The Ecological Consequences of Knotweed Invasion into Riparian Forests

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Abstract

The Ecological Consequences of Japanese Knotweed Invasion Into Riparian Forests

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Japanese (*Polygonum cuspidatum*), giant (*Polygonum sachalinense*) and bohemian (*Polygonum bohemicum*) knotweed are three closely related congeners invading riparian areas, roadsides, and parklands throughout the United States and Europe. The spread of knotweed along river corridors has been of particular concern to natural resource agencies and conservation organizations. Knotweed's invasion of riparian forests has the potential to alter critical ecological processes including streambank stability, channel morphology, nutrient cycling, forest and understory regeneration and organic matter inputs into aquatic food webs. Currently, there is limited field research documenting the level and significance of these suspected impacts.

This research investigates two suspected impacts of knotweed's invasion: 1) the displacement of native riparian plant communities and biodiversity, and 2) alteration of the quantity and nutrient quality of riparian leaf litter inputs into streams. Field data were collected in summer-fall 2004 at Grandy Creek, a tributary of the Skagit River densely colonized by giant knotweed, *Polygonum sachalinense*.

Study results indicate a negative correlation between knotweed invasion and the species richness and abundance of native understory herbs, shrubs, and juvenile trees. A reduction in riparian tree establishment could have detrimental and long lasting effects on the successional trajectory of riparian forests, bank stability, hydrology, nutrient loading, micro-habitat conditions and aquatic biota of adjacent lotic systems.

In addition to the displacement of native vegetation, data suggest that knotweed invasion alters stream nutrient subsidies from riparian litterfall. Results demonstrate an average 70% reduction of native litter inputs correlated with knotweed invasion. Additionally, the C:N of senesced knotweed leaves is 52:1, a value 38% (*Salix*) to 58% (*A. rubra*) higher than dominant

native riparian species.

Analysis of nutrient re-absorbance from senescing leaves reveals that knotweed reabsorbs 75.5% of its foliar nitrogen prior to litterfall. In contrast, native species reabsorb 2.3% (*A. rubra*) to 33% (*Salix*), thus contributing a greater proportion of their nitrogen resources to riparian soils and aquatic environments through leaf litter. Litterfall from riparian vegetation comprise a primary source of nutrients and energy in forested streams and backwater channels. By altering the composition and nutritional value of allochthonous litter, knotweed invasion could have a detrimental impact on the productivity of aquatic food webs.

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Chapter 1: Introduction

Three closely related species of knotweed are invading riparian areas, roadsides, and parklands throughout the United States and Europe. These include *Polygonum cuspidatum* Sieb. & Zucc. (Japanese knotweed), *Polygonum sachalinense* F. Schmidt ex Maxim. (Giant knotweed), and *Polygonum x bohemicum* (J. Chrtek & Chrtkovß) Zika & Jacobson (Bohemian knotweed). All three species, which I will collectively refer to as “Japanese” knotweed, are distinguished from other congeners by their height (2-5 m) and perennial habit with bamboo like stems and heart shaped or cuspidate leaves (Child and Wade 2000). Japanese knotweeds grow vigorously from rhizome fragments and form dense, monotypic stands that appear to exclude native vegetation and are extremely difficult to eradicate. The International Union for the Conservation of Nature recently named Japanese knotweed in their list of “100 of the World's Worst Alien Invasive Species" (Lowe et al. 2004). Throughout the Pacific Northwest, the spread of Japanese knotweed along river corridors is a growing concern of natural resource agencies and conservation organizations. Once introduced, these species spread throughout the riparian zone as flood waters pick up root and stem fragments and deposit them downstream.

Knotweed’s invasion of riparian forests is predicted to alter critical ecological processes including hydraulic regimes, stream-bank stability (Dawson and Holland 1999), channel morphology (Dawson and Holland 1999), nutrient inputs (Potash 2002), forest and understory regeneration (Beerling et al. 1994, Tickner et al. 2001) and aquatic food webs (Potash 2002). In 2004 and 2005, the Washington State legislature appropriated a supplemental budget of $500,000 to the Washington State Department of Agriculture (WSDA) for control of Japanese knotweed, first as a pilot project in southwest Washington, and then for the statewide expansion the program (WSDA 2006). Additional knotweed control work is ongoing throughout the State. Knotweed working groups have formed for the Skagit, Chehalis, and Olympic Peninsula watersheds in order to coordinate control efforts among restoration groups, government agencies, and private landowners on a landscape scale.

The allocation of limited resources to knotweed control is based on anecdotal evidence that these species are causing significant, long-term changes in the composition, structure and function of riparian systems which, in turn, affect the food availability, large wood recruitment, shade, and pool formation required by Pacific salmon. However, it is difficult to assess the relative importance of knotweed eradication versus alternative riparian restoration actions (i.e. barrier culvert removal and large woody debris (LWD) enhancement) without quantitative information demonstrating the ecological consequences of knotweed invasion. Research focused on the level and significance of suspected impacts will aid land managers in developing informed and effective restoration strategies.

This study had two inter-related objectives related to suspected consequences of knotweed invasion: 1) Does knotweed invasion alter the vegetation composition and diversity of riparian forest understory communities? 2) What is the effect of knotweed invasion on the quantity, species composition and nutrient quality of autumnal leaf litter inputs into streams? Field sampling was conducted at Grandy Creek, a tributary of the Skagit River that is densely colonized by giant knotweed, *Polygonum sachalinense.*

Chapter 2: Background

The Ecological Consequences of Plant Invasions

Invasions by non-native plants displace native species and can bring about dramatic alterations to ecosystem structure and function (Parker et al. 1999, Byers et al. 2002, Levine et al. 2003). The rampant spread of non-native invasive plants into natural areas is receiving increasing attention from ecologists, conservationists and land managers. The reduction or elimination of these species is often a time and energy consuming aspect of ecological restoration initiatives. Yet, our understanding of the causes and consequences of plant invasions remains limited and there is a shortage of quantitative information demonstrating effects of invaders on native biota and ecosystem functioning (Byers et al. 2002). As a result, management decisions are often based on anecdotal evidence or subjective assessments of negative impacts (Blossey 1999). It is difficult to weigh the management value of invasive plant removal versus alternative restoration strategies without having first quantified invasion effects. Research directed at the ecological consequences of plant invasions is needed both to aid land managers in setting effective invasive species control priorities and to enhance understanding of how species introductions and deletions affect indigenous communities and ecosystem processes.

Existing data on the ecological consequences of non-native invasive plants focus on species with “quirky” traits that introduce a novel function to the invaded ecosystem (Parker et al. 1999, Dukes and Mooney 2004). These species often possess the ability to directly alter ecosystem processes, such as nutrient cycling and disturbance regimes, and can lead to dramatic alterations of native systems (Vitousek 1990). In a seminal study, Vitousek et al. (Vitousek et al. 1987) demonstrated striking affects to the nutrient budget of young volcanic systems in Hawaii invaded by a nitrogen fixing shrub, *Myrica faya* (since reclassified *Morella faya*). Resulting increases in nitrogen inputs to this naturally low nutrient system led to greatly modified succession and species diversity. In another widely cited example, the invasion of C^4 grasses into Hawaiian submontane woodlands has altered community composition and nutrient budgets through the introduction of fire into systems where it was previously rare or absent (D'Antonio and Vitousek 1992).

Native species in these systems are not fire adapted whereas the introduced grasses are both highly flammable and regenerate readily after fire. As a result, a positive feedback cycle develops between grasses and fire which facilitates the spread and long-term dominance of these invaders.

Chapin and others (Chapin et al. 1996, Dukes and Mooney 2004) suggest that novel trait invaders are most likely to cause significant alterations in native ecosystems. However, a sub-set of invasive plants do not possess novel ecosystem-altering characteristics. These species differ from natives in traits that are continuously distributed such as litter quality or relative growth rate (Dukes and Mooney 2004). Continuous trait invaders can alter ecosystem structure and functioning by forming dense monotypic stands that displace diverse communities of native vegetation. Direct impacts occur once an invader supplants native species and ecosystem properties and processes shift towards qualities of the invader. Indirect impacts occur through the loss of native species and biodiversity (Walker and Vitousek 1991, Alvarez and Cushman 2002, Yurkonis and Meiners 2004). Loss of taxonomic and structural diversity can significantly impact community and ecosystem level properties and processes (Lawton 1994, Tilman et al. 1997, Naeem et al. 1999, Hooper et al. 2005)

Biodiversity Theory

Ecological theory suggests that simplification and alteration of vegetation resulting from non-native plant invasions can affect ecosystem processes (i.e. energy transformations and matter cycling) via two alternative mechanisms. First, taxonomic simplification can affect ecological functioning through the loss of species performing as “foundation species” (Ellison et al. 2005) or “ecosystem engineers”(Jones et al. 1994). Foundation species are “ single species that define much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes” (Dayton 1972, Ellison et al. 2005). Exclusion of these species can lead to significant and cascading effects throughout the ecosystem (Ellison et al. 2005). For example, introduction of the Hemlock wooly agelid into eastern U.S. forests has led to widespread mortality of a dominant tree species, *Tsuga canadensis* (eastern hemlock). Declines in *Tsuga canadensis* abundance have initiated a rapid shift from a coniferous to deciduous forest type and significantly impacted forest structure (Jenkins et al. 1999), avian (Tingley et al. 2002) and insect (Ellison 2005) community composition (Jenkins et al. 1999) and soil nitrogen cycling (Jenkins et al. 1999) within these systems.

Second, the complementary resource use hypothesis (CRU) asserts that each species provides a unique contribution to ecosystem functioning (Naeem et al. 1999, Hooper et al. 2005). This assumption is based on the principal of competitive exclusion, in which inter-specific competition for limited resources drives biodiversity by restricting similarity among competitors (Hardin 1960). Species must evolve distinct methods of resource capture in order to avoid competitive deletion. Therefore, greater species diversity can be equated to greater niche differentiation and diversity of resource acquisition strategies which, in turn, facilitates more complete use of available resources (Hooper 1998).

It is important to note that, whereas empirical evidence supports the relevance of CRU in species poor systems, the degree to which CRU applies to species rich systems, such as floodplain forests (Gregory et al. 1991, Naiman et al. 1993, Pollock et al. 1998), is unclear (Schwartz et al. 2000). Plants operate on a limited set of resource acquisition strategies, and greater diversity increases the likelihood that species will perform similar ecological roles. Thus, loss of a single species may be compensated for by the other, remaining species. However, even though the functional role of species diversity may not be presently apparent, individual species traits can play an important role under altered environmental conditions. For example, diversity may be integral in maintaining ecosystem functioning following external disturbance (Chapin III et al. 2000, McCann 2000).

Riparian Plant Invasions

Riparian forests are especially well suited for studying the ecological consequences of invasive plants resulting from their displacement of native species. The regular disturbance, high productivity, and geomorphic heterogeneity characteristic of riparian corridors result in a naturally high degree of floristic and structural diversity (Gregory et al. 1991, Naiman et al. 1993). Additionally, there is an extensive body of research demonstrating the functional role of riparian forests in regulating the microclimate, channel morphology, nutrients and energy resources of adjacent rivers and streams (Vannote et al. 1980, Cummins et al. 1989, Bilby and Ward 1991, Fetherston et al. 1995, Naiman et al. 1998, Tabacchi et al. 1998, Naiman et al. 2000, Wissmar and Bisson 2003). For instance, allochthonous litter inputs are a primary source of organic matter into streams and serve as food and habitat for aquatic macro-invertebrates (Cummins et al. 1989, Wallace 1997). The diverse structure of riparian vegetation provides an array of habitats for terrestrial and lotic organisms (Naiman et al. 2005). Shade from the riparian canopy controls the light and temperature of adjacent streams (Wissmar and Bisson 2003). Tree roots provide bank stability and downed riparian trees supply inputs of large woody debris-- a key regulator in the flow of water and sediment (Tabacchi et al. 1998).

Riparian corridors are also highly susceptible to invasions by non-native plants (Pysek 1994, Planty-Tabacchi et al. 1995). Regular flooding disturbance, ample nutrient availability and high degree of habitat connectivity provide the opportunity for introduced invaders to spread rapidly throughout riparian corridors (Naiman et al. 1993, Planty-Tabacchi et al. 1995, Tickner et al. 2001). Studies examining the landscape patterns of plant invasions demonstrate that early successional floodplain forests contain a greater number and cover of non-native plants than nearby upland and late successional riparian sites (DeFerrari and Naiman 1994).

Reduction of riparian invasive plants is a common goal of river restoration initiatives and often requires “comprehensive and complex management approaches” (Wissmar 2003). It is therefore surprising that quantitative evidence directly testing for effects of invasive plants on biological and physical processes within riparian zones is limited. The prioritization of invasive plant control as a riparian restoration strategy is based on presumed ecological roles and relationships, anecdotal evidence, and a few, well-documented case studies of ecological impact. For example, spread of the introduced *Tamarix ramosissima* along rivers throughout the southwestern US has been demonstrated to profoundly alter riparian community composition (Busch 1995, Sher 2002), terrestrial wildlife habitat, fresh water availability, soil salinity (Vitousek 1990), fluvial geomorphology (Tickner 2001), fire frequency, organic matter dynamics (Kennedy and Hobbie 2004) and aquatic food webs (Bailey et al. 2001).

