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Title: Negative Effect of Purple Loosestrife and Reed Canary Grass on the Diversity of Wetland Plant and Moth Communities.

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Invasive plants have the potential to reduce the diversity of species in plant and animal communities. I examined the negative effect of two invasive wetland plants, purple loosestrife and reed canary grass, on the species richness and diversity of plant and moth communities within 24 wetland study sites in the Pacific Northwest. I hypothesized that as the cover of the invasive species increased, the diversity of the local plant and moth community would decrease. Increasing cover of purple loosestrife and reed canary grass was associated with reduction in the diversity of wetland plant communities irrespective of the diversity measure examined. Moth species richness was positively correlated with plant species richness, but I found no detectable direct negative association between loosestrife and canary grass cover and moth community diversity. Wetland hydrology, soil characteristics, and topography were measured to control for potentially covarying and confounding influences on plant diversity. Temperature, ambient light, and surrounding land-use were measured to control for potentially covarying and confounding influences on moth sampling and diversity. None of these variables was significantly associated with invasive species abundance. This strengthens the conclusion that the invasive species are the cause of the decline in biotic diversity.

Understanding the mechanisms that influence plant invasions will lead to more effective management strategies. I examined the role of soil nutrients in the invasive potential of purple loosestrife. I hypothesized that nitrogen was the primary nutrient limiting plant growth and that higher soil nitrogen concentrations would increase the growth of purple loosestrife within 13 wetland sites in the Willamette Valley, Oregon. Using greenhouse experiments and field studies I found that nitrogen was the primary resource limiting both plant community biomass and purple loosestrife growth. Purple loosestrife grew well in soils taken from nine wetlands currently not colonized by loosestrife. Given their similar hydroperiods, this suggests that these wetlands will be susceptible to invasion should loosestrife colonize. Plant species richness was negatively associated with soil nitrate and ammonium concentrations. This trend included invaded and non-invaded sites. Therefore, to prevent repeated invasions, management strategies should consider methods for reducing soil nutrient concentrations, particularly nitrogen.

Negative Effect of Purple Loosestrife and Reed Canary Grass on the Diversity of Wetland Plant and Moth Communities.

by

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Negative Effect of Purple Loosestrife and Reed Canary Grass on the Diversity of Wetland Plant and Moth Communities.

Chapter 1

General Introduction

An invasive species is an "alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health" (Clinton Executive Order 132112, 1999, USA). Invasive plant species have been shown to reduce biological diversity and alter ecosystem processes (Randall 1996, Wilcove et al. 1998, Blossey 1999, Parker et al. 1999). They also can reduce agricultural, timber, and rangeland production (Radtke and Davis 2000). Physical, chemical and biological management strategies can be used to control populations of invasive plants but these methods impose both costs and risks (Myers and Bazely 2003). Therefore, quantifying the effects of invasive species is important in prioritizing control programs and analyzing whether the benefits of control are worth the costs. To create effective management strategies it is important to understand the ecology of the weed species and the mechanisms by which it is able to colonize and dominate plant communities (Levine et al. 2003, Myers and Bazely 2003). In addition, understanding mechanisms of invasion allows us to predict which habitats are at risk of invasion.

Chapter two of this dissertation examines the effect of two invasive wetland plants, purple loosestrife (*Lythrum salicaria*) and reed canary grass (*Phalaris arundinacea*), on the diversity of local wetland plant and herbivore communities. A biotic community is characterized by the number, traits, and relative abundance of species and their interactions through space and time (Begon et al. 1990). I hypothesized that as the cover of the invasive species increased, the diversity of the local plant and herbivore community would decrease. I sampled plant and moth communities over three years (2000-2002) at 24 wetlands in the Pacific Northwest. Within each wetland, a circular area was sampled (50m radius, 7,854m^2) for cover of plant species and abundance of moth species. Seven wetlands dominated by purple loosestrife and six wetlands dominated by reed canary grass were compared with eleven wetlands dominated by other plant species (reference wetlands). Environmental variables that might covary with invader abundance and confound the analysis were measured and analyzed.

Chapter three investigates a potential mechanism by which loosestrife is able to dominate the plant communities where it invades. In 2002, plant biomass, plant tissue nitrogen and phosphorus concentrations, and soil nutrient concentrations were sampled within thirteen wetlands in the Willamette Valley, Oregon. In a greenhouse phytometer study I grew purple loosestrife from seed in soil from each of the wetland sites to test whether the soils were conducive to loosestrife growth in the absence of other environmental constraints. Based on prior evidence, I hypothesized that nitrogen was the nutrient limiting primary production at the sites and that nitrogen would be positively correlated with purple loosestrife biomass. I also hypothesized that loosestrife spread in Oregon is currently restricted by colonization events and not habitat suitability. First, I used N:P ratios in plant tissue and the relationship between soil nutrient concentrations and plant community biomass to determine which soil nutrient is likely the main limitation to primary production. Second, I examined the relationship between soil nutrient concentrations and loosestrife biomass in invaded wetlands to determine whether loosestrife biomass was correlated with the limiting nutrient. Third, I examined the relationship between soil nutrient concentrations and loosestrife biomass in the greenhouse to determine whether the same result was found when examining growth at all sites in the absence of other environmental constraints. Finally, phytometer biomass is used as an indication of the potential for loosestrife to invade previously uncolonized sites.

Ecological Effect of Invasive Plants

Concerns over the negative effects of invasive species have been escalating due to both a greater number of species invading habitats throughout the world and an increase in scientific and public awareness of the problems associated with these invasions (Randall 1996, Wilcove et al. 1998, Blossey 1999, Parker et al. 1999). Quantifying the effect of the invader allows prioritization of management thus directing limited resources where they are most needed (Byers et al. 2002). Effects of invasive species can be measured as economic or ecological. Economic effects, such as reduction in rangeland capacity to rear cattle, are measured as dollars lost (Radtke and Davis 2000). Ecological effects can be summarized in the following conceptual equation:

$$I=R*A*E$$

where: I is the effect of the invader, R is the range of the invader, A is the abundance of the invader, and E is the effect per individual invader (Parker et al. 1999). The metrics R and A are self-explanatory as area and density of infestation respectively, however E (the effect) can be further split into effects upon: individuals, genetics, population dynamics, communities, and ecosystem processes (Parker et al. 1999). Ecosystem level effects may indirectly alter the community structure of invaded areas by changing the habitat in which they invade. Community level effects, within a given trophic level, are more likely caused by direct effects of interspecific competition (Levine et al. 2003). As both are relevant to this study, prior research is summarized below.

Ecosystem level effects

The ecosystem level of ecological integration includes both organisms and their environmemnt and is primarily concerned with the flow of energy and materials (Krebs 1994). Invaders that modify ecosystem processes have the potential for greatest effect. Alteration of ecosystem processes then can alter community structure and composition (Vitousek 1990). Ecosystem level changes can be defined as "those that alter the fluxes of water and energy or the cycling and loss of material" (Ramakrishnan and Vitousek

1989). Vitousek (1990) suggests that exotic species are likely to alter ecosystem processes when they differ from native species in resource acquisition or utilization, alter trophic structure, or alter disturbance frequency or intensity (where disturbance is an event that reallocates limiting resources). These species may be the most ecologically important invasive organisms because they do not just compete with native species, but change the rules of existence for all the species within that ecosystem.

Several authors present categorizations of ecosystem-level effect. Gordon (1998) divides effects into four major classes: altered geomorphological processes, altered hydrological cycling, altered biogeochemical cycling, and altered disturbance regimes. Parker et al. (1999) classify these effects as changes in: resource pools and supply rates, rates of resource acquisition by plants and animals, and disturbance regimes. Vitousek (1986) lists the collective properties that can be altered as: productivity, consumption, decomposition, water fluxes, nutrient cycling and loss, soil fertility, erosion, and disturbance frequency.

Geomorphological processes that might be affected by invasive species include: erosion rates, sedimentation rates, elevation, and water channels. Invasive species may affect hydrology through increased transpiration rates thus altering water-holding capacity, water-table depth, and surface-flow patterns (Gordon 1998). Blackburn et al. (1982) found that as salt cedar (*Tamarix spp.*) density increased along the edges of the Brazos River (TX) from 1941 to 1973, river sediments were stabilized, resulting in a mean accumulation of three meters of sediment. Graf (1978) reached similar conclusions in a study of the Green River (UT), where salt cedar was found to develop stabilized islands and bars that reduced the river channels 13% to 55% of their former width. Loope et al. (1988) found that the water table in a marsh in Death Valley National Monument was lower after being invaded by salt cedar and rose again when salt cedar was removed.

Biogeochemical cycling includes nutrient mineralization rates, nutrient immobilization rates, and soil and water chemistry (Gordon 1998). Invasive species that have been found to alter nutrient cycling include: iceplant (*Mesembryanthemum crystallinum*)(Kloot 1983, Vivrette and Muller 1977), purple loosestrife (*Lythrum salicaria*) (Emery and Perry 1996, Templer et al. 1998), mimosa (*Myrica faya*) (Vitousek et al. 1987, Vitousek and Walker, 1989), common reed (*Phragmites australis*) (Templer et al. 1998), and Chinese tallow (*Sapium sebiferum*)(Cameron and Spencer 1989).

Alteration of the type, frequency, intensity or duration of disturbance is considered an ecosystem-level effect (Gordon 1998). Many exotic grasses have been found to alter fire frequency and intensity (Hughes et al. 1991, D'Antonio and Vitousek 1992, Mack and D'Antonio 1998, D'Antonio et al. 2000). Hughes et al. (1991) found that three grasses (*Melinis minutiflora, Andropogon virginicus,* and *Schizachyrium condensatum*) were associated with increased fire frequency and area burned in Hawaii. Studying the same system in Hawaii, D'Antonio et al. (2000) found that submontane native species were less tolerant of fire than the invasive African grass, *Melinis minutiflora,* and were therefore displaced in this zone.

Organisms causing ecosystem level effects may indirectly alter the community structure of invaded areas by changing the habitat that they invade. Some, like iceplant, may modify the environment in favor of the plant's own fitness through salinification, while others, like *Myrica faya* may increase the speed of succession through fixing of nitrogen. Community level effects, within a given trophic level, are more likely caused by direct effects of interspecific competition.

Community level effects

Invasion of native wetland communities by introduced species is occurring in the Pacific Northwest. A recent study of 96 wetlands within the Portland Urban Growth Boundary documents the invasion of the regional wetland flora. Non-native species account for more than 50% of plant species present on both naturally occurring wetlands and in human created mitigation wetlands (Magee et al. 1999).

Invasion of native communities by introduced plant species is associated with decline in species richness and diversity of the plant community. The negative effect of introduced plant species on native plant communities has been extensively studied for introduced *Acacia* and *Pinus* species in the Fynbos biome of the Cape Province, South Africa. The studies have found that the introduced species: negatively effect species richness and diversity (Richardson and van Wilgen 1986, Richardson et al. 1989, Holmes and Cowling 1997a, Holmes and Cowling 1997b), suppress native seedling regeneration (Musil 1993), and alter plant community guild structure (Holmes and Cowling 1997a). Another well studied invasion is that of mimosa (*Mimosa pigra*) in tropical Australia (Lonsdale and Braithwaite 1988, Braithwaite et al. 1989). Braithwaite et al. (1989) found that herbaceous plant species richness was negatively correlated with mimosa cover. They also examined the animal community but the results discerned no clear pattern. Generalist animal species that used mimosa for cover, such as rodents, increased in abundance, while specialists, such as various bird species, tended to decline in abundance. Introduced beach grass (*Ammophila arenaria*) disrupts the structure of sand dune arthropod communities in California, USA. Slobodchikoff and Doyen (1977) found that even low percent cover of beach grass strongly depressed arthropod populations and arthropod community species richness as compared with dunes stabilized by native species. More recently, studies of the effect of the invasive vine, *Clematis vitalba,* in New Zealand have indicated of 24% decrease (45 to 34) of shrub and small tree species, and a 37% loss (51 to 32) of herbaceous flowering plants within the Taihape forest reserve (Ogle et al. 2000).

Effects on biotic communities and ecosystem processes are linked. Reduction in species diversity can alter ecosystem function. In experimental microcosms, Naeem et al. (1994) found that more diverse systems had greater rates of CO_2 flux, greater productivity, and greater accumulation of phosphorus and potassium. A number of other studies support the general conclusions that greater diversity leads to greater productivity in plant communities, greater nutrient retention in ecosystems, and greater ecosystem stability (Chapin et al. 2000, Tilman 2000). Therefore, invasive species may effect ecosystem functions directly (i.e. *Myrica faya* altering soil nitrogen concentrations) or indirectly through changes in community composition that then alter ecosystem processes.

The Study Organisms

This study examines the effect of two invasive wetland plant species, purple loosestrife and reed canary grass, on the diversity of wetland plant and herbivore communities. Purple loosestrife (*Lythrum salicaria* L.) is an invasive herbaceous plant species in the family Lythraceae and reed canary grass (*Phalaris arundinacea* L.) is an invasive grass species in the family Poaceae. These two invasive plants are often found in close association with on another throughout the wetlands of temperate North America. This association is found in the Pacific Northwest where reed canary grass was present at 60% (9 of 15) of the purple loosestrife sites examined in 1986 (Thompson et al. 1987).

Purple loosestrife

Purple loosestrife is a tall perennial wetland plant native to Europe. It probably arrived on the East coast of the United States before 1830 in ballast deposited by trading ships from Northern Europe (Thompson 1991). Purple loosestrife was first recognized as an aggressive invasive species during the 1930's in wetland pastures along the St. Lawrence River (Thompson et al. 1987) and has subsequently spread across the United States, aided recently by road construction and irrigation channels, as well as through the planting of seeds sold in wildflower mixes (Wilcox 1989). Loosestrife's mean rate of spread since 1940 has been estimated at 645 km^2 per year (Thompson 1991). Two excellent and thorough reviews of the biology, ecology, and history of invasion in North America of purple loosestrife are provided by Thompson et al. (1987) and Mal et al. (1992).

Purple loosestrife is an invasive species that is thought to displace native wetland vegetation in wetlands and riparian areas. Claims of negative effects prior to 1998 were criticized for being poorly substantiated (Anderson 1995, Hager and McCoy 1998). Subsequently, research has been published that both supports and refutes the hypothesis that loosestrife reduces wetland diversity and alters ecosystem processes. Two articles summarize what had been known as "suspected" and "documented" (Blossey 1999 and 2001).

Loosestrife has been shown to modify phosphorus cycling regimes. Phosphorus in loosestrife leaves and stems leaches into surrounding environment in fall and winter, as compared with native cattail species (*Typha* spp.) where phosphorus is retained until spring (Emery and Perry 1996). Purple loosestrife sequesters phosphorus in tissue, significantly reducing summer porewater phosphate concentrations to half that of the porewater of native cattail, *Typha angustifolia*, and the invasive reed *Phragmites australis* (Templer et al. 1998). In addition, phosphorus cycles through purple loosestrife 2 times and 1.5 times more quickly than through cattail and common reed respectively (Templer et al. 1998). However, because phosphate was more available throughout the year than nitrogen (measured as porewater ammonia) it is likely that available nitrogen was the nutrient limiting plant growth in these wetlands. It is not clear how these changes to phosphorus cycling would effect the plant community.

Purple loosestrife can persist at lower concentrations of soil nutrients than a native plant. Shamsi and Whitehead (1977a) compared the response of purple loosestrife and hairy willow-herb (*Epilobium hirsutum*) to varying concentrations of nitrogen (N), phosphorus (P), and potassium (K). They found that purple loosestrife growth was more tolerant of low concentrations of nutrients than hairy willow-herb. In a second experiment, they manipulated concentrations of N, P, and K separately and found that loosestrife growth was more sensitive to decreases in N than reduction of P or K (Shamsi and Whitehead 1977b). Although loosestrife was more tolerant of low nutrient conditions than hairy willow-herb, the studies did not examine competitive performance between the two species.

Direct evidence that purple loosestrife can dominate wetland plant assemblages and reduce species richness is supported by extended germination trials (Weiher et al. 1996), tests of competitive response (Johannsson and Keddy 1991, Keddy et al. 1998), loosestrife removal studies using herbicides (Gabor et al. 1996) and loosestrife reduction studies using biological control organisms (Landis et al. 2003). In a study by Weiher et al. (1996) the seeds from 20 wetland plant species were sown in 120 experimental microcosms representing 24 environmental treatments. During the first year, *Bidens cernua* was most prevalent, but by year five, loosestrife had become dominant in both high and low fertility treatments where the water level was held constant and subdominant (behind *Eleocharis smallii*) in high fertility treatments with fluctuating water levels (Weiher et al. 1996). In tests of competitive response of 48 wetland plants, purple loosestrife was found to reduce biomass of test plants by 90% (Keddy et al. 1998). Gabor et al. (1996) used herbicide treatments to reduce biomass of loosestrife at a wetland site in Canada. They found that in treated plots (3m x 10m) native vegetation replaced loosestrife for a limited time, but loosestrife reinvaded when treatment was discontinued. Landis et al. (2003) found a significant increase in nontarget plant species when biological control agents reduced biomass of loosestrife at five field sites in Michigan. The species richness remained unchanged or decreased in "control" sites where the biological control agents were not released and loosestrife abundance was not reduced.

However, not all studies agree that purple loosestrife reduces the diversity of the local wetland plant community. Morrison (2002) examined plant community diversity before and after removing purple loosestrife from three 1m^2 plots at two wetland sites in southeastern New York. She did not find a statistical difference in species richness, plant community diversity (Shannon diversity index), or percent cover after three years. This result may be a product of low replication and small spatial scale. With an effective sample size of two, the power to detect a significant difference is very low. In addition, species richness is dependent upon the size of the area sampled. Morrison acknowledges this and states, "A more exhaustive monitoring program over larger temporal and spatial scales is necessary to determine if native species are truly declining due to the presence of purple loosestrife". Two other studies, one by Farnsworth and Ellis (2001) and one by Treberg and Husband (1999) also did not detect an effect of purple loosestrife on plant community diversity, but again, both studies examined plant community diversity on a $1 m^2$ spatial scale.

Another means by which loosestrife has been shown to effect the local plant community is through competition for pollinators. Many herbaceous plant species rely upon insect pollinators to move pollen and fertilize conspecific plants in the short term and increase genetic mixing over the long term. Grabas and Laverty (1999) found that seed set of two co-flowering plant species, *Eupatorium perfoliatum* and *Impatiens capensis*, was reduced by 19 and 30% in plots with medium and high density of purple loosestrife respectively.

However, purple loosestrife does have benefits, both for human uses and possibly for native organisms. Bee keepers prize loosestrife as an abundant late season nectar source and many horticulturalists have cultivated purple loosestrife for its abundant and showy flowers. In addition, loosestrife may be an acceptable host plant for some native insect species. Purple loosestrife has been shown to host phytophagous insects in its introduced range. Hight (1989) identified 59 herbivorous insects, including 15 Lepidoptera species, which sporadically fed upon purple loosestrife in northeastern North America. However, he observed that none caused appreciable damage to the plant, suggesting the insects may be simply "sampling" and may not be able to complete their life-cycle on loosestrife. Barbour and Kiviat (1997) found that purple loosestrife supports several native Saturniid moths (*Hyalophora cecropia, Antheraea polyphemus,* and *Automeris io*) in the Hudson River Valley, New York. A census of 4th and 5th instar larvae found that moth larvae occurred more frequently on purple loosestrife than on a native host, gray dogwood (*Cornus racemosa*). The fitness of the resulting Saturniid adults was not examined and therefore the quality of purple loosestrife as an alternate host is not known. More testing is needed to examine whether these potential benefits to native insects are validated, particularly whether herbivore fitness is similar between native host plants and purple loosestrife. In addition, these three moth species are known to feed on many plant species (polyphagous).

In summary, a number of observational and experimental studies support the hypothesis that purple loosestrife may decrease wetland plant diversity, but some studies found no evidence of effect. In experimental microcosms invasive potential is increased with reduction in water level fluctuation and increase of nutrients. Loosestrife growth is particularly sensitive to available soil nitrogen concentrations. In addition, loosestrife has been shown to alter phosphorus cycling rates. However, it is prized for it nectar and flowers may also be an acceptable host plant for some native insect herbivores.

Reed canary grass

Reed canary grass is a coarse perennial wetland plant. Whether reed canary grass is a native or introduced species is currently in dispute. Some researchers believe it to be a "cryptogenic species" in that it is not possible to determine its true origin (Galatowitsch et al. 1999). Herbarium records support the claim that reed canary grass is native to temperate areas of Eurasia and North America (Naglich 1994).

However, others believe that, although the native reed canary grass ecotype is not considered to be aggressive, the Eurasian ecotype (or possibly the mixture of native plants and exotic cultivars) is an invasive plant that forms monospecific stands similar to those of loosestrife (Hutchinson 1992, Merigliano and Lesica 1998).

Reed canary grass is documented as a cultivated forage grass as early as 1749 in Sweden (Alway 1931). In Oregon, it was first cultivated in Coos County in 1885 (Finnell 1936). Canary grass has also been used to stabilize soils. However, "it is suggested that the species not be used to temporarily stabilize pond bottom soils because of its great and unexpected adaptability to aquatic situations" (LeFor 1987). Its tenacity and rapid growth make reed canary grass both a useful forage plant and an aggressive invader. It has completely eliminated all other plant species in the seedbank at a wetland site in Illinois, where it had been dominant for a period of over 40 years (Apfelbaum and Sams 1987). Reed canary grass has been shown to be associated with species poor plant communities in Wisconsin wetland meadows. Meadows dominated by *Carex stricta* and *Typha* spp. were found to support 29 and 28 additional plant species respectively while a meadow dominated by reed canary grass contained only 3 additional plant species (Werner and Zedler 2002). However, this study had no replication, potentially confounding differences in habitat were not controlled for, and size of meadow was not factored into species richness estimates. In addition, this study focused primarily on the effect of sedimentation on reducing the microtopography of wetland meadows and the associated response of the plant community. Because the single reed canary grass dominated site with a high sedimentation rate was compared with the other two reference sites without appreciable sedimentation, it is not clear whether the reduction of microtopographic variability or the increase of reed canary grass resulted in the observed difference in species richness.

Reed canary grass invasiveness has been shown to increase with increasing soil fertility. The plant can effectively utilize high nutrient concentrations to outgrow competitors, even across varying hydroperiods. Specifically, greater nitrate concentrations were shown to increase growth of reed canary grass which allowed it to out-compete various sedge meadow plant species in experimental mesocosms (Green and Galatowitsch 2001). Canary grass populations are negatively effected by reduced light availability. A study by Lindig-Cisneros and Zedler (2001) showed that changes in light frequency associated with shading reduced seed germination levels by 30%. In addition, canary grass rhizome survival was reduced by decreased light availability in field and greenhouse experiments (Maurer and Zedler 2002).

In summary, evidence from observations in the field and experiments in mesocosms support the hypothesis that reed canary grass can displace wetland plant species. In addition invasiveness is shown to increase with increases in soil nutrients (primarily soil nitrogen) and light availability. However, it has beneficial use as a forage source for livestock and as a means of controlling erosion.

Summary

Invasive plant species have been shown to alter ecosystem processes, the composition of plant communities, and interactions among plant species. Although purple loosestrife has been shown to decrease plant community diversity in experimental mesocosms, its effect on plant diversity under field conditions has not been fully resolved. In addition, there have been no studies that address the effect of purple loosestrife at higher trophic levels. Even less is known about the effect of reed canary grass. Chapter two of this dissertation evaluates the effect of purple loosestrife and reed canary grass on the diversity of plant and herbivore communities in the Pacific Northwest.

Mechanisms underlying ecosystem level effects are often examined and tested as a part of studies measuring effects at the ecosystem level, whereas studies investigating the effect of invasive plants on community structure rarely examine the mechanisms by which effect may occur. In a review of 150 studies examining the effect of invasive plants, Levine et al. (2003) found that although the number of studies examining effects to communities and ecosystems were roughly equal, nearly all of those examining ecosystem effects studied the mechanism of effect, whereas those studying community effect only investigated the mechanisms in 5% of the cases. In chapter three of this dissertation I examine mechanisms explicitly by studying the role of soil nutrients on the invasiveness of purple loosestrife.

The results of this study increase our understanding of both the effects and mechanisms driving the effects of invasive plant species. Knowledge of level of impact to biotic communities will help to prioritize efforts in controlling these species and create predictions of the benefits to be gained at various levels of reduction in invasive plant cover. Knowledge of mechanism underlying the effects may suggest new management strategies by which these invasive plants can be more effectively controlled. Currently, biological control methods using insect herbivores show great promise for reducing the density of purple loosestrife in Oregon and Michigan (Schooler 1998, Landis et al. 2003). Reed canary grass populations can be controlled using many strategies from flooding to shading (Maurer et al. 2003), but without sustained management reed canary grass reinvades and quickly returns to prior densities (Apfelbaum and Sams 1987).

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Chapter 2

Effect of purple loosestrife and reed canary grass on wetland diversity

Introduction

An invasive species is an "alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health" (Clinton Executive Order 132112, 1999, USA). The increasing abundance of invasive plant species is reducing biological diversity worldwide (Wilcove et al. 1998). In addition, invasive plant species have been shown to alter ecosystem processes (Randall 1996, Blossey 1999, Parker et al. 1999) and they negatively effect local and regional economies through reduced agricultural, timber, and rangeland production (Radtke and Davis 2000). Physical, chemical and biological management strategies can be used to control populations of invasive plants but these methods impose both costs and risks (Myers and Bazely 2003). Therefore, it is important to quantify the effects of invasive species in order to prioritize control programs and analyze whether the benefits are worth the costs.

Purple loosestrife (*Lythrum salicaria* L.) and reed canary grass (*Phalaris arundinacea* L.) are two invasive plants that are currently the dominant vegetation in many wetlands across the United States. Both species are known to form dense monospecific stands that may negatively effect local wetland plant and animal communities. Decline of vegetative diversity is known to alter wetland ecosystem function and services (Engelhardt and Ritchie 2001). Changes in the herbivore community will likely cause changes in the composition of trophic levels above (predators) and below (plants) the herbivore level.

In this study I examine the association between the abundance of purple loosestrife and reed canary grass (measured as % cover) and the species richness and diversity of wetland plant and herbivore communities. Moths are used as representatives of the herbivore community because, as consumers of living plants, they are likely to be sensitive to the vegetation changes caused by plant invaders. To control for potentially confounding environmental factors, I examined covariance between invader abundance and other variables that are known to influence plant diversity (hydrologic regime, topographic variation, and soil characteristics) and moth sampling and diversity (night-time illumination, temperature, and surrounding land-use).

The number and diversity of plant and moth species was sampled within 24 palustrine emergent wetlands in the Pacific Northwest. The plant community was sampled as the percent cover of each plant species at each site and the moth community was measured as the number of individuals of each species at each site. I expected that increasing cover of the introduced plant species would be associated with decreasing species richness and diversity of the local plant communities. Because many moth species are often associated with specific host plants, I hypothesized that as the species richness and diversity of plant hosts decline, so will the species richness and diversity of the moth community.

Purple loosestrife

Purple loosestrife is a tall perennial wetland plant native to Europe. It probably arrived on the East coast of the United States before 1830 in ballast deposited by trading ships from Northern Europe (Thompson 1991). The plant was first recognized as an aggressive invasive species during the 1930's in wetland pastures along the St. Lawrence River (Thompson et al. 1987) and has subsequently spread across the United States, aided by road construction and irrigation channels, as well as through the planting of seeds sold in wildflower mixes (Wilcox 1989). The mean rate of spread of loosestrife since 1940 has been estimated at 645 km^2 per year (Thompson 1991). Two thorough reviews of the biology, ecology, and history of invasion in North America of purple loosestrife are provided by Thompson et al. (1987) and Mal et al. (1992).

Purple loosestrife is an invasive species that is thought to displace native wetland vegetation in wetlands and riparian areas. Estimates of effect prior to 1998 were criticized for being poorly tested (Anderson 1995, Hager and McCoy 1998). Subsequently, research has been published that both supports and refutes the hypothesis that loosestrife negatively effects wetland diversity and ecosystem processes. Two articles summarize what had been known to date as "suspected" and "documented" (Blossey 1999 and 2001).

Direct evidence that purple loosestrife can dominate wetland plant assemblages and reduce species richness is supported by extended germination trials (Weiher et al. 1996), tests of competitive response (Johannsson and Keddy 1991, Keddy et al. 1998), loosestrife removal studies using herbicides (Gabor et al. 1996) and loosestrife reduction studies using biological control organisms (Landis et al. 2003). In a study by Weiher et al. (1996), the seeds from 20 wetland plant species were sown in 120 experimental microcosms representing 24 environmental treatments. During the first year, *Bidens cernua* was most prevalent, but by year five, loosestrife had become dominant in both high and low fertility treatments where the water level was held constant and subdominant (behind *Eleocharis smallii*) in high fertility treatments with fluctuating water levels (Weiher et al. 1996). In tests of competitive response of 48 wetland plants, purple loosestrife was found to reduce biomass of test plants by 90% (Keddy et al. 1998). Gabor et al. (1996) used herbicide treatments to reduce biomass of loosestrife at a wetland site in Canada. They found that native vegetation replaced loosestrife for a limited time, but loosestrife reinvaded when treatment was discontinued. Landis et al. (2003) found a significant increase in other plant species after biological control agents reduced biomass of purple loosestrife at five field sites Michigan. The species richness remained unchanged or decreased in "control" sites where the biological control agents were not released and loosestrife abundance was not reduced.

However, not all studies agree that purple loosestrife reduces the diversity of the local wetland plant community. Morrison (2002) examined plant community diversity before and after removing purple loosestrife from three 1m^2 plots at two wetland sites in southeastern New York. She did not find a statistical difference in species richness, plant community diversity (Shannon diversity index), or percent cover after three years. This result may be a product of low replication and small spatial scale. With an effective sample size of two, the power to detect a significant difference is very low. In addition, species richness is dependent upon the size of the area sampled. Morrison acknowledges this and states, "A more exhaustive monitoring program over larger temporal and spatial scales is necessary to determine if native species are truly declining due to the presence of purple loosestrife". Two other studies, one by Farnsworth and Ellis (2001) and one by Treberg and Husband (1999) also did not detect an effect of purple loosestrife on plant community diversity, but again, both studies examined plant community diversity on a 1m^2 spatial scale.

In summary, a number of observational and experimental studies support the hypothesis that purple loosestrife is able out-compete other wetland plants and that increasing abundance of loosestrife is correlated with decreasing wetland plant diversity. However, several studies found no association between purple loosestrife abundance and plant community diversity in invaded wetlands. Experimental evidence suggests that loosestrife invasiveness may increase with reduction in water level fluctuation and increase of soil nutrient concentrations.

Reed canary grass

Reed canary grass is a coarse perennial wetland plant. Its origin is currently in dispute and some believe it is a "cryptogenic species" in that it is not possible to determine its true origin (Galatowitsch et al. 1999). Evidence from herbaria records supports the claim that reed canary grass is native to temperate areas in both Eurasia and North America (Naglich 1994). However, others believe that, although the native reed canary grass ecotype is not considered to be aggressive, the Eurasian ecotype (or possibly the mixture of native plants and exotic cultivars) is an invasive plant that forms monospecific stands similar to those of loosestrife (Hutchinson 1992, Merigliano and Lesica 1998).

Canary grass is documented as a cultivated forage grass as early as 1749 in Sweden (Alway 1931). In Oregon, it was first cultivated in Coos County in 1885 (Finnell 1936). Canary grass has also been used to stabilize soils. However, "it is suggested that the species not be used to temporarily stabilize pond bottom soils because of its great and unexpected adaptability to aquatic situations" (LeFor 1987). Its tenacity and rapid growth make reed canary grass both a useful forage plant and an aggressive invader. It has completely eliminated all other species in the seedbank at a wetland site in Illinois, where it had been dominant for a period of over 40 years (Apfelbaum and Sams 1987). Reed canary grass has been shown to be associated with species poor plant communities in Wisconsin wetland meadows. Meadows dominated by *Carex stricta* and *Typha* spp. were found to support 29 and 28 additional plant species respectively while a meadow dominated by reed canary grass contained only 3 additional plant species (Werner and Zedler 2002). However, this study had no replication, potentially confounding differences in habitat were not controlled for, and size of meadow was not factored into species richness estimates. In addition, this study focused primarily on the effect of sedimentation on reducing the microtopography of wetland meadows and the response of the plant community. Because the single reed canary grass dominated site with a high sedimentation rate was compared with the other two reference sites without appreciable sedimentation, it is not clear whether the reduction of microtopographic variability or the increase of reed canary grass resulted in the observed reduced species richness.

In summary, evidence from observations and experiments in mesocosms support the hypothesis that reed canary grass can displace wetland plant species. In addition, competitive ability is shown to increase with increases in soil nutrients (primarily soil nitrogen) and light availability.

