, and rate of change of flood events on multiple scales (Poff and others 1997). Erosion and deposition 1) create new surfaces for colonization (Rood and others 1998); 2) rework sediment which alters floodplain and channel topography (Leopold and others 1964;

Nanson and Croke 1992), water table depth (Martin and Chambers 2001; Shafroth and others 2000) and channel planform (Merigliano and Polzin 2003; Micheli and others 2004), ultimately supporting a mosaic of riparian vegetation patch types; and 3) influence sediment residence time which adds successional diversity (Merigliano 1998; Mount and Louis 2005). The temporal and spatial heterogeneity of overbank flooding creates conditions which favor some organisms one year (e.g. salmonids or valley oak,) and other organisms another year (e.g. macroinvertebrates or Fremont cottonwood) (Trowbridge 2002). The lateral exchange of nutrients, sediment and organisms during flooding events promotes biodiversity and structural diversity through temporally and spatially variable connectivity among patches in the riparian landscape (Junk and others 1986; Thoms 2003). Thus, the diversity of physical processes in space and time combine to create heterogeneous ecological processes in a functioning riparian zone.

The interdependence between biological and physical processes is driven by a natural flow regime within the constraints of basin geology, topography, and climate. Any change to the natural flow regime can alter the riparian ecosystem at a given location. While there are a finite number of natural and anthropogenic processes impacting flow regimes, the magnitude of their combined affect at any one location along a riparian corridor is unique and ever-changing (Scott and others 1996). Thus, no two riparian areas are identical (Nilsson and others 1988). The affect of invasive plants on the drivers of riparian ecosystems has not been directly investigated. We have reviewed literature surrounding documented impacts of invasives on the drivers of natural flow regime. Our intent is to provide a foundation for future exploration to find direct evidence that supports or refutes perceived links between invasive plants (upland and riparian) and altered watershed hydrology and riparian ecology. We have organized our synthesis around impacts to major riparian functions and ecosystem traits, with limited attention to those of aquatic ecology.

Ecosystem Function

Sediment Trapping

Depending on morphology, vegetation can reduce water velocities, which cause suspended sediment to drop (Fetherston and others 1995; Gregory and Gurnell 1988). Young woody vegetation with leaves has high roughness compared to that of graminoids, which often lay flat during flood flows. In this way, a mosaic of floodplain vegetation can influence the detailed features of the flood plain through varied levels of deposition of sediment. Within the active channel, vegetation offers minimal sediment stabilization and resistance to flow. Once out of bank, floodwaters encounter vegetation whose structure varies, laterally across the floodplain, vertically with seral stage, and longitudinally along the length of a river (Schmitz 2003). For example, Birkeland (1996) and Graf (1980) found *Tamarix* spp. have higher sediment trapping abilities than native riparian vegetation (*Populus fremontii*, *Salix* spp.) when grown in dense stands.

Blackburn and others (1982) observed strong correlations between *Tamarix* spp. density and cover and stream stage, flow velocity, and overbank flow frequency on the Brazos River in Texas. They compared flood stages of floods of similar volume before and after *Tamarix* spp. presence. Flood stages were significantly higher (32-62%) after *Tamarix* spp. invasion. They also noted significant channel narrowing (43-71%) over the time period of *Tamarix* spp. invasion. The channel narrowing and stage increases could be due to several factors including increased upland erosion from farming practices, upland fires, or regulated hydrology upstream due to dams. Graf (1978) found similar results on the Green River, Canyonlands NP. He examined historical records and photographs and found that channel widths were in equilibrium

prior to *Tamarix* spp. invasion around 1925. Since then the channel has narrowed 13-55% and has reached a new equilibrium. Prior to 1934 and *Tamarix* spp. invasion, discharge in the Green River slowly decreased and new bars and islands formed. After 1955 and *Tamarix* spp. invasion the bars and islands were stabilized by *Tamarix* spp. despite a significant increase in discharge. However, the hydrology of this river is highly altered. The observations do not account for channel changes due to river regulation in these systems.

Most, if not all, studies on the effects of *Tamarix* spp. on hydrology and fluvial geomorphology have taken place in the southwest where the river systems are flashy. *Tamarix* spp. has expanded its distribution northward and now exists on the Snake, Yellowstone, and Missouri Rivers. It is unknown if the same responses will occur in the greater northwest under different climatic and hydrologic conditions.