Riparian Litterfall and Mixed Species Litter

Leaf litter from riparian vegetation is a primary contributor to nutrient cycling and energy dynamics within riparian forest soils and adjacent streams. The influence of litter decay on soil mineral cycling and vegetation productivity within forested ecosystems has long been recognized (Killham 1994, Cadisch and Giller 1997, Aerts and Chapin 2000). Riparian forests are characterized by higher total litter production and faster decomposition rates than upland systems (Xiong and Nilsson 1997). Therefore, leaf litter may be especially important in determining soil fertility and plant growth within riparian corridors.

A substantial body of research demonstrates the role of riparian litterfall as an important, primary source of nutrients and energy into aquatic food webs (Petersen and Cummins 1974, Cummins et al. 1989, Wallace et al. 1999). Within forested stream corridors, aquatic microbes and shredding macroinvertebrates rely on riparian leaf litter as a direct food source (Wallace 1997). Additionally, microbial decomposition, invertebrate fragmentation and ingestion of riparian leaf litter create fine particles of organic matter that are subsequently transported downstream and consumed by collector-gatherer and scraper macroinvertebrates (Naiman and Bilby 1998) . Shredder, collector-gatherer, and scraper macroinvertebrates, in turn, serve as a primary prey resource for higher trophic consumers such as fish (Naiman and Bilby 1998).

The initial chemical composition of leaf litter, particularly the carbon:nitrogen or lignin:nitrogen ratio, is a key determinant of decomposition rates and nutritional resource quality (Petersen and Cummins 1974, Irons et al. 1988, Naiman and Bilby 1998, Motomori et al. 2001). In general, the C:N or Lignin:N content of litter is negatively correlated with resource quality and the rate of nutrient release from decomposing plant material (Cadisch and Giller 1997). Lignin is a structural carbohydrate that provides rigidity to vascular plants and is the most recalcitrant out of all naturally produced organic chemicals (Cadisch and Giller 1997). This complex compound also retards leaf break-down by shielding other structural polysaccharides from microbial attack. Nitrogen, on the other hand, is commonly the limiting nutrient for microbial growth and turnover. Therefore, higher nitrogen concentrations facilitate the mobilization of litter constituents by microbial decomposers. Under low nitrogen conditions, decomposers are nitrogen limited and will retain available nitrogen in their own biomass, thereby making it unavailable to plants and other organisms. Decomposition rates and leaf litter palatability are also related to concentrations of secondary plant compounds (Boulton and Boon 1991, Hagerman and Butler 1991). For example, condensed tannins bind to proteins and decrease the availability of leaf nitrogen to stream organisms (Boulton and Boon 1991).

Leaves from various species with diverse chemical and physical characteristics differ in their breakdown rates and patterns of invertebrate colonization (Petersen and Cummins 1974, Parkyn and Winterbourn 1997, Quinn et al. 2000). The species richness (Gartner and Cardon 2004, Swan and Palmer 2004, Lecerf et al. 2005) and composition (Swan and Palmer 2006) of riparian litterfall can influence its value as a food resource for aquatic consumers. Peterson and Cummins (1974) describe a “processing continuum” along which nutrients from leaves with a range of decomposition rates sequentially become available for use by aquatic organisms. In this study, invertebrate colonization of leaf packs reflected the addition of new food sources as slower decomposing leaf species became functionally available. These findings suggest that a diversity of leaf types can increase the period of time over which allochthonous litter is available as a food resource.

Empirical evidence also demonstrates that interactions among multi-species leaf litter can affect decomposition rates and nutrient dynamics (Leff 1989, Blair et al. 1990, McArthur et al. 1994, Kaneko and Salamanca 1999, Smith and Bradford 2003, Gartner and Cardon 2004). Several alternate mechanisms can account for these results. First, mixing litter alters the chemical environment and facilitates the movement of nutrients and secondary chemicals among constituent species. For example, litter of high nitrogen status could enhance the decomposition of adjacent litters, while low quality litter can have the opposite effect (Wardle 1997). Second, mixing litter can affect decomposer biomass and activity. Multiple species can lead to increased microhabitat complexity and support a more diverse and abundant decomposer community (Gartner and Cardon 2004).

Pacific Northwest Riparian Forest Communities

An essential component in a study of the ecological consequences of non-native plant invasions is to consider the role of displaced native species in ecosystem functioning. River and riparian systems throughout the Pacific Northwest (PNW) are recognized as vital natural resources, particularly in relation to maintaining quality habitat for six species of federally protected salmon (Naiman and Bilby 1998). Consequently, an impressive body of research has demonstrated the role of riparian vegetation in controlling the structure and function of river corridors. This summary will focus on vegetation communities' characteristic of low elevation floodplain corridors and tributary channels because these habitats are frequently invaded by knotweed.

The structure of riparian forests throughout PNW floodplains is commonly a mosaic of forest patches composed of various species assemblages and successional stages. At a local scale, flooding disturbance (and related factors such as elevation above active channel and substrate texture) is a key process determining riparian community composition (Fonda 1974, Naiman et al. 2005). Low terrace and floodplain forests adjacent to the active channel are dominated by fast growing, highly productive species that can withstand frequent flooding such as *Alnus rubra*, *Populus balsamifera*, and *Salix* spp. Barring repeated disturbance, after around 100 years early pioneer communities are replaced by forests dominated by less flood tolerant, slower growing and long lived coniferous species such as *Picea sitchensis, Tsuga heterophylla, Thuja plicata,* and *Pseudotsuga menzenzii* (Agee 1988, Naiman et al. 2000). Coniferous forests are common on landforms where flooding disturbance is less frequent such as floodplain terraces, steep valley walls and farther back from the active channel.

Deciduous and coniferous trees are foundation species within riparian and river ecosystems. Riparian trees provide streambank stability, sequester nutrients, determine the microclimate and supply seasonal nourishment to adjacent lotic systems. Empirical investigations have focused on the functional role of *Alnus rubra* as a key early seral species. As a primary N-fixer and canopy dominant during the first 50-70 years of stand development, *A. rubra* appears to exhibit strong control over the nitrogen biogeochemistry within floodplain forests and adjacent lotic environments. Nitrogen has been shown to be a limiting nutrient within Pacific Northwest forests as well as rivers and streams (Chapin 1980, Chapin et al. 1986, Perrin et al. 1987, Volk 2004). Previous studies have demonstrated that the presence of red alder increases the nitrogen content of riparian soils and has a positive effect on growth of associated plant species (Binkley 1983, Binkley et al. 1992, Hibbs et al. 1994). Additionally, stream communities also benefit from *A. rubra* nitrogen subsidies. Nitrate resources leached from N-saturated alder are transported into aquatic systems via ground and surface waters and can enrich benthic production (Bechtold et al. 2003, Compton et al. 2003). Autumn inputs of nitrogen-rich red alder leaf litter provide an important source of nitrate and ammonia to aquatic detritivores and macro-invertebrate communities (Volk, 2003).

A key ecological function of coniferous riparian trees is their contribution of large woody debris (LWD) to the active channel and riparian floodplains (Fetherston et al. 1995, Naiman et al. 1998, Naiman et al. 2000). Instream LWD exerts local control over the routing of water and sediment which then influences channel morphology and habitat complexity for aquatic organisms (Bilby and Ward 1989, Bilby and Ward 1991, Fausch and Northcote 1992). Additionally, the reduction in shear stress immediately downstream of LWD provides sites for seedling germination of deciduous species (Fetherston et al. 1995). Within riparian floodplain and terrace forests, LWD inputs serve as important sites for the colonization and establishment of both coniferous and deciduous trees (Naiman and Bilby 1998). On terraces of the South Fork Hoh River, Olympic National Park, WA, over 90% of both western hemlock and Sitka spruce seedling recruitment occurs on LWD nurse logs (McKee et al. 1984).

Fewer studies have focused on the ecological role of understory riparian vegetation. Whereas the species richness of riparian tree canopy species is typically low, the ground layer is composed of a mixture of many herbaceous and shrub species.

Common riparian understory species, such as vine maple (*Acer circinatum*), contribute nutrient-rich litter to forest soils that positively impact site fertility and growth of neighboring coniferous trees (Tashe and Schmidt 2003). Furthermore, because of their higher turnover rates, herbaceous and shrub vegetation are thought to be useful indicators of current soil and hydrologic conditions (Naiman et al.2005).

Chapter 3: Study Organism and Study Site

Study Organism

The taxonomic classification of Japanese (*Polygonum cuspidatum*), giant (*Polygonum sachalinense*), and bohemian (*Polygonum x bohemicum*) knotweed is a subject of ongoing debate, and various authors place these species in the genera *Reynoutria*, *Polygonum*, or *Fallopia* (Shaw and Seiger 2002, Zika and Jacobson 2003, Yurkonis and Meiners 2004). This paper adheres to the *Polygonum* nomenclature because it is commonly used throughout the Pacific Northwest, North America (Zika and Jacobson 2003). All three congeners closely resemble one another in morphology and invasive habits; and are often grouped together under the general term "Japanese Knotweeds[1]."

Polygonum cuspidatum and *P. sachalinense* are native to northeastern Asia where *P. cuspidatum* is an early colonizer of volcanic slopes, riparian floodplains, and landslide scars and can usually be found in sunny places on hills and mountains (Seiger 1997). *P. sachalinense* is most common throughout Japan and the Sakhalin islands where it rapidly forms colonies along roadsides and river banks in gravelly soils (Inoue et al. 1992). Both species were first brought from Japan to Europe during the second half of the 19th century, and subsequently introduced to North America during the late 19th century as fodder and garden ornamental plants (Sukopp and Starfinger 1995). *P. x bohemicum* is the hybrid between *P. cuspidatum* and *P. sachalinense* and has, until recently, often been mistaken for the parental species *P. cuspidatum* throughout its introduced range (Seiger 1991, Zika and Jacobson 2003). Evidence suggests that the hybrid, *P. x bohemicum*, may be more abundant than either of the parental species in the United States (Zika and Jacobson 2003).

Japanese knotweeds are recognized as problem invaders of riparian and various human-disturbed habitats throughout North America, Europe, New Zealand and

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[1] *Polygonum polystachyum* Meissne (Himalayan knotweed) is another closely related congener invading the U.S. and Europe. *P. polystachyum* is excluded from mention in the text because the shallow, creeping rhizome system, lanceolate leaf morphology and shorter stature of this species differentiate it from *P. cuspidatum, P. sacchalinense, and P. bohemicum*. Additionally, throughout the Pacific Northwest, *P. polystachum* appears to be less abundant and more susceptible to eradication that the other three species.

Australia. In North America, Japanese knotweeds are commonly found on both east and west coasts, and have been observed as far North as Nova Scotia and Newfoundland, and as far south as North Carolina (Seiger 1991). Throughout the Pacific Northwest, knotweeds have been identified as noxious weeds in California, Oregon, Washington and British Columbia (Potash 2002). Within the state of Washington, invasive knotweeds are known to be spreading in all counties west of the Cascades (Potash 2002). The Washington State Weed Control Board currently lists all three species as class B noxious weeds and quarantines all three so that they may not be sold (although, they continue to be sold under the names *Fallopia* or *Reynoutria*).

Certain morphological, phenological and chemical characteristics of Japanese knotweeds appear to facilitate their invasion success. Like many non-native invasive plants, Japanese knotweeds are early seral species in their native habitats and thus are well suited to colonize disturbed sites (Seiger 1984). As herbaceous perennials, knotweeds are able to utilize energy stored in persistent tissues to grow rapidly in early spring (Brock et al. 1995). Knotweeds develop tall (3-5 m), dense colonies which produce a continuous leaf canopy and monopolize understory light resources. These species also form extensive rhizome systems that can extend 15-20 m from a parent plant and provide a competitive advantage in obtaining soil water and mineral nutrients. Additionally, the bamboo-like, ligneous stems of knotweed are slow to decompose and can form a thick litter layer that may inhibit the establishment of potential competitors (Beerling et al. 1994). Literature on the allelopathic potential of giant knotweed cites “potent” allelochemicals contained within rhizome, root and leaf extracts (Inoue, 1992).

Knotweed’s mechanisms of reproduction and dispersal contribute to their rapid invasion along river corridors. Within their introduced range, the principal mode of reproduction appears to be vegetative. Japanese knotweeds can regenerate from both rhizome and stem fragments (Brock et al. 1995) where lateral buds are located (Adachi et al. 1996). Knotweed rhizomes possess a particularly remarkable capacity to regenerate. Studies have shown that fragments as small as 0.7g can grow into a new plant. Additionally, rhizomes can regenerate when buried up to 1 meter deep, and have been observed growing through 5 cm of asphalt (Child and Wade 2000, Potash 2002).