Effect of invasive plant species on community structure

The effect of an introduced plant species on local species richness, identity, and relative abundance is somewhat of a paradox. Initially, an introduced invasive plant species will increase local species richness though itself and other organisms that are close associates (such as specialist herbivores and pathogens). As the species establishes and spreads, it will increase the evenness of species distributions. Finally, as the plant community approaches a monospecific stand, both species richness and evenness will decline through the displacement of other species and their associates due to competitive exclusion (Grime 1973, Grubb 1977). I expect that the slight positive effects of the two introduced plants will be imperceptible due to the natural variability between sites while the negative effect will become readily apparent at greater densities of the invasive species. Therefore, the hypotheses can be simplified to: (1) as the density of the invasive plant species increases, the species richness and diversity of the local plant community will decrease and (2) because moths are often associated with specific host plants, as the species richness and diversity of plant hosts declines, so will the species richness and diversity of the local herbivore (moth) community.

To link loosestrife and reed canary grass invasion to biodiversity loss, it is necessary to characterize the subject wetlands in regard to potentially covarying and confounding variables. The wetlands were characterized by the following additional explanatory variables: (1) topography, (2) hydrologic regime, (3) soil characteristics, (4) ambient night-time light, (5) trap event variables (temperature, rainfall, wind speed), and (6) surrounding landscape use. The first three variables are expected to influence the structure of the plant community while the last three pertain to variables potentially influencing moth community sampling and structure. I use these data to assess whether the wetlands are similar among attributes that may affect plant and moth species richness aside from the density of the invasive plant species. In particular it is important that the characteristics that define the invaded wetlands are interspersed within the characteristics of the reference wetlands. Low covariance between these environmental variables and invasive plant species abundance strengthens the conclusion that the invasive plant species themselves are responsible for the patterns of diversity found at the research sites.

Variables influencing the species richness and abundance of wetland plant communities

Measurements of the species richness and diversity of plant communities are influenced by both environmental variables and sampling bias. Several environmental factors potentially influence the species richness and diversity of wetland plant communities beyond the density of an invasive dominant plant species (Table 2.1). Duration of inundation is the primary factor influencing the plant community with the greatest number of plant species coexisting in seasonally flooded freshwater habitats (Keddy 2000) such as the wet meadows that are the focus of this study. A secondary influence is soil fertility, where more fertile conditions tend to be associated with fewer species and greater biomass of the dominant species (Weiher et al. 1996, Bedford et al. 1999, Keddy 2000).

The sampling bias contributing to variation within and between sites was reduced by: (1) assigning one observer to quantify the plant community composition at all the sites, (2) sampling all sites within a one month period, and (3) using visual aids to calibrate percent cover estimates before and after sampling. Habitat variables, including wetland history, hydrologic regime, and soil characteristics were measured and analyzed to determine their role in potentially confounding the cause of plant diversity patterns found at the sites.

Table 2.1 Factors influencing the species richness and diversity of wetland plant communities

Reference	Water level	Water fluctuation	Salinity	Soil fertility	Disturbance	Competition	Herbivory	Burial
Magee and Kentula 2002	X	X						
Azous and Cooke 2000	-	-			X (urbanization)			
Keddy 2000	- (1)	+ (1)	- (2)	- (3)	X (4, waves)	- (5)	X (6)	X (7)
Mitsch and Gosselink 2000	-	+		-				
Bedford et al. 1999				-				
Silvertown et al. 1999	X	X						
Weiher et al. 1996	- (1)			- (2)				
van der Valk et al. 1994	-							
Ehrenfeld and Schneider 1993				0	- (man-made) + (natural)			
Keddy 1984		+ (1)			X (2, waves)			
Auclair et al. 1976	X	X		- (1, Ca & P)	+ (2, fire)			

+ indicates positive relationship, - indicates negative relationship, X indicates a relationship but more complex, numbers indicate the relative strength of factor indicated in the study in order from greatest importance (1) to lowest (7), 0 indicates no relationship was found

Variables influencing the species richness and abundance of wetland moth communities

As with plant communities, measurements of the species richness and diversity of moth communities are influenced by both environmental variables and sampling bias. Aside from the composition of the host plant community, land-use surrounding the sites may influence local moth populations (Ricketts et al. 2001). In particular, increasing residential and urban percent cover is likely to decrease moth species richness and diversity by decreasing surrounding host plant habitat, inhibiting colonization from regional sources, and causing sampling and behavioral interference due to night-time illumination (Luff and Woiwod 1995).

Measurements of the species richness and numerical abundance of animal populations tend to be heavily influenced by the sampling method used (Southwood 1966). Using blacklight traps to sample moth populations is not an exception. Most importantly, light traps only attract positively phototaxic organisms. In addition, light trap catch is influenced by: (1) species of insect, (2) sex of insect, (3) design of trap, (4) light intensity, (5) light source, (6) distance to trap, (7) ambient light, (8) meteorological conditions (wind speed, wind direction, rainfall, and cloud cover), and (9) temperature (references listed in Table 2.2). Influential factors 3-7 were controlled for by using the same type of trap during synchronous new moon sampling periods for all sites. In addition, I measured the most important environmental factors which may vary between sites: wind speed, cloud cover, rainfall, temperature, ambient light, and land-use. As with the plant analysis, habitat variables including wind speed, cloud cover, rainfall, temperature, ambient light, and land-use were analyzed to determine their role in potentially confounding the cause of moth diversity patterns found at the sites.

Table 2.2 Environmental factors affecting light trap catch

reference	moth species	moth sex	trap type	light intensity	light source	ambient light	temperature	wind speed	wind direction	rain fall	cloud cover	dist. to trap
Intachat and Woiwod 1999			x									
Nabli et al. 1999					x							
Holyoak et al. 1997							+			-		
Yela and Holyoak 1997						-(2)	+(1)	0			-(3)	
Young 1997				x	x	-	+	-	x	+		-
McGeachie 1989	x					-	+	-				
McGeachie 1988								-				
Gaydecki 1984 (from Young 1997)							+(1)	-(2)				
Bowden 1982	x		x	x	x	x						-
Douthwaite 1978						-		-	0	+		
Persson 1976		x				-(3)	+(1)	-(2)		-		
Taylor and Brown 1972			x	x								
Plaut 1971												-
Stewart et al. 1969	x											-
Harling 1968							+	-	x	-	0	
Hartstack et al. 1968	x											
Stewart et al. 1967	x	x										

"+" indicates positive relationship, "-" indicates negative relationship, "x" indicates relationship but more complex, numbers in parentheses indicate the relative strength of factor indicated in the study, 0 indicates factor was studied but no relationship was found

Moths as indicators of effect to herbivore community

Although the negative effect of some plant invaders on plant species richness and diversity has been documented, little is known about the effect on other trophic levels. The presence and abundance of insects, identified to various taxonomic levels, have previously been used to convey information about the properties of the ecosystems in which they live (Hilsenhoff 1988, Growns et al. 1992, Kremen et al. 1993, Luff and Woiwod 1995, Resh et al. 1995, Wright et al. 1995, Anderson and Vondracek 1999, King and Brazner 1999). Herbivorous and detritivorous arthropods are notable for their numerical abundance, extreme diversity, and importance in food webs (Seastedt and Crossley 1984, Goyer et al. 1990). Experimental studies and environmental surveys have shown that increases in both the number of plant species and the number of plant functional groups result in increased numbers of arthropod species (Murdoch et al. 1972, Strong et al. 1984, Siemann et al. 1998, Wright and Samways 1998, Knops et al. 1999, Haddad et al. 2001, Hawkins and Porter 2003). In addition, experimental evidence suggests that generalist herbivores exhibit lowered biomass gain in species-poor plant communities (Pfisterer et al. 2003).

Lepidoptera have previously been found to be good indicators of environmental conditions (Kremen 1992, Luff and Woiwod 1995) and are known to be almost exclusively herbivorous and relatively host specific (Brues 1920, Brues 1924, Dethier 1952, Erlich and Raven 1964, Janzen 1987, Mitter and Farrell 1991, Young 1997). In addition, prior studies have found a positive correlation between the species richness of plants and Lepidoptera (Thomas and Mallorie 1985, Hawkins and Porter 2003). Therefore, I expect populations of Lepidoptera to exhibit detectable change associated with changes in local plant community composition.

In this study I compare the species richness and abundance of moths sampled throughout the growing season in light traps placed at sites with varying abundance of purple loosestrife and reed canary grass. Moths are used here as a biological indicator of the effect of increasing density of invasive plant species on the herbivore trophic level in wetland communities. Characteristics of an ideal biological indicator species are: (1) practical to monitor, (2) sensitive to the stressor of interest, (3) ubiquitous, (4) short generation times, and (5) play a key role in the functioning of the community (Parker et al. 1999). Moths exhibit the first four of these traits and arguably the fifth (Foote et al. 1988, Goyer et al. 1990). Moths are efficiently sampled by light traps and, as consumers of living plants, they are likely to be sensitive to vegetation changes caused by plant invaders (Janzen 1987, Pinheiro and Ortiz 1992). Moths in regional forests have been examined extensively in biodiversity studies at Oregon State University; photographs (Miller and Hammond 2000), voucher specimens (OSU Arthropod Collection), and local expertise (P. Hammond) were used in species level identification.

Materials and Methods

Study sites

Twenty-four wetland field sites were selected in 2000 and 2001 (Figure 2.1, Appendix A). Sixteen focal sites were established in the Willamette Valley, OR. Four study sites were established on islands within the Columbia River Estuary (three in northwestern Oregon and one in southwestern Washington) and an additional four sites were located east of the Cascade Mountain Range along the

Columbia and Snake Rivers (two in northeastern Oregon and two in southwestern Idaho respectively). Twenty sites are seasonally flooded emergent palustrine wetlands and four are tidally influenced (freshwater) wetlands inundated on a monthly cycle. The vascular plant community at all sites was dominated by herbaceous vegetation at the time they were selected.

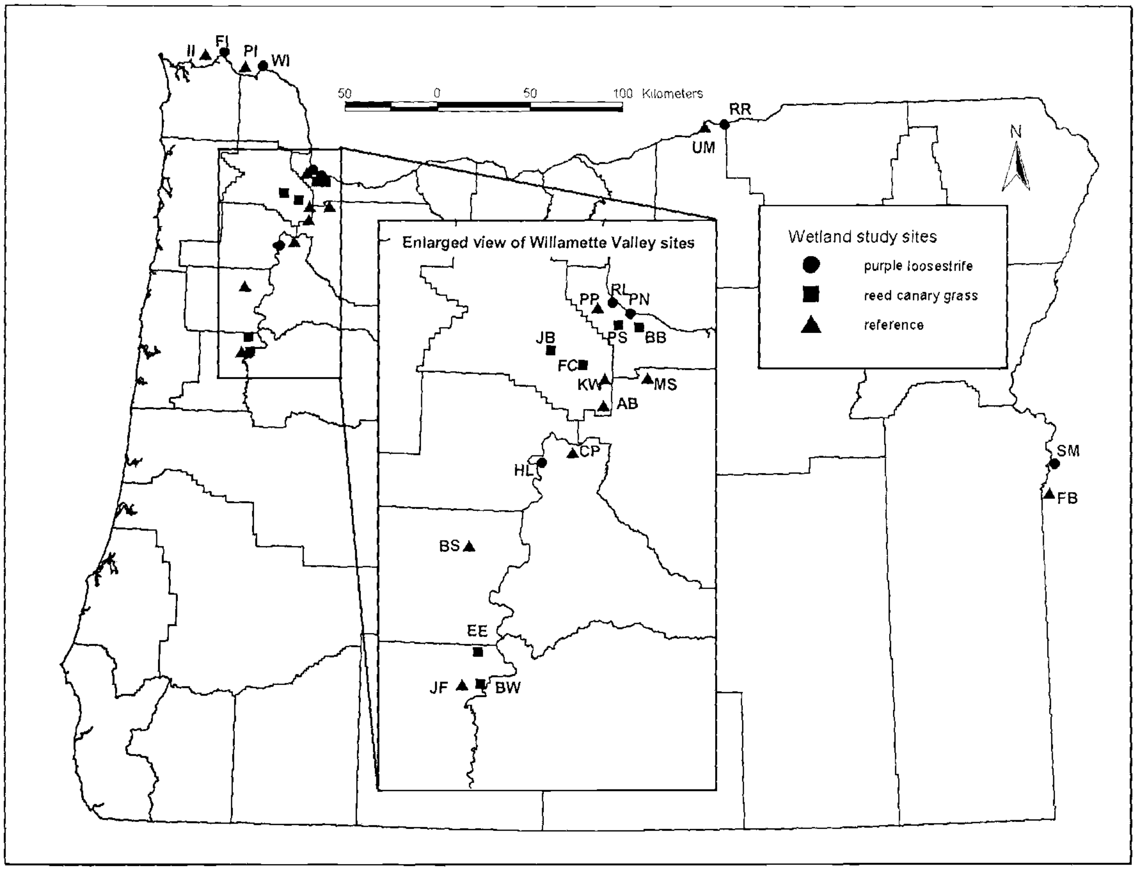


Figure 2.1. Map of wetland study site locations in the Pacific Northwest. Acronyms are used for site identification, see Appendix A for geographic coordinates and site contact information. All sites are in the state of Oregon except Simplot Marsh (SM) and Fort Boise (FB), which are in Idaho, and Puget Island (PI), which is in Washington. Thin lines denote county boundaries.

These sites were not selected randomly from a set of all possible wetlands. Instead they were chosen based on: (1) wetland type, (2) abundance of purple loosestrife or reed canary grass, (3) area and shape of invasive species stand (for light trap purposes), (4) accessibility, (5) permission to sample, (6) probability of site being modified during the study, and (7) risk of equipment to vandalism. Therefore, the species richness of the plant and moth communities may be driven by environmental factors other than invasive species cover, thereby confounding the relationship of greatest interest to this study. The most important environmental factors have been quantified to control potentially confounding results (Table 2.3). The wetlands were characterized by the following additional explanatory variables: (1) wetland microtopography, (2) hydrologic regime, (3) soil characteristics, (4) ambient nighttime light, (5) trap event variables, and (6) surrounding landscape use. The environmental data are used to assess whether the wetlands are similar among attributes other than invasion status and whether the observed patterns of species richness and diversity are associated with these potentially covarying and confounding variables.

Table 2.3 Environmental variables that may influence plant and moth diversity

Factors Influencing Plant Diversity		
Variable		**Measurement**
Topography		
	elevation	meters above sea level (m)
	microtopographic variation	mean basin depth (cm) standard deviation of basin depth range basin depth
Hydrologic Regime		
	Frequency	inundation cycle (monthly or yearly)
	Duration	time to 90% drawdown (months) time to 50% drawdown (months)
	Intensity	max and cumulative area inundated (m^2) max and cumulative water volume (m^3) max, mean, and range of water depth (m)
Soil characteristics		
	Conductivity/Salinity	mean and standard deviation (ds/m)
	Soil Acidity	mean and standard deviation (pH)
	Sand/Silt/Clay	mean and standard deviation (%)
	Organic Matter	mean and standard deviation (%)
	Nitrogen (total)	mean and standard deviation (ppm)
	Nitrogen (nitrate)	mean and standard deviation (ppm)
	Nitrogen (ammonia)	mean and standard deviation (ppm)
	Nitrogen (incubated)	mean and standard deviation (ppm)
	Phosphorus (total)	mean and standard deviation (ppm)
	Phosphorus (phosphate)	mean and standard deviation (ppm)
	Potassium	mean and standard deviation (ppm)
	Manganese	mean and standard deviation (ppm)
	Calcium	mean and standard deviation (meq/100g)
	Magnesium	mean and standard deviation (meq/100g)
Factors Influencing Moth Diversity		
Variable		**Measurement**
Nocturnal illumination		
	Ambient light (during new moon)	mean night sky illumination (lumens)
Trap event variables		
	Temperature	min night temp (degrees Celsius)
	Wind Speed	meters per second
	Rainfall	present/absent
Land use		
	Urban	percent
	Natural	percent
	Agricultural	percent
	Forest	percent

The plant community was sampled at all 24 sites. However, logistics, safety issues, and low moth catch in preliminary sampling precluded us from sampling moths at the four estuarine island sites (FI, WI, PI, and II). Therefore, moth community analyses were performed on the emergent palustrine sites only. Due to logistical limitations and site modification I was not able to quantify all site characteristics for all sites. Soil characteristics and wetland hydrology/microtopography were quantified at 13 of the 16 Willamette Valley focal sites (Table 2.4).

Table 2.4 Site characteristics measured by site and location

Site	ID	Location	Site characteristics measured							
			Plants sampled	Moths sampled	Elevation	Microtopography	Water level	Soil characteristics	Land-Use	Ambient night illumination
Apache Bluff	AB	Willamette Valley	X	X	X	X	X	X	X	X
Bird Blind Site	BB	Willamette Valley	X	X	X	X	X	X	X	X
Baskett Slough	BS	Willamette Valley	X	X	X	X	X	X	X	X
Boardwalk	BW	Willamette Valley	X	X	X	X	X	X	X	X
Champoeg SP	CP	Willamette Valley	X	X	X	X	X	X	X	X
EE Wilson	EE	Willamette Valley	X	X	X	X	X	X	X	X
Fanno Creek	FC	Willamette Valley	X	X	X	X	X	X	X	X
Horseshoe Lake	HL	Willamette Valley	X	X	X	X	X	X	X	X
Jackson Bottom	JB	Willamette Valley	X	X	X	X	X		X	X
Jackson-Fraizer	JF	Willamette Valley	X	X	X	X	X	X	X	X
Knez Wetland	KW	Willamette Valley	X	X	X	X	X	X	X	X
Minthorn Springs	MS	Willamette Valley	X	X	X				X	X
Prison Site North	PN	Willamette Valley	X	X	X	X	X	X	X	X
Pickle Pond	PP	Willamette Valley	X	X	X	X	X	X	X	X
Prison Site South	PS	Willamette Valley	X	X	X	X	X		X	X
Ramsey Lake	RL	Willamette Valley	X	X	X	X	X	X	X	X
Old Fort Boise	FB	East of Cascades	X	X	X				X	X
Rand Road	RR	East of Cascades	X	X	X				X	X
Simplot Marsh	SM	East of Cascades	X	X	X				X	X
Umatilla NWR	UM	East of Cascades	X	X	X				X	X
Fitzpatrick Island	FI	Columbia Estuary	X		X					
Ironson Island	II	Columbia Estuary	X		X					
Puget Island	PI	Columbia Estuary	X		X					
Wallace Island	WI	Columbia Estuary	X		X					

Clean protocol

In this study, multiple wetland sites were visited each day and seeds of exotic wetland plant species could potentially be spread to uncolonized reference sites. To prevent the spread, researchers carried a separate pair of boots for invaded and uninvaded sites and visited the sites in order from reference sites, to canary grass sites, to loosestrife sites. Because canary grass was prevalent at all the loosestrife sites, although not *vice versa*, loosestrife sites were visited last. Boots were brushed free of soil and all pockets and recesses of clothing were emptied before moving to a new site. At the end of each day, all boots and clothing were either cleaned or switched with previously cleaned clothing before subsequent sampling.

Light traps were stationed at a site for the duration of the monthly sampling event (four days). Before moving traps into reference wetlands they were brushed free of seeds and other plant material. All researchers were informed of protocol before visiting the sites.

Plant sampling

An estimate of percent plant cover was made at each of the 24 sites. Thirty 1.0m^2 plots (square) were randomly selected from within the effective trapping area of the light trap (50m radius, $7{,}850\text{m}^2$). This was done by randomly selecting a direction (1-360 with North at 360) and then randomly selecting a distance. The distance was initially selected randomly from between 0 and 2,500 and the square root of the result was the radial distance to the plot. This corrected for the bias in the exponentially increasing area with geometrically increasing distance from the center. The percent cover of each plant species was then visually estimated in each plot to the nearest one percent. Due to overlapping cover, the total cover for each plot sometimes exceeded 100%.

Plant abundance can be measured as density, biomass, or cover. Plant density is a problematic measure because of the extreme variation in the size of individuals and the difficulty in identifying an individual plant, particularly for clonal species. Biomass is arguably a more objective measure of plant abundance, but is also more destructive, time consuming, and difficult to sample repetitively. Hermy (1988) found that biomass data from a moss and herbaceous plant community were highly correlated (r=0.87) with visual estimates of plant cover in 0.25m^2 plots. His comparison suggested that "for monitoring changes in species abundance, community development and environmental correlation analysis, visual cover gives no significant loss in information compared to more time consuming methods". McCune (1990) reached a similar conclusion when comparing percent cover estimates with biomass for cryptogamic epiphytes on tree branches. He found that percent cover estimates were "strongly correlated [r^2=0.63 for bryophytes and 0.76 for lichens] with biomass for all species, sample totals, and species totals". These correlations between cover and biomass come from plant communities that have a limited third dimension (i.e. they are relatively flat). The relationship between cover and biomass would be weakened in plant communities with greater three-dimensional structure, such as forests.

Another standard method for estimating plant abundance uses a sample frame with a uniform array of pins extending downward. Where a pin touches a plant, the species is recorded. Sykes et al. (1983) compared point quadrat estimates (100 uniformly distributed pins in multiple 4m^2 plots over multiple sites) to visual cover estimates using 10 different observers. They found that variation between observers (90% CI: ±10-20%) was greater than the variation within observers (90% CI: ±5-15%).

In this study I sampled plant abundance using the visual cover estimation method because: (1) many of the sites were mitigation wetlands or in parks or other sensitive areas where I could not destructively sample biomass, (2) I was interested in all plant species and point estimates would be expected to lead to an underestimate of species richness because the finite points would likely miss small or rare species, and (3) given time constraints I chose to sample more plots with less accuracy rather than few plots with great accuracy. To avoid the additional source of error introduced by multiple observers (Sykes et al. 1983), one researcher (S.S. Schooler) sampled all sites. The observer was trained prior to making measurements by calibrating cover estimates using a series of charts where the percent cover had been calculated. The observer tested against the charts after measuring the sites to determine change in bias over time and experience.

The plant community at each of the sites was sampled during July, 2001. Species identifications follow Hitchock and Cronquist (1973). A voucher collection of the plant species sampled was assembled. Richard Halse (Department of Botany and Plant Pathology, Oregon State University) verified the voucher plant identifications and these specimens have been deposited in the Oregon State University Herbarium.

Moth sampling

The moth community at each site was sampled using an 8-watt blacklight trap (Ward's Natural Science, Rochester, NY) with a Diclorvos fumigant strip (Revenge: 2,2-Dichlorovinyl dimethylphosphate, Bioquip, Rancho Dominguez, CA). The traps were located at the center of the site and elevated so that the light was above the vegetation canopy. Each light trap sample was collected the following day to prevent decay of moth specimens. Sites were trapped for three moonless nights each month from May through August, resulting in a total of 240 samples collected in 2001.

The effective trapping distance of the light trap is important in determining the area of the vegetation to be sampled when correlating plant species with moth species. Researchers have studied the effect of distance using mark-recapture experiments (Plaut 1971) and behavioral observations of caged moths (Stewart et al. 1969, Plaut, 1971). Stewart et al. (1969) found that the limit of response of *Manduca sexta* was 135m and that of *Heliothis zea* was 90m using a 15-watt blacklight trap. However, the distance of attraction of caged moths doesn't indicate the probability that moths found at that distance will be caught in the trap. Plaut (1971) found that *Spodoptera littoralis* was attracted to a 6-watt blacklight at a distance of 200m. However, after releasing moths from differing distances from a 15-watt blacklight trap he found that only 0.6% of those released at 100m were recaptured in the trap during the next night. At 1, 10, and 50m he recaptured 14.7, 10.7, and 1.4% respectively (Figure 2.2). Therefore, the finding that *Spodoptera littoralis* is more sensitive than either *M. sexta* and *H. zea* to blacklight radiation and only 1.4% of individuals are recaptured from a cohort placed 50m from the light source indicates that most of lepidopteran individuals caught in an 8-watt blacklight trap were attracted from within 50m of the trap. However, this does not mean all the moths sampled in light traps have necessarily completed their larval stages on plants within 50m of the trap. Some moths may have flown into trap's attraction zone after feeding on host plants outside the sample area.

Several other researchers have also estimated the zone of effective catch of a light trap to be less than 50m (Baker and Sadovy 1978, McGeachie 1988, Roberts 1996 (graph from Young 1997)). Therefore, I used 50m as the effective area of the light traps and restricted vegetation sampling to within that area (7,850m^2). This assumption was tested by matching moth host plant associations with site plant composition. If a significant number of moths are mismatched with available host plants, larvae may be feeding on plants outside the assumed trap area and larger areas may need to be sampled to link plant communities with moth communities. Preliminary data collected in 2000 indicate that few moth species are necessarily feeding on vegetation from outside the sampling area.

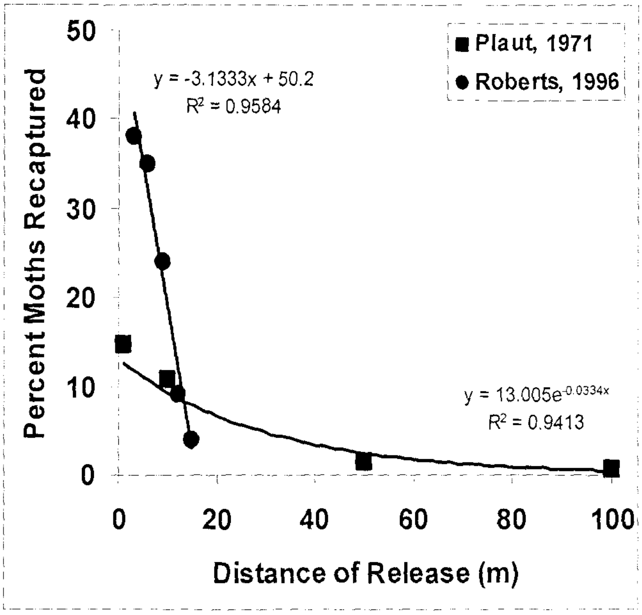


Figure 2.2. Percent of moths recaptured decreases with increasing distance from the blacklight trap. Plaut (1971) studied *Spodoptera littoralis.* Roberts (1996) captured and released various moth species.

The species richness of the moth community is expected to be positively correlated with the species richness of the plant community (Erhardt and Thomas 1991, Kremen 1992, Kremen et al. 1993, Luff and Woiwod 1995, Siemann et al. 1998) and negatively correlated with habitat loss and increasing human development (due to mating disruption in high-light night environment) (Ricketts et al. 2001). I used a GIS-based land-use data layer (imagery collected in 1993) to calculate percent urban land-use in a series of ten concentric circles with increasing radii (100, 200, 300, 400, 500, 1000, 1500, 2000, 2500, 3000m) centered about each light trap location. Percent urban cover was then plotted against moth species richness and abundance. At each scale the percent of the area in each of four land-use categories was summarized as forest, natural non-forest, agricultural, and urban (after Shaffer et al. 1999) for each site. Correlation coefficients were used to determine which land-use practices most affect the moth community species richness and abundance at various scales. Ricketts et al. (2001) found that a "halo" of increased moth species richness extended from 1.0-1.4km from the forest edge into agricultural fields and therefore agricultural sites within 1.0km of a forest fragment had significantly greater species richness and abundance than sites farther than 3.5km from the forest edge. I expected the local moth communities to react at similar scales and have therefore chosen to quantify land-use composition in a series of ten concentric radii up to 3000m around each site.

I examined potential biases in sampling method due to local environmental site conditions. Variables of primary interest that might affect trap catch and vary between sites on a given night are: (1) temperature, (2) wind speed, (3) rainfall, and (4) cloud cover. In addition, ambient light associated with urban environments may impact trap catch, but is unlikely to vary much during a given night. Temperature is likely the most influential factor in light trap catch (Table 2.2). Air temperature was recorded when the traps were set and again when samples were collected. A max-min thermometer was attached to each trap (north side in shade of trap) and these temperatures were recorded when the traps were serviced the following day. Current and maximum temperatures were heavily influenced by the time of day the trap was set, and this varied between sites depending upon the sequence they were tended. Therefore, only the minimum temperature was used to quantify temperature differences between the sites. Also, it is likely that minimum temperatures most influence trap catch as moths stop flying when temperatures reach a minimum threshold. Wind speed was measured at dusk at all twelve sites in 2000 using a digital wind speed meter (Kestrel 1000, Nielsen-Kellerman, Chester, PA, USA) and was found to be negligible. This was probably because most sites exist within topographic depressions and many are surrounded by forest, thus I observed wind speeds of less than 0.3 meters per second. In addition, presence or absence of rainfall and an estimate of percent cloud cover were recorded for each trap event. Some traps were located in urban environments where ambient light may affect trap catch. Light intensity measurements were taken on a new-moon night in August 2001 for sites in eastern Oregon and in September 2001 for Willamette Valley sites. A standard photographers' light meter (Gossen Luna-Pro, Bogen Inc., London, UK) was used to measure the ambient light intensity (lumens) of the night sky at nine points (horizon (N,E,S,W), 45° (N,E,S,W), and 90° (directly overhead). The mean of these nine locations was used as the measure of nocturnal light intensity at each site.

After collection, the moth samples were frozen and transported to Corvallis for identification to species. Paul Hammond (Department of Zoology, Oregon State University) assisted by identifying and verifying specimens. A voucher collection for the moths was assembled and was deposited in the Oregon State University Arthropod Collection (OSAC).

Quantifying hydroperiod and topographic variation

Wetland plant species richness is primarily influenced by hydroperiod (references in Table 2.1). Topographic variation coupled with cyclic water level fluctuation create a landscape of waxing and waning soil oxygen concentrations dependent upon the duration, intensity, and frequency of inundation. Plant roots need oxygen to respire and standing water slows the rate at which plant roots receive oxygen from the environment. In addition, water depth influences seed germination rates and photosynthetic ability (Keddy

2000, Cronk and Fennessy 2001). Theoretically, habitats with greater topographic heterogeneity should provide a greater diversity of niches and thereby allow a greater number of species to coexist (Whittaker 1965, Grime 1973, Grubb 1977). Therefore, reduced variation in hydrologic conditions should lead to a fewer number of plant species per unit area regardless of invasive species dominance. The hydroperiod of fourteen wetlands was examined to determine whether the inundation patterns of reference wetlands successfully circumscribed the conditions of the invaded wetlands.

The hydroperiod (hydrologic state or water budget) of a wetland is defined as "the balance between the inflows and outflows of water" and can be expressed as the change in the volume of water over a given change in time. Water volume is a function of the area of inundation and mean water depth (Mitsch and Gosselink 2000). Therefore, the flooding regime of a wetland can be defined by the fluctuation of water depth, area of inundation, and water volume over time. To compare the hydrological properties of the study sites, I first qualitatively examined the wetlands by examining plots of water depth, area, and volume measured in monthly increments. Second, I quantified attributes using disturbance ecology as a guide. Inundation (flooding) is a disturbance in that it reallocates limiting resources. It can be quantified through its components: frequency, duration, and intensity (Pickett and White 1985). Since the focal study sites are all seasonal wetlands, the frequency of inundation disturbance is on a yearly cycle (1/yr). The intensity of disturbance at the sites was compared using four metrics, mean water depth (cm), maximum water depth (cm), range of water depth (cm), and volume (cumulative monthly m^3/year). Duration of flooding was quantified as: area inundated (cumulative monthly m^2/year), maximum area inundated (m^2), and the number of months to 50 and 90% drawdown.

Elevation and topographic variation were included as separate variables as they may influence plant diversity independent from their role in defining flooding. Elevation above sea level for each site was acquired from digital elevation models (USGS-DEM). Surveying and GIS techniques were used to quantify microtopographic elevation (Louchaichi et al. 2001) for the basin of each site. The basin morphology was then linked to monthly water level measurements to determine the area inundated, mean water depth and standing water volume for each month at each site.

In March and April 2001 a shallow well was sunk at each of the Willamette Valley focal sites to measure water level throughout the year. Wells consisted of a 1.3m PVC tube (5cm inside diameter) with opposing perforations (1cm diameter) at 10cm intervals down each side. The bottom was capped and had two perforations. The tube was then wrapped with fiberglass window-screening (approx. 2mm mesh) on the exterior to prevent sediment accumulation. The wells were installed so to extend one meter below the ground surface by digging a hole with a soil auger, inserting the well, and filling in with sand. Digging, rather than driving, prevented soil compaction around the wells, and sand fill facilitated water flow (pers com M. Kentula, US-EPA, Corvallis, OR). Two wells 100m apart were installed at one site (JF) to determine whether one central well was adequate to measure surface water characteristics.

Water can be below or above the soil surface. If the water level was below ground, it was measured using a 1.5m measuring stick. The stick was lowered into the well while observing the reflectance of the water's surface. When the stick broke the water surface the reflectance change was visible and the depth was recorded, minus the wetted portion of the stick (usually 1-4cm), minus the distance to the ground from the lip of the well. This was the depth of the water below the ground surface at that location. Water above the soil surface was measured by placing the measuring stick beside the well and recording the depth of standing water. The ground surface at the well head was considered the zero point and negative numbers indicated the depth of water below the surface and positive numbers indicated surface water depth. Water levels were taken at monthly intervals over a span of 21 months.

The microtopographic basin survey method used a surveyor grade differentially correcting GPS receiver (Trimble Surveyor) in conjunction with a rotating laser level to obtain a digital elevation model (DEM, grid-based contour map) of each site. A laser level was set at each site and the distance to ground from the laser plane was measured at the well (usually within 2m from center). A laser sensing device and stadia rod were used to map deviation from the laser level plane to the ground surface for multiple locations (50-100) at each site.