Cortaderia jubata (pampas grass) and *Arundo donax* (Giant reed) have invaded California river margins. Hoshovsky (1988) suggested that *Arundo donax* can trap and stabilize more sediment than native vegetation, decrease river channel width, and reduce shading of streams leading to increased stream temperatures. There was no published data to support these observations.

Sediment trapping is a function of any vegetation in a riparian zone, and it is naturally highly variable. To define sediment trapping as a negative impact of invasive plants in a riparian zone is misguided. Those studies that have compared the sediment trapping of native vegetation to that of invasive species have not addressed the natural range of variability. Further, comparisons were made by comparing conditions at one point in time under one flow regime to another point in time under a different flow regime. Thus, the vegetation, channel, and flow changes may be responses to changes in flow regime rather than impacts due to *Tamarix* spp. More likely, the impacts of sediment trapping are deemed incompatible for a particular management objective and the current vector of sediment deposition deemed the driver. In California, levees on the Sacramento River are intentionally devegetated to increase flow velocities, regardless of species (Greco 2004).

Flood Attenuation

When a flood exceeds the river banks and flows across the floodplain, the roughness of the floodplain due to vegetation, topography, or substrate slows water velocities to varying degrees (Graf 1978). In this way, channel and floodplain forms which redirect river flow onto the floodplain prompt temporary flood storage. Vegetation and topography are major drivers of flood attenuation. Water managers and agriculturists in floodplain environments often remove vegetation to enhance flood conveyance to reduce the time a tract of land is inundated by flood waters. Fisheries biologists, riparian ecologists, and conservationists work to increase flows onto floodplains because of the exchange of nutrients, sediment, and water which creates juvenile fish habitat, hot spots for diversity, and encourages trophic transfer between aquatic, riparian, and upland communities.

The role invasive plants play in flood attenuation is largely unexplored. Where invasive plant species alter floodplain roughness, there may be an impact to flood control. However, in most cases where impacts of invasives on riparian function have been addressed, the overarching impact is due to altered flow regime (e.g. Graf 1980). Stromberg and Chew (2002) hypothesized that *Tamarix* spp. may become dominant along highly altered waterways where native vegetation can not survive the altered conditions. This being the case, they offer that native communities would be competitive with *Tamarix* spp. if a natural flow regime were restored (Junk and others

1986; Poff and others 1997). Further, eradication of *Tamarix* spp. without restoring a natural flood pulse could do more damage than good (Glenn and Nagler 2005).

Water Purification

In areas where subsurface flow occurs in the root zone, riparian vegetation can play a significant water purification role (Hill 1996). Denitrification is the major process in reducing groundwater nitrate levels before entering a waterway (Martin and others 1999). Riparian vegetation has been observed to immobilize nitrate (Schade and others 2005) and produce the high quantities of organic matter (above and below ground) required for denitrifying bacteria to convert nitrate to gaseous nitrogen (Lowrance and others 1997). Changes in riparian plant composition and structure due to invasive plants may alter this process in areas where subsurface water flows through the root zone. Invasive species may have different root densities than natives at depths where significant subsurface flow occurs, thus altering nutrient buffering capacity of riparian zones. Currently, there is no conclusive data to support this hypothesis.

Changes in community structure may alter sediment trapping from upland erosion or overbank flooding (Corley and others 1999). Aggradation of sediment may alter topography and increase depth to groundwater, thus reducing soil moisture beyond what native vegetation can survive (Stromberg and others 1996). Clement and others (2002) measured denitrification rates in France under three different riparian vegetation types to find that topography was the dominant control. Corley and others (1999) have observed *Poa pratensis* in montane riparian areas where active nitrogen and phosphorus removal has occurred.

The effects of *Elaeagnus angustifolia* on riparian nutrient cycling was reviewed by Katz and Shafroth (2003). They found no data to directly support the hypothesis. Significant research has suggested connections. Tickner and others (2001) build a framework for *Elaeagnus angustifolia* to alter floodplain roughness. Simons and Seastedt (1999) found *Elaeagnus angustifolia* to withdraw less nitrogen from the western riparian environments than *Populus deltoides*. Royer and others (1999) found that while *Elaeagnus angustifolia* leaves had higher nitrogen concentrations and carbon: nitrogen ratios than native *Populus tremuloides* and *Cornus* spp. leaf decomposition rates varied between two Idaho streams suggesting that generalities based on leaf nutrient content are not supported.