Until recently, it was thought that invasive knotweed populations reproduce solely by vegetative means outside of their native habitats. However, Forman and Kesseli (2003) tested the germinability and survival knotweed seeds collected from the East Coast, U.S., and found a high % germinability, observed wild seedlings at several field sites, and recorded seedling survival over winter with re-sprouting the following spring. Within the Pacific Northwest, knotweed seeds also have a high germination rate (R.T. Haard, Fourth Corner Nurseries, Bellingham, WA, personal communication) and wild seedlings have been sighted (personal observation). However, the role of sexual reproduction in knotweed's spread throughout riparian corridors remains poorly understood.

Despite their similarities, Japanese knotweeds can be distinguished from each other on the basis of several morphological characteristics (Zika and Jacobson 2003). *Polygonum sachalinense* commonly grows to a height of 5 m, whereas *P. cuspidatum* is usually 1.5-2 m tall. The leaves of *P. sachalinense* are larger than *P. cuspidatum* and have a deeply cordate base, whereas the leaves of *P. cuspidatum* are truncate to slightly acuminate. The inflorescence length of *P. sachalinense* is shorter than the length of a subtending mid-branch leaf, whereas *P. cuspidatum* inflorescence is longer than the subtending leaf. *P. bohemicum* is generally characterized as having an intermediate form in regards to these properties. According to identifying characteristics described in Zika and Jacobson (2003), the dominant species colonizing Grandy Creek was positively identified as *P. sachalinense*.

Functional attributes such as reproductive capacity (Bimova et al. 2003, Pysek et al. 2003, Bimova et al. 2004), response to control (Bimova et al. 2001) and genetic variation, (Hollingsworth et al. 1998, Hollingsworth et al. 1999, Mandak et al. 2003) also differ between species. Bimova et al. (2003), compared the regeneration capacity among invasive *Polygonum* congeners and found the hybrid, *P. x bohemicum* to be the most successful taxon in terms of regeneration and establishment of new shoots. The hybrid taxon has also been shown to be the most difficult to control (Bimova et al. 2001). Several studies examined levels of genetic variation among the three congeners in Europe, and found *P .x bohemicum* to have the greatest number genotypes. In contrast, *P. sachalinense* has limited genetic variation, and *P. cuspidatum* appears to be genetically uniform within its introduced range (Hollingsworth et al. 1998, Pysek et al. 2003).

Study Site

This study was conducted at Grandy Creek, a tributary of the mid-lower Skagit River located in Skagit County, Washington. The local climate is typical for the Puget Sound region, with measurable precipitation occurring an average of 157 days per year, typically between the months of September and April (WDFW 2004). The lowlands of western Skagit County receive approximately 89 cm of measured precipitation (Klungland and McArthur 1989), while the Concrete area, at 59 m elevation, receives 170 cm of precipitation annually (Weisberg and Riedel 1991).

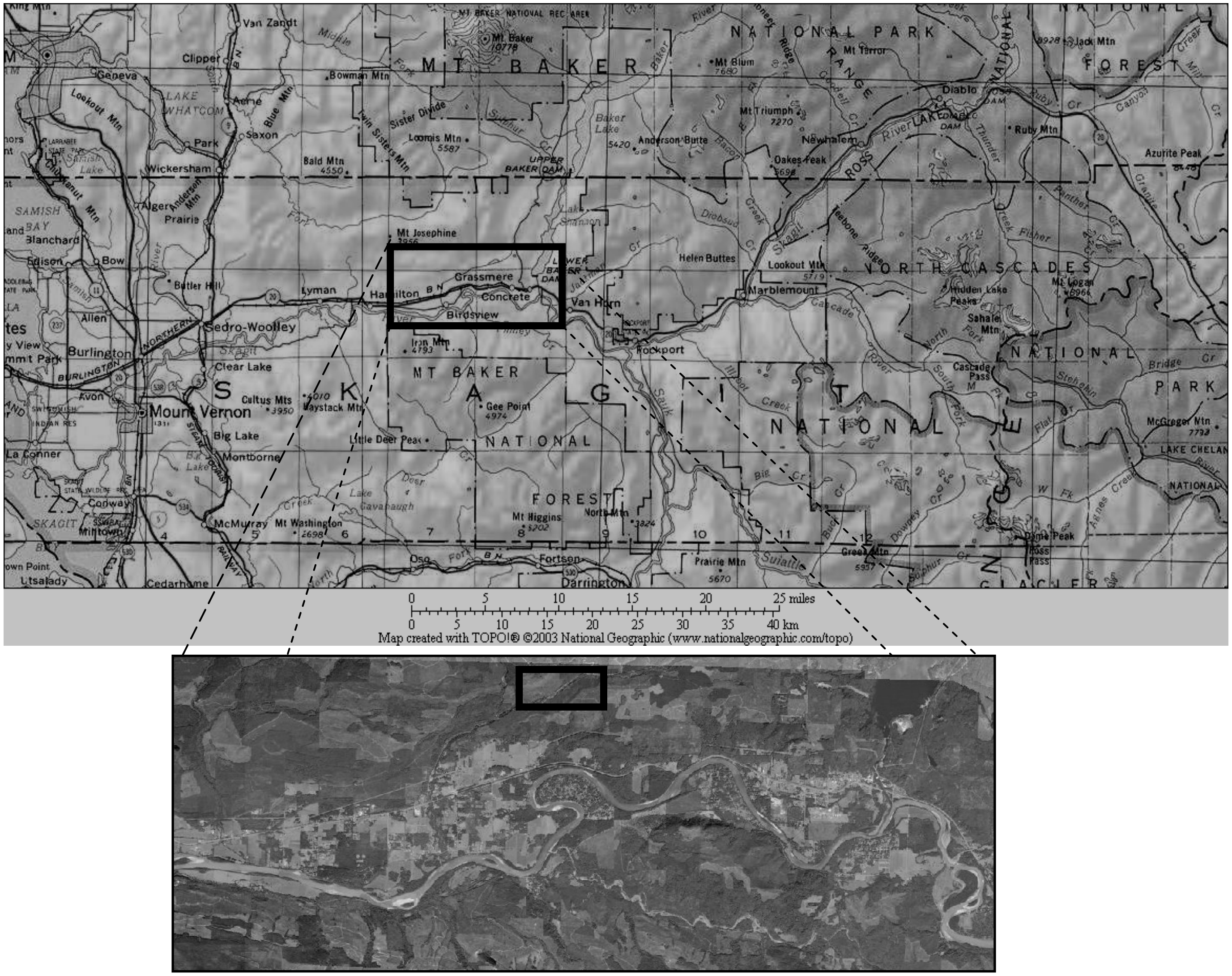
The Skagit River is one of the largest rivers in Washington State and the largest river in the Puget Sound region (Williams et al. 1975, DeShazo 1985). The 259 km long, Skagit mainstem lies within the North Cascades mountain range and the Skagit watershed encompasses over 8060 km^2 within the North Cascades spanning Snohomish, Skagit, and Whatcom counties and has headwater regions in British Columbia (WDFW 2004). This system is considered one of the largest and last remaining strongholds of fish and wildlife habitat in the Puget Sound region (DeShazo 1985, Beamer et al. 2003).

Grandy Creek meets with the Skagit at river km 73 (Ames and Bucknell 1981). The headwaters of Grandy Creek originate 1.6 km above the inlet of Grandy Lake, and it flows for approximately 12.2 km until reaching the Skagit (WDFW 2004). Grandy Creek is a meandering, braided channel that ranges from approximately 9 to 30 m wide (WDFW 2004). The Grandy Creek watershed drains approximately 31.7 square km and includes Grandy Lake, tributaries upstream of the lake, and small fish bearing tributaries to Grandy Creek (WDFW 2004). The watershed varies in elevation from about 35 m near the confluence, to over 366 m along the eastern watershed boundary (WDFW 2004). Washington Department of Fish and Wildlife recorded Grandy Creek discharge from November 2002 through March 2003 and calculated a 2.28 cms winter daily average with a low of 0.18 cms in early November and a high of 7.2 cms in March (WDFW 2004).

Within its section of the Skagit, Grandy Creek is utilized extensively by salmonids (Williams et al. 1975). Anadromous fish known to spawn in Grandy Creek include steelhead (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), coastal cutthroat, chinook salmon (*Oncorhynchus tshawytcha*), pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) (WDFW 2004). The species that have been known to spawn with greatest frequency include cutthroat, steelhead and coho (WDFW 2004). Because its headwaters originate at Grandy Lake, there is more flow stabilization at Grandy Creek than other nearby streams (WashingtonTrout 2004). Additionally, Grandy Creek tends to have somewhat warmer winter and spring temperatures than the mainstem Skagit and other nearby tributaries because of its south facing aspect (WashingtonTrout 2004).

The riparian forest community along Grandy Creek is dominated by deciduous tree species including red alder (*Alnus rubra)*, big-leaf maple, black cottonwood (*Populus trichocarpa)* and willows *(Salix spp.)* in the overstory. Common understory species include salmonberry (*Rubus spectabilis*), thimbleberry (*Rubus parviflorus*), vine maple (*Acer circinatum*), stinging nettle (*Urtica dioica*), and sword fern (*Polystichum munitum*). Western red cedar (*Thuja plicata*), Douglas fir (*Psudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) are the most common coniferous trees. *Polygonum sachalinense* was the dominant non-native invasive plant colonizing the riparian corridor along my study reach. There were a number of common co-occuring invaders including Himalayan blackberry (*Rubus discolor*), reed canary grass (*Phalaris arundinacea*) and butterfly bush (*Buddleja davidii*).

The study reach spanned approximately 1.6 river km in length. The start of the study reach was randomly selected from within the portion of Grandy Creek below Grandy Lake with the largest riparian buffer, in order to reduce effects from an adjacent road. The upland areas surrounding the study reach were predominantly owned by commercial timber companies.



Map created with TOPO!® ©2003 National Geographic (www.nationalgeographic.com/topo)

Figure 1. Map of Grandy Creek field site. The illustration, above, shows the location of Grandy Creek along the Skagit River, Skagit County WA. The bottom photo shows the field site location along Grandy Creek (www.skagitcounty.net).

Chapter 4: Methods

Composition and Diversity of Riparian Understory Vegetation

Vegetation was sampled within floodplain forest patches experiencing varying levels of knotweed invasion to assess differences in native species diversity and community composition. Forty, 10 x 2 m belt transects were placed perpendicular to the stream channel at randomly determined locations spaced 10-20 m apart. Transect locations were determined randomly according to a number table. Sample plots were restricted to early-mid successional (i.e. deciduous dominated) riparian communities colonizing in-stream gravel bars or low-terrace floodplains. Sampling was confined to these areas because they represent the riparian habitats and community associations most commonly invaded by knotweed (Beerling et al. 1994, Dawson and Holland 1999, Collingham et al. 2000, Bimova et al. 2004) and because autumnal senescence of deciduous forest communities is a primary contributor of allochthonous litterfall to streams (Volk et al. 2003, Hart 2006) . Additionally, sampling plots were confined to riparian forest patches that contained at least one native understory (height > 3m, diameter at breast height (dbh) <5cm) or overstory (dbh >5cm) tree. The purpose of this criterion was to avoid sampling freshly established gravel bars where knotweed is growing on bare mineral substrate because it was unclear whether native species would have had adequate time to establish in these areas.

Along each transect the density of knotweed stems, shrubs and large herbs, tree seedlings (<0.5 m tall) saplings (0.5-3.0 m tall) and understory trees (dbh<5cm) were tallied and individuals identified to species or genus. Herbaceous species taller than 0.5 meters were included within the “shrub” data set. Tree and shrub counts were based on primary stems without accounting for the clonal nature of various riparian species. Ground species cover and composition was measured in 2, 1 m^2 quadrats randomly placed within the front and back five meters of each transect, relative to the stream channel. Results from the two quadrats were averaged for each vegetation sampling transect. All plants with a height of less than 0.5 m were considered ground species and included in these measurements. Percent cover of each species within the quadrat was visually estimated and quantified according to a 6 grade Daubenmire cover scale, <5%, 5-25%, 25-50%, 50-75%, 75-95%, >95% (Mueller-Dombois and Ellenberg 1974). Unidentified plants were collected for later identification in the herbarium.

Data on height above wetted channel (m), slope (˚), average overstory tree diameter (dbh), overstory tree density (m^2), and percent canopy cover were collected at each transect. Overstory tree diameter and stem density were determined at 2.5 m and 7.5 m along each transect using a point-quarter-method in which the diameter and distance to the closest tree were measured in each cardinal direction (Mueller-Dombois and Ellenberg 1974). Percent canopy cover was measured with a densiometer at random locations within the front and back five meters of each transect and quantified according to the Daubenmire cover scale (Mueller-Dombois and Ellenberg 1974).