The accuracy of the model depends on how well the site is surveyed. A grid system for locating points would be the most objective method, but would often miss break points in the terrain (mounds, ditches, etc.) and would be logistically difficult to maintain when working through brush and shrubs. A randomized approach would pose similar problems. Therefore, I chose a more subjective, but probably more accurate method (Louchaichi et al. 2003). I started at 60m from the center stake and surveyed the perimeter in 10m increments in a clockwise direction (approx. 30 point locations). Meanwhile, I looked for topographic features (break points) greater than 50cm in height (or depth) and greater than $10m^2$ in area (approx. 3m x 3m). These areas were then surveyed at the edges and central points so that the interpolation would recognize the unique aspects of the area and model them accurately. Once the outer perimeter was surveyed, I moved to a 30m radius (20 points), then to 10m (10 points and center) and repeated the process.

The data were then downloaded and differentially corrected using Pathfinder software (Trimble) and exported as ArcView shapefiles in Universal Transverse Mercator projection using North American Datum 1927. The GPS receiver, through real-time and post-processing differential correction, was able to locate the horizontal position of a given survey point within a calculated precision of <1.0m. Louchaichi et al. (2001) have studied this technique and report a vertical accuracy of 1-3cm. Using ArcView (version 3.2, ESRI), the elevation of each point in relation to the ground surface at the well was calculated by subtracting the deviation of the laser level plane to the ground surface at each survey location from the deviation of the laser level plane to ground surface at the well (surface of ground at well was then relativized to 0).

These point data were then used to interpolate an elevation grid with 1m x 1m cells (7,854 cells) for each site. I chose to use the inverse distance weighted (IDW) interpolator method over the spline method because the spline method was observed to over-correct when it encountered sharp breaks in the landscape. The inverse distance weighted (IDW) interpolator assumes that each input point has a local influence that diminishes with distance. It weights the points closer to the processing cell greater than those farther away. I chose to use the six nearest neighboring survey points with the root of the distance (2nd power) as the weighting factor. Once the elevation grid was calculated, the grid values were exported to a spreadsheet. The area of inundation was then calculated for each site during each month by determining the number of cells below the measured water level.

Quantifying soil characteristics

Nitrogen is considered the primary limiting nutrient for plant growth in emergent marsh ecosystems (available as nitrate and ammonium), followed by phosphorus (available as soluble phosphate) (Bedford et al. 1999, Keddy 2000, Mitsch and Gosselink 2000, Bridgham et al. 2001). However, there is evidence that phosphorus may be limiting in urban wetlands (Woo and Zedler 2002). Carbon, potassium, and micronutrients (primarily Mn, Mg, and Ca) may also be limiting nutrients for plant growth, but I found no prior literature that presents evidence that these nutrients are limiting in wetland ecosystems.

I examined the soil characteristics of a given site by directly measuring an array of soil nutrient concentrations (Stolt et al. 2001). The direct measurements included the variables: total nitrogen, nitrate, ammonium, mineralizable ammonium, total phosphorus, phosphate, organic carbon, potassium, magnesium, calcium, manganese, conductivity, acidity, and percent sand/silt/clay. Since variation of nutrients within a site may contribute to diversity, I also included the standard deviation of the soil character variables in the analysis.

To assess soil characteristics I collected soil samples from four randomly selected locations within 13 focal wetland sites (52 samples) during June of 2002. Soil samples were taken by first removing the top 5cm of soil from the center of the plot using a spade. Then the next 5cm (approx. 2 liters) were placed into a paper bag. If the soil was wet, the paper bag was set into a plastic bag for transport. Prior studies have found no significant difference in soil properties (organic C, cation exchange capacity (CEC), N, pH, Ca, and Mg) within small (0.25-0.35ha) palustrine wetland sites between samples taken at the same depth (Stolt et al. 2001). Therefore, I restricted soil sampling to the root zone at a single depth (5-10cm below surface) within and across sites. Samples were brought back to the lab, removed from plastic bags, and dried. Soil nutrient analyses were conducted by the OSU Department of Crop and Soil Science soils laboratory and physical soil properties were measured by a technician (C. Meston) under the direction of Crop and Soil Science staff using their protocols (Horneck et al. 1989).

Quantifying land-use using GIS spatial datasets

Increasing urbanization may influence moth population dynamics and community structure by decreasing host plant habitat and inhibiting colonization. Urbanization is also positively correlated with nocturnal light. I used ArcView (3.2) with the PNW-ERC Willamette River Basin Mapping Project theme to quantify surrounding land-use (www.fsl.orst.edu/larse/wrb/wrb.html) for the Willamette Valley sites and the Oregon and Idaho Gap Land Cover Analysis (Oregon Natural Heritage Program) to estimate land-use surrounding the east Oregon and west Idaho sites. The Gap GIS coverage was not as detailed as the Willamette coverage and visual estimates were used at the smaller scales of observation. Land-use was measured at ten scales, 100, 200, 300, 400, 500, 1000, 1500, 2000, 2500, and 3000m around each site. At each scale the fraction of the area in each of four land-use categories, natural (natural/park), forest, agriculture (fields/ orchards), and urban (residential/ commercial/ industrial/ transportation corridor) was summarized (after Shaffer et al. 1999). See “moth sampling” for a more complete description of methods.

Quantifying Species Diversity

Similar analysis procedures were used for both the plant and moth communities. First, sampling adequacy was analyzed by constructing species-area curves for each site using multivariate analysis software (PC-ORD, McCune and Mefford 1999). The species-area curves were calculated using a nonparametric resampling procedure called a “jackknife”. This procedure determines the number of unique species in 500 randomly selected “resampled” combinations of subsamples ($1 m^2$ plots) for each increase in level of sampling area (1-30 plots) (McCune and Mefford 1999, McCune and Grace 2002). Then, the mean and standard deviation are calculated for each level of effort (stepwise increase of total area sampled). If the mean number of species reaches a plateau, it suggests fewer species are being added through a stepwise increase in sample area. Presence of a plateau indicates that most of the species in the habitat were sampled at least once.

The structure of a biotic community consists of a number of species with associated abundance values (Fisher et al. 1943, Whittaker 1965) and is often quantified as the two components of biological diversity: (1) the total number of species in a given area, or the species richness (S), and (2) the evenness between species abundance or equitability (J). The community structure can be qualitatively examined and compared between sites using rank-abundance diagrams (Whittaker 1965, Magurran 1988, Begon et al. 1990). Rank-abundance diagrams plot mean species abundance against species rank, thereby visually integrating the two diversity components, species richness and equitability (Magurran 1988, Begon et al. 1990, Krebs 1999). These diagrams can be used to compare the communities between sites and contrast with proposed theoretical distributions such as the log normal series, log series, geometric series, and broken stick model (Whittaker 1972, Magurran 1988, Begon et al. 1990, Gotelli and Graves 1996).

Four standard nonparametric community diversity descriptors were used to quantitatively evaluate the plant community at each wetland site. These were, (1) species richness (S), (2) species equitability (J),

(3) Shannon-Wiener function (H'), and (4) Simpson's Index (D). A single quantitative index of community diversity incorporates both the total number of species and the equitability in distribution of those species (Whittaker 1972, Magurran 1988, Begon et al. 1990, Krebs 1999). Community ecologists and statisticians have made many attempts to create an index that accurately represents the combination of species richness and equitability, but a consensus has not yet been reached (Whittaker 1972, Hurlbert 1971, Hill 1973, Wolda 1983, Magurran 1988). This is partially because each index emphasizes different community traits (*i.e.* H' tends to emphasize the less abundant species whereas D emphasizes dominant species) (Hill 1973, Magurran 1988), and either index may be preferred depending upon the question being asked or hypothesis being tested. Since I am interested in the response of both dominant and rare species I calculate both Shannon-Wiener and Simpson indices and contrast the results.

The Shannon-Wiener function (H') is a measure of the information content of the sample and integrates species richness and equitability. The function is defined as the sum across all species of the total number of species multiplied by the proportion of the total sample belonging to a particular species (Table 2.5). Thus, for a given richness, H' increases with equitability, and for a given equitability, H' increases with richness. The Shannon-Wiener function is most strongly affected by the species in the middle of the sequence and is therefore not as sensitive to the abundances of the first few dominant species, as compared with Simpson's index (Whittaker 1972).

Simpson's index (D) is similar to H' in that it integrates species richness and abundance. It can be thought of as the probability that two individuals, drawn at random from the sample population, are of different species. It is calculated as one minus the sum across all species of the squared proportion of abundance of each species (Table 2.5). As with H', for a given richness, D increases with equitability, and for a given equitability, D increases with richness. The Simpson index is strongly influenced by the abundances of the first few dominant species, and can therefore be regarded as a measure of dominance (Whittaker 1972).

Species equitability (J) is a measure of how evenly species abundances are distributed throughout the community. It is usually calculated as the observed H' divided by the maximum H' (=ln S) of the community. An equitability value of one indicates a completely even distribution of species abundances and values decrease with increasing disparity between species abundance.

Diversity indices have a long history in the analysis of arthropod communities sampled with blacklight traps (Fisher et al. 1943, Pielou 1966, Kempton and Taylor 1974, Taylor et al. 1976, Wolda 1983, Barlow 1989). Because blacklight trap collections are not considered random samples and because they tend to have many rare species (perhaps due to vagrant arthropods passing through the collecting area), there are additional published recommendations for analysis of these communities. Therefore, I used a slightly different set of five diversity indices to examine the moth communities as compared to those used in the plant community analysis. These were: (1) species richness (S), (2) species equitability (J), (3) Brillouin's Index (H), (4) Simpson's Index (D) and (5) Fisher's log-series index (α).

Many researchers suggest that the indices H' and D are not optimal integrators of species richness and abundance (Pielou 1966, Hurlbert 1971, Hill 1973). Pielou (1966) states that since light trap collections are not random, they can not be considered a random sample of the insects in a given region and should therefore be regarded as populations in themselves. She suggests that a population measure of diversity, such as Brillouin's Index (H), is more appropriate. Therefore, Brillouin's Index (H) replaced H' in the analysis of moth community diversity.

A problem with H, H', and D as characterizations of community diversity is that once the initial components (species richness and abundance) have been combined, the specific information inherent in each is lost. Some researchers argue that indices based on theoretical distributions (log-normal, log-series, geometric series, etc.) provide better diversity estimates in that they preserve the relationship between the component variables (Whittaker 1972, Kempton and Taylor 1974, Taylor et al. 1976, Wolda 1983). Wolda (1983) studied the diversity of tropical cockroaches using blacklight traps and found that the diversity index "α" of the log series was the most satisfactory single measure of diversity (over Hurlbert's "S_m" (Hurlbert 1971)) or Hills's series (which include Simpson's D and Shannon-Wiener H' (Hill, 1973)). However, he also found that the much simpler statistic of "species richness per unit effort can be at least as useful" (Wolda 1983). Therefore, in addition to the above nonparametric estimates of biodiversity, I also calculated the log-series diversity index, α. The log-series index was one of the first diversity indices, originally proposed by Fisher, Corbet and Williams in 1943. It is a parametric statistic that has been used extensively for studying light trap collections of Lepidoptera (Kempton and Taylor 1974, Taylor et al. 1976). Studies have found it robust to deviations from the underlying distribution and that it behaves more consistently and predictably than the Shannon-Wiener and Simpson indices (Taylor et al. 1976).

Table 2.5 Formulas used to compute diversity indices

Index	Symbol	Formula	Reference
Plant Diversity			
Species Richness	S	= total number of species	Whittaker 1972 (p.214)
Shannon-Wiener	H'	$= -\Sigma p_i \log p_i$	McCune and Grace 2002 (p.26)
Equitability	J (Pielou's J)	= H'/log S	McCune and Grace 2002 (p.32)
Simpson's Diversity	D	$= 1-\Sigma p_i^2$	McCune and Grace 2002 (p.26)
Moth Diversity			
Species Richness	S	= total number of species	Whittaker 1972 (p.214)
Brillouin	H (HB)	$= (\log N! - \Sigma \log n_i!) / N$	Magurran 1988 (p.37)
Simpson's Diversity	D	$= 1-\Sigma p_i^2$	McCune and Grace 2002 (p.26)
Equitability	J	= D/S	Krebs 1999 (p.449)
Log Series	α	= see reference	Williams 1964 (p.308)

Data Analysis

Random number generation and data entry were performed in Excel (Office XP, Microsoft 2002). Spatial data were collected using a Trimble Surveyor (XR Pro) global positioning system receiver (GPS) with real-time and post-processing differential correction capable of sub-meter spatial accuracy. Spatial data were differentially corrected using Pathfinder Office software (version 2.70, Trimble 2000). ArcView (version 3.2, ESRI 1999) was used to calculate basin topography and summarize land-use spatial datasets. Linear and multiple regression analyses were performed using Excel and S-plus (version 6.1, Insightful 2002). The community analysis software PCOrd (version 4.17, MjM 2002) was used to compute species-area curves and implement canonical correspondence analysis (CCA) ordination procedures.

Interpreting statistical significance of plant and moth community impact analyses

In the following statistical analyses I use linear regression to examine the relationship between a single explanatory variable (percent cover of the invasive plant species) and 12 different response variables. Each test increases the probability of a Type I Error (rejecting the null hypothesis when the null hypothesis is actually true). A solution is to adjust the α level using a Bonnferoni correction (Ramsey and Schaffer 1997, Scheiner 1993). To retain an overall α of 0.05, I divided α by 12 (the number of tests) for an adjusted $\alpha' = 0.0042$. A one-sided correction was used because I expected unidirectional response, the reduction in diversity measures with increasing cover of the invasive species. The Bonnferoni method is a conservative approach. The correction only applies to analyses where percent cover of purple loosestrife or percent cover of reed canary grass is the explanatory variable.

Results

Wetland Study Sites

The 24 wetland study sites selected for the study are located in Washington, Oregon, and Idaho. They are emergent-nonpersistent wetlands under the Cowardin system (Cowardin et al. 1979). Twenty sites are palustrine, with a yearly inundation cycle, and four sites are riverine with a monthly tidal influence (Table 2.6). Most sites are located in a floodplain and have the potential to be riverine impounding wetlands during winter months when high water flows in the adjacent rivers (Willamette, Tualatin, Snake, and Columbia) rise out of the river channel and fill the depressions.

Table 2.6 Wetland study site classification

Site	ID	County	State	HGM class	HGM subclass	Cowardin System: Subsystem	Cowardin Class	Cowardin Subclass
Apache Bluff	AB	Washington	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Bird Blind Site	BB	Multnomah	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Baskett Slough	BS	Polk	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Boardwalk	BW	Benton	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Champoeg SP	CP	Marion	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
EE Wilson	EE	Benton	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Old Fort Boise	FB	Canyon	ID	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Fanno Creek	FC	Washington	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Fitzpatrick Island	FI	Clatsop	OR	Estuarine fringe	river sourced	Riverine:Tidal	emergent	nonpersistent
Horseshoe Lake	HL	Marion	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Ironson Island	II	Clatsop	OR	Estuarine fringe	river sourced	Riverine:Tidal	emergent	nonpersistent
Jackson Bottom	JB	Washington	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Jackson-Fraizer	JF	Benton	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Knez Wetland	KW	Washington	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Minthorn Springs	MS	Clackamas	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Puget Island	PI	Wahkiakum	WA	Estuarine fringe	river sourced	Riverine:Tidal	emergent	nonpersistent
Prison Site North	PN	Multnomah	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Pickle Pond	PP	Multnomah	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Prison Site South	PS	Multnomah	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Ramsey Lake	RL	Multnomah	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Rand Road	RR	Morrow	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Simplot Marsh	SM	Payette	ID	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Umatilla NWR	UM	Morrow	OR	Depressional	closed nonpermanent	Palustrine	emergent	nonpersistent
Wallace Island	WI	Columbia	OR	Estuarine fringe	river sourced	Riverine:Tidal	emergent	nonpersistent

Dominant Species Status

Nine plant species were dominant (most abundant in the community) across the 24 wetland sites (Table 2.7). Purple loosestrife was dominant at seven sites (13.8-91.7% cover), reed canary grass dominated six sites (18.8-94.7%), and the remaining 11 sites were dominated by seven other plant species (12.5-47.8%).

Table 2.7 Dominant plant species of wetland field sites

Site	ID	Dominant Plant	Mean cover (%)
Apache Bluff	AB	*Alopecurus pratensis*	12.5
Bird Blind Site	BB	*Phalaris arundinacea*	87.4
Baskett Slough	BS	*Juncus effusus*	17.7
Boardwalk	BW	*Phalaris arundinacea*	53.8
Champoeg SP	CP	*Alopecurus pratensis*	47.8
EE Wilson	EE	*Phalaris arundinacea*	18.8
Old Fort Boise	FB	*Typha latifolia*	28.1
Fanno Creek	FC	*Phalaris arundinacea*	94.7
Fitzpatrick Island	FI	*Eleocharis palustris*	27.9
Horseshoe Lake	HL	*Lythrum salicaria*	91.7
Ironson Island	II	*Scirpus microcarpus*	18.5
Jackson Bottom	JB	*Phalaris arundinacea*	66.1
Jackson-Fraizer	JF	*Oenanthe sarmentosa*	30.6
Knez Wetland	KW	*Carex obnupta*	27.8
Minthorn Springs	MS	*Veronica americana*	14.1
Puget Island	PI	*Eleocharis palustris*	16.7
Prison Site North	PN	*Lythrum salicaria*	19.5
Pickle Pond	PP	*Lythrum salicaria*	13.8
Prison Site South	PS	*Phalaris arundinacea*	78.0
Ramsey Lake	RL	*Lythrum salicaria*	14.1
Rand Road	RR	*Lythrum salicaria*	65.7
Simplot Marsh	SM	*Lythrum salicaria*	83.8
Umatilla NWR	UM	*Typha latifolia*	28.0
Wallace Island	WI	*Lythrum salicaria*	47.2

Abiotic factors potentially influencing plant community diversity

Plant diversity is expected to be influenced by wetland topography, hydrology, and soil characteristics. Hydrologic variables were calculated using the monthly water depth measurements coupled with the basin microtopographic surveys. The adequacy of one central well to measure surface water at the 50m radius sites was examined by installing two wells, 100m apart, at the Jackson-Frasier (JF) wetland site and correlating the resultant water depths (Figure 2.3a). Water levels were highly correlated between the two locations (r=0.96) and the slope of the regression line (m=1.09) indicates an approximate 1:1 relationship. The levels of standing water exhibited greater correlation than subsurface water levels. In addition, visual estimates of percent inundation were taken each month for each site. This was done to check the accuracy of the calculated percent inundation estimates against subjective estimates. Visual estimates were highly correlated (r=0.93) with the calculated inundation (Figure 2.3b). However, visual estimates of percent inundation tended to over-estimate the area inundated when it was above 50% and under-estimated the percent inundation when it was below 50%.

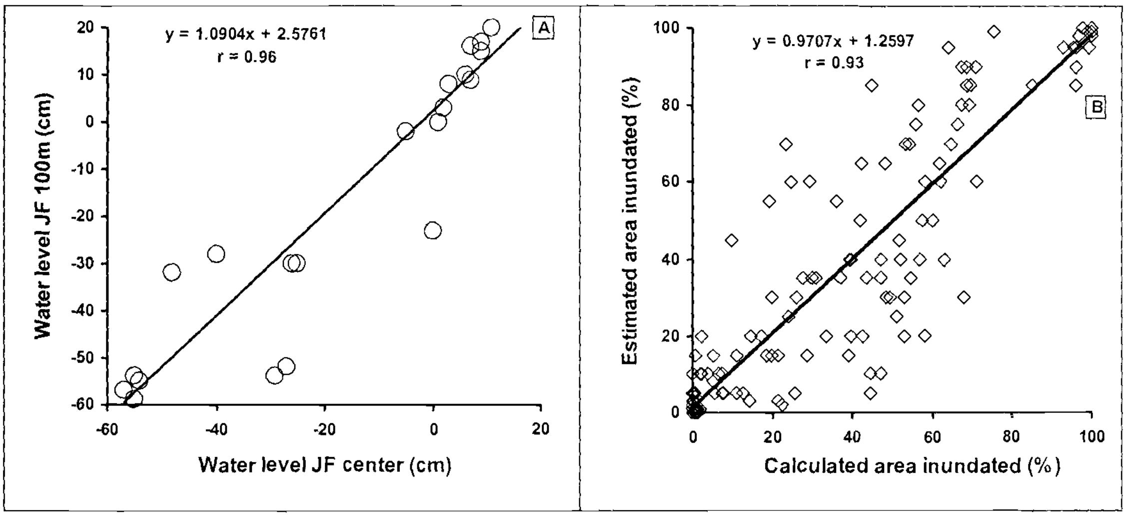
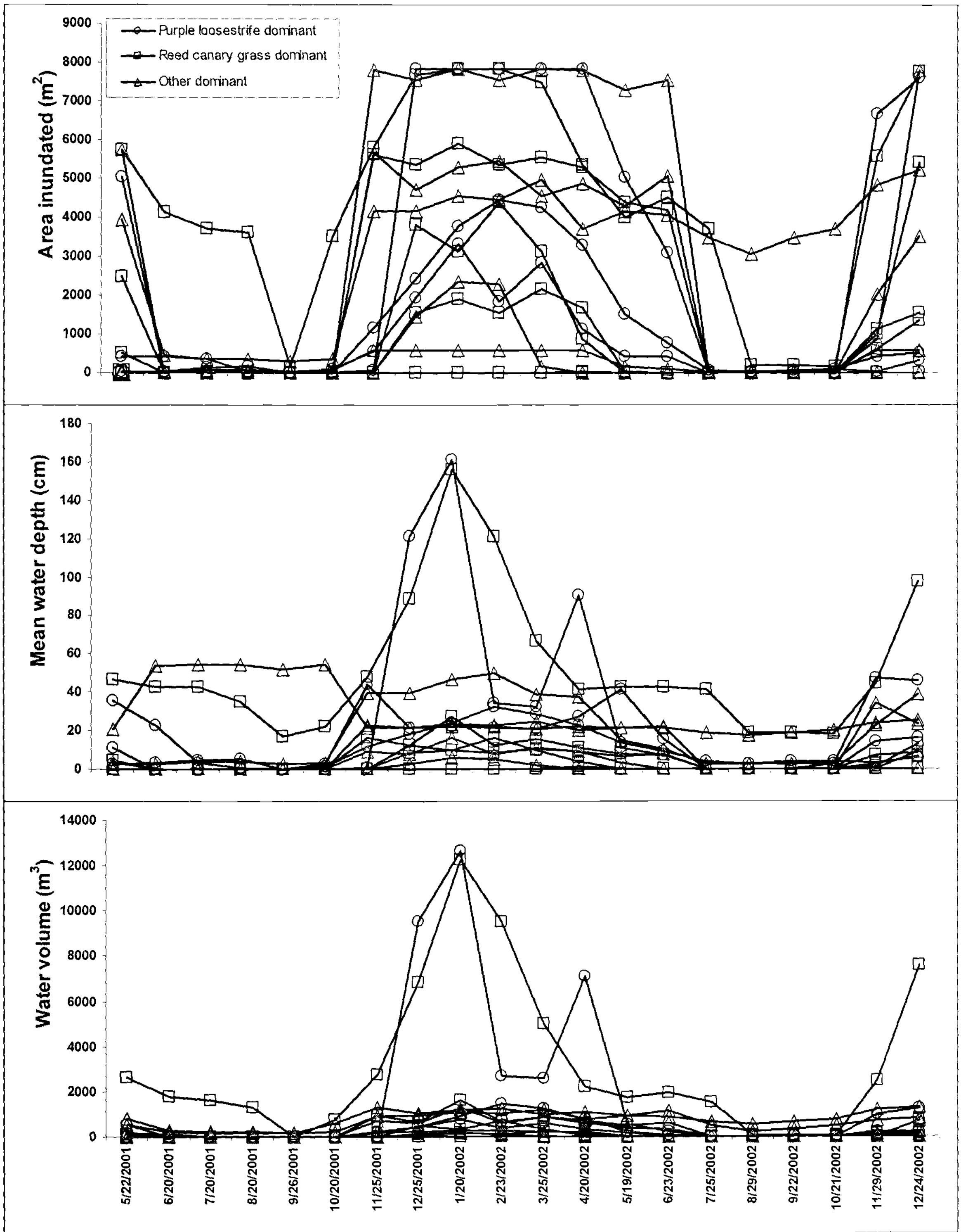


Figure 2.3a-b Assessment of the accuracy of water level and area inundated measurements. (a) Water levels were highly correlated between two locations 100m apart (r=0.96). Subsurface water levels were less correlated than surface water. (b) Visual estimates of percent inundation were highly correlated (r=0.93) with calculated estimates.

Wetland plant community composition is primarily influenced by inundation cycles (see Table 2.1 for references). A visual examination of the monthly area of inundation suggests that hydroperiods of the invaded wetlands are interspersed with those of the reference wetlands (Figure 2.4a). However, graphs of mean water level and water volume indicate that two invaded wetlands exhibit higher flooding peaks during winter months (Figure 2.4b-c) than their reference counterparts. Canonical correspondence analysis and pair-wise correlations were used to further determine whether the conditions of the reference wetlands adequately represented those of the invaded wetlands.



Figures 2.4a-c. Study site hydrology. The area of inundation (a) of the reference sites is interspersed with that of the invaded sites whereas the related parameters of mean depth (b) and water volume (c) indicate more intense flooding during winter months at two invaded sites.

Canonical Correspondence Analysis (CCA) is a direct gradient analysis method that seeks to structure one data matrix so as to maximize the strength of the relationships with a second matrix (McCune and Grace 2002, Anderson and Willis 2003). I used the method to constrain an ordination of the site characteristics by the abundance of loosestrife and canary grass. A Monte Carlo test was then used to evaluate whether the environmental variables were significantly related to the abundance of the invasive plant species. Specifically, the Monte Carlo procedure randomly reassigned the abundances of the invasive species within rows of the second matrix, which eliminates the relationship between the two matrices. A finding of no significant difference between the correlations of the real dataset and the randomized datasets suggests that the relationship between the matrices is not stronger than that expected by random chance and supports the hypothesis of no linear relationship between the two matrices (Ramsey and Schafer 1997, McCune and Grace 2002).

The main data matrix consisted of the wetland habitat parameters (13 sites and 44 variables) and the second matrix contained the mean proportional cover of the loosestrife and reed canary grass for the 13 wetlands. Since CCA incorporates linear regression, assumptions of normality and constant variance were examined for the abundances of invasive species in the second matrix. Normality was improved using an arcsine square root transformation on the proportional cover data. Row and column scores were standardized by centering and normalizing.

There was a negative correlation between the abundances of the two invasive species comprising the second matrix ($r= -0.39$). Axis one was primarily associated with the abundance of purple loosestrife ($r= -0.99$), while axis two was associated with the abundance of reed canary grass ($r= -0.86$). The Monte Carlo randomization procedure was run 100 times and the result was compared with that of the nonrandomized data. The Monte Carlo test statistic indicated that the relationship between loosestrife abundance (axis 1) and the environmental variables was not significantly greater than expected by chance ($p=0.17$). The relationship between reed canary grass abundance (axis 2) and the environmental variables was also not statistically significant ($p=0.47$). I conclude that the variables of interest, purple loosestrife and reed canary grass abundance, vary independent of variation in topography, hydrology, and soil variables.

Abiotic factors potentially influencing moth community diversity

Local temperature influences the flight behavior of moths and lower temperatures are expected to result in reduced light-trap catches. If wetlands dominated by invasive species tend to have lower night temperatures than reference wetlands, moth species and abundance may be reduced regardless of invasive presence. Minimum night-time temperatures were plotted against invasive species cover in order to determine whether the reference wetlands had similar temperature regimes as the invaded wetlands. Minimum monthly mean night temperature during trap events ($n=3$ nights/month) varied from 2.9 to 17.2

degrees Celsius depending on the month and site (Figure 2.5). There was no apparent trend of decreasing temperature with regard to invasive species abundance.

Ambient night illumination is expected to be negatively correlated with light-trap catch. Illumination varied from 0.10 to 2.0 lux with a mean of 0.24 lux. Most sites had low ambient illumination during new moon nights, except Knez Wetland (2.0 lux), which was illuminated by a nearby billboard. No apparent trend of increasing illumination with regards to invasive species abundance was found (Figure 2.6).

Precipitation and wind speed can influence trap catch. There was no precipitation during the nights moths were sampled. During a preliminary study in 2000, wind speed was measured at the sites when the traps were set in the evenings and at dawn when the moths were collected. All wetlands were in depressions in the landscape. This topography caused winds to be so light that they rarely registered on the wind speed meter (start-up speed 0.3m/sec.). We discontinued wind speed measurements for moth sampling in 2001.

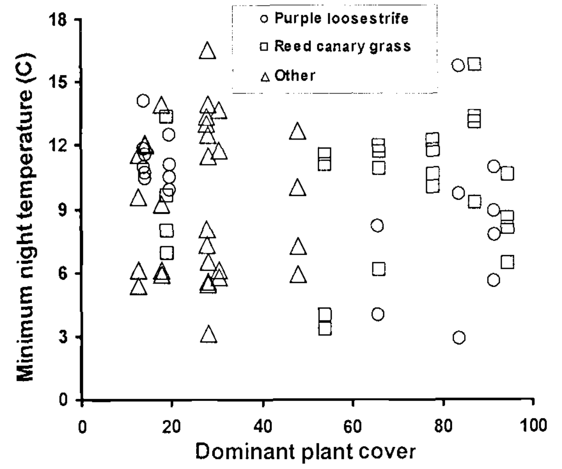


Figure 2.5. Comparison of temperatures between reference and invaded wetlands during sampling events. Reference site temperature during light-trap sampling nights circumscribes the temperatures of the invaded sites. Temperature was summarized as mean minimum temperature by month (n=3).

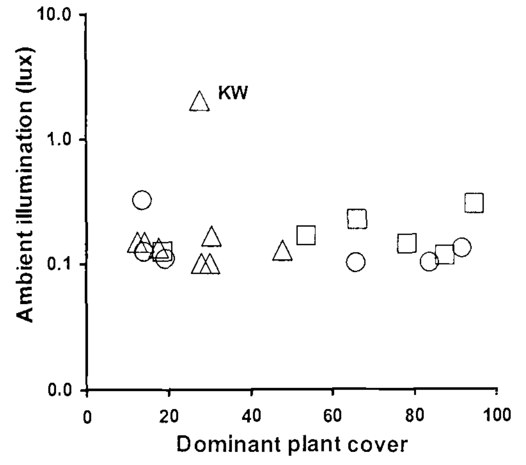


Figure 2.6. Reference site night-time illumination circumscribes the ambient light of the invaded sites. Illumination was quantified as mean lux per site on new moon night (n=9). Knez wetland (KW) was illuminated by a nearby billboard and highway.

The land cover surrounding the wetland sites is expected to influence the species richness and abundance of the moth community. Increasing urban and agricultural cover may increase fragmentation of preferred habitat, which may increase population extinctions and decrease colonization probability of moth species. Sites with high surrounding urban and agricultural area are expected to have lower moth species richness and abundance regardless of the abundance of invasive species. I used CCA to determine whether land-use trends were correlated with the abundance of invasive species.

The main data matrix consisted of the twenty Willamette Valley and Eastern Oregon sites, each with four surrounding land-use categories (forest, natural non-forest, agricultural, and urban) at the ten spatial scales (100, 200, 300, 400, 500, 1000, 1500, 2000, 2500, and 3000) for a total of 20 sites and 40 variables. The second matrix contained the mean proportional cover of the loosestrife and reed canary grass for the 20 wetlands. Normality was improved using an arcsine square root transformation on the proportional cover data. Row and column scores were standardized by centering and normalizing.

The abundances of the two invasive species comprising the second matrix were negatively correlated (r= -0.41). Axis one was primarily associated with the abundance of purple loosestrife (r= -0.98), while axis two was associated with the abundance of reed canary grass (r= -0.82). The Monte Carlo randomization procedure was run 100 times and the result was compared with that of the nonrandomized data. The Monte Carlo test statistic indicated that the relationship between loosestrife abundance (axis 1) and the land-use variables was not significantly greater than expected by chance (p=0.12). The relationship between reed canary grass abundance (axis 2) and the environmental variables was also not statistically significant (p=0.49).

Summary of environmental analysis

Wetland hydrology, soil characteristics, and topography were measured and analyzed to control for covarying and confounding influence on plant diversity. Temperature, ambient light, wind speed, precipitation, and surrounding land-use were measured and analyzed to control for covarying and confounding influence on moth sampling and community structure. I detected no significant covariance between the environmental variables and the abundance of invasive species that would be expected lead to lower plant or moth species richness at the study sites. Therefore, patterns of plant and moth species richness and abundance that are correlated with invasive species abundance are likely a result of the effect of the invasive species and not the underlying environment.

Plant Community

Overview of plant community

The regional wetland plant community (or gamma diversity) of the 24 sites consisted of 196 vascular plant species distributed within 36 families (Appendix B). The six most speciose families were the: Poaceae (23), Fabaceae (17), Asteraceae (17), Cyperaceae (17), Rosaceae (11), and Juncaceae (9). Native species comprised 60% of the regional wetland flora (118 species) while 34% (67) were exotic plant species. The status of 11 species (6%) was unknown. Forty-six (25%) of the species were obligate wetland plant species (United States Fish and Wildlife Service National Wetlands Inventory (www.nwi.fws.gov)). An additional 46 (25%) of the plant species were facultative wetland species, 58 (31%) were species that occur in equal probability in wetland and uplands, two (1.0%) were obligate upland species, and the remaining 34 (18%) were either not classified or not listed.