Ecosystem Traits

Riparian Habitat Quality

Of all the ecosystem traits characteristic of riparian areas, habitat quality to incredible numbers of species in many plant and animal taxa is the most cited and well documented. The impacts of invasive plants to riparian habitat quality are not clear. Several studies document reduced species richness in the presence of invasive plant species such as *Phalaris arundinaceae* in Oregon (Fierke and Kauffman 2006), *Tamarix* spp. (Hunter and others 1988; Wiesenborn 2005) and *Elaeagnus angustifolia* in greater western North America, *Acer platanoides* in Montana (Reinhart and others 2005), and *Lythrum salicaria* in greater northwestern North America (Mullin 1998). Avian species appear to be less sensitive to plant composition if structural complexity is present (Fleishman and others 2003). Through a functional comparison between *Tamarix chinensis* and *Populus fremontii*, a common native riparian tree displaced by *Tamarix* spp., Stromberg (1998b) found that the two species are similar in riparian function, morphology, phenology, and soil requirements. Busch and Smith (1995) examined *Tamarix* spp. in two communities along the Lower Colorado, a regulated river, and the Bill Williams River, a

less altered river. Following *Tamarix* spp. removal, *Salix* spp. showed lower water potentials, higher leaf conductance, and increase productivity.

Anderson and others (1977) observed higher riparian bird species diversity and density in native riparian vegetation communities compared to young monocultures of *Tamarix* spp. and they were most different during winters in the southwest (Anderson and others 1977; Hunter and others 1988). Further, bird species diversity and density in *Tamarix* spp. communities were similar to riparian habitat converted to orchard. Anderson and others (1977) suggested that fire prevents *Tamarix* spp. communities from developing their full structure and predicted that bird species diversity and density would be higher in older, mature stands compared to young stands. Hunter and others (1988) found that seasonal bird species diversity, density, and distribution increased with the expansion of *Tamarix* spp. into southwest New Mexico and southeast Texas. They attributed these range expansions to the historic structure of native riparian vegetation communities, which lacked diversity in structure.

Soil environments have been investigated under *Tamarix* spp. Compared to Bermuda grass, annual weeds, and bareground, *Tamarix* spp. can extract water from deeper in the soil profile leading to lowered water tables (Weeks and others 1987) and saline conditions in arid environments. However, this would be the case when comparing any riparian woody species to herbaceous species. Also, *Tamarix* spp. has the ability to extrude salts into the soil and survive saline soil conditions better than native woody species (Shafroth and others 1995). Berry (1970) found that the water potential of the root environment induced *Tamarix aphylla* to exude salts depending on the ions present in the soil environment. In addition, *Tamarix* spp. were found to be physiologically adapted to survive in saline conditions due the ability to manipulate its internal ionic concentrations. These observations suggest that *Tamarix* spp. responds to saline conditions rather than creates them. There is much discussion in the literature about the ability of *Tamarix* spp. to cause an increase in soil salinity. However, we found no data to substantiate this claim. However, the ability of *Tamarix* spp. to survive in dry and saline soil conditions may give it an advantage over native riparian vegetation (Busch and Smith 1995).

Successional Diversity

Riparian ecosystems are known for their diversity in successional stages. Dependent on flood disturbance, which is variable in magnitude and frequency, succession can follow many pathways and exist in many stable states (Baker and Walford 1995; Chambers 2000). Cleverly and others (1997) analyzed growth ring data from *Tamarix* spp. and natives riparian species in the Mohave Desert over 50 years. They found that *Tamarix* spp. grew more slowly than natives but eventually dominated the communities due to recurring drought where natives died back. Cooper and others (2003) have aged over 800 riparian woody plants along the Yampa and Green Rivers dating back to 1962. They concluded that flow regulation mimicked drought conditions on floodplain surfaces which once supported native woody vegetation, and now favors *Tamarix* spp. Dixon and Johnson (1999) along the middle Snake River and Brothers (1981) along the Owens made similar observations regarding *Elaeagnus angustifolia*.