Multiple linear regression analysis was performed using a stepwise selection method (holding P to enter at 0.05 and P to remove at 0.10) to assess the relationship between knotweed stem density and the species richness and/or abundance of native herbs, shrubs and juvenile trees while adjusting for plot-level environmental characteristics. Separate models were considered for each understory vegetation response variable: juvenile coniferous tree density (20 m^2), juvenile deciduous tree density (20 m^2), juvenile red alder density (20 m^2), shrub density (20 m^2), shrub species richness (20 m^2), percent herbaceous cover (m^2), herbaceous species richness (m^2), native herbaceous cover (m^2), native herbaceous species richness (m^2), introduced herbaceous cover (m^2), and introduced herbaceous species richness (m^2). Dependent variables were Log_{10} transformed as needed to normalize data distributions for statistical analysis.

Independent variables included in the model selection process were knotweed stem density (20 m^2), average overstory dbh (cm), percent tree canopy cover, overstory tree density (m^2), height above wetted channel (m), and slope (º). Prior to model selection, bivariate analysis was performed with Spearman's Rank Correlations (r_S) to test for collinearity among independent variables. Significantly correlated variables were not included in the same regression models. Polynomial terms of independent variables were also included in the model selection when associations with understory vegetation response variables appeared to be non-linear. A two-sided 0.05 level test determined statistical significance for all analyses.

Additionally, knotweed density/transect was divided into three categories based on natural breaks in the data: low density (0-15 stems, n = 13), medium density (16-89 stems, n = 16), and high density (≥90 stems, n = 10). Parameters describing the composition and abundance of the native understory vegetation were compared across these three levels of knotweed invasion.

Litterfall Quantity

Autumn litterfall was collected in seven knotweed invaded and seven un-invaded forest patches with three (38cm X 60cm) traps placed ≤ 2m from the stream edge and adjacent to a vegetation sampling transect. Litter sampling sites were selected to reflect the range of overstory tree density and basal area measured in the vegetation transects. Traps were constructed from laundry baskets with window screen mesh fastened to the insides and elevated several cm above the ground. To prevent trap movement and loss of contents during storm events, two metal stakes were hammered through the center of each basket. In order to deter and detect public tampering, a weather-proofed notice was attached to each trap and a small stone was placed inside trap nets to mark whether contents had been displaced.

Accumulated litter was collected weekly throughout autumnal senescence (September 13 - November 18, 2004). Upon collection, the litter was dried in an oven at 40˚C for 5-7 days, sorted by native or knotweed and weighed to the nearest 0.1 g. These data were used to compare the type and quantity of allochthonous litter inputs into streams within knotweed invaded and uninvaded sites. Although stream litter inputs were not measured directly, placing traps on the stream bank was considered a suitable surrogate because 1) vertical litter fall would probably not differ; 2) horizontal litter inputs enter streams from the riparian forest floor; and 3) it minimized loss of samples from flooding disturbance.

Student’s t-test was used to detect differences in the average quantity and type of autumnal leaf litter inputs from knotweed invaded versus un-invaded, native floodplain forest stands. Statistical significance was determined at a two-sided 0.05 level.

Litter Nutrient Quality

To assess differences in the nutrient quality of *P. sachalinense* leaves versus leaves of dominant native riparian flora, litter from mature green leaves and newly abscised leaves of *Polygonum sachalinense, Alnus rubra, Salix sp., Populus deltoides,* and *Rubus spectabilis* were collected and pooled into a single sample for each species. Only leaves that detached when plants were shaken to simulate wind were collected. Leaves were oven dried at 50˚C, ground with a mortar and pestle and analyzed for % carbon and nitrogen. Nutrient analysis was conducted by dry combustion using a CHN Analyzer, Perk Elmer model
2400, at the University of Washington, College of Forest Resources analytical laboratory. The amount of each nutrient withdrawn before abscission was then estimated as:

Nutrient absorbed = 100 x (Fresh Leaf Concentration – Dead Leaf Concentration/
Fresh Leaf Concentration) (Lindsay & French, 2005)

Chapter 5: Results

Composition and Diversity of Riparian Understory Vegetation

Spearman's rank correlations (r_S) among transect-level environmental variables and knotweed stem density illustrate significant collinearity among average overstory dbh and percent canopy cover ($r_S = 0.563$); slope and height above wetted channel ($r_S = -0.444$); knotweed stem density and percent canopy cover ($r_S = -0.472$); knotweed stem density and slope ($r_S = -0.367$) (Table 1). Subsequently, significantly correlated variables were included in separate multivariate regression models.

Results from step-wise multiple regression (Table 2) illustrate a significant negative association between the species richness and/or abundance of native herbs, shrubs and juvenile trees (dependent variables) and knotweed stem density while adjusting for plot-level environmental characteristics (independent variables). Of the six independent variables included in the regression analyses, knotweed stem density was the only factor included in all eleven models. Average overstory dbh and height above wetted channel were also included in several models. Standardized regression coefficients were computed to assess the relative importance of each independent variable while adjusting for all other factors included in the final model. Standardized regression coefficients represent the amount of change in the dependent variable per one standard deviation unit of change in the independent variable.

The best-fitting stepwise regression model ($R^2 = 0.341$) for juvenile conifer density included knotweed stem density, knotweed stem density^2, and average overstory dbh. Both factors exhibited a significant negative association with juvenile conifer density. The standardized regression coefficient for knotweed stem density ($\beta_{std} = -1.166$) was thirty times greater than average overstory dbh ($\beta_{std} = -0.037$). This suggests that of these measured factors knotweed stem density exhibited the strongest association with juvenile conifer density.

Knotweed stem density, average overstory dbh, and height above wetted channel were included in the best fit models for both juvenile deciduous tree density ($R^2=0.562$) and juvenile *A. rubus* density ($R^2=0.567$). All three factors exhibited a significant negative association with both juvenile deciduous tree and *A. rubus* density. The standardized regression coefficient for average overstory dbh (β_{std} = -0.521) was slightly greater than knotweed stem density (β_{std} = -0.413) and height above wetted channel (β_{std} = -0.336) in the regression model for juvenile deciduous tree density. This suggests that all three factors had similar associations with juvenile deciduous tree density. In contrast, the standardized regression coefficient for knotweed stem density (β_{std} = -0.364) was considerably greater than average overstory dbh (β_{std} = -0.011) and height above wetted channel (β_{std} = -0.021) in the regression model for juvenile *A. rubus* density. This suggests that, of these measured factors, knotweed stem density exhibited the strongest association with juvenile red alder density.

Knotweed stem density and average overstory dbh were included in the best fit models for shrub density (r^2= 0.489) and shrub species richness (r^2=0.534). Knotweed stem density exhibited a significant negative association with both shrub density and species richness whereas average overstory dbh's association was positive. The standardized regression coefficient for knotweed stem density (β_{std} = -0.510) was slightly greater than average overstory dbh (β_{std} = 0.465) in the regression model for shrub density. This suggests that both factors had similar associations with shrub density, but in the opposite direction. Similar results were obtained from the regression model for shrub species richness.

Knotweed stem density was the only factor included in the best fit models for herbaceous percent cover (r^2=0.462, $\beta_{std.}$=-0.648) and species richness (r^2 0.243, $\beta_{std.}$=-0.493). Knotweed remained the only factor included in the final model when the herbaceous data were broken down into native percent cover (r^2=0.453, β_{std} =-0.673) and species richness (r^2=0.283, β_{std} = -0.532) and introduced percent cover (r^2=0.162, β_{std} =-0.002) and species richness (r^2=0.25, β_{std} = -0.354). This suggests that knotweed stem density was the only measured factor significantly associated with herbaceous percent cover and herbaceous species richness.

Classifying transects into low, medium, and high *P. sachalinense* stem density illustrated decreasing herbaceous, shrub, and juvenile tree richness and/or abundance across knotweed density categories (Figure 1). Median ground and shrub species richness were reduced by 75% and 73% in high knotweed density as compared to low knotweed density plots. Percent herbaceous cover exhibited a 91% reduction in high density knotweed plots; shrub density exhibited a similar 81% reduction. Presence of conifer and deciduous juvenile tree densities were reduced by 41.5% and 61.9%, respectively, in high density plots. Presence of juvenile *A. rubus* was reduced by 43.8% in high knotweed density plots as compared to low density plots.

Litterfall Quantity

Comparison of autumnal litter quantity between native, uninvaded and knotweed invaded forest patches suggest that knotweed invasion alters the type but not quantity of allochthonous leaf litter inputs to Grandy Creek (Figure 2). The quantity of total allochthonous litter inputs (native plus knotweed leaves) was not significantly different across vegetation type. However, the quantity of native litter inputs was significantly lower in knotweed invaded stands. Throughout autumnal senescence, mean native inputs were 2014.6 kg/ha in native stands as compared to 625.0 kg/ha in knotweed invaded stands. This equates to an average 70% reduction of native litter inputs correlated with knotweed invasion.

Nutrient Composition

Nutrient analysis of green and senesced leaves from Grandy Creek illustrate striking differences between knotweed and native species in foliar nitrogen composition and autumnal re-absorption (Table 3). The C:N of senesced knotweed leaves is 51.5:1. This value is 38% (*Salix*) to 58% (*A. rubra*) higher than the C:N of senesced leaves from dominant native species at Grandy Creek. In contrast, the C:N of green, pre-senesced knotweed leaves is 13.3:1, a value 36% (*Salix*) to 61% (*A. rubra*) lower than dominant native species. Knotweed re-absorbs 75.5% leaf nitrogen prior to senescence whereas nitrogen re-absorption among dominant native species ranges between 4.8% in *A. rubra* to 33% in *Salix* species.

Table 1: Spearman rank correlations (r_S) between knotweed stem density/$20m^2$ and transect-level environmental variables. Spearman's correlation coefficient (above) and p-value (below) is noted for each variable. Canopy cover and average overstory dbh; height above wetted channel and slope; knotweed stem density and canopy cover; knotweed stem density and slope were significantly correlated and, subsequently, not included in the same multivariate linear regression models.

	Slope (˚)	**Height Above Wetted Channel (m)**	**Canopy Cover (%)**	**Average Overstory Tree DBH (cm)**	**Overstory Tree Density (m^2)**
Knotweed Stem Density	-0.367 0.022	0.273 0.097	-0.472 0.002	-0.127 0.440	0.306 0.058
Slope (˚)	-----	-0.444 0.005	0.036 0.826	0.198 0.226	0.11 0.946
Height Above Wetted Channel (m)	-----	-----	0.056 0.736	0.041 0.806	-0.049 0.767
Canopy Cover (%)	-----	-----	-----	0.563 <0.001	-0.165 0.341
Average Overstory Tree DBH (cm)	-----	-----	-----	-----	0.262 0.980

Table 2: Regression coefficients and *P* values from multivariate linear regression using a stepwise selection method modeling understory vegetation parameters (dependent variable) against knotweed stem density, 20m^2, and transect level environmental variables (independent variables). Transect level environmental variables included overstory tree density (m^2) average overstory dbh (cm), canopy cover (%), height above wetted channel (m), and slope (˚). Herbaceous species richness and percent cover were measured in 1m^2 quadrats. All other vegetation variables were measured in 20 m^2 belt transects.