Each species was also associated with a particular plant guild. I used the guilds: "hardwood" for woody dicots, "herbs" for non-woody dicots, and "grasses" for monocot species. Fifty-six species (30%) were grasses, 104 species (56%) were herbs, and 26 species (14%) were hardwoods. Two species of fern (*Azolla mexicana* and *Athyrium filix-femina*) were sampled. These were included in the herbaceous category.

Sampling accuracy

Sampling accuracy was assessed for both the estimation of plant abundance (percent cover) and the number of species (species richness). Accuracy of cover estimates was determined by creating a series of 14 cards with differing "densities" arranged in various patterns. The observer who estimated cover (S.S. Schooler) was tested before and after field observations to determine changes in accuracy (Figure 2.7a). Both "before" and "after" estimates of cover were highly correlated with actual cover (r=0.98 and 0.99, respectively). Slopes of the relationship indicate a slight trend to overestimate cover before sampling (1.11) and to underestimate cover after sampling (0.97).

Adequate sampling is important when studying the species composition of biotic communities because species richness estimates are positively correlated with the area sampled. Species-area curves are a means of determining sampling adequacy (McCune and Mefford 1999). If the mean number of new species detected reaches a plateau as the area sampled (or sample effort) increases, it suggests that area has been sampled adequately. The species-area curves reached a plateau for the plant communities at most of the wetland sites, while the number of species at some sites continued to increase at a reduced rate with increasing sampling effort (Figure 2.7b).

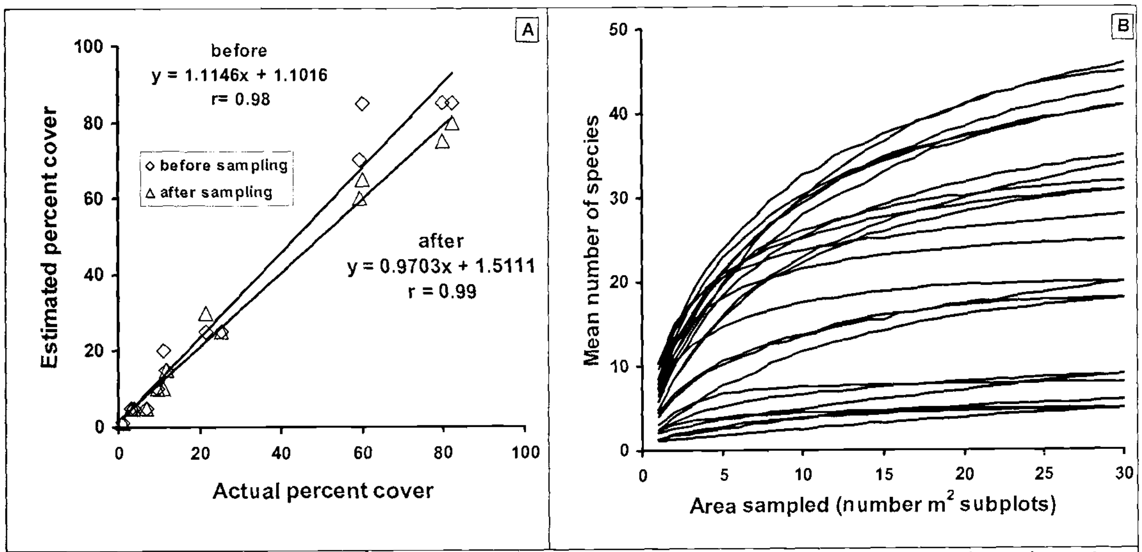


Figure 2.7a-b. Estimation of plant species sampling accuracy. (a) Accuracy of percent cover estimates was examined using cards (20cm x 20cm) with differing proportions filled in to represent plant cover in a field plot. The observer was tested before and after sampling to assess change in accuracy. (b) Species accumulation curves for the plant community approach a plateau with increasing sampling effort indicating fewer species are gained with each subsequent increase in sampling effort.

Impact of purple loosestrife and reed canary grass on wetland plant species diversity

The basic structure of a biotic community consists of a number of species with associated abundance values. This structure can be visually examined and compared between sites using rank-abundance diagrams (Whittaker 1972, Magurran 1988, Begon et al. 1990). Rank-abundance diagrams indicate that both species richness and equitability decrease with increasing dominance of a single plant species (Figure 2.8). Reference sites tend to have a greater number of species and have more equitable distributions of abundance between species than those dominated by loosestrife or reed canary grass. This result is consistent with the hypothesis that invasion by an invasive plant species decreases species richness and equitability of the local plant community.

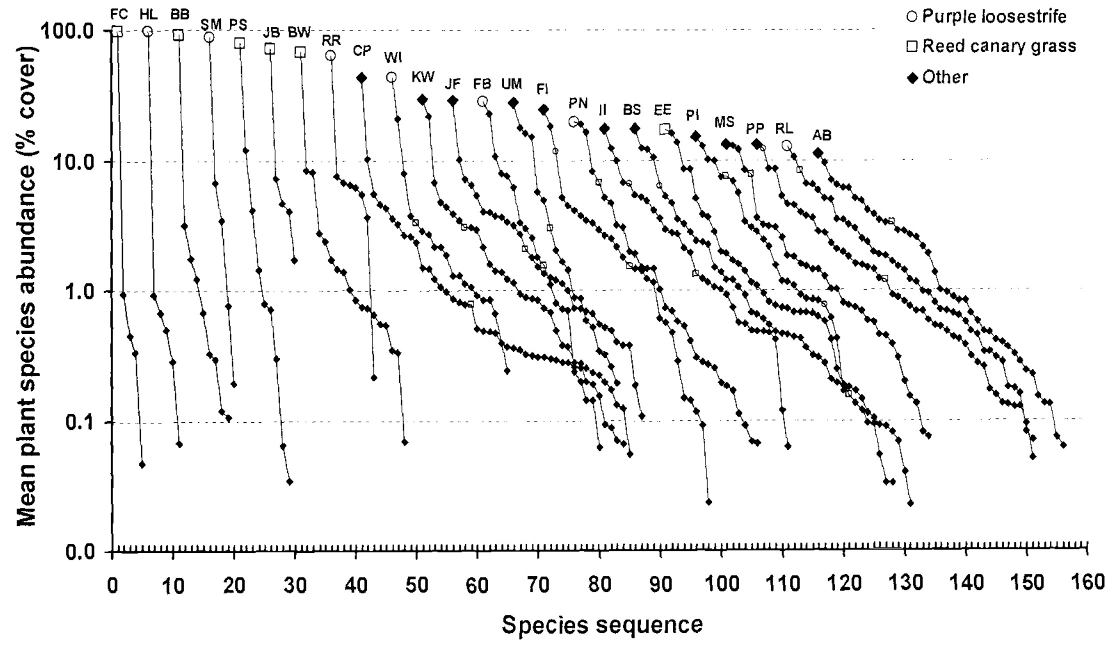


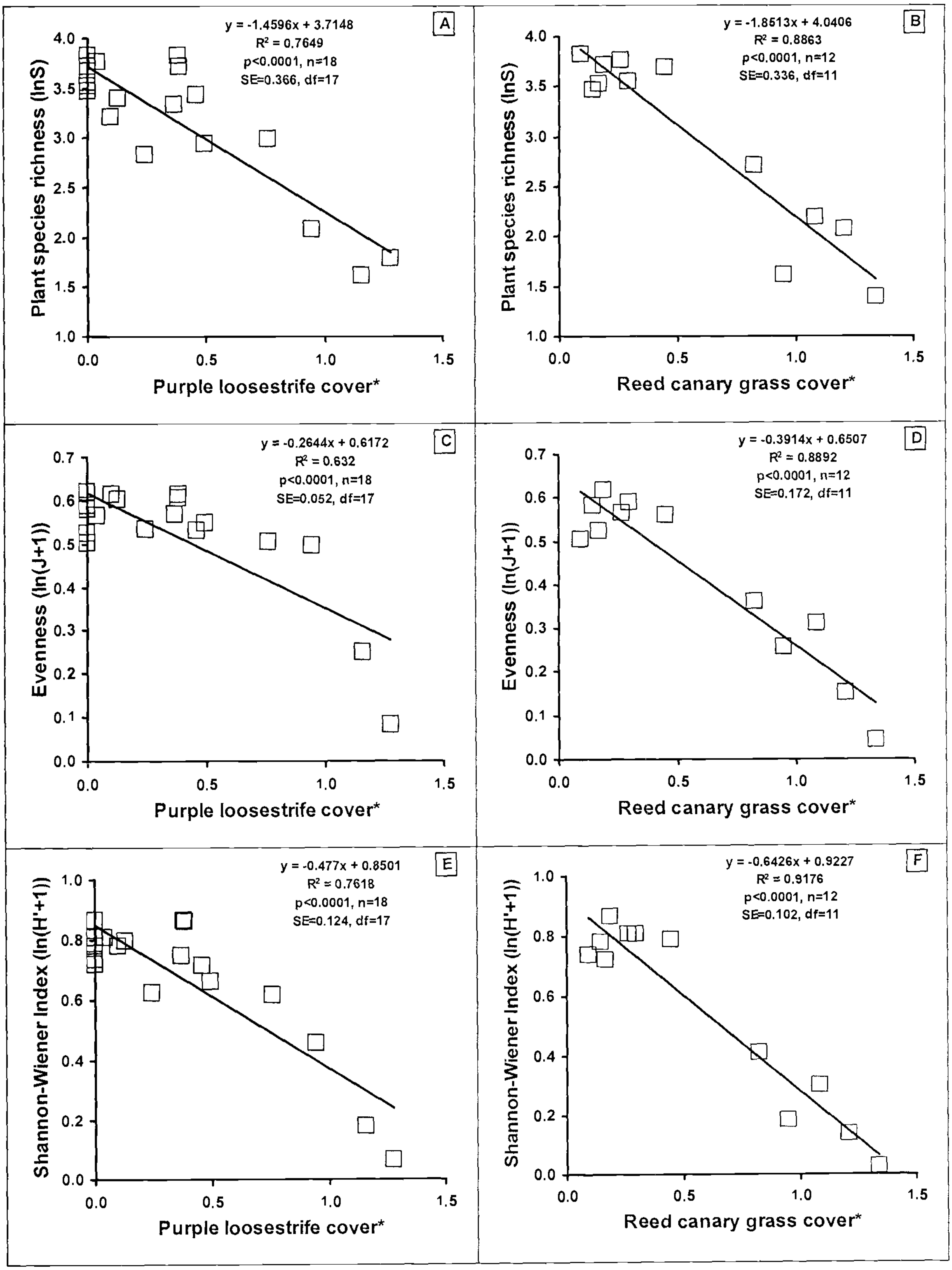
Figure 2.8. Rank-abundance curves for 24 wetlands in the Pacific Northwest. Mean percentage cover values of plant species are plotted for the sequences from the most to the least abundant species for each site. Means are computed from thirty 1m² plots per site. Curves are labeled according to site using a two-letter acronym (defined in Appendix A) and are arranged in the order of decreasing abundance of the dominant plant species. Circles are purple loosestrife, squares are reed canary grass, and diamonds are other species. The curves, separated by 5 unit intervals, start at various points on the species sequence in order to fit them into the same figure. Thus the curve for Apache Bluff (AB) begins at point 120 and ends at point 156 on the species sequence. Rank-abundance curves visually integrate the species richness (spread of the curve) and evenness (slope of the curve) of the plant community. The curves show that as the abundance of the dominant species within a community decreases from left to right in the figure, species richness and evenness increase.

Diversity measures calculated for the plant community included species richness, equitability, the Shannon-Wiener Index and Simpson's Index. The species richness (S) of each site ranged from 4 to 46 species (Figure 2.9a-b). Fanno Creek (FC), an urban site dominated by reed canary grass (95%) included only three other plant species (all introduced species) within the 7,854m^2 sampling area including: *Rubus discolor, Galium aparine, and Solanum dulcamara.* An urban site, Pickle Pond (PP), and a rural site, Champoeg State Park (CP), tied for a total of 46 plant species despite CP being dominated by the introduced grass, short-awned foxtail (*Alopecurus pratensis* (48%)) and PP being a restored urban wetland (Rivergate Industrial District) with small amounts of both reed canary grass (1.5%) and purple loosestrife (14%). Plant species richness declined from 46 to 4 with the increasing abundance of both reed canary grass and purple loosestrife (Figure 2.9a-b). I used linear regression to determine whether the slope of the relationship was statistically different from zero (null hypothesis). The natural log of species richness was used to better meet the assumption of constant variance and percent cover was arcsine square root transformed. For both plant species, the low p-value ($p<0.0001$) indicates that the null hypothesis should be rejected and therefore the negative relationship between the number of plant species and the abundance of the invasive species is significantly different from zero.

Evenness (or equitability J) ranged from 0.04 at Fanno Creek (FC) to 0.86 at Apache Bluff Wetland (AB). Apache Bluff is an urban wetland (Tualatin) dominated by short-awned foxtail (13%). As with species richness, evenness declined with the increasing abundance of the invasive species (Figure 2.9c and d). However, the relationship is different for the two invasive species. Evenness declines linearly with increasing cover of reed canary grass (Figure 2.9d), whereas evenness remains high (>0.6) until the cover of loosestrife reaches 80%, then declines steeply to 0.09 at 92% loosestrife cover (HL) (Figure 2.9c). Linear regression was used to determine whether the slope of the relationships between invasive plant abundance and plant community evenness was significantly different from zero. For the invasive plant species, percent cover was arcsine square root transformed and evenness was transformed by the natural log ($\ln(J+1)$) to better meet the assumptions of linear regression analysis. The low p-value ($p<0.0001$) indicated that the slope of the regression line was significantly different from zero for both invasive species.

The Shannon-Wiener Index (H') ranged from 0.06 (FC) to 3.18 (AB and PP). As with species richness, H' declined in a linear trend with the increase of invasive plant cover (Figure 2.9e-f). Linear regression was used to test significance. Invasive species cover was arcsine square root transformed and H' was natural log transformed ($\ln(H'+1)$). The p-values for both plant species were less than 0.0001. This indicates that the slopes were significantly different from zero, suggesting that plant community diversity is negatively correlated with invasive plant cover.

Simpson's Index of Diversity (D) ranged from 1.02 (FC) to 18.81 (AB). Although the trend of decreasing diversity with increasing invasive plant cover continues with this index, the relationship resembled a negative exponential function prior to transformation (Figure 2.9g-h). The natural log transformation was applied to D to even variance across values of invasive plant cover and improve the linearity of the trend. The p-value of less than 0.0001 for both invasive plant species indicate the slope of the relationship was significantly different from zero.


A
y = -1.4596x + 3.7148
R^2 = 0.7649
p<0.0001, n=18
SE=0.366, df=17
Plant species richness (lnS)
Purple loosestrife cover*
B
y = -1.8513x + 4.0406
R^2 = 0.8863
p<0.0001, n=12
SE=0.336, df=11
Plant species richness (lnS)
Reed canary grass cover*
C
y = -0.2644x + 0.6172
R^2 = 0.632
p<0.0001, n=18
SE=0.052, df=17
Evenness (ln(J+1))
Purple loosestrife cover*
D
y = -0.3914x + 0.6507
R^2 = 0.8892
p<0.0001, n=12
SE=0.172, df=11
Evenness (ln(J+1))
Reed canary grass cover*
E
y = -0.477x + 0.8501
R^2 = 0.7618
p<0.0001, n=18
SE=0.124, df=17
Shannon-Wiener Index (ln(H'+1))
Purple loosestrife cover*
F
y = -0.6426x + 0.9227
R^2 = 0.9176
p<0.0001, n=12
SE=0.102, df=11
Shannon-Wiener Index (ln(H'+1))
Reed canary grass cover*

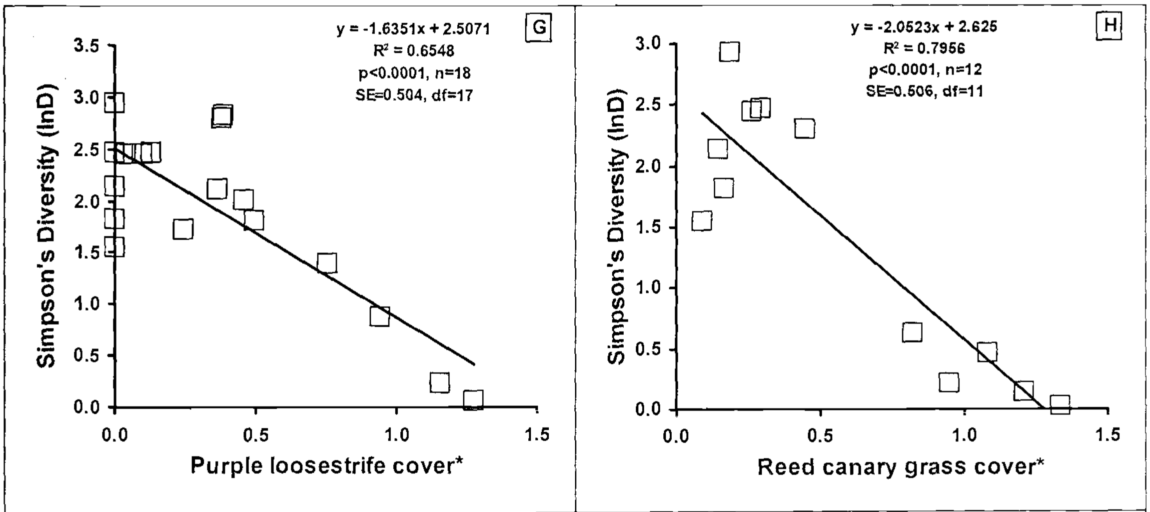


Figure 2.9a-h. All measures of diversity decrease with increasing abundance of the invasive plant species. Species richness and diversity indices were natural log transformed. *Percent cover of the invasive plant species was arcsine square root transformed.

Effect of purple loosestrife and reed canary grass on plant family richness

Although biological diversity is usually studied at the species level of taxonomic resolution, invasive species may effect other taxonomic levels differently. The hypothesis that the slope was significantly different from zero was tested using linear regression. Invasive species abundance was arcsine square root transformed before analysis. The p-value was less than 0.0001 for both invasive plant species indicating that the negative relationship between plant family richness and invasive plant cover was significant (Figure 2.12a-b).

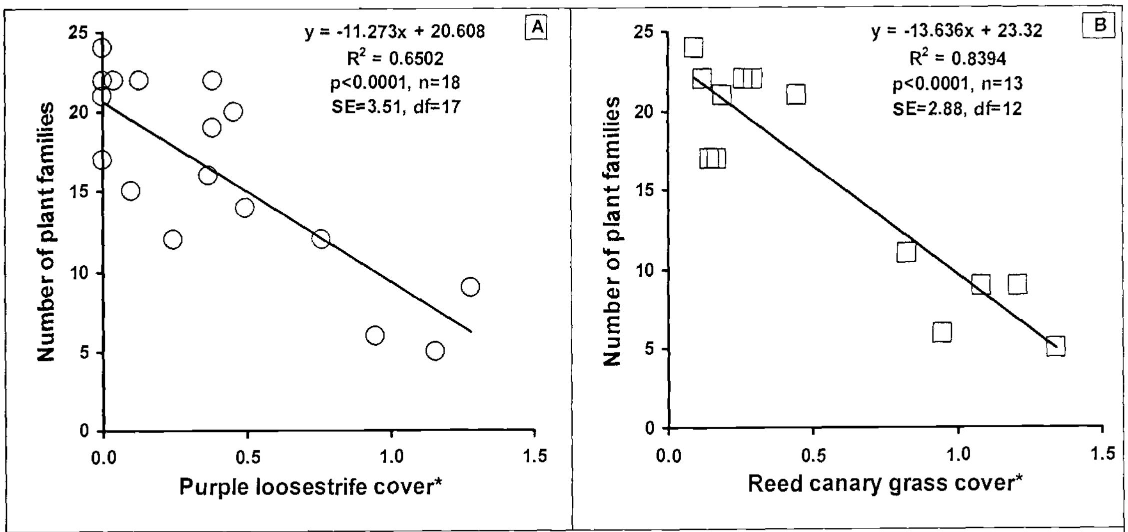


Figure 2.10a-b. The number of plant families per site decreases with increasing invasive cover. *Percent cover of the invasive species was arcsine square root transformed.

Effect of purple loosestrife and reed canary grass on individual plant species

Correlation was used to determine the relationship between the abundance of the invasive species and the abundance of the other plants at the sites. Many plant species were found at just a few sites. Correlations can produce inaccurate results with small sample sizes so I first removed plant species that occurred in less than five of the sites. Thirty-two plant species remained in the purple loosestrife analysis and eighteen species remained in the reed canary grass analysis (Table 2.8).

Table 2.8 Plant species correlations with purple loosestrife and reed canary grass cover

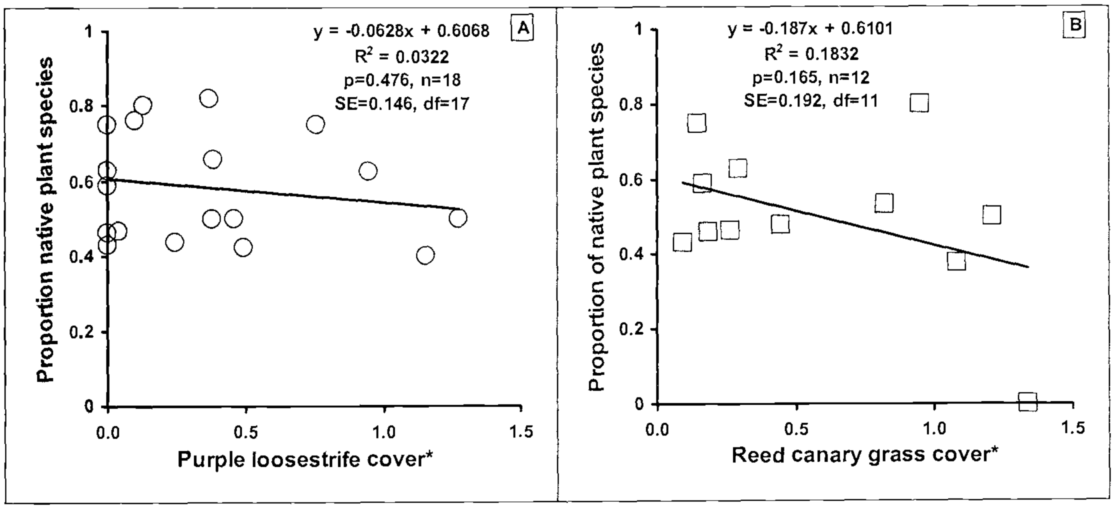
Purple loosestrife			Reed canary grass		
Plant species	Origin	*r*	Plant species	Origin	*r*
Cirsium vulgare	I	-0.42	*Cirsium vulgare*	I	-0.38
Solanum dulcamara	I	-0.38	*Solanum dulcamara*	I	-0.37
Galium trifidium	N	-0.37	*Carex densa*	N	-0.33
Juncus effusus	N	-0.32	*Typha latifolia*	N	-0.31
Carex densa	N	-0.31	*Epilobium ciliatum*	N	-0.27
Holcus lanatus	I	-0.30	*Myosotis discolor*	I	-0.26
Myosotis discolor	I	-0.28	*Juncus effusus*	N	-0.26
Veronica americana	N	-0.28	*Eleocharis palustris*	N	-0.25
Gnapthalium uliginosum	I	-0.27	*Veronica americana*	N	-0.24
Bidens cernua	N	-0.26	*Rumex acetosella*	I	-0.24
Epilobium ciliatum	N	-0.24	*Galium aparine*	I	-0.23
Scirpus microcarpus	N	-0.23	*Cirsium arvense*	I	-0.21
Carex scoparius	N	-0.23	*Vicia tetrasperma*	I	-0.21
Rumex acetocella	I	-0.23	*Fraxinus latifolia*	N	-0.20
Cirsium arvense	I	-0.22	*Agrostis stolonifera*	I	-0.20
Oenanthe sarmentosa	N	-0.20	*Holcus lanatus*	I	-0.17
Alisma plantago-aquatica	N	-0.20	*Galium trifidium*	N	-0.15
Deschampsia cespitosa	N	-0.20	*Rubus discolor*	I	-0.10
Rubus discolor	I	-0.19			
Salix lassiandra	N	-0.17			
Salix lucida	N	-0.15			
Agrostis stolonifera	I	-0.13			
Parentuccellia viscosa	I	-0.13			
Hypericum perforatum	I	-0.12			
Lotus purshiana	N	-0.10			
Juncus oxymeris	N	-0.09			
Typha latifolia	N	-0.04			
Ludwigia palustris	I	-0.04			
Eleocharis palustris	N	0.01			
Scirpus acutus	N	0.05			
Polygonum hydropiperoides	N	0.11			
Scirpus americanus	N	0.22			

N = native in origin, I = introduced species, *r* is the correlation coefficient of the correlation between that species and the invasive plant species, purple loosestrife or reed canary grass

The mean abundance of the plant species was correlated with the mean abundance of the invasive species at each site (Table 2.8). Interestingly, both loosestrife and reed canary grass were most negatively correlated with two other introduced species, bull thistle (*Cirsium vulgare*) and European bittersweet (*Solanum dulcamara*). Dense sedge (*Carex densa*), common rush (*Juncus effusus*), and small bedstraw (*Galium trifidium*) were the most negatively correlated native plant species. Although reed canary grass was not positively correlated with any plant species, purple loosestrife was positively correlated with four native species, American bulrush (*Scirpus americanus*), waterpepper (*Polygonum hydropiperoides*), hard-stem bulrush (*Scirpus acutus*), and creeping spike-rush (*Eleocharis palustris*).

Effect of invasive plant species on native plant species

I also examined whether native plant species richness and abundance were associated with increasing cover of the invasive species. I discerned no clear pattern that indicated the number of native species was reduced more than that of the introduced species (Figure 2.11a-b). The exception was one reed canary grass site (FC) that contained only four plant species and none were native (Figure 2.11b). However, abundance of the native species declines with increasing cover of the invasive species (Figure 2.11b-c). Note that for the purposes of this study I classified reed canary grass as an introduced species.



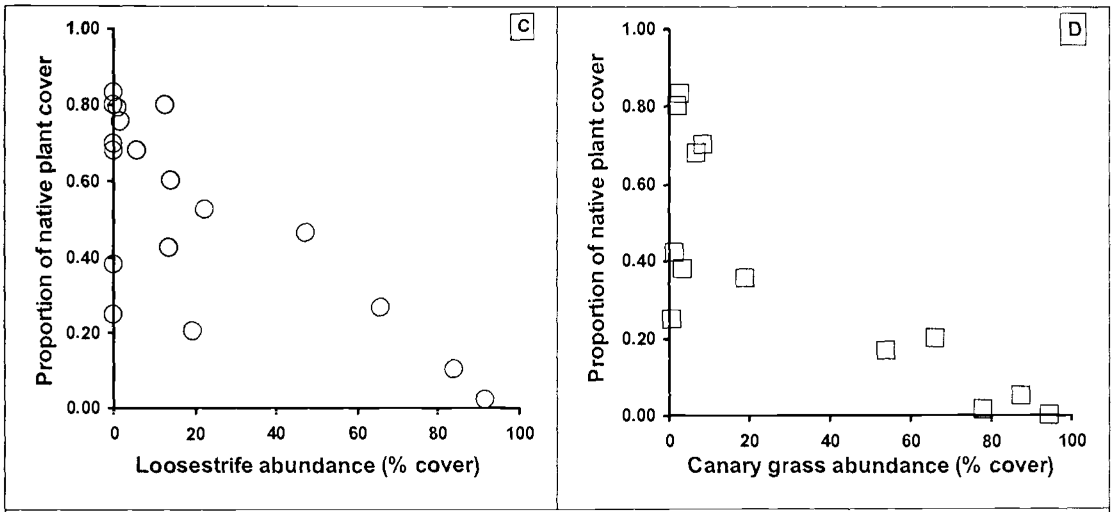
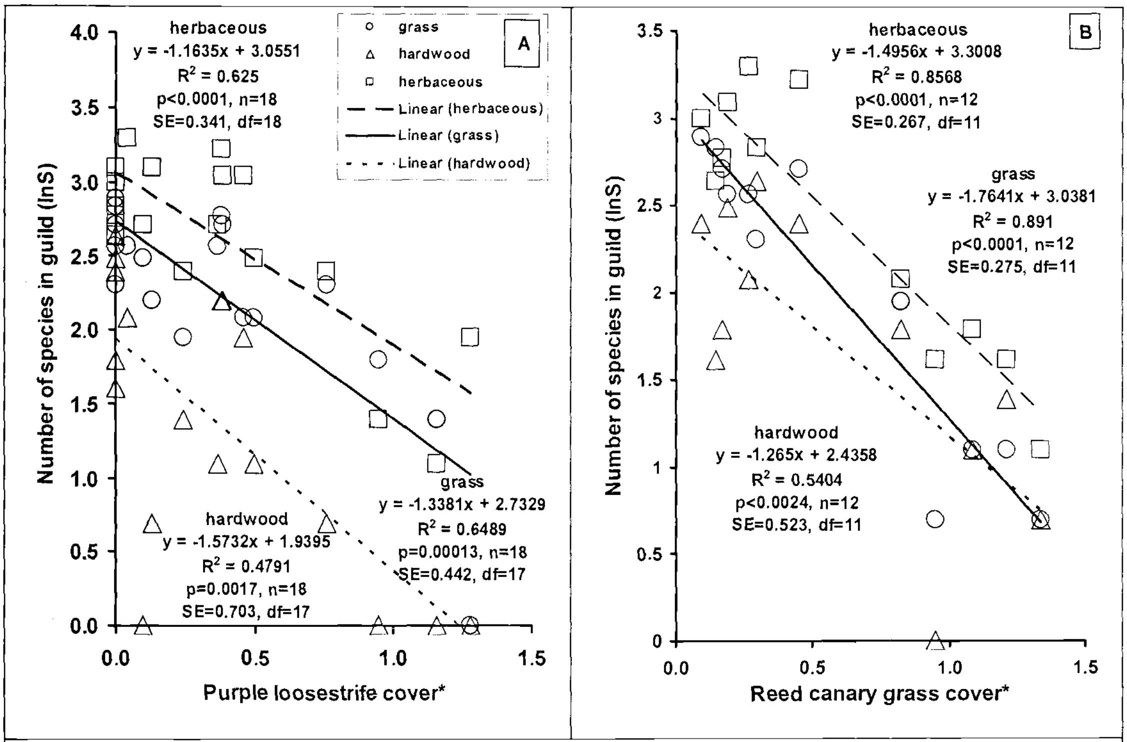


Figure 2.11a-d. Effect of invasive species on native plant species and abundance. (a-b) The number of native and introduced plant species decrease at an equal rate with increasing invasive cover for both (a) loosestrife and (b) reed canary grass. (c-d) Native plants comprise approximately 50% of the cover in reference sites and abundance decreases with increasing invasive plant cover. *In Figures a and b percent cover is arcsine square root transformed.

Effect of invasive plant species on plant guilds

After investigating the effect of the invasive species on the taxonomic diversity of the plant community, I examined the response from a functional perspective. The plant community was divided into grasses (monocots), herbaceous plants (non-woody dicots), and hardwood shrubs and trees (woody dicots). The number of plant species in each guild decreased with increasing cover of the invasive plant species. This trend was statistically significant in all cases. The number of species of herbaceous plants tended to be greater than grasses in the reference wetlands and decreased to a similar number in dense stands of the invasive species (Figures 2.10a-b). There tended to be fewer hardwood species within the study sites, presumably due to intolerance of extended hydroperiods (Keddy 2000), and most of these were shrubs such as willows, roses, or hawthorns. The abundance of these species also declined significantly with the increasing cover of the invasive plants.



Figures 2.10a-b. The number of plant species declines with the increase of invasive species cover for all plant guilds. Species number was log normal transformed and percent cover of the invasive species was arcsine square root transformed before applying linear regression analyses.

Effect of the scale of observation on results

The primary study units of this survey are the wetland sites (24 circular plots 50m in radius, 7,854m^2). Prior studies have examined the effect of purple loosestrife and reed canary grass at the 1m^2 spatial scale. I plotted the data for each of the 30 plots (1m^2) within each site to contrast with the results from the species richness at the 7,854m^2 scale. Since the 1m^2 sample plots are spatially autocorrelated within sites, the data violate the assumption of independence necessary for parametric statistical analyses. The plant species richness in a given plot varies from 1-21 in the absence of purple loosestrife and reed canary grass and from 1-4 when cover of the invasive species exceeds 90%. This indicates that the conclusions of studies examining the effect of these species at small scales are greatly influenced by the number of plots and where the plots happen to be located.