Cottonwood decline has also been seen without major infestations of invasive species on the St. Mary's River (Rood and others 1995), Marias River (Rood and Mahoney 1995), and upper Colorado and Rio Grande Rivers (Snyder and Miller 1992) where flow regimes have been altered for hydropower, water storage, flood control, and development. Along the Sacramento River, old fields are being restored to riparian communities. Peterson (2000) has observed a "founders effect" where weed species that establish in old fields determine the successional trajectory and make restoration exceptionally difficult.

Aquatic Ecology

Aquatic ecosystems are dependent on periodic connection to riparian environments. The exchange of nutrients, water, sediment, and organisms has long been recognized by aquatic and riparian ecologists in most conceptual frameworks. And virtually all of them are based on hydrology. The river continuum concept describes zones along a longitudinal gradient in which ecological processes respond to changes in fluvial geomorphology (Vannote and others 1980). Nutrient (resource) spiraling refers to changes in nutrient retention in channels and hyporheic zones during downstream transport (Elwood and others 1983; Newbold and others 1983). The serial discontinuity concept (Poole 2002; Ward and Stanford 1995) and hyporheic corridor concept (Stanford and Ward 1993) incorporate ecological responses to irregularities in longitudinal profile associated with anthropogenic and hydrogeomorphic (respectively) impacts. The ecological responses to lateral exchanges between channel and floodplain are the focus of flood pulse concept (Junk and others 1986), the most widely used approach.

Invasive plants in upland and riparian ecosystems can impact aquatic systems through changes in watershed function and riparian ecology, as described above. Specifically, changes in upland or riparian community composition can alter organic matter inputs into aquatic systems. Organic matter in the form of large woody debris creates complexity of aquatic landforms for spawning, macroinvertebrate refugia, and cover for all aquatic species (e.g. Malanson and Butler 1990). Coarse particulate organic matter and fine particulate organic matter provide energy sources for aquatic organisms (e.g. Minshall 1988).

CONCLUSION

Our review showed that there is substantial scientific basis to expect that invasive plants would impact watershed hydrology and riparian ecology. However, it also shows a great amount of variability in hydrologic and ecologic response to invasives due to the interdependence of environmental factors in any given location. We found that environmental response to invasives does not lend itself to generality. Due to this fact, it is imperative that empirical studies be conducted to characterize impacts prior to taking major action on such grounds.

We have identified several research needs regarding the impacts of invasives on watershed hydrology and riparian ecology. The morphological, phenological, and physiological differences between invasives and natives have been shown to be instrumental in hydrologic and ecologic changes. Ehrenfeld (2003) stated the need to determine the magnitude of the morphological or physiological differences between invasive and native plants necessary to alter ecosystem processes. This gap remains unfilled, based on our findings.

We note a dearth of studies which adequately quantify the impacts of upland invasive plants on water yield. Lewis and others (2000) quantified the effect of woodland oak removal on stream discharge in the Sierra Nevada foothills. They measured precipitation, stream flow, and potential evapotranspiration continuously for 3 years prior to a 14% conversion and 14 years after. Such an approach needs to be applied to invasions of non-native plant species to confirm, quantify, and appropriately manage landscapes for hydrologic impacts of invasive vegetation. Further, the existing studies on the effects of vegetation on hydrology pertain exclusively to woody species. There needs to be studies carried out on herbaceous invasives to either support or refute the claim that invasive species impact hydrology processes.

While riparian zones are considered havens for invasive species (Masters and Sheley 2001; Stohlgren and others 1998), we found no studies that directly attributed changes in the drivers of

riparian ecology to invasives – namely floodplain geomorphology, flow magnitude, flow frequency, sediment regime, or nutrient cycling between stream and floodplain. Those studies measured hydrologic, geomorphic, or nutrient parameters as they related to invasives in riparian zones could not account for the effects regulated flow or upland landuse changes at the time of data collection.

Future research is needed in western North America to 1) quantify the effects of invasives on the sediment regime, nutrient fluxes, and flow regime of rivers; 2) distinguish between the effects of altered hydrology and invasive plants in riparian zones; 3) characterize water, sediment, and nutrient budgets for entire watersheds accounting for fluxes in upland, riparian, and aquatic systems. Studies of these types would require highly controlled paired watershed experimental designs. Such research should be an integral to assessing the impacts of invasive species on watershed hydrology and riparian ecology.

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