Understory Vegetation Response Model	**β**	**β_{std}**	***P*-value**
Log_{10} Juvenile Conifer Density ($R^2 = 0.341$)			
Intercept	0.807	--	0.001
Knotweed Stem Density	-0.008	-1.166	0.007
Knotweed Stem Density^2	<0.0001	0.835	0.049
Average Overstory DBH	-0.027	-0.037	0.011
Log_{10} Juvenile Deciduous Density ($R^2 = 0.562$)			
Intercept	1.871	--	<0.001
Knotweed Stem Density	-0.005	-0.413	0.001
Average Overstory DBH	-0.065	-0.521	<0.001
Height Above Wetted Channel	-0.841	-0.336	0.006
Log_{10} Juvenile Red Alder Density ($R^2 = 0.567$)			
Intercept	1.379	--	<0.001
Knotweed Stem Density	-0.003	-0.364	0.003
Average Overstory DBH	-0.058	-0.011	<0.001
Height Above Wetted Channel	-0.526	-0.273	0.021
Shrub Density ($R^2 = 0.489$)			
Intercept	12.552	--	0.081
Knotweed Stem Density	-0.187	-0.510	<0.001
Average Overstory DBH	1.699	0.419	0.001
Shrub Species Richness ($R^2 = 0.534$)			
Intercept	2.290	--	0.023
Knotweed Stem Density	-0.027	-0.508	<0.001
Average Overstory DBH	0.272	0.465	<0.001
Log_{10} % Herbaceous Cover ($R^2 = 0.462$)			
Intercept	1.821	--	<0.001
Knotweed Stem Density	-0.041	-0.648	<0.001
Herbaceous Species Richness ($R^2 = 0.243$)			
Intercept	2.851	--	<0.001
Knotweed Stem Density	-0.015	-0.493	<0.001
Log_{10} % Native Herbaceous Cover ($R^2 = 0.453$)			
Intercept	1.521	--	<0.001
Knotweed Stem Density	-0.008	-0.673	<0.001
Native Herbaceous Species Richness ($R^2 = 0.283$)			
Intercept	1.988	--	<0.001
Knotweed Stem Density	-0.011	-0.532	<0.001
Log_{10} % Introduced Herbaceous Cover ($R^2 = 0.162$)			
Intercept	1.105	--	<0.001
Knotweed Stem Density	-0.006	-0.002	0.011
Introduced Herbaceous Species Richness ($R^2 = 0.25$)			
Intercept	1.042	--	<0.001
Knotweed Stem Density	-0.006	-0.354	0.027

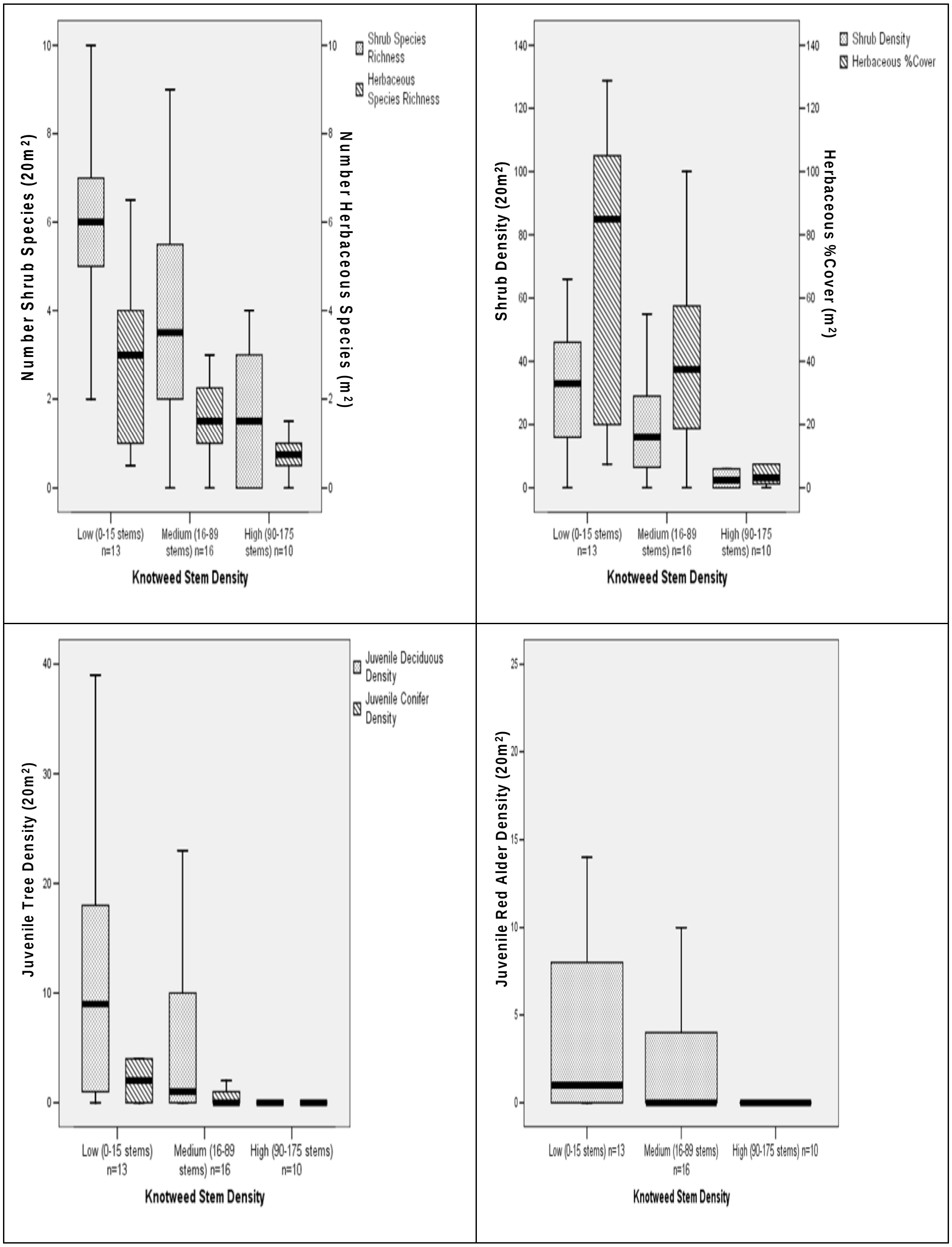


Figure 2 Species richness and occurrence of native understory herbs, shrubs and juvenile trees across categories of knotweed stem density. Knotweed density was classified into three categories: low density, 0-15 stems/transect (n=13), medium density, 16-90 stems/transect (n=16), high density, 91-165 stems/transect (n=10) based on natural breaks in the data set. Sampling areas for herbaceous species richness and percent cover were 1m^2 quadrats. All other vegetation variables were measured in 20 m^2 belt transects

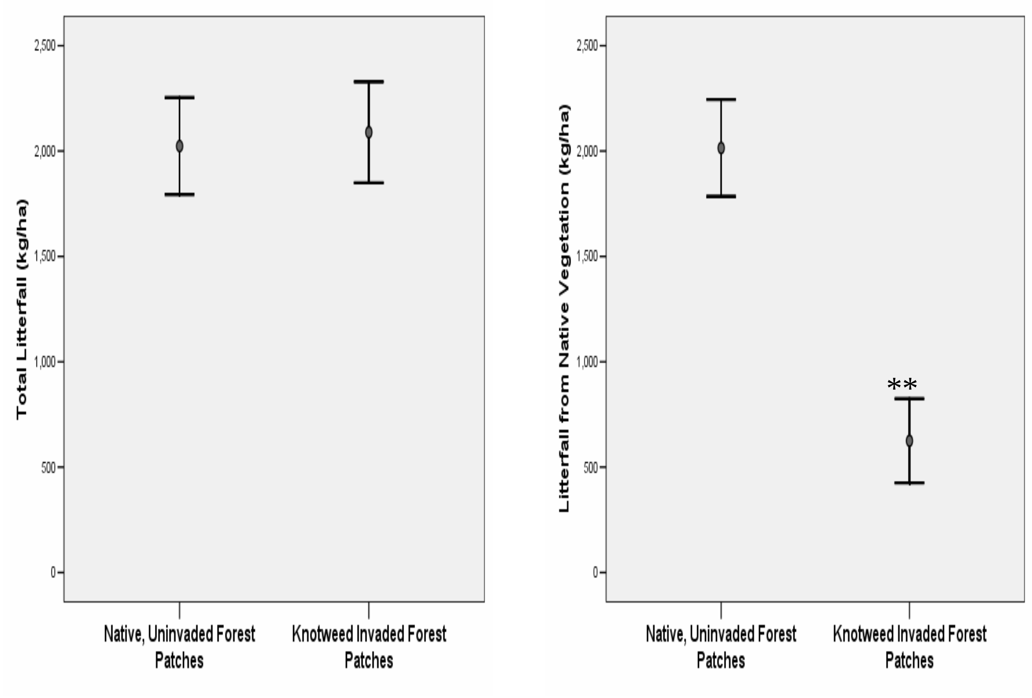


Figure 3. Mean biomass of autumnal leaf litterfall from knotweed invaded (n = 7) and native, uninvaded (n = 7) forest patches. Error bars = ± SEM. Statistically significant differences across vegetation types are indicated with ** at the 0.01 level.

Table 3. % Carbon (%C), % nitrogen (%N) and carbon: nitrogen (C:N) of green and senesced leaves from knotweed and the dominant native species along Grandy Creek. Nutrient content is based on a single bulk sample of leaves collected on site. * Nutrient values for senesced *Rubus spectabilis* leaves are froma study located along the Nooksack River, Whatcom County, Washington (Gwozdz 2003).

	%C Green Leaves	**%C Senesced Leaves**	**%N Green Leaves**	**%N Senesced Leaves**	**C:N Green Leaves**	**C:N Senesced Leaves**	**%C Resorbed**	**% N Resorbed**
A. rubra	47.6	48.3	2.4	2.3	20.1:1	21.4:1	-1.4	4.8
Salix sp.	46.3	45.7	2.2	1.4	21.5:1	31.7:1	2.3	33.1
R. spectabilis	45.0	44.1*	2.3	1.8*	19.9:1	24.5:1*	2.1	20.3
P. balsamifera	---	45.9	---	1.6	---	29.2:1	---	---
P. sachalinense	47.5	44.8	3.7	0.9	13.3:1	51.5:1	5.6	75.5

Chapter 6: Discussion and Conclusions

Ecological Significance

Unlike the majority of research investigating the ecological consequences of non-native invasive plants, this study does not focus on a species that introduces a novel, ecosystem altering trait into invaded systems. Knotweed differs from native riparian flora in traits that are continuously distributed (i.e. litter quality, relative growth rate). The ecological impacts of continuous trait invaders have often be overlooked in the scientific literature because these species are considered less likely to bring about dramatic changes in native ecosystems. However, empirical and theoretical evidence suggest that continuous trait invaders can significantly alter ecosystem structure and functioning by forming dense stands that dominate colonized areas and displace diverse communities of native vegetation.

Study results indicate direct and indirect mechanisms by which knotweed invasion can alter the nutrient cycling and productivity of riparian forests and adjacent aquatic food webs. Direct consequences of knotweed invasion are associated with an advanced ability to acquire and retain available nitrogen. Greater nitrogen content in knotweed's green leaves as compared to dominant native species is indicative of high uptake of nitrogen resources, nitrogen use efficiency or both. This explanation is substantiated by studies from *P. cuspidatum's* native habitat on Mt. Fuji where it functions as a primary colonizer following volcanic disturbance. Knotweed's rapid growth rate within this nitrogen-limited system has been demonstrated to be a consequence of both its high capacity to acquire nitrogen and efficient use of acquired nitrogen (Hirose 1984, Chiba and Hirose 1993).

Whereas knotweed's green leaves are rich in nitrogen, senesced knotweed leaves contain considerably less nitrogen than dominant native species. Nutrient reabsorbance from senescing leaves is a primary mechanism of nutrient conservation in perennial plants (Aerts 1996). Analysis of foliar nitrogen dynamics during senescence indicate that knotweed reabsorbs 75.5% of leaf nitrogen prior to leaf abscission while native species reabsorb 2.3-33%. This pattern suggests that knotweed transports a majority of foliar nitrogen resources down into its own rhizome system for reuse during subsequent growing seasons. In contrast, native species contribute a greater percent of their nutrient resources to riparian soils and aquatic environments through their leaf litter.

Price and colleagues (Price et al. 2001) investigated seasonal patterns of carbohydrate use and storage in *P. cuspidatum* introduced to United Kingdom and demonstrated a tight recycling of energy resources in this species. In this study, photoassimilate was reabsorbed upon leaf senescence, efficiently stored in the rhizome system prior to shoot death and then remobilized to new shoots early the next spring. Knotweed's efficient recycling of both nutrient and energy resources has important implications for invasion impacts on riparian forest communities and river ecosystems. At the community level, this trait can grant knotweed a competitive advantage over native species by enabling the rapid growth, early emergence, and high equilibrium biomass of knotweed populations (Aerts 1996). At the ecosystem level, knotweed's resorption of nutrients can affect the nutrient cycling and productivity of both riparian forest soils and aquatic food webs by sequestering available nitrogen and reducing the quantity of nutrients input through litterfall (Tateno and Chapin 1997).

Leaf litter from riparian vegetation comprises a primary source of organic matter in forested streams and backwater channels (Petersen and Cummins 1974, Cummins et al. 1989, Wallace 1997). Analyses of allochthonous litter inputs at Grandy Creek suggest that knotweed invasion can alter this important subsidy of nutrients and energy into aquatic food webs. Comparison of litter inputs from within knotweed invaded and knotweed free riparian forest patches demonstrate an average 70% reduction in native litter associated with knotweed invasion and the replacement of diverse native litter inputs with monotypic knotweed leaves. Changes in the composition and diversity of leaf species have been empirically demonstrated to affect the value of riparian litter as a food resource for aquatic consumers (Petersen and Cummins 1974, Blair et al. 1990, Boulton and Boon 1991, Gartner and Cardon 2004).

Results of litter nutrient analysis illustrate that the C:N of knotweed leaf litter is 50:1 whereas litter from native species varies between 20:1 (*A. rubra*) to 30:1 (*Salix*). The chemical composition, particularly the C:N, of species litter is a primary determinant of decomposition rates and resource quality (Melillo et al. 1984, Irons et al. 1988, Ostrofsky 1997, Quinn et al. 2000). Previous research demonstrates a positive association between litter nitrogen content and the feeding preferences, survivorship, growth rate and fecundity of litter feeding aquatic macro-invertebrates (“shredders”) (Ostrofsky 1997, Graca et al. 2001). By displacing leaf litter inputs from native vegetation and providing litter of lower nutritional quality, knotweed invasion could negatively impact the productivity of aquatic macroinvertebrate consumers. Shredding macro-invertebrates play a critical role in the energy dynamics of streams and constitute a primary food source for stream fishes (Petersen and Cummins 1974, Cummins and Klug 1979, Cummins et al. 1989, Naiman and Bilby 1998). Consequently, reductions in litter nutrient quality associated with knotweed invasion could potentially have cascading affects through stream food-webs.