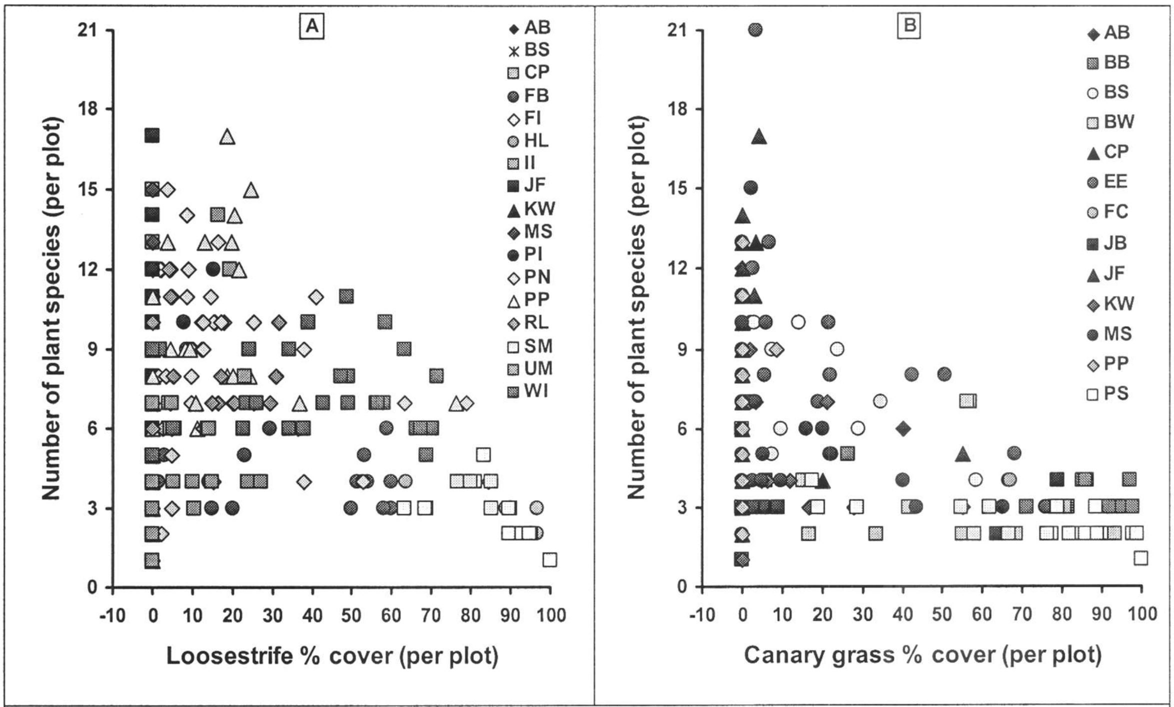


Figure 2.13a-b. Effect of invasive species at the 1m² spatial scale. Individual sample plots (1m²) varied in species richness from one to 21 species in plots with low density of loosestrife and canary grass, whereas plots with greater than 80% cover of the invasive species varied from one to four species. In figure a, n=510 plots, in figure b, n=390 plots.

Moth Community

Overview of the moth community

The regional wetland moth community at the 20 sampled sites (moths were not sampled on the four estuarine islands) consisted of 177 moth species distributed across 14 families (Appendix C). Nine individuals could not be associated with a particular species, although they were identified to genus (5) or family (4). The four most speciose families, including 88% of all the moth species, were the Noctuidae (88 species), Geometridae (31), Pyralidae (26), and Arctiidae (10). Native species comprised 92% of the regional wetland moth species (162 species) while 3% (6) were exotic moth species. The native status was not known for the additional nine taxa (5%) because they could not be attributed to a particular species.

Based on literature reviews, databases, and local knowledge, 152 (86%) moth species were assigned to six general feeding guilds. No information was available on the remaining 25 (14%) species. Sixty-one species (34%) feed on hardwoods, 54 (31%) feed on herbaceous hosts, 31 (18%) feed on grasses, 3 (2%) feed on lichen, 2 feed on conifers, and 1 feeds on algae. The host plants of some species were known in greater detail (see Appendix C). For example, 15 (25%) of the hardwood feeders are known to feed on willows (*Salix* spp) and five (8%) feed on oaks (*Quercus* spp). Of the herbaceous feeders, five are known to specialize on peas (Fabaceae), three feed on plants in the Asteraceae, and one feeds only on oak mistletoe (*Phoradendron flavescens*: Loranthaceae). The grass feeders tend to be host generalists, but four are known to feed exclusively on cattails (Typhaceae), two on sedges (Cyperaceae), and one on rushes (Juncaceae).

Sampling accuracy

As with the plant community, species-area curves were plotted for the moth data to determine whether the sampling effort was adequate to sample the species diversity of the local moth community. Unlike the plant community, the accumulation of new species did not appear to reach a plateau, although the rate of accumulation appears to slow with increasing sampling effort (Figure 2.14). This result may be the effect of sampling a community that is more dynamic temporally than that of the plant community. The active flight periods of moths wax and wane over the year, so samples are not drawn from the same assemblage of species for each sample event.

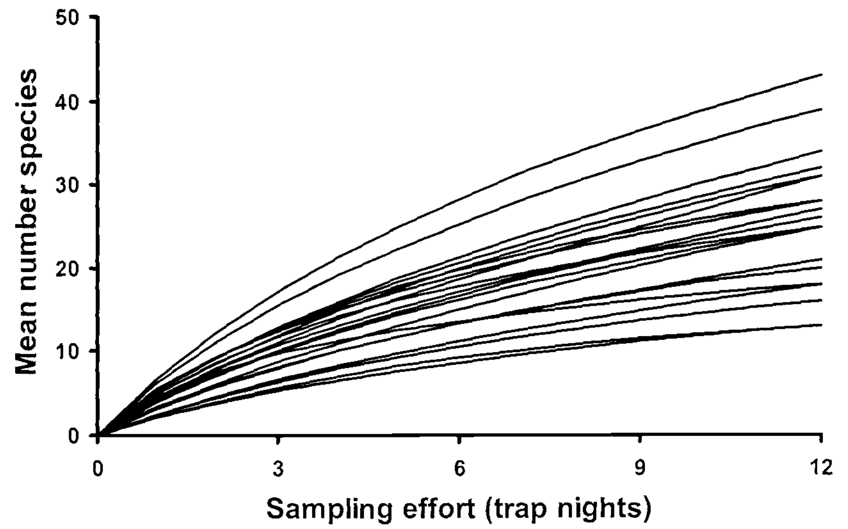


Figure 2.14. Moth species accumulation curves continue to rise with increasing sampling effort.

Relationship between plant and moth species richness

Moth species richness increased weakly with plant diversity at all sites (Figure 2.15a). Although the p-value was low ($p=0.095$) linear regression indicated that the slope of the relationship was not significantly different from zero, but there was a serious outlier. This result led us to examine additional explanatory factors that might affect either trap catch (effectiveness) or moth population dynamics (survival and reproduction). The most direct explanation is that ambient nocturnal light may have reduced trap catch at a particular site. Knez Wetland (KW) was located directly underneath a billboard (not recognized at the time of site selection) which increased the nocturnal illumination an order of magnitude (KW was 2.0 lux where the mean for all other sites was 0.15 lux) beyond that of all other sites (see Figure 2.6). Because the trapping method used light to attract moths and moth behavior is likely to be disrupted by such a strong light source, I removed Knez Wetland from the analysis (Figure 2.15b). When Knez Wetland was removed from the analysis the slope of the regression increased and differed significantly from zero (p=0.041). Knez Wetland was removed from subsequent moth analyses.

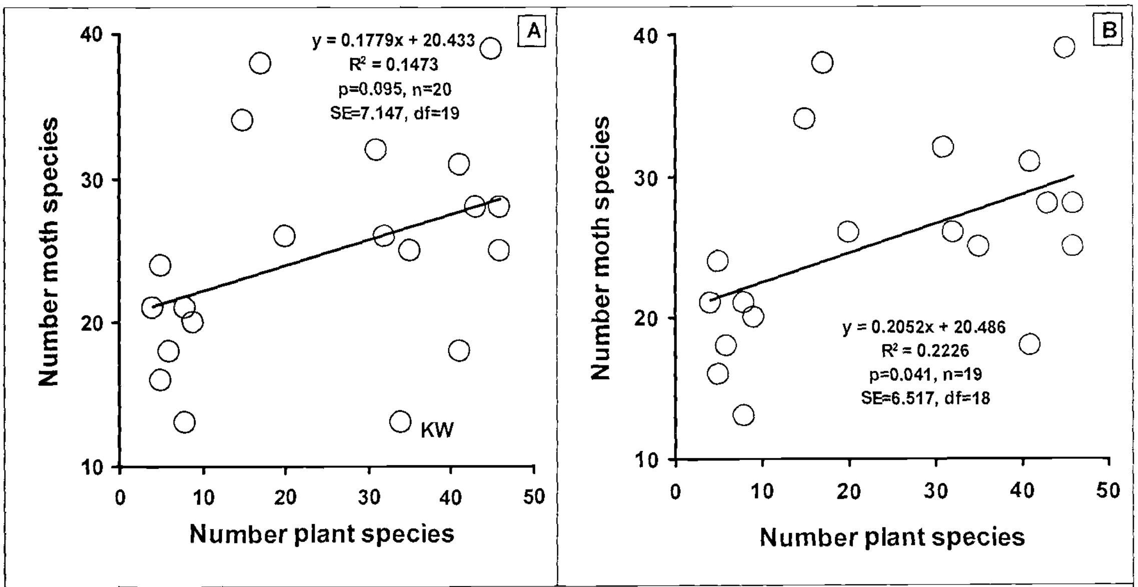


Figure 2.15a-b. Moth species richness is positively correlated with plant species richness. (a) Plant species richness is correlated with moth species richness at all sites but the slope is not significant (p=0.095). (b) When Knez Wetland was removed from the analysis the slope of the regression increased and differed significantly from zero (p=0.041)

Effect of purple loosestrife and reed canary grass on wetland moth species richness and diversity

The structure of the moth communities differed from that of the plant communities at the wetland study sites. Moth communities tended to include a large number of species represented by only a single individual (Figure 2.16a-c).

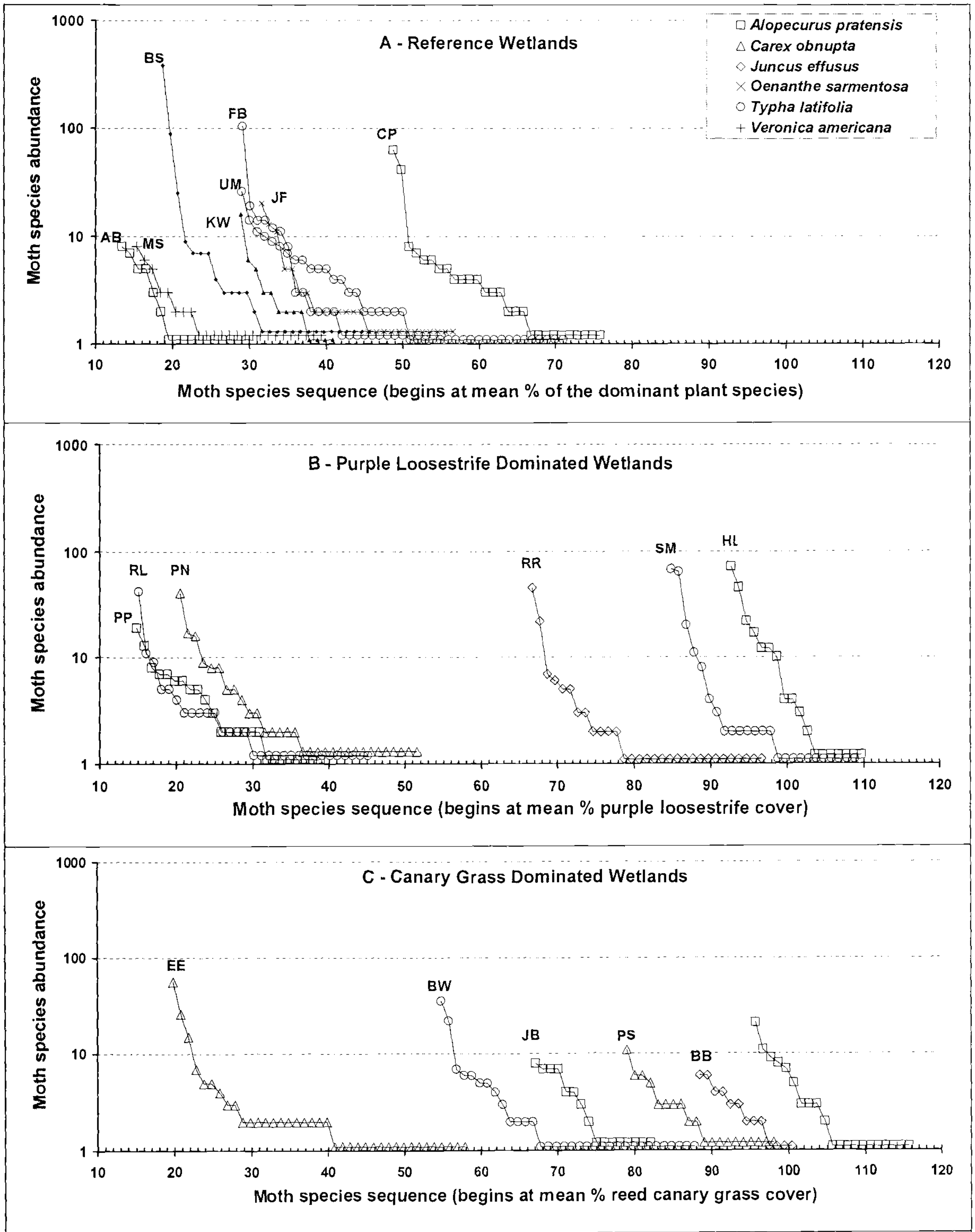


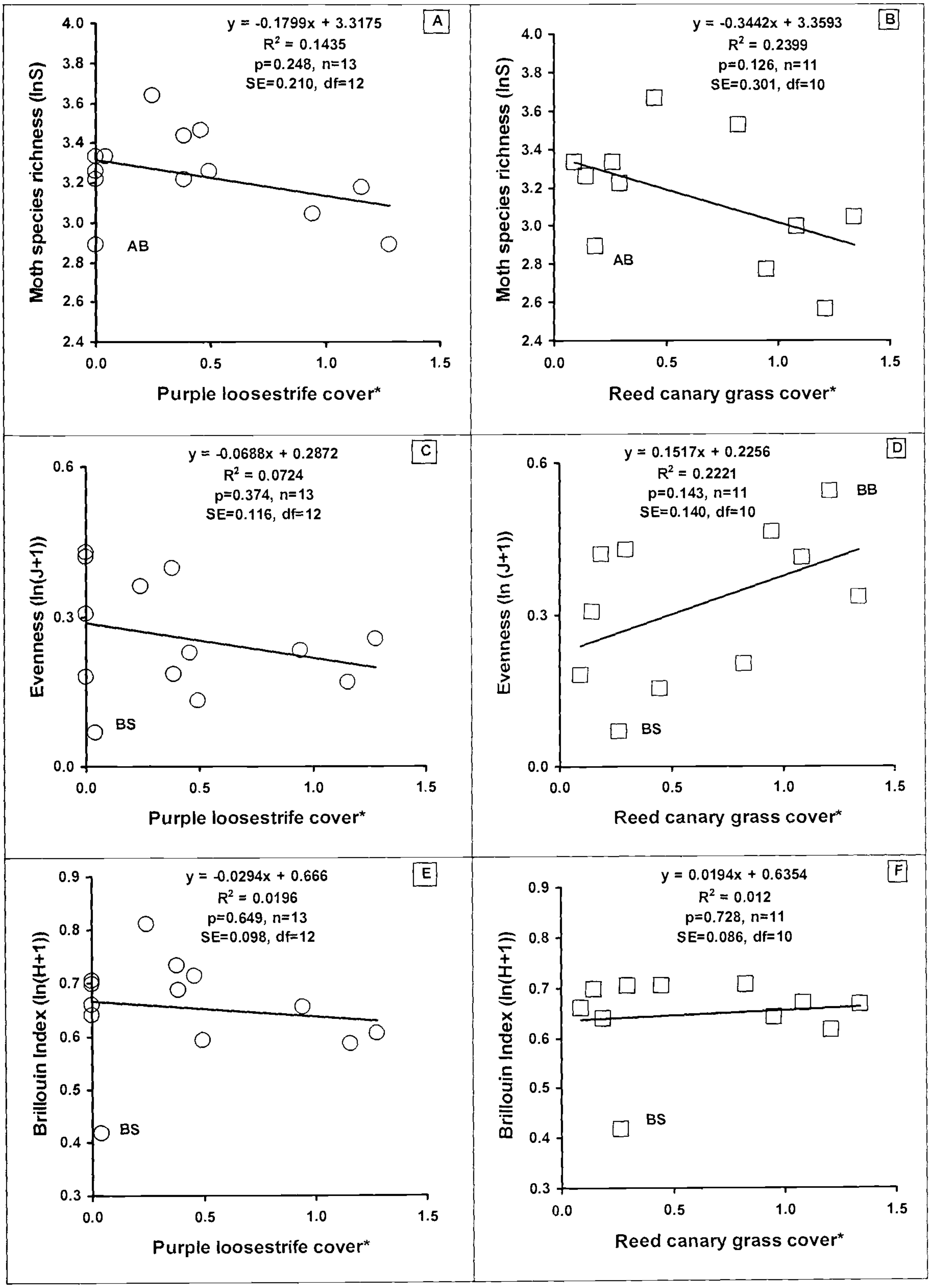
Figure 2.16a-c. Rank abundance plots of the 20 moth communities. Communities are arranged so they begin at the mean percent cover of the dominant plant species. Species represented by a single individual have been adjusted along the y-axis to prevent overlap. Symbols in Figure 2.16a indicate the dominant plant in that community. See Figure 2.8 for a more detailed description of these curves.

Measures of moth community diversity (Figure 2.17a-b) did not show the clear and consistent trends that were found in the measures of the plant community diversity (2.9a-h). Linear regression was used to identify significant trends ($\alpha'=0.0041$). Percent cover of the invasive species was arcsine square root transformed and diversity measures were natural log transformed prior to analysis.

As expected from the result that moth species richness is correlated with plant species richness, moth species richness appears to decline with increasing abundance of both invasive plant species. However, this trend was not significant for either purple loosestrife ($p=0.248$) or reed canary grass ($p=0.126$). The result is heavily leveraged by low species richness at Apache Bluff Wetland (AB). This is a wetland in a residential district adjacent to a golf course. Therefore, it is possible that insecticide application may have reduced the number of moth species at this site.

Evenness (J) showed no trend in the case of purple loosestrife (Figure 2.17c) and appeared to increase with invasive species abundance for reed canary grass (Figure 2.17d), although the trend was not significant ($p=0.143$). The Brillouin's (H), Simpson's (D), and log series (α) indexes of diversity also showed no significant trend (Figure 2.17e-j). The log series index of diversity appeared to be slightly more effective at dealing with the disparity in total moth abundance. Although the disparity of abundance between the dominant moth species and other moth species Baskett Slough (BS) produced a very low score, the trend of the other sites indicated a decrease in diversity with increasing invasive plant abundance (Figure 2.17i and j).

Baskett Slough (BS) was an outlier that heavily leveraged the linear regression analysis of the relationship between Brillouin's (H), Simpson's (D), and log series (α) indexes of diversity and invasive species cover. The outlier also reduced the equality of variation, thereby violating an assumption of linear regression. The conclusion of no significant trend was protected from the influence of a single site by re-examining these relationships after removing that site (BS) from the analysis. The result was the same as that of the original analysis. No significant association between invasive plant cover and moth community diversity was found.


A
y = -0.1799x + 3.3175
R^2 = 0.1435
p=0.248, n=13
SE=0.210, df=12
Moth species richness (lnS)
Purple loosestrife cover*
AB
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
0.0
0.5
1.0
1.5
B
y = -0.3442x + 3.3593
R^2 = 0.2399
p=0.126, n=11
SE=0.301, df=10
Moth species richness (lnS)
Reed canary grass cover*
AB
C
y = -0.0688x + 0.2872
R^2 = 0.0724
p=0.374, n=13
SE=0.116, df=12
Evenness (ln(J+1))
Purple loosestrife cover*
BS
0.6
0.3
0.0
D
y = 0.1517x + 0.2256
R^2 = 0.2221
p=0.143, n=11
SE=0.140, df=10
Evenness (ln (J+1))
Reed canary grass cover*
BB
BS
E
y = -0.0294x + 0.666
R^2 = 0.0196
p=0.649, n=13
SE=0.098, df=12
Brillouin Index (ln(H+1))
Purple loosestrife cover*
BS
0.9
0.8
0.7
0.6
0.5
0.4
0.3
F
y = 0.0194x + 0.6354
R^2 = 0.012
p=0.728, n=11
SE=0.086, df=10
Brillouin Index (ln(H+1))
Reed canary grass cover*
BS

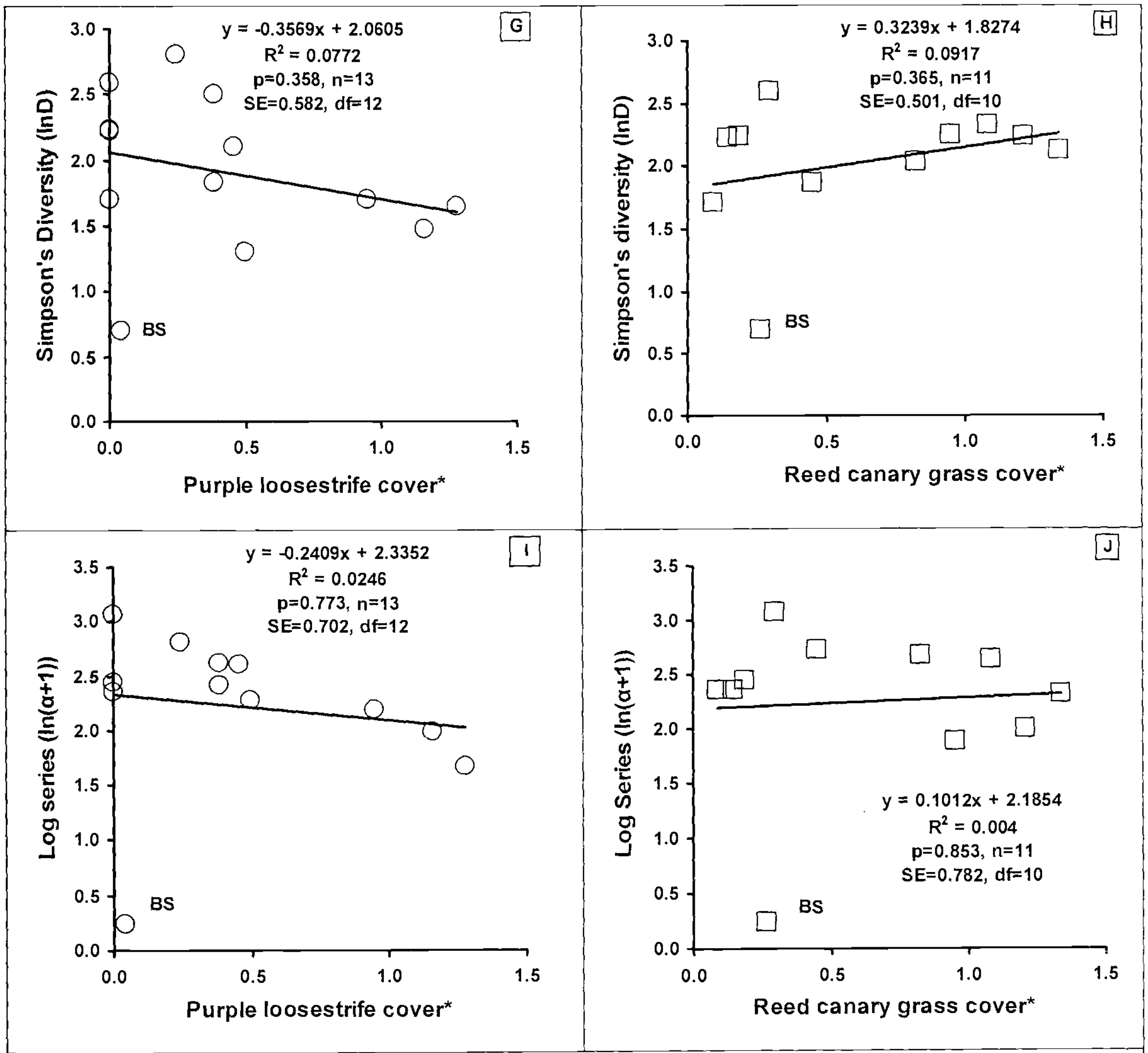


Figure 2.17a-j. Diversity measures of the moth community. No significant trends of decreasing moth diversity with increasing invasive species abundance were observed. Acronyms identify specific sites, see Appendix A for details. *Percent cover of the invasive plant species was arcsine square root transformed. Diversity measures were natural log transformed. An outlier (BS) in Figure 2.17e-j. prompted six additional analyses where the outlier was removed. These analyses also indicated no significant trend.

Effect of purple loosestrife and reed canary grass on moth family richness

I also examined the effect of the invasive plant species on moth family richness. Minthorn Springs (MS), an urban reference site, had nine moth families while Bird Blind, an urban reed canary grass site (87%), had the fewest with four families of moths. Although sites with high cover of the invasive plant species tended to have fewer families of moths, some reference sites also had few moth families (Figure 2.18a-b). The trend of decreasing number of moth families with increasing invasive plant cover produced a low p-value (p=0.020) for reed canary grass, but after adjusting for multiple tests and examining outliers it is likely not a significant result. The trend was also not significant for purple loosestrife (p=0.071).

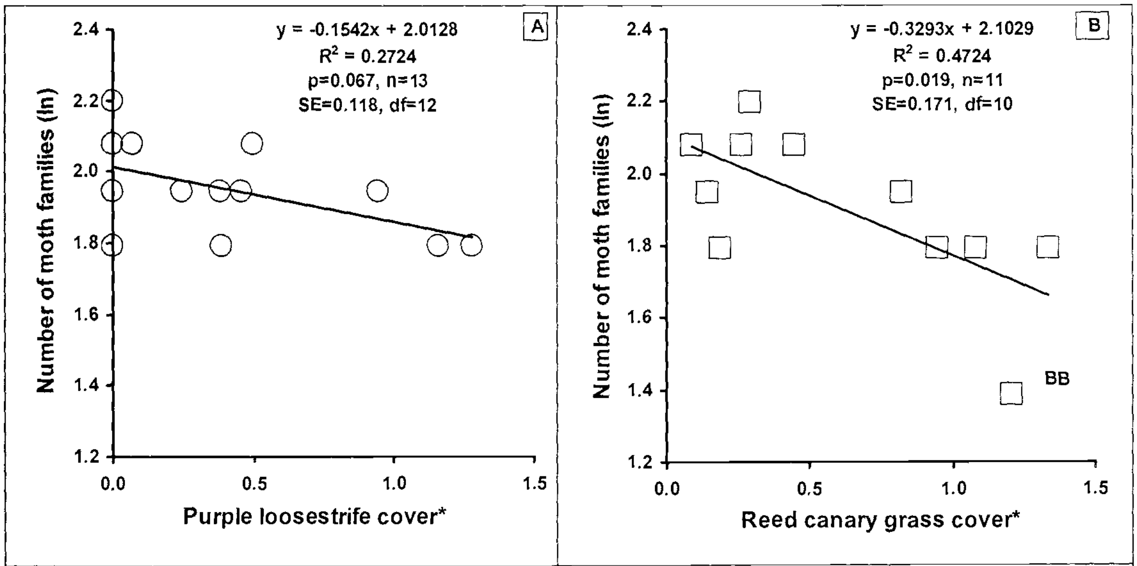


Figure 2.18a-b. Effect of invasive species on moth family richness. Although the number of moth families tends to be reduced in sites with increasing density of the invasive plant species, some reference sites also have few moth families. (a) Increasing purple loosestrife cover appears to be associated with a decline in moth family richness, the trend was not significant (p=0.067). (b) Reed canary grass cover was negatively associated with moth family richness, but the trend was not significant after adjusting for multiple tests (p=0.019). *Percent cover of the invasive plant species was arcsine square root transformed and moth family richness was natural log transformed before analysis.

Discussion

Purple loosestrife and reed canary grass are capable of forming dense stands approaching 100% cover in Pacific Northwest wetlands (Figure 2.8). These populations can exceed 0.75ha in spatial extent and occur over a wide range of hydrologic regimes and soil nutrient concentrations. The size and density of these populations negatively effects the diversity of plant communities. The negative effect on moth communities is less certain. I found that although the species richness of the moth community was positively correlated with the moth community, the direct association between moth species richness and invasive plant cover was not significant.

Effect of invasive species on the diversity of the plant community

Increasing cover of purple loosestrife and reed canary grass led to decreases in all measures of plant community diversity (Figure 2.9a-h). In most cases the relationship between invasive plant cover and reduction in plant diversity was similar for reed canary grass and purple loosestrife. However, the evenness of the plant community appeared to be less effected at intermediate levels of loosestrife cover than for reed canary grass (Figure 2.9c and d). This may be due to the different traits of the invasive species. Reed canary grass often spreads by clonal growth *via* rhizomes and creates a dense mat of vegetation and a thick layer of litter. Due to these traits, Boutin and Keddy (1993) classify reed canary grass as a "matrix: clonal dominant" species. Purple loosestrife spreads primarily by seed and does not generally form a dense vegetative mat or cause an accumulation of litter. This lets more light through the canopy to the ground and appears to allow other species to coexist at higher levels of abundance even when loosestrife cover approaches 80%. Boutin and Keddy classify loosestrife as a "ruderal: facultative annual" characterized by a high percentage of flowering, no lateral spread, and a few tall stems with a small crown area.

The hypothesis that purple loosestrife reduces the diversity of wetland plant communities has been examined in prior studies, with conflicting results. Thompson et al. (1987) and Mal et al. (1992) report that loosestrife is a threat to native plants and animals. However, these conclusions were based primarily on professional opinion and a single observational study by Rawinski and Malecki (1984). Rawinski and Malecki claimed loosestrife displaced cattails and negatively effected muskrats, deer, and four bird species on the Montezuma National Wildlife Refuge, NY. However, they found no statistically significant results and subsequent analysis indicated that the results were inconsistent and inconclusive (Hager and McCoy 1998).

In addition, in 1995 Anderson reviewed 34 papers that examined the interactions between purple loosestrife and native plant species. He found that sometimes native species out-competed loosestrife and sometimes loosestrife out-competed native species. He concluded that there was insufficient evidence to support the claim that loosestrife had negative effects. In 1999, Blossey published a review of prior studies that documented the effects of purple loosestrife. At that time the only research to provide evidence that loosestrife reduced plant biodiversity was an experimental microcosm study where loosestrife was found to dominate wetland plant assemblages consisting of 20 selected plant species under conditions of low water fluctuation or high nutrient concentration (Weiher et al. 1996). This study indicated the potential for loosestrife to reduce the diversity of plant communities, but was not evidence of effect.

Since Blossey's review, four additional studies have been published that examined the negative influence of purple loosestrife on plant community diversity (Treberg and Husband 1999, Farnsworth and Ellis 2001, Morrison 2002, Landis et al. 2003). Treberg and Husband (1999) examined forty-one 2 x 2m plots at a single site along the Bar River, Ontario, Canada. They found no significant effect of presence of loosestrife or cover of loosestrife on mean species richness. Farnsworth and Ellis (2001) studied the effect of purple loosestrife abundance at five wetland sites in Connecticut. They examined species richness in thirty $1m^2$ plots arrayed in a grid within each wetland. They found no significant relationship between purple loosestrife density and species richness at the $1m^2$ scale, although dense stands of loosestrife maintained greater above-ground biomass than uninvaded sites. Morrison (2002) examined the effect of loosestrife on plant community diversity at two wetland sites in New York. At each site, nine $1m^2$ plots were established within three blocks. Within each block, one plot was an unmanipulated control, one plot had all vegetation removed and loosestrife was weeded twice each year for three years, and one plot had all vegetation removed and was subsequently unmanipulated. She detected no difference in species richness between any of the treatments after three years. She observed that the manipulated plots were usually colonized by one or two sedge species. Landis et al. (2003) examined the response of plant communities after the reduction in abundance of purple loosestrife by biological agents at five sites in Michigan. They measured species diversity using 1, 3.7, and 7.1m^2 plots, first in 1995 before the biological control agents reduced biomass of loosestrife, then again in 2000 and 2001 after the agents reduced biomass. They found that plant species richness significantly increased after the decline of loosestrife biomass at all five sites.

Why did three of these four studies not observe the declines in plant species diversity that are found to be significant in this study? These inconsistent results are likely the product of the spatial scale at which plant diversity was measured. Species richness is positively correlated with sample area (Magurran 1988). The three studies that found no response of plant diversity to increases in loosestrife abundance measured species richness at spatial scales of 4m^2 (Treberg and Husband 1999) or 1m^2 (Farnsworth and Ellis 2001, Morrison 2002). When I examined the impact of the invasive species at the 1m^2 spatial scale I found the plant community at many plots consisted of one or two plant species (Figure 2.13). These scales would be appropriate if purple loosestrife existed in wetlands as a patchy mosaic of 1 and 4m^2 stands, such as *Carex obnupta* and *Juncus effusus*. However, both purple loosestrife and reed canary grass are known to form dense stands that can cover many hectares. Thus it is appropriate to examine the response of the plant community at larger spatial scales in order to better estimate the effect of invasive species that act upon the plant community at those scales.

I also examined the effect of the invasive species abundance on plant family richness. Although biological diversity is usually studied at the species level of taxonomic resolution, invasive species may impact other taxonomic levels more or less severely. An invasive species that reduces the total number of plant *species* from 40 to 10 may not alter the number of families present. In this case, less diversity is lost than if the invasive species reduced the number of plant *families* from 25 to 10. I found that increasing cover of purple loosestrife and reed canary grass was significantly associated with declines in plant family richness. This is not surprising given the reduction in the number of species. However, it does confirm that a similar trend is detected for diversity measured at the family level as that measured at the species level and the diversity of functional groups.

The influence of the invasive species on individual plant species was examined using correlation coefficients (Table 2.8). Interestingly, both loosestrife and reed canary grass were most negatively correlated with two other introduced species, bull thistle (*Cirsium vulgare*) and European bittersweet (*Solanum dulcamara*). Bull thistle tends to be an early successional species that thrives in areas recently disturbed. This suggests that either loosestrife and reed canary grass inhibit disturbance, or more likely, may quickly out-compete bull thistle in disturbed areas. Dense sedge (*Carex densa*), common rush (*Juncus effusus*), and small bedstraw (*Galium trifidium*) were the native plant species most negatively correlated with invasive species abundance. Dense sedge and small bedstraw are diminutive plants that are likely simply overgrown by loosestrife and canary grass. Common rush is a larger plant (up to 100cm) that grows in tussocks. Interestingly, it also thrives in disturbed areas (Guard 1995). As with bull thistle, this suggests that loosestrife and canary grass can out-compete early successional species. It may also be indicative of environmental condition and that these wetlands are being disturbed regularly enough to promote strong competition between early successional species. Although reed canary grass was not positively correlated with any specific plant species, purple loosestrife was positively correlated with four native species, American bulrush (*Scirpus americanus*), waterpepper (*Polygonum hydropiperoides*), hard-stem bulrush (*Scirpus acutus*), and creeping spike-rush (*Eleocharis palustris*). All of these species tend to be found in habitats with long durations of standing water and may coexist with purple loosestrife because these conditions represent the edge of loosestrife's competitive range (realized niche). Thus, these plants may have a spatial refuge in deeper water habitats where the competitive ability of loosestrife is reduced.

One of the primary concerns of loosestrife and canary grass invasion is the negative effect on native plant species richness and abundance. During field sampling I observed that native species richness appeared to be more greatly reduced than introduced species in wetlands with high densities of loosestrife and canary grass. However, after plotting the proportion of native species against the percent cover of the invasive species I discerned no clear pattern that indicated the number of native species was reduced more than that of the introduced species (Figure 2.11a-b). However, abundance of native species declined with increasing cover of the invasive species (Figure 2.11b-c). This is somewhat tautological because the x-axis represents increasing abundance of an introduced species, however I include the data to show that in the absence of the invasive species, native plants usually comprise a large portion of the plant community.

I also classified the diversity of the plant community based on plant guilds. The plant community was divided into grasses, herbs, and hardwoods. The number of plant species in each guild decreased with increasing cover of the invasive plant species. The number of species of herbaceous plants tended to be greater than grasses in the reference wetlands and decreased to equal numbers in dense stands of the invasive species (Figures 2.10a-b). There tended to be fewer hardwood species within the study sites, presumably due to intolerance of extended hydroperiods or herbivory by beaver (*Castor canadensis*) and nutria (*Myocastor coypus*), and most of these were shrubs such as willows, roses, or hawthorns. These results suggest that the diversity of non-woody dicots is more greatly impacted than that of monocots or woody plants.

In summary, both purple loosestrife and reed canary grass cover are negatively correlated with all aspects of plant community diversity. Reed canary grass appears to have a greater negative effect on species richness and evenness than loosestrife at intermediate levels of abundance, but diversity is reduced by a similar amount at high densities.

In addition, I found evidence that both invasive plants appear able to out-compete early successional plants, including the invasive bull thistle. Because both plants are also known to be able to persist as dense stands for long periods in the absence of disturbance, this implies that purple loosestrife and reed canary grass may be able to effectively "halt" the successional processes (*i.e.* disturbance reallocates limiting resources) that are thought to maintain diversity (Whittaker 1965).

Grime (1979) proposed that plants can be divided into functional groups based on their abilities to colonize and persist in the environment during three successional stages. He calls these groups, C-types (competitors), S-types (stress tolerators) and R-types (ruderals). In this study I find that purple loosestrife and reed canary grass appear to fit into all three of these categories, they out-compete ruderal species for available resources after disturbance, they tolerate a wide range of environmental conditions, and they can invade and dominate relatively undisturbed communities. Presumably, trade-offs between physiological costs of each strategy would normally limit plants to one of the guilds. For example, the cost of producing aerenchyma tissue to provide oxygen to roots under conditions of standing water has a cost which reduces the ability of the plant to compete for nitrogen in dry habitats.

I hypothesize that invasive plants are able to excel at all three strategies for two reasons. First, the absence of specialized herbivores may allow these plants to reallocate resources from anti-herbivore defenses to competition, stress-tolerance, and reproduction. This may occur during an individual plant's lifetime through phenotypic plasticity, or plants may evolve over time through the natural selection of more competitive genotypes. Blossey and Notzold (1995) call this the Evolution of Increased Competitive Ability (EICA) hypothesis and provide evidence that this has occurred for purple loosestrife. Landis et al. (2003) found evidence that the absence of specialized herbivores did allow purple loosestrife to dominate plant communities. When specialized host-specific herbivores (biological control agents) reduced the abundance of purple loosestrife at five sites in Michigan, the researchers found that the species richness of the plant community significantly increased at all five sites. At nearby "control" sites, where no agents were released, loosestrife biomass was not reduced and the diversity of the plant community was unchanged.

While invasive species appear to thrive at all three strategies, appearances may be deceiving in this case. It may be that the underlying environment has been modified, thus changing the rules of the game. For competitors to benefit from their ability to efficiently gather and use scarce resources, resources must be scarce. However, if resource levels are increased, there is no benefit to be an efficient competitor, rather there is a benefit to grow and reproduce quickly even if done less efficiently. For example, if the limiting resource for primary production of wetland plants is nitrogen (Koerselman and Mueleman 1996, Bedford et al. 1999, Keddy 2000, Mitsch and Gosselink 2000, Bridgham et al. 2001) and human activities are effectively doubling the natural rate of nitrogen addition (Vitousek et al. 1997, Tilman and Lehman 2001), efficient competitors will be displaced by less efficient ruderals. Therefore, it may not be the case that loosestrife and canary grass are particularly good competitors, but rather competition (at least for nitrogen and phosphorus) has been made an irrelevant strategy. In the next chapter I investigate this hypothesis for purple loosestrife.

Effect of invasive species on the diversity of the moth community

I found that moth species richness was positively correlated with plant community richness (Figure 2.15). This suggests that declines in plant species richness associated with increasing cover of purple loosestrife and reed canary grass might result in reduction of moth species richness. However, when I examined the direct relationship between moth diversity and invasive plant cover I could not detect an effect with my limited sample (Figure 2.16a-b).

Moth diversity measures that included species equitability showed no trend in relation to increasing invasive plant cover (Figure 2.17c-j). These measures of moth community diversity include moth abundance in order to estimate the equitability or evenness of the community. Samples of many of the reference wetlands had a large number of individuals of a single moth species that dwarfed the abundance of moths of the other species (see Figure 2.16a), thereby decreasing measurements of equitability and diversity. The extreme case was Baskett Slough (BS), a United States Fish and Wildlife Service National Wildlife Refuge. The site was surrounded by grass fields planted as forage for Dusky Canada Geese (*Branta canadensis occidentalis*). This likely increased populations of the grass feeding moth *Euchromius ocelleus* (Noctuidae), such that I trapped 385 individuals in 2001. The abundances of the next most populous moth species were 89 individuals of *Aletia oxygala* and 25 individuals of *Crymodes devastator*. The remaining 25 species added a total of 63 individuals to the samples. These trends made the communities very inequitable when compared to communities that had fewer rare species and individuals. For example, at the Bird Blind site (BB), with a mean of 87.43% reed canary grass, I trapped a total of 36 individuals of 13 species in 2001. *Caenurgina erechtea* and *Aletia oxygala* tied for most abundant at six individuals each. These factors resulted in estimates of evenness (J) that either showed no trend in the case of purple loosestrife (Figure 2.17c) or appeared to increase with invasive species abundance for reed canary grass (Figure 2.17d), although the trend was not significant ($p=0.145$). The Brillouin's (H) and Simpson's (D) indices of diversity showed similar results, probably for the same reason (Figure 2.17e-h).

The log series appeared to be slightly more effective at dealing with the disparity in total moth abundance and the large number of rare species than the other measures of diversity. Although Baskett Slough was still given a very low score, the trend of the other sites did suggest a decrease in diversity with increasing invasive plant abundance (Figure 2.17i-j). This is not unexpected as the log series measure of diversity was developed for moth community data collected with light traps (Taylor et al. 1976).

Moth diversity was also measured at the taxonomic level of family. Reduction in the number of families is a greater overall loss of diversity than reduction of potentially closely related species. The number of moth families tended to decrease with increasing cover of both invasive plant species, however the trend was not significant after adjusting for multiple tests (Figure 2.18). Also, five moth families were represented by a single species (Cossidae, Lymantriidae, Plutellidae, Pterophoridae, and Saturniidae).

In conclusion, although plant diversity decreases with increasing abundance of the invasive plant, and plant species richness increases with moth species richness, I detected no decrease in moth diversity with increase of invasive species cover. This contradictory result is most likely the product of inadequate sample size, although variability in the data due to sample methods and other factors may have exacerbated the effect. The key is that there was a significant association between the species richness of the plant community and the species richness of the moth community. The p-value of 0.040 indicates a significant, but weak, association. This analysis included 19 sites. However, when the dataset was split to examine the effect of loosestrife cover and reed canary grass cover on moth species richness, the number of sites is each analysis was reduced to 13 and 11, respectively. By reducing the number of sites included in the analysis, the power to detect a significant result was also reduced.

Environmental analysis

I excluded potentially covarying and confounding environmental variables by identifying and measuring those factors most likely to influence plant and moth community diversity. Wetland hydrology, soil characteristics, and topography were measured and analyzed to control for covarying and confounding influences on plant diversity. Temperature, ambient light, and surrounding land-use were measured and analyzed to control for covarying and confounding influences on moth sampling and diversity. Canonical correspondence analysis (CCA) in conjunction with Monte Carlo tests of significance indicated that none of these variables were linearly associated with the abundance of the invasive species. The analysis indicated that these factors were not associated with invasive plant cover, and therefore they are not the mechanisms driving the patterns of community diversity that I observed in this study. This strengthens the causal link between the cover of the invasive species and the response of the plant and herbivore communities.

In addition, the measurements of ambient nocturnal light were important in identifying the likely reason why Knez Wetland had a depauparate moth community despite a high diversity of host plants (Figure 2.6). These measurements provided evidence that allowed us to remove the site from the moth diversity analysis. However, the result that Apache Bluff Wetland had few moth species (18) despite having a high number of plant species (41) was not explained by the environmental data. I hypothesize that that the reduction of moth abundance was due to the adjacent golf course, since golf courses are known for heavy insecticide use to control turf insects.

Conclusion

I found that both purple loosestrife and reed canary grass reduce the diversity of the wetland plant communities they invade. Species richness, evenness, the Shannon-Wiener Diversity Index and Simpson's Diversity Index all declined with increasing cover of the invasive plant species. Moth species richness increased with increasing plant species richness. However, moth diversity did not appear to decline with increasing cover of the invasive species. Wetland hydrology, soil nutrients, and topography were measured and analyzed to control for covarying and confounding influence on plant diversity. Temperature, ambient light, and surrounding land-use were measured and analyzed to control for covarying and confounding influence on moth sampling and moth community structure. No associations were found that suggested environmental factors other than invasive plant abundance were responsible for the decline in plant and moth diversity.

Future research

This study documents a strong negative association between the abundance of two invasive plant species and plant community diversity. Although potentially confounding environmental factors were considered, none-the-less there is the possibility that the patterns I found were caused by something other than the invasive plant species. However, this study allows us to predict the effect on plant diversity should the abundance of the invasive species be reduced. If diversity increases by the predicted amount with a given reduction of invasive plant cover it strengthens the conclusion of a cause and effect relationship.

Therefore, if the abundance of these invasive species can be reduced I can test my predictions. Purple loosestrife abundance can be reduced using introduced biological control agents. These insects were released at or near all of the loosestrife dominated wetland sites in this study. Although the insects are currently not in high enough densities to suppress loosestrife populations, I expect insect populations to grow, spread, and reduce loosestrife biomass by 90% as found in other studies (Schooler 1998, Landis et al. 2003). Reed canary grass is being actively managed throughout the Willamette Valley and several of the sites are targeted for control. This generally involves manipulating water levels to drown roots, planting trees to reduce sunlight, or physically removing plants and litter. I am less hopeful about these methods, because the manipulation is not selective and will effect the entire plant community. I intend to return to these study sites in the coming years to sample plant populations in order to verify my predictions.

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Chapter 3

The growth of purple loosestrife is positively associated with soil nitrogen concentrations

Introduction

Plants differ in their ability to acquire and use nutrients. There is a trade-off between speed (power) and efficiency of resource use, such that increases in one come at the expense of the other (Odum and Pinkerton 1955, Calow 1977). Some plants are more efficient at extracting nutrients when nutrients are present at low soil concentrations and therefore gain a competitive advantage when these nutrients are scarce. Other plants can take up abundant nutrients and convert these to growth and reproduction more quickly, but less efficiently, thereby displacing more efficient competitors when resources are plentiful. These different competitive strategies and abilities may allow plant species to coexist across subtle nutrient gradients in otherwise homogeneous environments, thereby increasing species richness in plant communities (Whittaker 1965).

Furthermore, invasive plants can dominate habitats and reduce the diversity of previously species-rich communities when nutrient concentrations are increased (Tilman and Lehman 2001). Human activities have approximately doubled the rate of nitrogen input into terrestrial ecosystems (Vitousek et al. 1997), and we are increasing levels of soil nitrogen and phosphorus in ecosystems around the world (Tilman and Lehman 2001). Since nitrogen, available to plants as ammonium or nitrate, is most often the nutrient limiting plant growth in terrestrial ecosystems, it is no surprise to many ecologists that invasive plant species are a major threat to biodiversity in the United States (Wilcove et al. 1998).

Purple loosestrife (*Lythrum salicaria* L.) is an invasive species that displaces native wetland vegetation in wetlands and riparian areas (see Chapter 2). In this chapter I examine which nutrients are limiting the production of vegetative biomass in wetland plant communities in the Willamette Valley of Oregon and the role of soil nutrients in the growth and invasiveness of purple loosestrife. I then assess the risk of invasion to nine wetlands currently not colonized by purple loosestrife. I found that nitrogen is most likely the nutrient limiting plant community biomass and purple loosestrife biomass in field plots. In addition, loosestrife biomass increased with increasing concentration of soil nitrogen in a greenhouse experiment where environmental constraints other than soil nutrients were controlled. The results of this study indicate that soil nitrogen may enhace the invasiveness of purple loosestrife and wetlands where purple loosestrife is currently absent will be susceptible to invasion should loosestrife colonize these sites.

Role of nutrients in plant competition

Competition between plant species for scarce resources is an important factor governing plant community composition. The main limiting resources for plants are light, water, and nutrients. Water is rarely a limitation for wetland plants, although standing water can be a problem for plants that do not have adaptations to move oxygen to root tissue (Keddy 2000). Light is generally available for herbaceous plants in emergent wetlands due to the inability of woody plants to tolerate long periods of inundation (Keddy 2000). Therefore, nutrients are most often the factor limiting plant growth in emergent wetland ecosystems (Keddy 2000, Mitsch and Gosselink 2000). Nitrogen is considered the primary limiting nutrient for plant growth in emergent marsh ecosystems (available as nitrate and ammonium), followed by phosphorus (available as soluble phosphate) (Koerselman and Mueleman 1996, Bedford et al. 1999, Keddy 2000, Mitsch and Gosselink 2000, Bridgham et al. 2001). However, phosphorus may be limiting in urban wetlands (Woo and Zedler 2002). Carbon, potassium, and micronutrients (primarily Mn, Mg, and Ca) may also be limiting nutrients for plant growth, but I found no prior literature that presents evidence that these nutrients are limiting in wetland ecosystems.

The ratio of nitrogen to phosphorus in plant tissues is an indication of which nutrient is limiting for a given wetland vascular plant species (Koerselman and Mueleman 1996, Bedford et al. 1999). In a review of 40 European wetland plant community fertilization studies, Koerselman and Mueleman found that a plant tissue N:P ratio of less than 14 indicated nitrogen was the limiting nutrient while a plant tissue N:P ratio greater than 16 indicated phosphorus was limiting plant biomass. The nature of nutrient limitation was ambiguous at plant N:P ratios between 14 and 16 (Koerselman and Mueleman 1996).

Effect of nutrients on the competitive ability of purple loosestrife

Direct evidence that nutrients alter purple loosestrife's ability to dominate wetland plant communities is supported by extended germination trials (Weiher et al. 1996) and in tests of competitive response (Shamsi and Whitehead 1977a and b). In a study by Weiher et al. (1996), the seeds from 20 wetland plant species were sown in 120 experimental microcosms representing 24 environmental treatments. During the first year *Bidens cernua* was the most prevalent plant, but by the fifth year purple loosestrife had become dominant in both high and low fertility treatments where the water level was held constant. However, when water levels were manipulated to mimic seasonal flooding, loosestrife attained dominance only in high fertility treatments (Weiher et al. 1996). Shamsi and Whitehead (1977a) compared the response of purple loosestrife and hairy willow-herb (*Epilobium hirsutum*) to co-varying concentrations of nitrogen, phosphorus, and potassium. They found that purple loosestrife growth was more tolerant of low concentrations of nutrients than hairy willow-herb, although they did not test competitive ability between the plant species at low nutrient concentrations. In a second experiment they manipulated concentrations of N, P, and K independently and found that loosestrife growth was more sensitive to decreases in N than reduction of P or K (Shamsi and Whitehead 1977b). These experiments support the hypothesis that increased nutrients, particularly nitrogen, may enhance the competitive ability of purple loosestrife in seasonally flooded wetlands, such as those in the Willamette Valley.

Effect of purple loosestrife on nutrient concentration and cycling

Although it is widely acknowledged that nutrients affect organisms, organisms can also alter the availability and cycling of nutrients. In a much simplified example, annual uptake by plants depletes soils of nutrients during the growing season and then these nutrients are released back into the ecosystem after plant tissues decompose the following fall through spring. Different plants have different nutrient cycling rates. Loosestrife has been shown to modify phosphorus cycling regimes in wetlands. Emery and Perry (1996) found that the phosphorus in loosestrife leaves and stems leaches into surrounding environment in fall and winter, as compared with native cattail species (*Typha* spp.) where phosphorus is retained until spring. Templer et al. (1998) found that purple loosestrife sequesters phosphorus in tissue, significantly reducing summer porewater phosphate concentrations to half that of the porewater of native cattail, *Typha angustifolia*, and the invasive reed *Phragmites australis*. They also found that phosphorus cycles through purple loosestrife 2 times and 1.5 times more quickly than through cattail and common reed respectively. Although this hoarding of phosphorus may be a manifestation of competition for limited resources, it is likely that available nitrogen was the primary limiting nutrient in these wetland ecosystems because phosphate was more available throughout the year than nitrogen (measured as porewater ammonia).

Objectives of this study

The role of nutrients in the invasibility of wetlands is not clear. The objectives of this study are to determine: (1) which nutrients limit plant growth in regional palustrine emergent wetlands, (2) which nutrients are likely limiting the growth of purple loosestrife in regional wetlands, and (3) whether currently uncolonized wetlands will be susceptible to invasion should loosestrife colonize. Based on previous studies and observations I proposed the following hypotheses: (1) nitrogen is the primary limiting nutrient for plant species within the study sites, (2) nitrogen is the primary limiting nutrient for purple loosestrife growth, and (3) soil conditions at currently uncolonized wetlands are suitable to loosestrife invasion. I also examine the association between the abundance of the limiting nutrient and the species richness of the plant community.

Since there are multiple means of measuring soil nitrogen I refined my general predictions. Nitrate is the most available form of nitrogen and will be scarce when and where nitrogen is limiting due to plant uptake. Ammonium can be used by many plants, however it is toxic at high concentrations and is therefore a less available form of nitrogen and will persist at higher concentrations in the soil. In addition, since it is the precursor to nitrate I expect plant biomass to be positively correlated with ammonium (ammonium as indicator of potential nitrate). For the same reasons I expect concentrations of total nitrogen to vary more widely in the soil than nitrate and to exhibit a positive correlation with plant biomass (as potential ammonium). However, microorganisms can also fix nitrogen directly from its most abundant and ubiquitous form, the atmospheric gas (N_2).

If phosphorus is not limiting, I expect the available form, phosphate, to persist in the soil in greater concentrations than nitrate and not be associated with plant biomass. In addition, if phosphorus is not limiting plant growth, I expect total phosphorus, as potential phosphate, to exhibit no significant association with plant biomass.

Materials and Methods

Study sites

Thirteen wetland sites were selected in the Willamette Valley, OR (Figure 3.1, Appendix A). The Willamette Valley is considered a Mediterranean climate with cool wet winters and hot dry summers. All sites were seasonally flooded emergent palustrine wetlands (after Cowardin et al. 1979) and the vascular plant community was dominated by herbaceous vegetation.

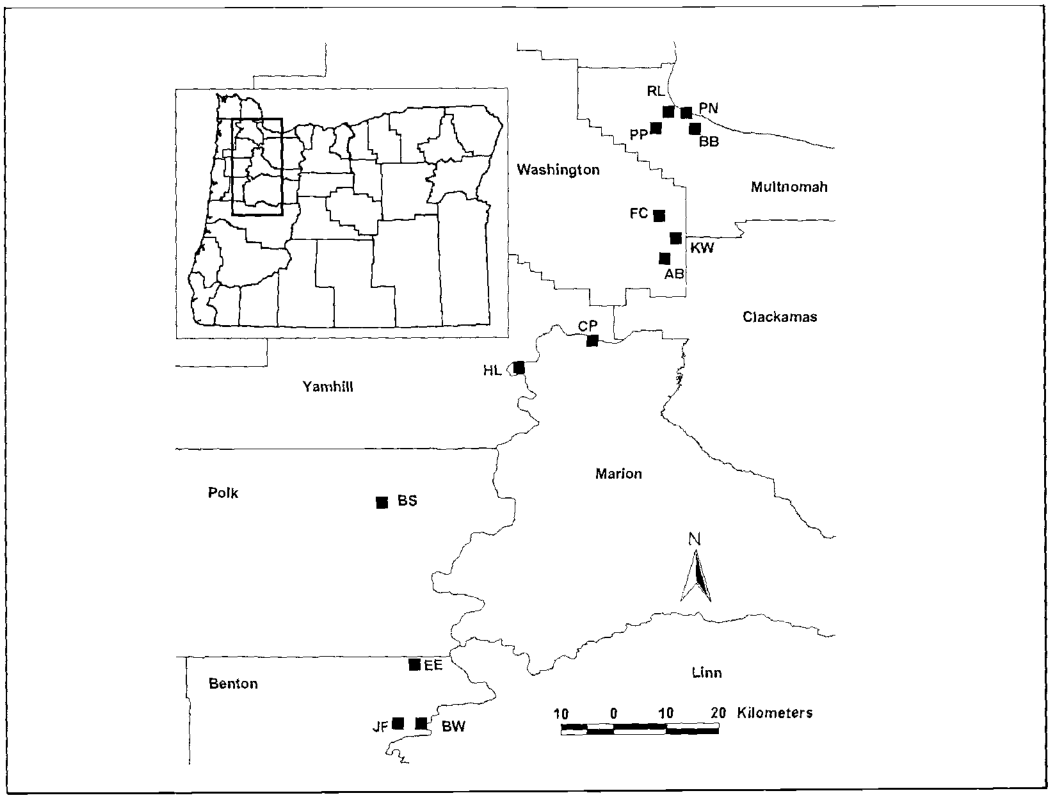


Figure 3.1. Wetland study site locations in the Willamette Valley, Oregon. The two letter acronyms identify specific sites. See Appendix A for full site names, geographic coordinates, and site contact information. Thin lines denote county boundaries.

Quantifying site hydrology

In March and April of 2001 a shallow well was sunk at each of the sites to measure monthly water levels. Wells consisted of a 1.3m PVC tube (5cm inside diameter) with opposing perforations (1cm diameter) at 10cm intervals down each side. The bottom was capped and had two perforations. The tube was then wrapped with fiberglass window-screening (approx. 2mm mesh) on the exterior to prevent sediment accumulation. The wells were installed so to extend one meter below the ground surface by digging a hole with a soil auger, inserting the well, and filling in with sand. Digging, rather than driving, prevented soil compaction around the wells, and sand fill facilitated water flow (pers. com. M. Kentula, US-EPA, Corvallis, OR). This method allowed us to record above and below ground water level through the year.

To determine percent inundation I surveyed relative elevation, created digital elevation models (DEMs), and related these to water levels for each site. The basin microtopography survey method used a surveyor grade differentially correcting GPS receiver (Trimble Surveyor ProXR, sub-meter accuracy) in conjunction with a rotating laser level to obtain a high resolution (1m^2) digital elevation model of each site. The laser level was set at each site and the distance to the ground from the laser plane was measured at the well and at 50 to 85 additional locations depending upon the evenness of the terrain (see Louhaichi et al. 2003 for more extensive description of method and accuracy). These point data were then used to interpolate an elevation grid with 1m x 1m cells (7,854 cells) for each site. The area of inundation was calculated for each site during each month by determining the number of cells below the measured water level.

Quantifying soil characteristics

I examined the soil characteristics of a given site by: (1) directly measuring an array of soil nutrient parameters (Stolt et al. 2001), (2) using the primary focal plant species, purple loosestrife, as a "phytometer" species (Clements and Goldsmith 1924, Clements 1935, Keddy 2000), and (3) measuring nutrient ratios in the dominant vegetation in order to determine which nutrient is likely the limiting nutrient for the plant species at that location (Koerselman and Mueleman 1996). The direct measurements include the parameters: total nitrogen, nitrate, ammonium, mineralizable ammonium, total phosphorus, phosphate, organic carbon, potassium, magnesium, calcium, manganese, conductivity, acidity, and percent sand/silt/clay.

To assess soil characteristics I collected soil samples from 13 wetlands in the Willamette Valley. Within the wetlands I identified sampling sites of 50m in radius that were homogeneous with respect to hydrologic regime. Within each site, four randomly selected locations were sampled during June of 2002. Prior to collecting the soil samples I clipped all plant material within a 1m^2 plot (square) centered on the sample location. The above ground material was sorted to species, dried to constant weight, and weighed to nearest 0.1g. The dominant plant species at each plot was then analyzed for total nitrogen and phosphorus concentrations in above-ground tissue.

Soil samples were taken by first removing the top 5cm of soil from the center of the plot using a spade. Then the next 5cm (approx. 2 liters) were placed into a paper bag. If the soil was wet, the paper bag was set into a plastic bag for transport. Prior studies have found no significant difference in soil properties (organic C, CEC, N, pH, Ca, and Mg) within small (0.25-0.35ha) palustrine wetland sites between samples taken at the same depth (Stolt et al. 2001). Herbaceous wetland plants tend to have shallow root zones due to anoxic conditions inhibiting deep roots and abundance of water near the surface (Mitsch and Gosselink 2000). Therefore, I restricted soil sampling to the root zone at a single depth (5-10cm below surface) within and across sites. Samples were brought back to the lab, removed from plastic bags, and dried. After all samples were collected, half of the material was separated and analyzed to determine soil characteristics and half was used in the phytometer study. Soil nutrient analyses were conducted by the OSU Department of Crop and Soil Science soils laboratory and physical soil properties were measured by C. Meston under the direction of Crop and Soil Science staff using their protocols (Horneck et al. 1989).

Phytometer Experiment

The phytometer approach simply means using plant growth as an indicator of soil suitability (Clements and Goldsmith 1924). Growing plants in field soil isolated in a greenhouse provided a safe alternative to planting the invasive species within currently uncolonized field sites. In addition, growing plants in the greenhouse allowed us to control for potentially confounding organism interactions and environmental conditions.

The portion of the soil from each sample location not allocated toward chemical and physical analysis was transferred to two plant pots (14cm diameter). Five loosestrife seeds, collected from a local loosestrife population at Baskett Slough National Wildlife Refuge in the fall of 2001, were sown in each pot. Once the seeds germinated, plants were thinned to one per pot. Plants were kept in a greenhouse and grown from January through April 2003 with the aid of fluorescent lights (40 GE Gro bulbs) on a 16:8 light:dark cycle. They were then harvested (above and below ground), dried to constant weight, and weighed. The resulting biomass was the phytometric measure of soil suitabilty for loosestrife growth.

Data Analysis

I generated random numbers and entered data in Excel (Office XP, Microsoft 2002). Spatial data were collected using a Trimble Surveyor (XR Pro) global positioning system (GPS) with real-time and post-processing differential correction capable of sub-meter spatial accuracy. Spatial data were differentially corrected using Pathfinder Office software (version 2.70, Trimble 2000). Multiple regression analyses were performed using Excel and S-plus (version 6.1, Insightful 2002). Data were transformed to meet the assumptions of regression prior to analysis. The assumption of independence between explanatory variables was assessed using scatter plots. Variables tended to exhibit weak correlation. Exceptions were: manganese was positively correlated with the four measures of nitrogen, phosphate and phosphorus were positively correlated, and measures of soil nitrogen were positively correlated.

Results

Site hydrology

The emergent wetland sites exhibited the predicted hydrologic cycle with waxing area of inundation during the winter and waning inundation during the summer (Figure 3.2). Two exceptions were the Bird Blind site (BB) which did not accumulate above-ground water in the winter of 2001 and the Baskett Slough (BS) site which only drew down to 50% inundation during the summer of 2002. The hydrologic regimes of both sites were being actively modified by land managers. The Bird Blind site is on the Smith and Bybee Lakes Management Area, a wildlife refuge in the Rivergate District of Portland, Oregon. Water retention at the Bird Blind site was reduced by the opening of a water control structure in the summer of 2000 at the adjacent Smith Lake by the wetland managers (Portland Metro Parks and Greenspaces). This was done to increase summer drawdown and thereby increase wetland plant production to provide more forage for wetland bird populations. The opening of this control structure also lowered the water levels at the BB study site. Baskett Slough is a United States Fish and Wildlife Service National Wildlife Refuge. The managers control the hydrologic regime to maximize forage production for dusky Canada geese (*Branta canadensis occidentalis*). A part of their strategy is to retain water in reservoirs in areas of higher elevation to flood lower elevation wetlands later in the year. This late season flooding stimulates the growth of wetland plants, thereby increasing the forage for geese populations. The amount of water in the reservoirs varies from year to year and resulted in extended inundation in 2002 at the study site located within an upstream wetland on the refuge.

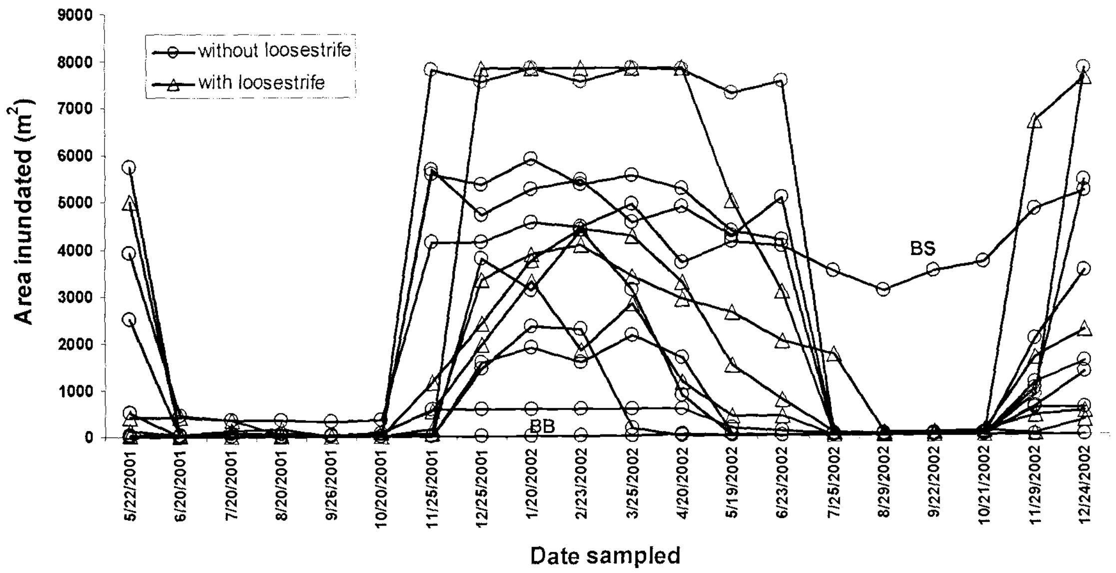


Figure 3.2. Wetland site hydrology. Sites exhibited the typical seasonal palustrine emergent wetland hydrologic cycle with waxing area of inundation during the winter and waning inundation during the summer.