Indirect consequences of knotweed invasion are likely to result from its exclusion of native species. Knotweed has wide ecological amplitude within riparian corridors and commonly colonizes freshly deposited gravel bars, floodplain forests, and low terrace forests beneath a deciduous canopy. Results from this study demonstrate a significant negative association between knotweed stem density and the species richness and/or abundance (density or percent cover) of native understory herbs, shrubs and juvenile trees while adjusting for average overstory dbh, percent canopy cover, slope, height above wetted channel and overstory tree density in these habitats. European studies investigating the effects of knotweed invasion on riparian community composition in have produced similar results (Beerling et al. 1994, Bimova et al. 2004). Bimova (2004) examined the effects of *P cuspidatum*, *P. sachalinense*, and *P. bohemicum* on vegetation communities along the Jizera River, Czech Republic and found all three species greatly reduced the occurrence and richness of resident herbs, shrubs and tree seedlings. Only three types of vegetation were found co-existing with knotweed species in this study: (1) other clonal ruderal species, (2) geophytes which complete their entire in early spring before knotweeds establish full biomass and (3) adult trees taller than 2 m which appear to be invasion resistant.

Among the species apparently displaced by knotweed include several foundation species within Pacific Northwest riparian forests. For example, the abundance of deciduous and coniferous juvenile trees declined with increasing knotweed stem density. Loss of juvenile trees in the understory can result in reductions of overstory tree density and canopy cover over time and alter the successional trajectory of riparian forests (Agee 1988). Empirical evidence from the region has demonstrated that loss of riparian trees has detrimental effects on the bank stability, hydrology, nutrient loading, micro-habitat conditions and aquatic biota of adjacent lotic systems (Bilby and Ward 1991, Naiman et al. 1998, Naiman et al. 2000).

Additionally, reductions in juvenile *A. rubra* abundance associated with knotweed invasion are of critical importance to the nitrogen biogeochemistry of both riparian forests and adjacent streams. *A. rubra* forms a symbiotic relationship with nitrogen fixing *Frankia* bacteria (Hibbs et al. 1994), and apparently does not have much need to re-absorb foliar nitrogen upon autumnal senescence (see Table 3). Nutrient rich *A. rubra* litter provides an important source of available nitrogen to both riparian forest vegetation and aquatic food-webs (Binkley 1983, Binkley et al. 1992, Hibbs et al. 1994, Compton et al. 2003, Volk et al. 2003). Consequently, knotweed invasion may alter the nutrient cycling and productivity within riparian corridors both directly, through nitrogen uptake and storage, and indirectly, through the competitive exclusion of *A. rubra*, a species recognized to play a key role in the nitrogen biochemistry of river corridors.

Study Limitations

Vegetation Sampling

The vegetation sampling portion of this study establishes a correlation between knotweed invasion and reductions in native plant diversity and/or abundance. Therefore, my data do not irrefutably establish that the loss in native species was actually caused by the invading knotweed. It remains possible that an external factor is driving both knotweed presence and native species absence within riparian forest plots. However, causal linkages may be inferred by considering the results of this study in light of field observations from knotweed control projects. Within Pacific Northwest watersheds, natural recruitment of native tree species can occur within one or two growing seasons following knotweed eradication. In sites where knotweed has been removed from young floodplain forest patches, regeneration of alder can occur within a single growing season (F. Geyer, personal communication, Quilayute tribe natural resources). Where knotweed has been removed from beneath an alder canopy, conifer regeneration occurs in areas previously containing a dense knotweed monoculture (F. Geyer, personal communication, Quilayute tribe natural resources). A combination of quantitative data illustrating strong negative correlations between knotweed density and field observations exhibiting native regrowth in knotweed control sites, provides strong evidence that knotweed invasion is prohibiting the establishment of native species in areas where they would otherwise be present.

Litterfall

Autumnal leaf litterfall from knotweed invaded sites (2089.2 kg/ha) were similar to native, uninvaded sites (2023.6 kg/ha) along Grandy Creek. These values are comparable to deciduous riparian sites in the Oregon Coast Range where 669.8 kg/ha/month have been recorded throughout autumn (Hart 2006), equating to 2009.4 kg/ha of leaf litterfall from September-November.

Regional studies examining total annual litterfall in early seral riparian sites demonstrate values of 2410 kg/ha/yr in a Coastal British Columbia (Neaves 1978), 3840 kg/ha/yr in Coastal Washington (Volk et al. 2003) and 5040 kg/ha in the Oregon Coast Range (Hart 2006). Greater litter quantities recorded in annual versus autumn litter studies reflect the fact that autumnal leaf senescence is not the sole source of riparian litterfall inputs to streams. Litter inputs can occur throughout several seasons and may be composed of assorted materials including leaves, twigs, fruits, flowers and seeds. For example, within PNW riparian corridors, red alder begins to shed its leaves in summer (Hart 2006) and a pulse of alder catkins, seeds, and bud scales occurs in early spring (Volk et al. 2003). These nitrogen rich spring/summer litter inputs represent a potentially important nutrient subsidy to aquatic detritivores (Volk et al. 2003, Hart 2006) .

In contrast to red alder, Japanese knotweed litter appears to enter the stream almost exclusively in autumn. This study measured leaf litterfall from September-November, coinciding with Japanese knotweed litter inputs. As a result, the total contribution of native litter to streams is underestimated, and there may be greater differences in the quantity of litterfall between knotweed invaded and un-invaded sites than those presented in this study.

Management Implications and Future Research

Human land use including deforestation, irrigation, agriculture, urbanization, dam and road construction have led to the degradation and simplification of riparian and river systems throughout the world. In response to the threat of losing the economically, environmentally and culturally important resources provided by ecologically healthy watersheds, there is a growing focus on watershed restoration and rehabilitation. This is especially true for the Pacific Northwest (PNW), North America where land conversion and intensive harvest of salmon and timber have led to extensive habitat degradation and placed salmon productivity and survival at risk. Stocks of Pacific salmon *Oncorhynchus spp* and steelhead *Oncorhynchus mykiss* are increasingly listed as threatened or endangered under the Endangered Species Act (ESA) and large amounts of money, time and resources are currently dedicated to the restoration of the Pacific Northwest's riparian and river systems (Wissmar and Bisson 2003, Roni 2005, SERF 2005).

Effective management and rehabilitation of PNW watersheds requires thoughtful evaluation of complex ecological interactions and restoration alternatives. Maintaining healthy functioning riparian forests is increasingly recognized to be an essential component of restoring in-stream water quality and wildlife habitat over the long term. However, control of riparian invasive plants is commonly overlooked by restoration programs and funding opportunities focused on improving in-stream habitat. With limited resources available for river restoration and rehabilitation, it is difficult to prioritize invasive plant control above alternative restoration strategies (ie. riparian plantings, barrier culvert removal) when empirical information demonstrating extent and/or mechanisms of invasion impact are lacking.

This study represents a first attempt at quantifying the ecological consequences of knotweed invasion in PNW riparian corridors. Results suggest that knotweed has the potential to disrupt riparian and river processes by precluding the regeneration of native riparian herbs, shrubs and tress; reducing the nutritional quality of riparian litterfall; and retaining a higher percentage (75.5%) of foliar nitrogen during autumnal senescence than native species. Additional research is needed to investigate whether the patterns recorded at Grandy Creek apply across invaded watersheds and invasive congeners. However, these findings suggest that Japanese knotweed invasion should be considered among the targets of both riparian and river restoration initiatives.

Future studies are also needed to examine the response of aquatic consumers to knotweeds alteration of riparian litterfall diversity and nutrient composition (see Appendix A) and to examine the competitive mechanisms underlying knotweed's displacement of riparian deciduous and coniferous trees. The physical effects of knotweed invasion represent another unknown and a fertile area for research. The shallow rooting depth of knotweed as compared to native trees suggests that banks dominated by Japanese knotweed, may be less stable and more prone to slumping. Additionally, in contrast to native trees and shrubs, knotweed dies back in the winter, thereby leaving river banks more exposed to erosive forces.

Ecological consequences of knotweed invasion may be magnified when viewed within the context of contemporary forms of river and riparian degradation and restoration practices. In order to fully consider knotweed's impacts, future studies should examine knotweed interactions with other forms of river and riparian degradation (ie. reductions in nitrogen inputs through salmon escapement; loss of mature tree canopy resulting from human land use) and assess knotweed effects on the outcome of riparian restoration initiatives such as riparian silviculture and conservation buffer zones.

Final Remarks

Many of Washington State's most ecologically and economically important river systems are experiencing high levels of Japanese knotweed (*Polygonum cuspidatum, P. sachalinense,* and/or *P. x bohemicum*) colonization. Knotweed eradication efforts within these watersheds have had mixed results. The most effective programs have combined public outreach and education with multiple years of intensive herbicide treatment and surveying. A preferred approach is to start from the top of the watershed and work down, because any plants located upstream will continue to recolonize controlled areas.

Even under the most ideal circumstances (in which there is large public involvement, inter-agency coordination, access to upstream infestations, and funding for post-control surveys) knotweed’s eradication is extremely difficult. It takes multiple years of herbicide application to kill the rhizome, and treated populations may be redistributed downstream before 100% mortality has been achieved. Any viable rhizome or stem fragment remaining has the ability to re-infest an area. The particularly long term and concerted control program required to eradicate knotweed once it has established, underscores the need to quantify the effect of knotweed invasion on riparian forest community and ecosystem level processes.

This study illustrates direct and indirect mechanisms by which Japanese knotweed invasion may impact the nutrient cycling and productivity of riparian forests and adjacent lotic systems. Direct consequences of knotweed invasion are associated with an advanced ability to retain and recycle nutrient resources. Indirect effects are related to knotweeds displacement of native flora, including deciduous and coniferous juvenile trees. These results will form the basis of future experiments to further elucidate the ecological impacts of knotweed on riparian forests and adjacent aquatic food-webs.

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Appendix A: Decomposition and Invertebrate Colonization of Knotweed Leaf Litter versus Litter from Native Riparian Species

Introduction

As a complement to the vegetation and litterfall studies presented in this thesis, a leaf pack experiment was attempted in fall of 2004 at Grandy Creek. The purpose of this experiment was to compare in-stream decomposition and invertebrate colonization of knotweed leaf packs to leaf packs composed of mixed native species. Knotweed leaf packs contained a single species with high C:N, and thus were expected to decompose at a slower rate and experience lower abundance and taxonomic richness of aquatic macro-invertebrate colonizers than leaf packs composed of several native species.

After 28 days, this investigation was truncated by a storm event which destroyed the majority of litter samples. Twenty-eight days is inadequate time to assess litter decomposition dynamics. Hence, study results are inconclusive. However, this experiment represents a first attempt at quantifying the trophic consequences of knotweed invasion. Additionally, leaf pack experiments are a time consuming and elaborate process. Methods are provided here to offer a reference for graduate students interested in incorporating leaf pack analysis into their research.

Background

Leaf litter from riparian vegetation is an important direct source of nutrients and energy for aquatic microbes and macro-invertebrates (Petersen and Cummins 1974, Vannote et al. 1980, Cummins et al. 1989). The breakdown of leaf litter in freshwater streams typically involves the rapid loss of soluble inorganic and organic materials from leaching followed by a slower decline of leaf material resulting from microbial decomposition, mechanical erosion, invertebrate fragmentation and ingestion (Webster and Benfield 1986, Naiman and Bilby 1998). Studies show that aquatic invertebrates preferentially select and feed on microbially colonized leaves (Petersen and Cummins 1974, Barlocher 1985). This preference may be the result of changes in leaf chemistry carried out by the microbial community or the presence of fungal hyphae, which can have a higher nutrition value than the leaves themselves (Graca et al. 2001).