Evidence for nutrient limitation using N:P ratios in plant tissues

The N:P ratios of the dominant plants varied from 3:1 to 11:1 but were all below 14:1, indicating nitrogen is likely the primary limiting nutrient at the study sites (Figure 3.3).

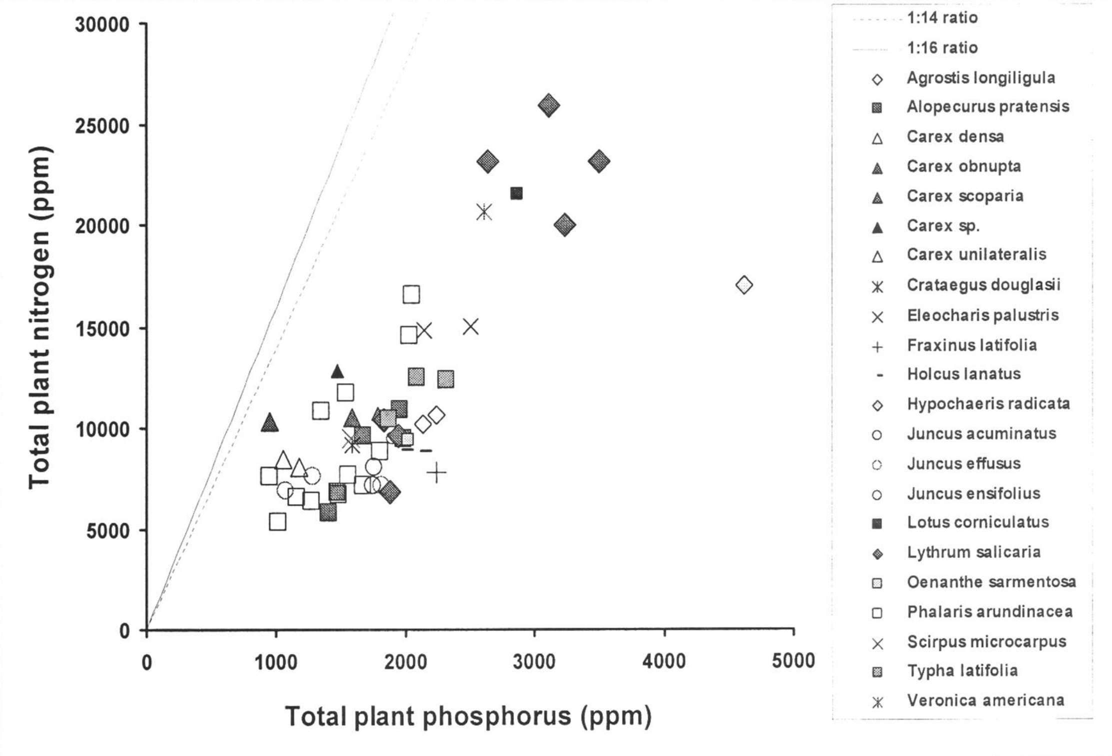


Figure 3.3. N:P ratios in dominant plant tissue was less than 14:1 in all cases (n=52). This indicates nitrogen is the limiting nutrient. The solid line designates the 1:16 phosphorus to nitrogen ratio and the broken line designates the 1:14 phosphorus to nitrogen ratio.

Evidence for nutrient limitation using nutrient association with plant community biomass

As expected under the hypothesis that nitrogen is the primary limiting nutrient, the most available form of nitrogen, nitrate, is present at low concentrations in the soil (Figure 3.4a). The precursors of nitrate, soil ammonium and total soil nitrogen, were found in the soils at greater concentrations (Figures 3.4b-c). Mineralizable ammonium is a measurement of the potential of the soil to generate ammonium and nitrate through anaerobic fixation by bacteria (Figure 3.4d).

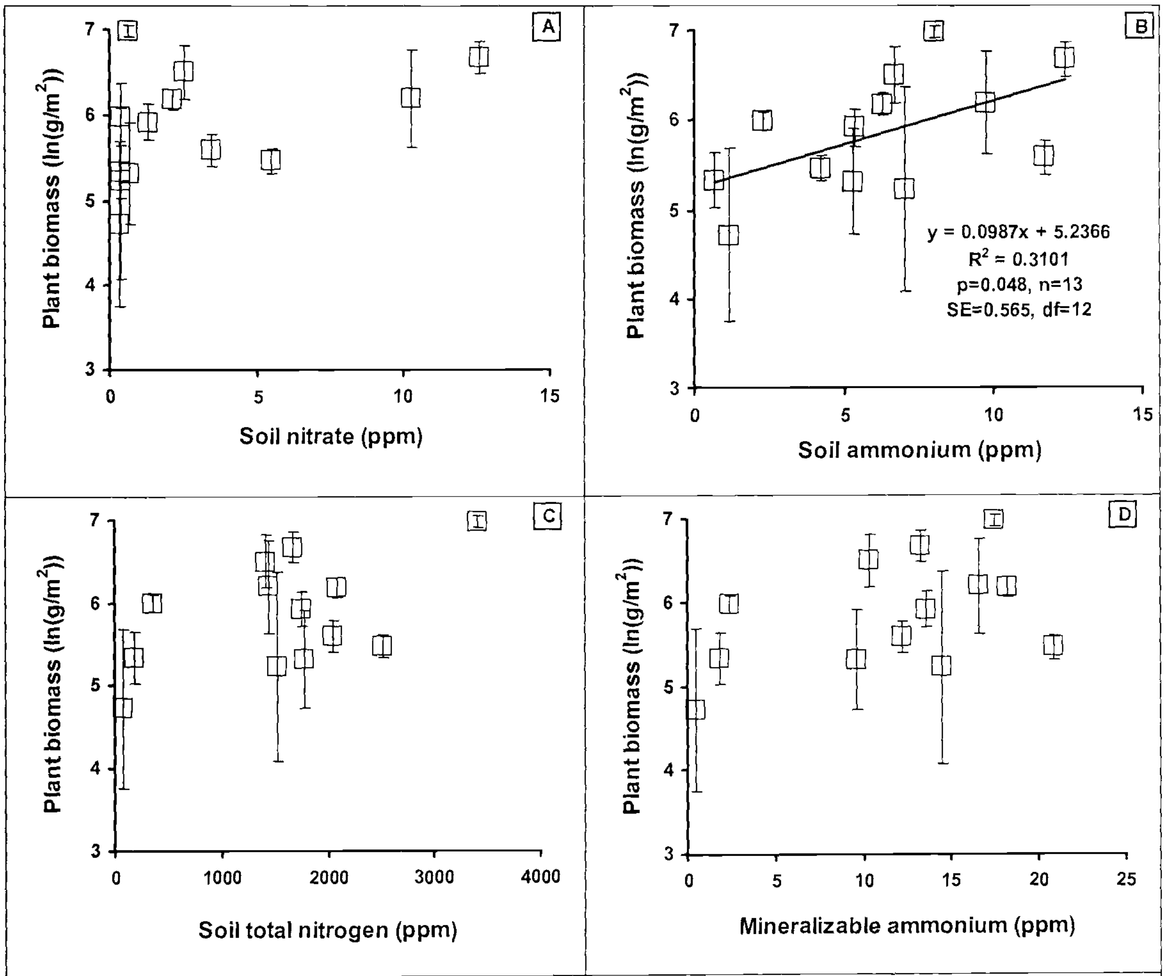


Figure 3.4a-d. Relationship between soil nitrogen concentration and plant biomass. Plant biomass is the natural log of the mean above-ground dry weight of vascular plants within four randomly selected 1m² plots per site. Multiple linear regression indicated that a model including only soil ammonium (b) had the best fit and the slope was significantly different from zero.

Soil phosphorus is the precursor to the available form of phosphorus, phosphate (Figure 3.5a). Concentrations of phosphate in the soil tended to be higher than nitrate (Figure 3.5b).

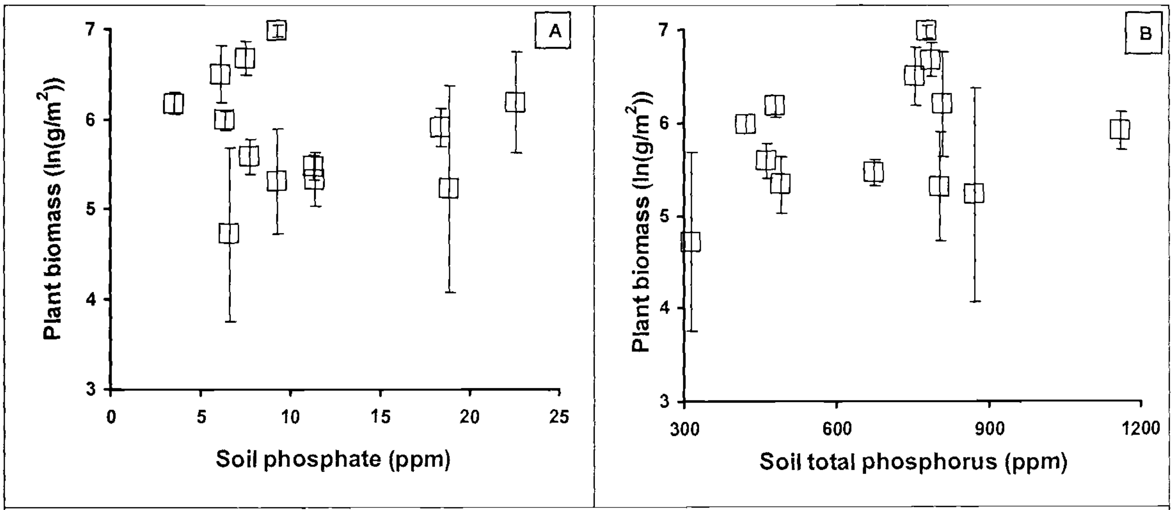


Figure 3.5a-b. Relationship between soil phosphorus concentration and plant biomass. Plant biomass is the natural log of the mean total above-ground biomass of vascular plants within four 1m^2 plots per site dried to constant weight.

Multiple regression was used to statistically examine the role of the multiple explanatory variables (soil nutrients) on the response (total plant biomass). The main question of interest was whether any of the measures, or combinations of measures, of nitrogen and phosphorus explained the observed variation in plant biomass. I expected that the most available form of the limiting nutrient (nitrate or phosphate) would not be associated with plant biomass because plant uptake would have removed it from the soil. However, precursors of the available form of the limiting nutrient (total nitrogen, ammonium: soil and mineralizable, and total phosphorus) would be positively associated with plant community biomass. I considered these as measures of the potential of the soil to produce the preferred available forms of the limiting nutrient. Micronutrients were not included in this analysis because, as with nitrogen and phosphorus, if they were limiting biomass I would expect their soil concentrations to be low and not associated with biomass. Plant biomass was natural log transformed to equalize variance before assessing the fit of the models. I performed a stepwise regression procedure using a combination of forward and backward selection to select the model with the best fit (Ramsey and Schafer 1997, p. 337). The Cp statistic was used to select the best model. A simple model including only soil ammonium had the best fit and the slope was statistically significant (p=0.048, n=13).

I sampled wetland soils during the growing season and expected that if nitrogen was limiting plant growth the concentration of available nitrogen (nitrate) would be less than that of available phosphorus (phosphate). A paired t-test for site means was used to assess whether the data supported the hypothesis. I found that soil nitrate concentrations were significantly lower than soil phosphate concentrations (2-tailed p=0.001, n=13).

Evidence for nutrient limitation for purple loosestrife in field sites

Four of the thirteen wetland sites were colonized by purple loosestrife (HL, PP, RL, and PN) and purple loosestrife was present in all of the four randomly chosen quadrats at each site. Even with the natural log transformations, the correlations, particulary with nitrate, are highly leveraged by a single site (Horseshoe Lake) and there are no intermediate values of nitrogen represented in the samples. As expected, purple loosestrife biomass was positively associated with three of the four measures of soil nitrogen: ammonium, total nitrogen, and mineralizable ammonium (Figure 3.6b-d).

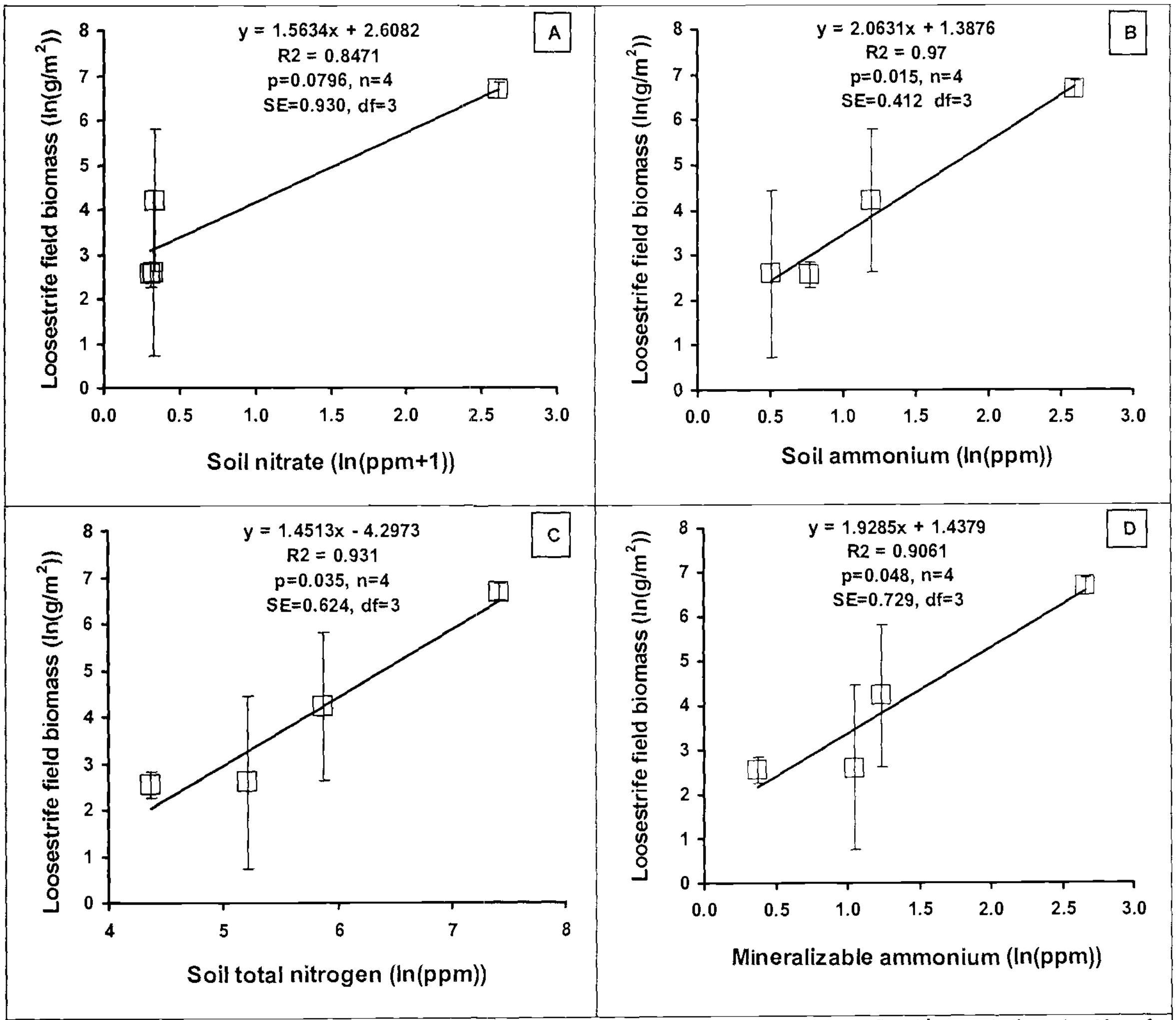


Figure 3.6a-d. Relationship between soil nitrogen concentration and loosestrife biomass. Loosestrife field biomass is the natural log of the mean total biomass of purple loosestrife within four 1m² plots per site dried to constant weight. Loosestrife biomass increases with three measures of soil nitrogen : ammonium, total nitrogen and mineralizable nitrogen. Measurements of soil nitrogen were natural log transformed. Bars indicate standard deviation of log transformed data (n=4).

Soil phosphate and total phosphorus were not associated with loosestrife biomass (Figure 3.7a-b).

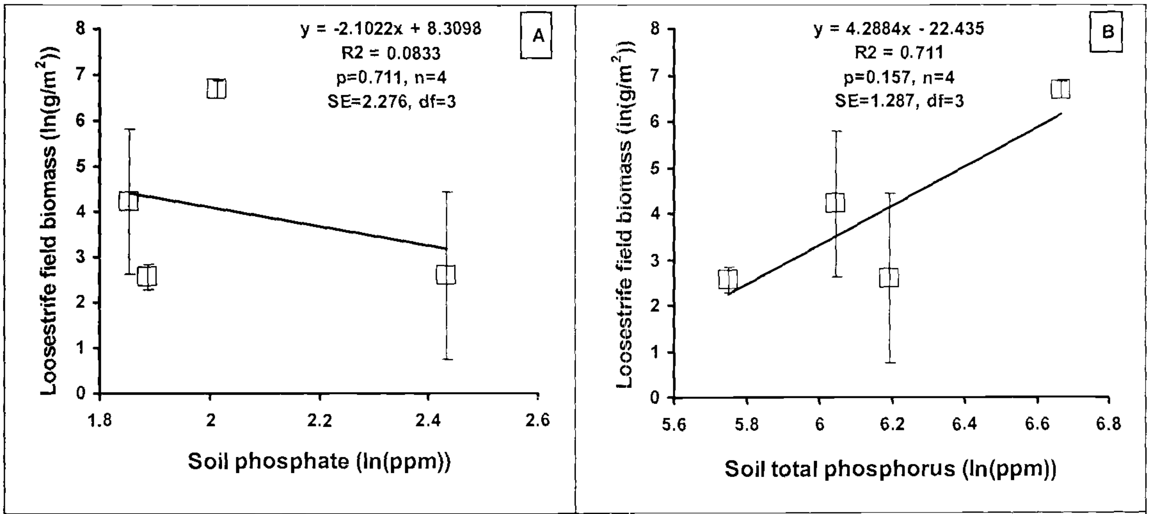


Figure 3.7a-b. Relationship between soil phosphorus concentration and loosestrife biomass. Loosestrife field biomass is the natural log of the mean total biomass of purple loosestrife within four 1m² plots per site dried to constant weight. Measures of soil phosphorus were natural log transformed. Bars indicate the standard deviation of the natural log transformed data (n=4).

I only had four sites with loosestrife field biomass data and I therefore could not perform a multiple linear regression on these data because I lacked the necessary degrees of freedom. However, the associations between loosestrife biomass and the soil nutrients were examined using linear regression. Loosestrife biomass increased with increasing concentration of ammonium, total soil nitrogen, and mineralizable ammonium (Figure3.6b-d). This result supports the hypotheses that precursors of nitrate will be positively associated with loosestrife biomass and measures of phosphorus will show no association with loosestrife biomass.

Evidence for limiting nutrients from loosestrife phytometer experiment

In the phytometer experiment I grew loosestrife in soils from all thirteen field sites under greenhouse conditions. This controlled for all factors potentially influencing purple loosestrife growth other than soil properties. Soil fertility measurements were conducted before growing the plants. Therefore, the analysis is more straightforward than analysis of field biomass where soil nutrient samples were taken when plant biomass was harvested.

Soil nitrate was weakly associated with loosestrife biomass in the phytometer study (Figure 3.8a). Soil ammonium was most highly associated with loosestrife biomass and the trend was positive and roughly linear (Figure 3.8b). Total soil nitrogen and mineralizable ammonium were positively associated with loosestrife biomass but the relationship was less clear (Figures 3.8c-d).

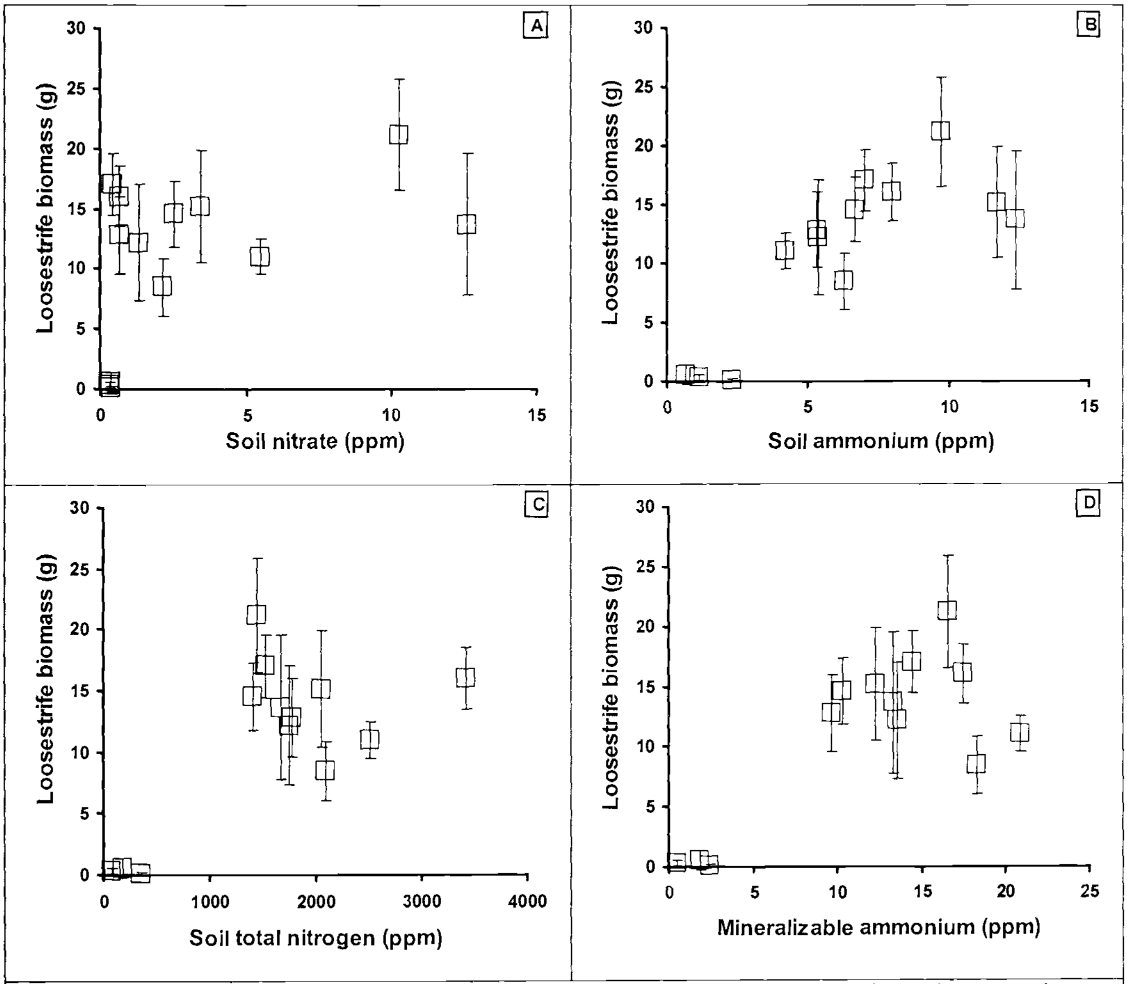


Figure 3.8a-d. Relationship between soil nitrogen concentration and loosestrife growth. Loosestrife biomass is the mean dry weight of eight entire purple loosestrife plants grown from seed in soil collected from each of thirteen field sites. Four plots were randomly selected at each site and two plants, in separate pots, were grown from each sample. Plants were grown in a greenhouse under identical conditions. Bars indicate standard deviation (n=4).

Soil phosphate was weakly associated with loosestrife biomass (Figure 3.9a). Three sites with relatively high soil phosphate concentrations produced very low biomass of purple loosestrife. Total soil phosphorus was positively associated with loosestrife biomass (Figure 3.9b). However, there was a high variation in the loosestrife biomass response around the 500ppm concentration, which indicates other variables may be influencing the result.

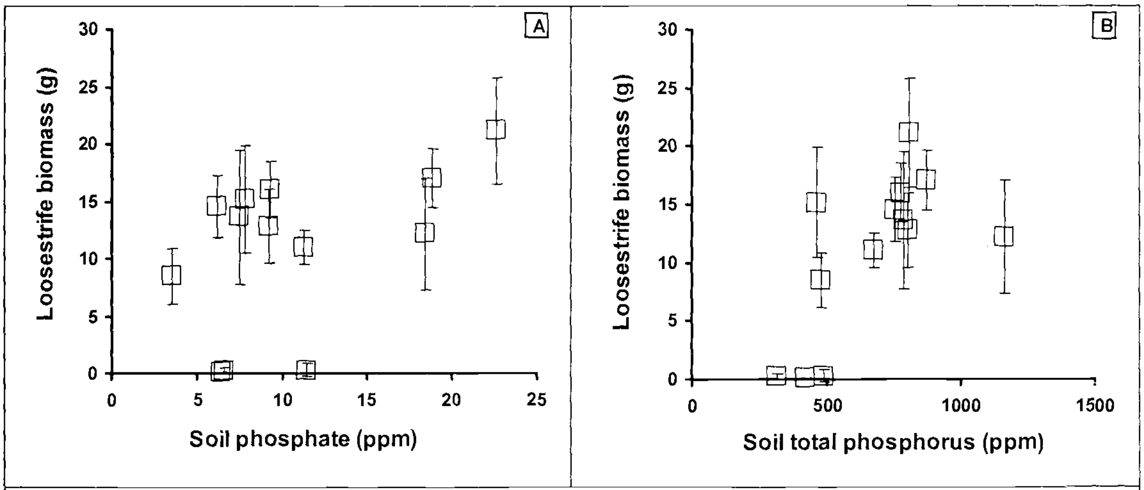


Figure 3.9a-b. Relationship between soil phosphorus concentration and loosestrife growth. Loosestrife biomass is the mean dry weight of eight entire purple loosestrife plants grown from seed in soil collected from each of thirteen field sites. Four plots were randomly selected at each site and two plants, in separate pots, were grown from each sample. Plants were grown in a greenhouse under identical conditions. Bars indicate standard deviation (n=4).

As with the analysis of soil nutrients and plant community biomass, I used stepwise multiple linear regression to assess which nutrient variables best explained the response (loosestrife biomass). However, in this analysis I included additional nutrients (K, Ca, Mg, Mn) because the measures now represented the initial condition of the soils. I performed a stepwise regression procedure using a combination of forward and backward selection to select the model with the best fit. The Cp statistic was used to select the best model.

The phytometer experiment yielded a similar result as that for the field biomass data. The model with the best fit (lowest Cp statistic) included all the soil nitrogen variables (nitrate, ammonium, mineralizable ammonium, and total nitrogen). However, the model also included the micronutrient, manganese. The model was significantly different from the null hypothesis that nutrients were unrelated to loosestrife biomass (p=0.00084). However, although the Cp statistic identifies the model that explains the most variation, it does not indicate whether all of the variables are significant. Based on prior literature and analyses I hypothesized that manganese was correlated with nitrogen and explained some variation but that the amount it explained was not significant to the model. This was analyzed using an extra sum-of-squares F-test. The rich model including the nitrogen measures and manganese was contrasted with the reduced model including only the measures of nitrogen. As expected, manganese did not explain a significant amount of the variation beyond that explained by nitrogen measures (F=4.34, df=1/7, p>0.05). The reduced model including only measures of soil nitrogen was significant (Table 3.1).

Table 3.1 Multiple linear regression results for soil nutrient and loosestrife biomass analysis

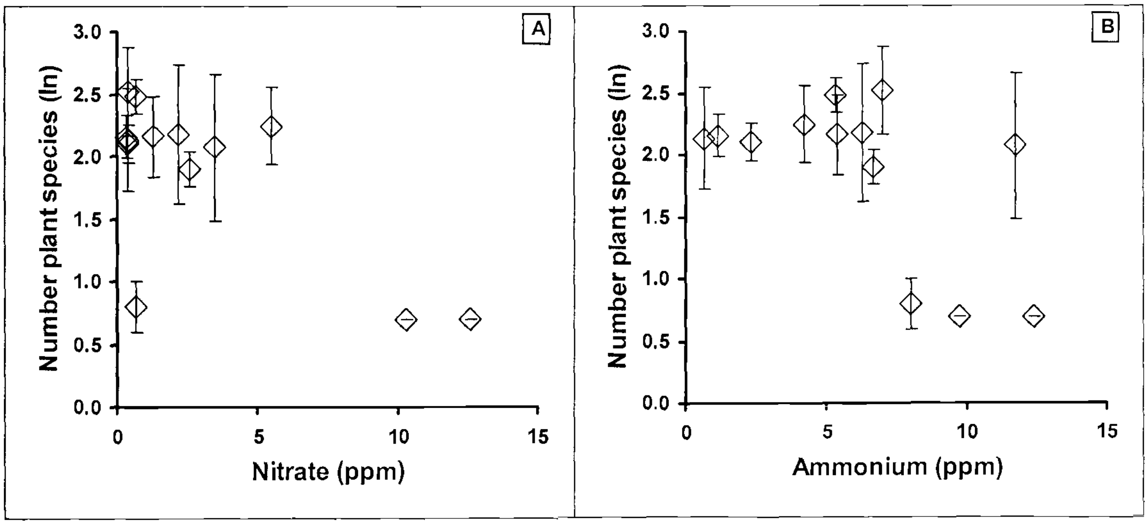
y = 0.0306 + (total nitrogen)(-0.0001) + (ammonium)(0.1856) + (nitrate)(-0.0651) + (mineralizable ammonium)(0.1132) + e

Variable	Coefficient	Standard Error	t-value	p
Intercept	0.0306	0.3299	0.0926	0.9285
Total nitrogen	-0.0001	0.0004	-0.2849	0.7829
Ammonium	0.1856	0.0703	2.6386	0.0298
Nitrate	-0.0651	0.0616	-1.0576	0.3211
Mineralizable ammonium	0.1132	0.0562	2.0138	0.0788

Residual standard error = 0.5106 on 8df, Multiple R-Squared = 0.8615, F-statistic = 12.44 on 4 and 8 df
p-value = 0.001638

Relationship between limiting nutrients and species richness

If abundance of the primary limiting nutrient favors the growth and domination of invasive plant species I would expect to see an overall trend of reduced plant diversity in sites with high concentrations of the limiting nutrient. I examined the relationship between soil nitrogen concentrations and the number of plant species. The mean number of plant species was negatively associated with both soil nitrate and soil ammonium (Figure 3.10a-b). Total soil nitrogen and mineralizable ammonium were weakly associated with plant species richness (Figure 3.10c-d).



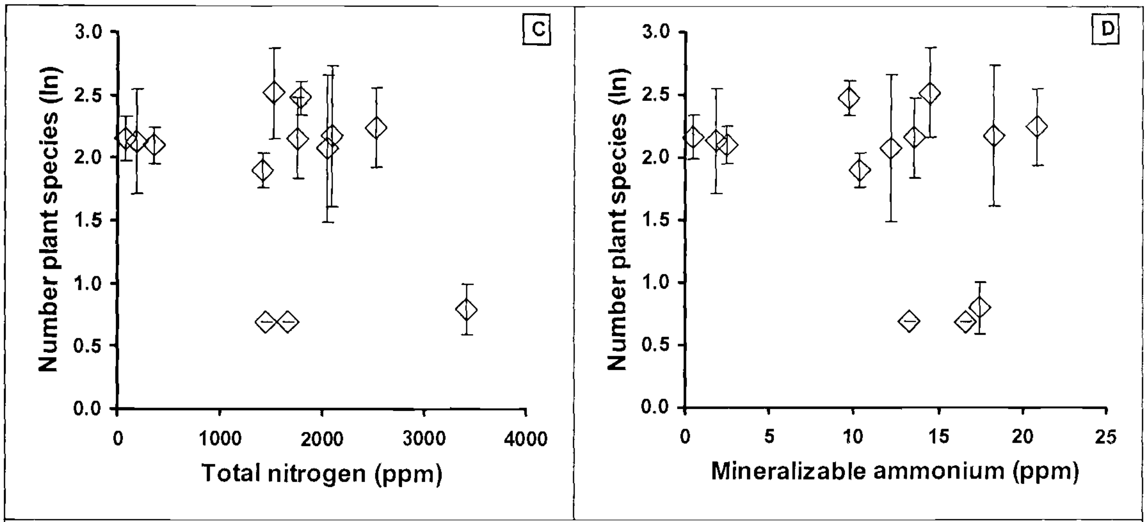


Figure 3.10a-d. Relationship between soil nitrogen concentration and plant species richness. Number plant species is the log transformed mean number of vascular plant species sampled per 1m² plot for each of 13 wetland field sites. Bars indicate standard deviation (n=4).

Although prior evidence strongly indicates that nitrogen is the nutrient limiting primary production in these wetlands, I also examined whether soil phosphorus concentrations were negatively associated with the number of vascular plant species within the 13 study sites. Soil phosphate and total phosphorus were weakly associated with the mean number of plants per site (Figure 3.11a-b).