The chemical changes that accompany litter decomposition involve an initial increase in nitrogen resulting from microbial immobilization, followed by a decline in nitrogen as these nutrients are mineralized and become available for use by stream organisms (Melillo et al. 1984, Webster and Benfield 1986, Boulton and Boon 1991). The initial chemical composition of leaf litter, particularly the carbon:nitrogen or lignin:nitrogen ratio, is a key determinant of decomposition rates and patterns of nutrient availability (Petersen and Cummins 1974, Irons et al. 1988, Naiman and Bilby 1998, Motomori et al. 2001). In general, the C:N or Lignin:N content of litter is negatively correlated with resource quality and the rate of nutrient release from decomposing plant material (Cadisch and Giller 1997). Lignin is a structural carbohydrate that provides rigidity to vascular plants and is the most recalcitrant out of all naturally produced organic chemicals (Cadisch and Giller 1997). This complex compound also retards leaf break-down by shielding other structural polysaccharides from microbial attack. Nitrogen, on the other hand, is commonly the limiting nutrient for microbial growth and turnover. Therefore, higher nitrogen concentrations facilitate the mobilization of litter constituents by microbial decomposers. Under low nitrogen conditions, decomposers are nitrogen limited and will retain available nitrogen in their own biomass, thereby making it unavailable to plants and other organisms. Decomposition rates and leaf litter palatability are also related to concentrations of secondary plant compounds (Boulton and Boon 1991, Hagerman and Butler 1991). For example, condensed tannins bind to proteins and decrease the availability of leaf nitrogen to stream organisms (Boulton and Boon 1991)

The effects of riparian invasions on allochthonous litterfall dynamics and aquatic macroinvertebrate communities have been the subject of a few investigations. This area of research has produced variable, and occasionally contrasting, results. Several studies exhibit measurable ecological consequences of riparian plant invasions including shifts from autochthonous to allochthonous production (Kennedy and Hobbie 2004), alterations in the seasonal timing and quantity of litterfall (Abelho and Graca 1996, Ellis et al. 1998), altered rates of litter breakdown (Bailey et al. 2001, Kennedy and Hobbie 2004), altered aquatic macroinvertebrate community composition and lower colonization of instream leaf-packs (Bailey et al. 2001). Other studies (occasionally investigating the same invasive species documented to have significant effects) have found no differences in decomposition rates or macro-invertebrate preferences for native versus introduced species (Canhoto and Graca 1995, Raviraja et al. 1996, Parkyn and Winterbourn 1997, Sampaio et al. 2001).

Literature describing the effects of invasive plants on allochthonous litter inputs suggests several conclusions. First, introduced plant species will differ in litterfall chemistry, timing and degree to which they vary from the native community so not all invaders will have measurable effects. Second, many invasive species lie within the range of litter chemistry and breakdown rates characteristic of native flora. Therefore, experimental results may be dependent upon the native species chosen for comparison. Third, whereas previous experiments compared introduced species litter to that of individual native species, it would be more ecologically meaningful to compare the introduced litter to that produced by a typical mixed assemblage of native species. Empirical evidence suggests that a diversity of litter types can enhance the value of allochthonous litterfall as a source of food, energy and habitat for aquatic macroinvertebrate communities (Lecerf et al. 2005). Therefore, taxonomic simplification in addition to alteration of leaf litter represents both a potentially important and often overlooked consequence of riparian invasions and offers the opportunity to examine the indirect consequences of plant invasions, exerted through the displacement of native species and biodiversity.

Methods

Leaves of giant knotweed, red alder, black cottonwood, and willow were collected from Grandy Creek just prior to autumn abscission. Only leaves that detached when plants were shaken to simulate wind were collected. Leaves were air-dried for 2 weeks and weighed into 8 g leaf packs composed of knotweed leaves or a mixture alder, willow and cottonwood leaves in a proportion of 4g alder: 2.5g willow: 1.5g cottonwood. Dried leaves were moistened to prevent fragmentation and packed into bags composed of plastic hardware mesh bags (20cm x 20cm in size, 1 mm mesh openings). This mesh size was chosen to allow entrance of all macroinvertebrates potentially present in the stream.

On October 21 2004, 120 leaf packs were fastened to 40, 40lb concrete bricks with fishing wire and placed facing the stream current. Each brick was stabilized with two rebar stakes pinned to the stream bottom. Bricks were placed along two transects located adjacent to the stream bank. The upstream transect was located adjacent to a bank with a high density of *P. sachalinense* whereas the downstream transect was located adjacent to a stream bank colonized by an un-invaded, alder dominated community. Each transect consisted of 20 bricks with three native or knotweed packs alternately attached to each brick.

Care was taken to place the experimental packs along a stretch of stream bank with visually uniform micro-environment. Micro-environmental conditions were not measured. A StowAway temperature datalogger was placed adjacent to each transect to monitor stream temperature throughout the experiment. Water chemistry samples were collected at transect sites on October 24, and November 11, (three and twenty one days after the onset of the experiment) and analyzed for F, Cl, NO^2, NO^3, Br, PO^4, SO^4 (mg/L) using the ion chromatography (IC) method (DIONIX Co., model DX120). Water sample analysis was conducted at the University of Washington, College of Forest Resources analytic laboratory.

After 10 days, five randomly selected packs of each litter type were removed from each transect. Site inspection at 28 days indicated nearly all packs were destroyed during high flow events and the remaining fifteen packs (7 knotweed, 8 native) were collected. Transect samples were combined in subsequent analysis because many samples were lost during flood events, ten day samples indicated no differences between transects and transects were located on a single stream reach. The temperature datalogger at site two was also lost during flooding.

Upon returning to the lab, the 20 leaf packs collected after 10 days, and 15 packs collected after 28 days within the stream were analyzed for mass loss in grams ash free dry weight (AFDW), % carbon and % nitrogen. AFDW was determined by weighing samples before and after burning off the organic matter portions in a muffle furnace. The remaining sample was considered to be sediment accumulated on the packs, and subtracted from the leaf pack weight to obtain AFDW. Additionally, five knotweed and five native packs not used in the decomposition experiment were analyzed to quantify initial AFDW and nutrient composition. Percent initial biomass and nitrogen lost were compared within and between leaf pack types for ten and twenty eight days within the stream.

The remaining packs collected after 28 days (7 knotweed, 6 native) were analyzed for macroinvertebrate colonization. Upon returning to the lab, and within three hours of collection, the invertebrate samples were preserved in 90% ETOH. To analyze differences in community composition and abundance between pack types, the macroinvertebrates were carefully washed and removed from each pack, total abundance was tabulated, and specimens were identified to order or genus.

Kruskall-Wallis ($p \leq 0.05$) was used to compare changes in leaf pack biomass and nitrogen content within knotweed and native leaf packs throughout 0, 10, and 28 days in Grandy Creek. Mann-Whitney U ($p \leq 0.017$) was applied to these results as a post-hoc test to detect where statistically significant differences occurred across sampling days. Mann-Whitney U ($p \leq 0.05$) was also employed to examine differences between knotweed and native leaf packs within each sampling day.

Results

Stream temperature ranged between 3.9 and 8.22 ˚C throughout the 28 day decomposition experiment. Because the downstream datalogger was lost during a flood event, temperature data are only presented for the upstream site. There were no measured differences in water quality parameters between litter pack transect sites (Table 4).

Biomass loss and nitrogen dynamics of knotweed and mixed, native leaf packs are presented in Figure 4 and Tables 5 and 6. Leaf pack type was not a significant factor determining rates of biomass loss after 10 ($p = 0.597$) or 28 ($p = 0.105$) days at Grandy Creek. Percent initial nitrogen remaining also did not significantly differ after 10 ($p = 0.199$) and 28 ($p = 0.105$) days across leaf pack types. However, the data exhibited a strong, but not significant, trend of increasing %N among native leaf packs and decreasing %N among knotweed leaf packs. Initial differences between knotweed and native leaves in litter C:N and %N persisted throughout the decomposition experiment.

There were no differences in the composition or diversity of aquatic macroinvertebrates colonizing knotweed or mixed-native leaf packs after 28 days in Grandy Creek (Tables 5 and 6) . The great majority of invertebrate colonizers of both leaf pack types were collector-gatherer or scraper feeders from the orders Ephemeroptera or Plecoptera.

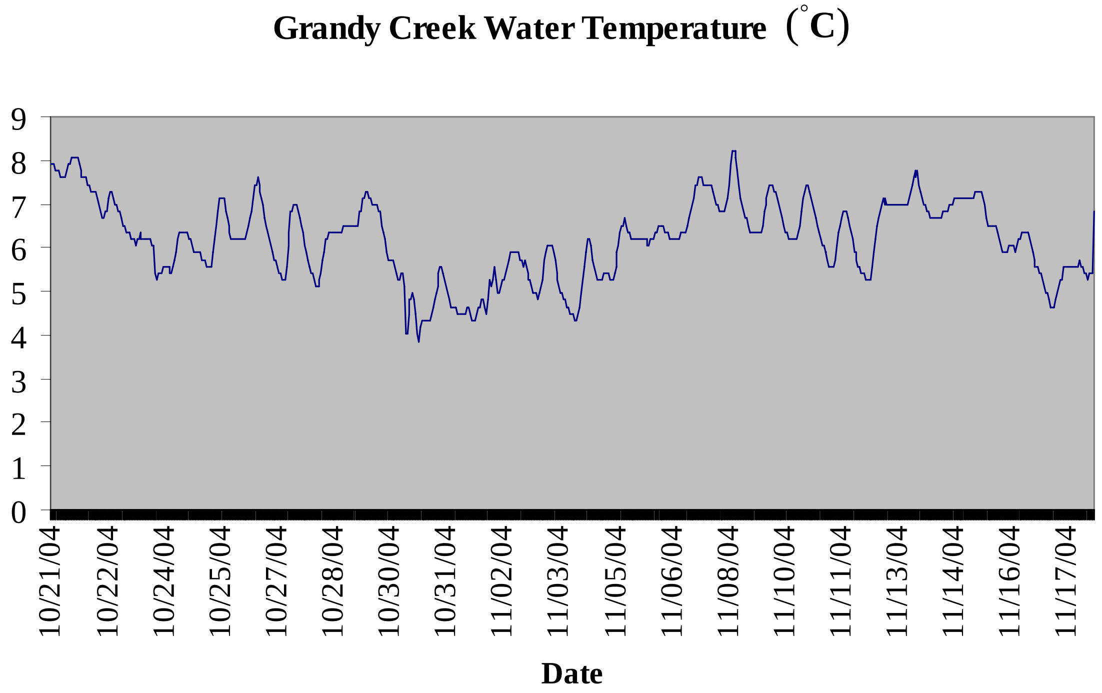

Figure A.1. Continuous temperature recordings in Grandy Creek, Washington. Temperature was recorded throughout the litter pack decomposition experiment, October 21, 2004 through November 18, 2004.

Table A.1.: Water Quality Analysis. Chemical analysis of Grandy Creek samples collected from leaf pack transect sites. The upstream site was located adjacent to a bank densely colonized by *P. sachalinense* and the downstream site was located adjacent to a stream bank populated by an un-invaded, *A. rubus* dominated community. ND=not-detected.

	F mg/L	**Cl** mg/L	**NO_2** mg/L	**Br** Mg/L	**NO_3** mg/L	**PO_4** mg/L	**SO_4** Mg/L
Upstream Site 10/24	0.004	1.253	ND	ND	0.058	0.012	1.088
Downstream Site 10/24	0.01	1.218	ND	ND	0.097	ND	1.287
Upstream Site 11/17	0.001	2.469	ND	ND	0.082	ND	1.037
Downstream Site 11/17	0.01	1.267	ND	ND	0.172	ND	1.328

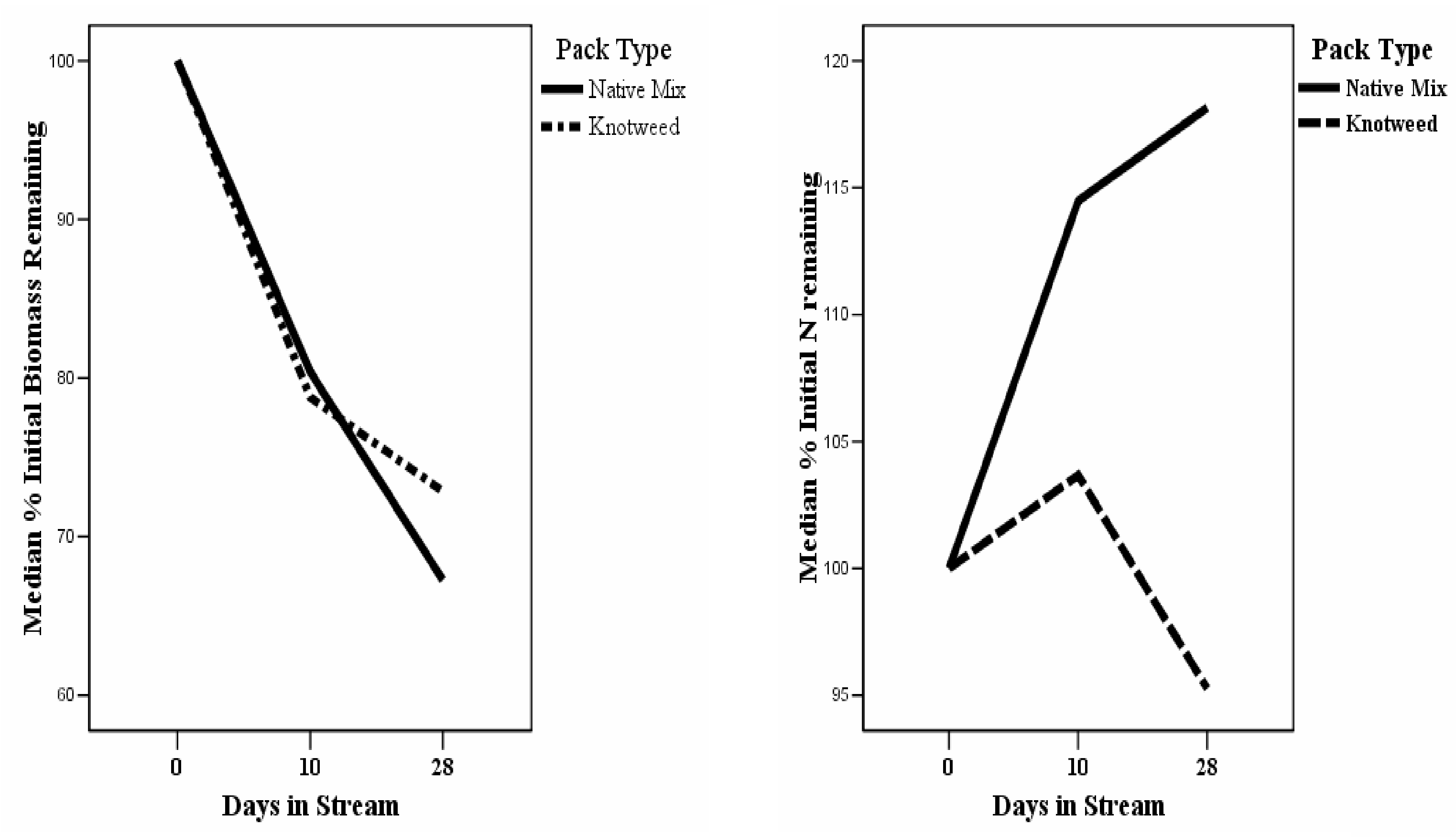

Figure A.2. Leaf Pack Decomposition Experiment. Median values for biomass loss (A) and nitrogen dynamics (B) of knotweed and mixed, native leaf packs after 0, 10 and 28 within Grandy Creek.

Table A.2: Changes in Leaf Pack Decomposition and Nutrient Dynamics Over Time. Kruskal-Wallis (K-W) tested for differences in knotweed or mixed, native leaf packs across 0, 10, 28 days within Grandy Creek ($p \leq 0.05$). Mann-Whitney U (MWU) was used as a post-hoc test to examine pair-wise comparisons between sampling dates ($p \leq 0.017$).

			% Initial Biomass Remaining				**% Initial Nitrogen Remaining**				**Leaf Litter C:N**			
	Time (days)	**N**	**Median**	**25% 75% Quartile**	**K-W**	**MWU 0-10 10-28**	**Median**	**25% 75% Quartile**	**K-W**	**MWU 0-10 10-28**	**Median**	**25% 75% Quartile**	**K-W**	**MWU 0-10 10-28**
Knotweed	0	5	100	NA	0.001	0.002 0.079	100	NA	0.62	1.00 0.283	49.7	49.0 54.9	0.097	0.066 0.922
	10	10	78.8	72.2 83.6			103.7	90.3 120.7			42.5	37.0 50.3		
	28	7	72.9	66.6 76.4			95.3	83.6 118.5			44.7	35.5 47.3		
Native	0	5	100	NA	<0.001	0.002 0.003	100	NA	0.17	0.061 0.722	25.0	24.3 26.9	0.002	0.002 0.110
	10	10	80.4	77.8 84.9			114.5	103.9 124.4			18.8	17.2 20.3		
	28	8	67.3	48.1 70.7			118.1	99.9 129.5			17.9	15.8 18.7		

Table A.3. Comparison of Leaf Litter Decomposition Across Pack Types. Mann-Whitney U test was used to examine differences between knotweed and native leaf packs after 10 and 28 days within Grandy Creek ($p \leq 0.05$).

			% Initial Biomass Remaining		% Initial Nitrogen Remaining		Leaf Litter C:N		Leaf Litter %N	
Days in Stream	**Leaf Pack Type**	**N**	**Median**	**Mann Whitney U**	**Median**	**Mann Whitney U**	**Median**	**Mann Whitney U**	**Median**	**Mann Whitney U**
0	Knotweed	5	100	NA	100	NA	49.7	0.009	1.89	0.009
	Native	5	100		100		25.0		0.89	
10	Knotweed	10	78.7	0.597	103.7	0.199	42.5	<0.001	0.91	<0.001
	Native	10	80.4		114.5		18.8		2.12	
28	Knotweed	7	72.9	0.105	95.3	0.105	44.7	0.001	0.83	0.001
	Native	8	67.3		118.1		17.9		2.19	

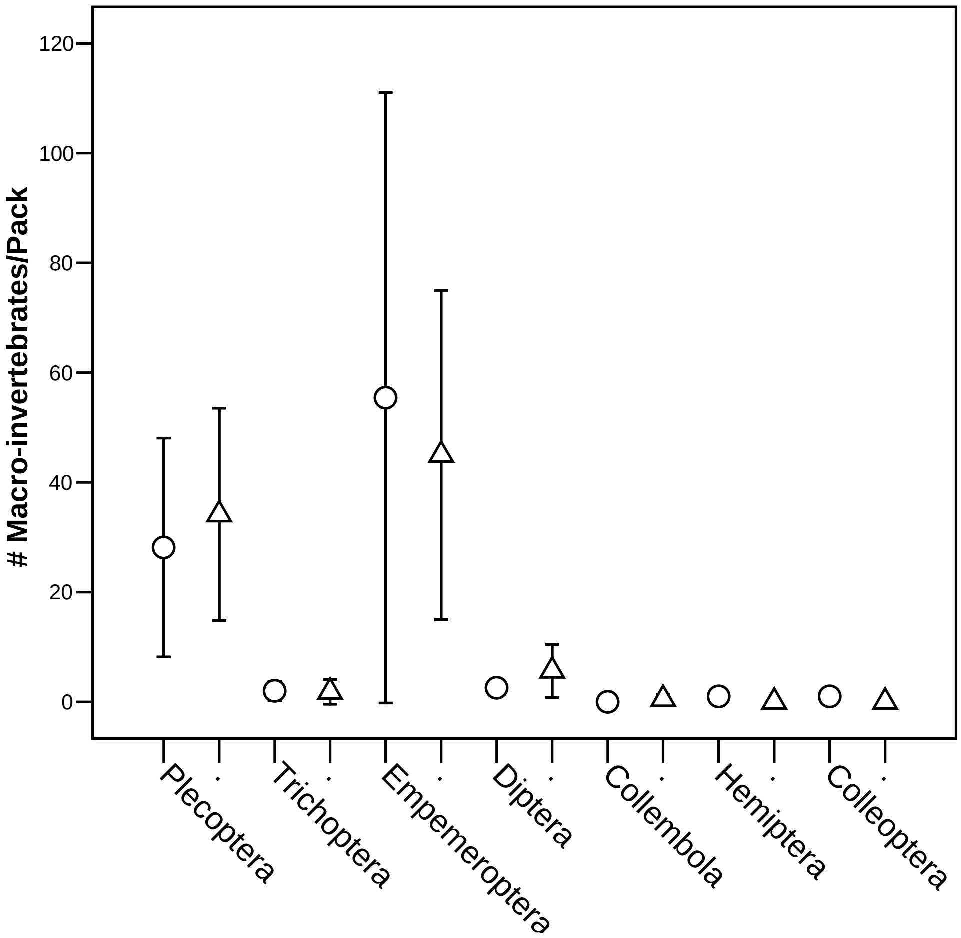

Figure A.3. Composition of aquatic macro-invertebrate assemblages colonizing knotweed (O) and native (Δ) leaf packs after 28 days within Grandy Creek. There were no differences between pack types.

Table A.4. Functional feeding groups of the aquatic macro-invertebrates colonizing knotweed and native leaf packs after 28 days in Grandy Creek. There were no differences between pack types.

Leaf Pack Treatment	Shredders	Collector Gatherers	Collector Filter Feeders	Scrapers	Predators
Knotweed	0	65	5	65	12
Knotweed	1	114	7	111	31
Knotweed	0	46	7	43	12
Knotweed	0	124	4	121	5
Knotweed	0	27	4	27	28
Knotweed	0	1	1	0	1
Knotweed	0	6	4	3	8
Native	0	88	7	82	12
Native	0	6	2	5	7
Native	0	12	6	4	10
Native	1	90	16	86	27
Native	2	25	1	23	17
Native	0	64	11	59	23

Discussion

Allochthonous litter inputs from riparian vegetation are an important source of nutrients and energy into aquatic food webs. The chemical make-up and species composition of riparian litterfall influence litter breakdown rates and food resource quality which, in turn, can affect the growth and feeding rates of aquatic microbe and macroinvertebrate consumers (Petersen and Cummins 1974, Irons et al. 1988, Naiman and Bilby 1998, Motomori et al. 2001, Swan and Palmer, 2006). Results from Grandy Creek illustrate knotweed leaf litter has a C:N of 50:1 whereas to leaf litter from native species vary between 20:1 (*A. rubra*) to 30:1 (*Salix*). Higher C:N in riparian litterfall has been linked to slower instream decomposition rates and lower nutritional value for aquatic consumers. Additionally, study results illustrate an average 70% decline in the quantity of native species litterfall associated with knotweed invasion, thus indicating a replacement of speciose native litter inputs with monotypic knotweed leaves. To examine the implications of these findings for aquatic food webs, decomposition (% biomass loss and nitrogen gain) and invertebrate colonization were compared between experimental leaf packs composed of knotweed leaves and leaf packs composed of a mixture of dominant native species at Grandy Creek (red alder, willow and black cottonwood). Knotweed litter packs were expected to exhibit slower decomposition (measured as % biomass loss and % nitrogen gain over time) and lower density and taxonomic richness of aquatic macroinvertebrates as compared to mixed, native species packs.

Unfortunately, twenty-eight days after the initiation of the experiment a flood event destroyed many of the remaining leaf packs and prematurely ended the study. After 28 days within Grandy Creek, patterns of biomass loss, nitrogen dynamics and invertebrate colonization of knotweed and native litter packs were more similar than expected. This is not surprising, given the inadequate duration of the experiment. However, some trends, although not statistically significant, indicated potential differences in decomposition dynamics between knotweed and native pack types.

Initial differences in C:N and %N between knotweed and native leaf packs persisted throughout the 28 day decomposition study. Both knotweed and native litter packs exhibited declining biomass throughout the experiment and the percent initial biomass remaining after 10 (p= 0.597) or 28 days (p=0.105) within Grandy Creek were not significantly different between pack types. This result is contrary to the expectation that knotweed leaf packs would decompose more slowly and lose less biomass over time than native leaf packs. The limited study length may have contributed to this result. Leaf litter breakdown in freshwater streams typically involves the rapid loss of soluble inorganic and organic materials from leaching followed by a slower decline of leaf material resulting from microbial decomposition, mechanical erosion, invertebrate fragmentation and ingestion (Webster and Benfield 1986, Naiman and Bilby 1998). It is possible that twenty eight days permitted measure of biomass loss during the initial leaching period, but not the successive stages of decomposition which involve aquatic microbes and macroinvertebrates. It is the later stages that are more likely to reflect differences in nutrition quality and composition between knotweed and native leaf packs.

Percent initial nitrogen remaining also did not significantly differ between pack types after 10 (p=0.199) or 28 (p= 0.105) days within Grandy Creek. However, median trends exhibit increased %N in native leaf packs throughout the experiment whereas knotweed packs exhibited a decline in %N between 10 and 28 days within Grandy Creek. This pattern is reflected within pack C:N dynamics. The C:N of knotweed leaf packs did not change throughout the experiment (p= 0.097), whereas the C:N of native leaf packs significantly declined (p= 0.002), indicating greater %N and/or lower %C. Increasing %N during leaf decomposition is thought to result from microbial colonization and/or nutrient immobilization. Therefore, declining C:N in native leaf packs may indicate greater microbial colonization and greater increases in palatability over time as compared to knotweed leaf packs.

There were no differences in the composition or abundance of aquatic macroinvertebrates colonizing knotweed and native leaf packs. The majority of invertebrates on both pack types were collector-gatherers and scrapers from the orders Ephemeroptera and Plecoptera. These results are contrary to expectations that the macroinvertebrates colonizing knotweed leaves would exhibit lower density and taxonomic richness than the macroinvertebrate assemblages on native leaf packs. Again, the length of this experiment was likely not adequate to provide a reliable estimate of invertebrate colonization.

Additionally, previous studies have compared invertebrate colonization of real versus plastic leaf litter and found no differences between leaf types, especially during high flow conditions. These findings suggest that aquatic invertebrates can use leaf packs as shelter as well as a food resource (Graca and Pereira, 1995). It is possible that macroinvertebrates using knotweed leaf packs as habitat masked potential differences between pack types.

This experiment represents a first attempt at quantifying the trophic consequences of knotweed invasion. Unfortunately, natural events truncated the decomposition experiment and, as a result, the findings are inconclusive. Additional research is needed to examine the ecological consequences of knotweed's displacement of native species and the resulting replacement of high quality, specious leaf litter with lower nutrient quality, monotypic knotweed leaves.