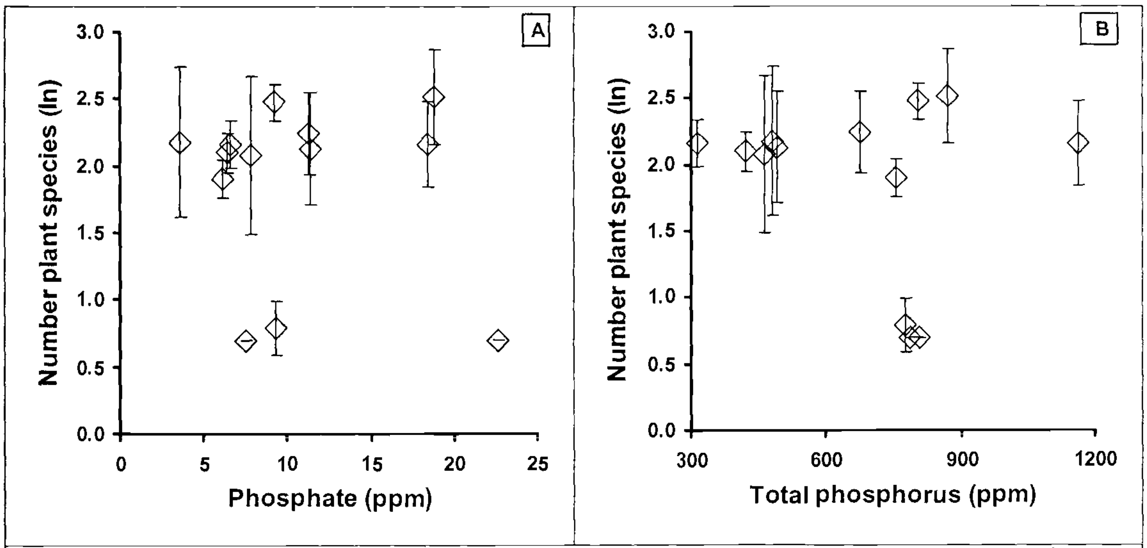


Figure 3.11a-b. Relationship between soil phosphorus concentration and plant species richness. Number plant species is the log transformed mean number of vascular plant species sampled per 1m² plot for each of 13 wetland field sites. Bars indicate standard deviation (n=4).

I used multiple linear regression with a stepwise testing procedure to assess which nutrients were most important in explaining the pattern of plant species richness found across the 13 study sites. I performed a stepwise regression procedure using a combination of forward and backward selection to select the model with the best fit. The Cp statistic was used to select the best model. Plant species richness was natural log transformed before implementing the analysis.

The model that best explained the pattern of species richness included only soil nitrogen variables (nitrate, total nitrogen, and mineralizable ammonium). The decrease in species richness was significant (Table 3.2). This result supports the hypothesis that increasing concentrations of nitrogen in the soil negatively effects the number of plant species within these 13 wetland field sites.

Table 3.2 Multiple linear regression results for soil nutrient and plant species richness analysis

y = 2.2921 + (total nitrogen)(-0.0006) + (nitrate)(-0.1463) + (mineralizable ammonium)(0.0857) + e

Variable	Coefficient	Standard Error	t-value	p
Intercept	2.2921	0.2722	8.4208	0.0000
Total nitrogen	-0.0006	0.0003	-1.9615	0.0815
Nitrate	-0.1463	0.0400	-3.6605	0.0052
Mineralizable ammonium	0.0857	0.0495	1.7322	0.1173

Residual standard error = 0.4613 on 9 df, Multiple R-Squared = 0.6368, F-statistic = 5.259 on 3 and 9 df
p-value = 0.02273

Discussion

Nitrogen as the nutrient limiting plant community biomass

The results of this study strongly support the hypothesis that nitrogen is the primary nutrient limiting plant production at the thirteen wetland sites. First, the N:P ratios in dominant plant tissue in all of the plots were less than 14:1 (Figure 3.3). This indicates nitrogen availability is limiting biomass production (Koerselman and Meuleman 1996). Second, multiple linear regression analysis determined the model that best explained the observed variability included only soil ammonium and that the trend was significant (p=0.038, n=13). Third, since soil samples were taken during the growing season, if nitrogen was limiting I expected the most available form of nitrogen (nitrate) to be present in the soil at lower concentration than phosphate. A paired t-test for site means indicated that soil nitrate concentrations were significantly lower than soil phosphate concentrations (2-tailed p=0.001, n=13).

These conclusions are supported by prior research. Multiple studies have found evidence that nitrogen is often the primary nutrient limiting plant growth in emergent marsh ecosystems (Koerselman and Mueleman 1996, Bedford et al. 1999, Keddy 2000, Mitsch and Gosselink 2000, Bridgham et al. 2001).

Nitrogen as the nutrient limiting purple loosestrife biomass

I also found that nitrogen was likely the nutrient limiting growth of purple loosestrife within the study sites. First, N:P ratios in loosestrife tissue were less than 14:1 (Figure 3.3), indicating nitrogen is the limiting nutrient. Second, loosestrife field biomass was positively asociated with the three measures of potential soil nitrogen: ammonium, total nitrogen and soil nitrogen (Figure 3.6b-d). However, I only had four sites with purple loosestrife and only one had a high concentration of nitrogen (HL). This single site was driving these correlations. Third, in a greenhouse phytometer study, loosestrife biomass was positively associated with soil nitrogen concentrations. A stepwise multiple regression analysis found that the model that best explained the variation in biomass included only measures of soil nitrogen and the slope differed significantly from zero (p=0.002).

Published studies have found that loosestrife growth and competitive ability are positively affected by nutrient concentrations. Weiher et al. (1996) and Shamsi and Whitehead (1977a) found that increased nutrients favored loosestrife growth over that of other plant species. In addition, Shamsi and Whitehead (1977b) manipulated concentrations of N, P, and K independently and found that loosestrife growth was more sensitive to decreases in N than reduction of P or K (Shamsi and Whitehead 1977b).

Invasion status of purple loosestrife

Results from the phytometer study indicate that the nine wetlands that are currently not colonized by loosestrife have soils suitable for loosestrife growth. In fact, loosestrife grew better in soils from these nine wetlands than it did in three of the four sites currently colonized by loosestrife (Figure 3.12). This suggests that the soils of these sites are capable of supporting dense stands of loosestrife like those found at Horseshoe Lake (HL).

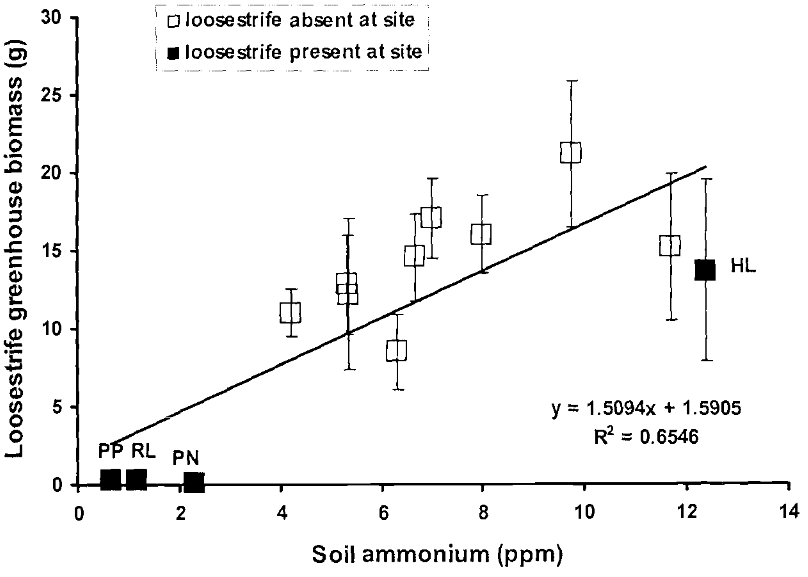


Figure 3.12 Potential for loosestrife invasion of uncolonized sites. Loosestrife greenhouse biomass is the mean dry weight of eight purple loosestrife plants grown from seed in soil collected from each of thirteen field sites. Four plots were randomly selected at each site and two plants were grown from each soil sample. Solid symbols represent sites where loosestrife is present and open symbols indicate loosestrife has not yet colonized the site. Sites where loosestrife is currently absent have higher concentrations of ammonium than 3 of 4 sites currently colonized.

Does abundance of the limiting nutrient favor invasive dominance?

Although purple loosestrife is known to be an invasive species with formidable competitive abilities, I found that the correlation between increased nitrogen availability and decreased species richness extended beyond just those wetlands colonized by loosestrife (Figure 3.10a-d). This suggests that just managing individual invasive species may not result in a more diverse plant community. Often one invasive plant species, such as loosestrife, may be controlled just to have another take its place, such as reed canary grass, with no net gain in native plant diversity. A more integrated approach to management may be needed. For example, the underlying mechanism of invasion for many introduced plant species may be the increase of nutrients that simplify formerly multidimensional resource gradients, thus reducing opportunities for niche differentiation and coexistence for competitors (Whittaker 1965, Tilman 1985). Therefore, without controlling the input of nutrients in these systems we may be destined to continue indefinitely on the invasive plant treadmill where we reduce the abundance of one invasive plant only to have another take its place.

Implications for invasive weed management

Many factors are responsible for limiting and regulating plant populations including: soil nutrients, soil moisture, soil disturbance, climate, light, interspecific competition, herbivores and diseases (Myers and Bazely 2003). This study examines one factor that may explain the invasiveness of purple loosestrife, namely the abundance of limiting soil nutrients. However, it is unlikely that soil nutrients alone are responsible for the invasive abilities of loosestrife and other introduced plants. For example, damage caused by herbivory and diseases may outweigh the benefits of abundant soil nutrients, i.e. reduction of photosynthetic tissue (leaves) and nutrient uptake tissue (roots) will alter the competitive ability of these plants. Since the invasive plant will no longer be able to quickly acquire and convert nutrients to growth and reproduction, its competitive ability will decrease and population densities will decline in the face of interspecific competition. Evidence of this is provided in the literature on classical biological control programs. There have been many successes using host-specific herbivores to control populations of invasive plants (Myers and Bazely 2003). The control of purple loosestrife using four beetle species that feed on leaves, roots, and seeds is an emerging success (Schooler 1998, Landis et al. 2003). However, not all populations of purple loosestrife are controlled by the introduced herbivores and not all biological control programs are successful. The reasons for failure in these programs may be due to these other factors.

In conclusion, multiple interacting factors govern invasive plant populations and these need to be considered when creating management strategies in a combinatorial approach (McEvoy and Coombs 1999). Before risking the introduction of biological control agents, other management options, such as manipulating resources, disturbances, and interspecific competition, including combinations of treatments, should be tested. If biological control agents are used but do not reduce invasive plant populations, integrated strategies may produce success.

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Chapter 4

General Conclusion

Invasive plants can reduce the number of species and the equitability of their abundances in plant and animal communities. The reduction in biotic diversity might alter ecosystem processes and cause additional ecological and economic harm. This first part of this study examined the effect of two invasive wetland plants, purple loosestrife and reed canary grass, on the species richness and diversity of plant and moth communities within 24 wetlands in the Pacific Northwest. The second part studied whether soil nutrient concentrations are a potential mechanism by which purple loosestrife is able to dominate wetland plant communities within 13 wetlands in the Willamette Valley, Oregon.

Chapter two of this dissertation examined the effect of purple loosestrife and reed canary grass on the species richness and diversity of local wetland plant and moth communities. I found that both purple loosestrife and reed canary grass significantly reduce the diversity of wetland plant communities within circular study plots (50m radius, 7,854m^2). Species richness, evenness, the Shannon-Wiener Diversity Index and Simpson's Diversity Index all significantly declined with increasing cover of the invasive plant species. Moth species richness was correlated with plant species richness, thus suggesting that declines in the number of potential host plants leads to reduction in the number of moth species. However, when moth diversity measures were examined in relation to invasive species cover I found no significant trend. Wetland hydrology, soil nutrients, and topography were measured and analyzed to assess their potentially covarying and confounding influence on plant community diversity. Temperature, ambient light, and surrounding land-use were measured and analyzed to assess their potentially covarying and confounding influence on moth sampling and community composition. Canonical correspondence analysis found no significant linear association between the environmental variables and the cover of the two invasive plant species. This strengthens the conclusion that the reduction in biotic diversity is caused by the abundance of the invasive plant and is not a product of underlying environmental variables.

Chapter three addresses the role of soil nutrients on the invasive potential of purple loosestrife. I found that nitrogen was likely the primary resource limiting both plant community biomass and purple loosestrife growth. Purple loosestrife grew well in soils taken from nine wetlands currently un-colonized by loosestrife. Given their similar hydroperiods, this indicates that these wetlands will be susceptible to invasion should loosestrife colonize these sites. Plant species richness was negatively associated with nitrate, mineralizable ammonium, and total nitrogen. This trend included sites where neither purple loosestrife nor reed canary grass were the dominant vegetation. These results suggest that soil fertility may be a factor that increases the propensity for a site to become dominated by an invasive plant species. Therefore, to prevent repeated invasions management strategies should consider methods for reducing soil nutrient concentrations, particularly nitrogen.

Two suggestions for the general improvement of ecological research

This study demonstrates the need to consider multiple interacting biotic and abiotic factors when studying the effects of invasive plant species. Interactions between organisms and the environment are complex. Conclusions of ecological studies depend upon the spatial scales at which the interactions were studied and the organisms and environmental variables that were examined.

First, effects on spatially dependent variables need to be measured at the appropriate spatial scales. All prior studies of the effect of purple loosestrife abundance on plant community diversity measured diversity at spatial scales of less than $10m^2$ while purple loosestrife was observed to dominate wetlands at the scale of square kilometers. The result of these methods were contradictory conclusions that caused controversy over biological control as a means to manage purple loosestrife populations. Biological control agents were released and subsequent studies have documented the increase of plant species richness at the sites, despite the prior reports of no negative effect of the invasive plant.

Second, observational field studies and experimental laboratory studies should be used together to strengthen conclusions in ecological research. Observational field studies allow ecologists to examine interactions in realistically complex conditions and at appropriate spatial and temporal scales. However, there is always the possibility that observed associations are the product of confounding factors. Laboratory and greenhouse studies allow scientists to control confounding variables, but such extreme simplification of complex systems may not represent actual conditions. Therefore, predictions based on these experiments may not be applicable to management practices. There are two solutions to this dilemma. One solution is to identify and measure the most important potentially confounding environmental variables and determine whether they are correlated with the explanatory variable of interest. The second solution is to perform both observational field studies and laboratory experiments and compare the results. Using these methods to strengthen cause and effect relationships under realistic conditions will increase the predictability of ecological research and lead to more effective environmental management strategies.

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APPENDICES

Appendix A. Study site location and contact information

Site name	ID	County	State	Latitude	Longitude	Ownership	Contact	Phone
Apache Bluff	AB	Washington	OR	45.396290	-122.778750	Wetlands Conservancy	Mary Anne	503-691-1394
Bird Blind Site	BB	Multnomah	OR	45.616070	-122.726880	Portland Metro Parks	Elaine Stewart	503-797-1515
Baskett Slough	BS	Polk	OR	44.981670	-123.264480	USFWS: Baskett Slough NWR	Jim Houck/Jacque Beall	541-757-7236
Boardwalk RCG	BW	Benton	OR	44.606150	-123.236610	Benton County Parks	Mary Simpson/Bob Frankel	541-766-6871
Champoeg State	CP	Marion	OR	45.256650	-122.903530	Oregon Parks and Recreation	Dennis Wiley	503-678-1251 ext 230
EE Wilson	EE	Benton	OR	44.702380	-123.218990	Oregon Dept of Fish and Wildlife	Dave Budeau	541-745-5334
Fort Boise	FB	Canyon	ID	43.810740	-116.991440	USFWS: Old Fort Boise NWR		
Fanno Creek Park	FC	Washington	OR	45.467520	-122.789280	Tualatin Hills Parks and Recreation	Ralph Cook	503-645-6433
Fitzpatrick Island	FI	Clatsop	OR	46.262730	-123.495900	USFWS: Julia Butler Hanson NWR	Joel David	360-795-3915 ext224
Horseshoe Lake	HL	Marion	OR	45.212030	-123.028800	Private	Harold Brentano	503-633-4272
Ironson Island	II	Clatsop	OR	46.242770	-123.535970	USFWS: Julia Butler Hanson NWR	Joel David	360-795-3915 ext224
Jackson Bottom	JB	Washington	OR	45.502600	-122.982830	Jackson Bottom Wetlands Preserve	Pat Willis	503-681-6206
Jackson-Fraizer	JF	Benton	OR	44.606140	-123.239520	Benton County Parks	Mary Simpson/Bob Frankel	541-766-6871
Knez Wetland	KW	Washington	OR	45.430760	-122.759520	Wetlands Conservancy	Mary Anne	503-691-1394
Minthorn Springs	MS	Clackamas	OR	45.441520	-122.622250	Wetlands Conservancy	Mary Anne	503-691-1394
Puget Island	PI	Wahkiakum	WA	46.150690	-123.322630	USFWS: Julia Butler Hanson NWR	Joel David	360-795-3915 ext224
Prison North	PN	Multnomah	OR	45.629050	-122.754690	Portland Metro Parks	Elaine Stewart	503-797-1515
Pickle Pond	PP	Multnomah	OR	45.617840	-122.777030	Port of Portland	Scott Carter	503-944-7510
Prison South	PS	Multnomah	OR	45.623240	-122.756070	Portland Metro Parks	Elaine Stewart	503-797-1515
Ramsey Lake	RL	Multnomah	OR	45.632780	-122.761700	Port of Portland	Scott Carter	503-944-7510
Rand Road PLS	RR	Morrow	OR	45.903880	-119.438560	Private	Tim Bevington	541-561-7651
Simplot Marsh	SM	Payette	ID	43.966980	-116.937930	Private: Simplot	Rory Clinton	208-278-3452
Umatilla NWR	UM	Morrow	OR	45.894940	-119.560620	USFWS: Umatilla NWR	Gary Hegedorn	509-545-8588
Wallace Island	WI	Columbia	OR	46.150050	-123.246670	USFWS: Julia Butler Hanson NWR	Joel David	360-795-3915 ext224

Appendix B. Plant species information

Plant species	Family	Guild	Origin	Wetland Indicator Status	Common name
Agropyron intermedium	Poaceae	grass	exotic	NL	intermediate wheatgrass
Agropyron repens	Poaceae	grass	exotic	FACU	quackgrass
Agrostis capillaris	Poaceae	grass	exotic	FAC	colonial bentgrass
Agrostis exarata	Poaceae	grass	exotic	FACW	spike bentgrass
Agrostis longiligula	Poaceae	grass	native	FAC	pacific bentgrass
Agrostis stolonifera	Poaceae	grass	exotic	FACW	spreading bentgrass
Aira caryophyllea	Poaceae	grass	exotic	NL	silver hairgrass
Alisma plantago-aquatica	Alismataceae	herb	native	OBL	broad-leaf water plantain
Alisma triviale	Alismataceae	herb	native	OBL	northern water plantain
Alnus rubra	Betulaceae	hard	native	FAC	red alder
Alopecurus pratensis	Poaceae	grass	exotic	FACW	foxtail
Amelanchier alnifolia	Rosaceae	hard	native	FACU	saskatoon
Anthoxanthum odoratum	Poaceae	grass	exotic	FACU	sweet vernal grass
Asclepias fascicularis	Asclepiadaceae	herb	exotic	FAC-	narrow-leaf milkweed
Aster subspicatus	Asteraceae	herb	native	FAC+	Douglas' aster
Athyrium filix-femina	Dryopteridaceae	herb	native	FAC	lady fern
Azolla mexicana	Salviniaceae	herb	native	OBL	mosquito fern
Beckmannia syzigachne	Poaceae	grass	native	OBL	American sloughgrass
Bellis perennis	Asteraceae	herb	exotic	NL	English daisy
Bidens cernua	Asteraceae	herb	native	FACW+	nodding beggar-ticks
Bidens frondosa	Asteraceae	herb	native	FACW+	devil's beggar-ticks
Brodiaea congesta	Liliaceae	grass	native	NL	northern saitas
Brodiaea elegans	Liliaceae	grass	native	FACU	harvest brodiaea
Bromus mollis	Poaceae	grass	native	NL	soft brome
Bromus sitchensis	Poaceae	grass	native	NL	Alaska brome
Callitriche heterophylla	Callitrichaceae	herb	native	OBL	water starwort
Camissia quamash	Liliaceae	grass	native	FACW	camassia
Carex aperta	Cyperaceae	grass	native	FACW	Columbia sedge
Carex aquatilis	Cyperaceae	grass	native	FACW	water sedge
Carex densa	Cyperaceae	grass	native	FACW+	dense sedge
Carex feta	Cyperaceae	grass	native	FACW	green-sheathed sedge
Carex obnupta	Cyperaceae	grass	native	OBL	slough sedge
Carex ovalis	Cyperaceae	grass	native	FAC	eggbract sedge
Carex scoparia	Cyperaceae	grass	native	NL	pointed broom sedge
Carex stipata	Cyperaceae	grass	native	NL	sawbeak sedge
Carex tumulicola	Cyperaceae	grass	native	NL	foothill sedge
Carex unilateralis	Cyperaceae	grass	native	FACW	one-sided sedge
Centaurium erythraea	Gentianaceae	herb	exotic	FAC-	European century
Ceratophyllum demersum	Ceratophyllaceae	herb	native	OBL	common hornwort

Appendix B. Plant species information continued

Plant species	Family	Guild	Origin	Wetland Indicator Status	Common name
Cicuta douglasii	Apiaceae	herb	native	OBL	western water hemlock
Cirsium arvense	Asteraceae	herb	exotic	FACU+	Canada thistle
Cirsium vulgare	Asteraceae	herb	exotic	FACU	bull thistle
Conium maculatum	Apiaceae	herb	exotic	FAC+	poison hemlock
Convolvulus arvensis	Convulvulaceae	herb	exotic	NL	field bindweed
Cornus stolonifera	Cornaceae	hard	native	FACW	red-osier dogwood
Crataegus douglasii	Rosaceae	hard	native	FAC	Douglas' hawthorn
Crataegus monogyna	Rosaceae	hard	exotic	FACU+	English hawthorn
Cyperus strigosus	Cyperaceae	grass	native	FACW	flat sedge
Daucus carota	Apiaceae	herb	exotic	FAC+	wild carrot
Deschampsia cespitosa	Poaceae	grass	native	FACW	tufted hairgrass
Dipsacus fullonum	Dipsaceceae	herb	exotic	FAC	teasel
Downingia elegans	Campanulaceae	herb	native	OBL	downingia
Elaeagnus angustifolia	Elaeagnaceae	hard	exotic	FAC	Russian olive
Elatine triandra	Elatinaceae	herb	native	OBL	water-wort
Eleocharis acicularis	Cyperaceae	grass	native	OBL	needle spike-rush
Eleocharis ovata	Cyperaceae	grass	native	OBL	ovate spike-rush
Eleocharis palustris	Cyperaceae	grass	native	OBL	creeping spike-rush
Elodea nuttallii	Hydrocharitaceae	herb	native	OBL	Nuttall's water weed
Elymus glaucus	Poaceae	grass	native	NL	blue wildrye
Epilobium angustifolium	Onagraceae	herb	native	FACU+	fireweed
Epilobium ciliatum	Onagraceae	herb	native	FACW-	hairy willow-herb
Epilobium denisflorum	Onagraceae	herb	native	NL	dense spike primrose
Epilobium hirsutum	Onagraceae	herb	exotic	NL	hairy willow herb
Equisetum arvense	Equisetaceae	herb	native	FAC	field horsetail
Equisetum hyemale	Equisetaceae	herb	native	FACW	rough horsetail
Equisetum telemateia	Equisetaceae	herb	native	FACW	giant horsetail
Fauria crista-galli	Menyanthaceae	herb	native	OBL	deer-cabbage
Festuca arundinacea	Poaceae	grass	exotic	FACU-	tall fescue
Fraxinus latifolia	Oleaceae	hard	native	FACW	Oregon ash
Galium aparine	Rubiaceae	herb	exotic	FACU	catchweed bedstraw
Galium parisiense	Rubiaceae	herb	exotic	UPL	wall bedstraw
Galium trifidium	Rubiaceae	herb	native	FACU	small bedstraw
Geranium dissectum	Geraniaceae	herb	exotic	NL	cutleaf geranium
Glyceria elata	Poaceae	grass	native	NL	tall mannagrass
Gnaphalium uliginosum	Asteraceae	herb	exotic	FAC+	cudweed
Gnaphlium stramineum	Asteraceae	herb	native	FAC+	cotton-batting cudweed
Grindelia integrifolia	Asteraceae	herb	native	FACW	Puget-sound gumweed
Heracleum lanatum	Asteraceae	herb	exotic	FAC	cow-parsnip
Holcus lanatus	Poaceae	grass	exotic	FAC	velvetgrass, Yorkshire fog

Appendix B. Plant species information continued

Plant species	Family	Guild	Origin	Wetland Indicator Status	Common name
Hordeum brachyanthemum	Poaceae	grass	native	FACW	meadow barley
Hypericum perforatum	Hypericaceae	herb	exotic	NL	St. Johnswort, Klamathweed
Hypochaeris radicata	Asteraceae	herb	native	FACU	cat's ear, false dandelion
Impatiens capensis	Balsaminaceae	herb	native	FACW	spotted touch-me-not
Iris pseudacorus	Iridaceae	grass	exotic	OBL	yellow-flag iris
Iva axillaris	Asteraceae	herb	native	FAC	small-flower sumpweed
Juncus acuminatus	Juncaceae	grass	native	OBL	tapertip rush
Juncus articulatus	Juncaceae	grass	native	OBL	jointed, jointleaf rush
Juncus balticus	Juncaceae	grass	native	OBL	baltic rush
Juncus effusus	Juncaceae	grass	native	FACW	common or lamp rush
Juncus ensifolius	Juncaceae	grass	native	FACW	swordleaf rush
Juncus nevadensis	Juncaceae	grass	native	FACW	Sierra rush
Juncus oxymeris	Juncaceae	grass	native	FACW+	pointed rush
Juncus patens	Juncaceae	grass	native	FACW	spreading rush
Juncus tenuis	Juncaceae	grass	native	FACW-	slender rush
Lathyrus angulatus	Fabaceae	herb	exotic	NL	angled pea
Lathyrus palustris	Fabaceae	herb	native	OBL	vetchling peavine
Leersia oryzoides	Poaceae	grass	native	OBL	rice cutgrass
Lemna minor	Lemnaceae	herb	native	OBL	lesser duckweed
Lepidium latifolium	Brassicaceae	grass	exotic	FAC	broad-leaf peppergrass
Leucanthemum vulgare	Asteraceae	herb	exotic	NL	oxeye-daisy
Lilaeopsis occidentalis	Apiaceae	herb	native	OBL	western lilaeopsis
Lotus corniculatus	Fabaceae	herb	exotic	FAC	bird's foot trefoil
Lotus denticulatus	Fabaceae	herb	native	NL	riverbar bird's-foot trefoil
Lotus micranthus	Fabaceae	herb	native	NL	desert deervetch
Lotus purshiana	Fabaceae	herb	native	NL	Spanish clover
Lotus uliginosus	Fabaceae	herb	exotic	FAC	big trefoil
Ludwigia palustris	Onagranaceae	herb	exotic	OBL	marsh seedbox
Lupinus polyphyllus	Fabaceae	herb	native	FAC+	bigleaf or marsh lupine
Lycopus americanus	Lamiaceae	herb	native	OBL	American bugleweed
Lycopus uniflorus	Lamiaceae	herb	native	OBL	northern water-horehound
Lysimachia nummularia	Primulaceae	herb	native	FACW	creeping Jennie
Lythrum salicaria	Lythraceae	herb	exotic	OBL	purple loosestrife
Melilotus alba	Fabaceae	hard	exotic	FACU	white sweetclover
Mentha arvensis	Lamiaceae	herb	native	FAC	field mint
Mentha piperita	Lamiaceae	herb	exotic	FACW+	peppermint
Mentha pulegium	Lamiaceae	herb	exotic	OBL	penny-royal
Mimulus guttatus	Scrophulariaceae	herb	native	OBL	common monkey-flower
Myosotis discolor	Boraginaceae	herb	exotic	FACW	yellow and blue forget-me-not
Myosotis laxa	Boraginaceae	herb	native	OBL	bay forget-me-not

Appendix B. Plant species information continued

Plant species	Family	Guild	Origin	Wetland Indicator Status	Common name
Myosotis scorpioides	Boraginaceae	herb	exotic	FACW	true forget-me-not
Nemophila parviflora	Saxifragaceae	herb	native	OBL	nemophila
Nepeta cataria	Lamiaceae	herb	exotic	FAC	catnip
Nuphar polysepalum	Nymphaeaceae	herb	native	OBL	yellow pond-lily
Oenanthe sarmentosa	Apiaceae	herb	native	OBL	water-parsley
Parentuccellia viscosa	Scrophulariaceae	herb	exotic	FAC-	yellow parentucellia
Phalaris arundinacea	Poaceae	grass	exotic	FACW	reed canary grass
Phleum pratense	Poaceae	grass	exotic	FACU	timothy
Plagiobothrys figuratus	Boraginaceae	herb	native	FACW	fragrant popcorn-flower
Plantago lanceolata	Plantaginaceae	herb	exotic	FAC	narrowleaf plantain
Plantago major	Plantaginaceae	herb	exotic	FAC+	commom plantain
Polygonum hydropiper	Polygonaceae	herb	exotic	OBL	smartweed, marsh-pepper
Polygonum hydropiperoides	Polygonaceae	herb	native	OBL	swamp smartweed
Polygonum persicaria	Polygonaceae	herb	native	FACW	spotted knotweed
Populus balsamifera	Salicaceae	hard	native	FAC	balsam poplar
Potamogeton crispus	Potamogetonaceae	herb	exotic	OBL	curly pondweed
Potentilla pacifica	Rosaceae	herb	native	FAC	pacific silverweed
Prunella vulgaris	Lamiaceae	herb	native	FACU+	healall, selfheal
Quercus garryana	Fagaceae	hard	native	NL	garry oak
Ranunculus orthorhynchus	Ranunculaceae	herb	native	FACW-	straight-beak buttercup
Ranunculus repens	Ranunculaceae	herb	exotic	FACW	creeping buttercup
Ribes aureum	Grossulariaceae	hard	native	FAC+	golden current
Rorippa curvisiliqua	Brassicaceae	herb	native	FACW+	curve-pod yellow-cress
Rosa elegans	Rosaceae	hard	exotic	NL	sweetbrier
Rosa nutkanana	Rosaceae	hard	native	NL	nootka rose
Rosa pisocarpa	Rosaceae	hard	native	FAC	cluster rose
Rubus discolor	Rosaceae	hard	exotic	FACU-	Himalayan blackberry
Rubus laciniatus	Rosaceae	hard	exotic	FACU+	cutleaf blackberry
Rubus ursinus	Rosaceae	hard	native	FACU	California blackberry
Rumex acetosella	Polygonaceae	herb	exotic	FACU	sheep sorrel
Rumex crispus	Polygonaceae	herb	exotic	FACW	curly dock
Sagittaria latifolia	Alismataceae	herb	native	OBL	common arrowhead, wapato
Salix lucida var. lasiandra	Salicaceae	hard	native	FACW+	pacific willow
Salix scouleriana	Salicaceae	hard	native	FACW	Scouler's willow
Salix sessilifolia	Salicaceae	hard	native	FACW	northwest sandbar willow
Salix sitchensis	Salicaceae	hard	native	FACW	sitka willow
Sambucus racemosa	Caprifoliaceae	hard	native	FACU	red elderberry
Scirpus acutus	Cyperaceae	grass	native	OBL	hard-stem bullrush
Scirpus americanus	Cyperaceae	grass	native	OBL	three-square bullrush
Scirpus microcarpus	Cyperaceae	grass	native	OBL	smallfruit bulrush

Appendix B. Plant species information continued

Plant species	Family	Guild	Origin	Wetland Indicator Status	Common name
Senecio jacobaea	Asteraceae	herb	exotic	NL	tansy ragwort
Setaria viridis	Poaceae	grass	exotic	NL	bottle or green bristle grass
Sium suave	Apiaceae	herb	native	OBL	water parsnip
Solanum dulcamara	Solanaceae	herb	exotic	FAC	bitter nightshade
Solidago canadensis	Asteraceae	herb	native	FACU	Canadian goldenrod
Sonchus asper	Asteraceae	herb	exotic	FAC-	prickly sowthistle
Sphaerophysa salsula	Fabaceae	herb	exotic	UPL	swainsonpea
Spiraea douglasii	Rosaceae	hard	native	FACW	Douglas's spirea
Stachys rigida	Lamiaceae	herb	native	FACW-	rigid hedgenettle
Stellaria borealis	Caryophyllaceae	herb	native	FACW+	northern starwort
Symphoricarpos albus	Caprifoliaceae	hard	native	FACU	snowberry
Tanacetum vulgare	Asteraceae	herb	exotic	NL	common tansy
Toxicodendron diversilobum	Anacardiaceae	hard	native	FACU	poison oak
Trifolium arvense	Fabaceae	herb	exotic	NL	hare's foot
Trifolium incarnatum	Fabaceae	herb	exotic	NL	crimson clover
Trifolium repens	Fabaceae	herb	exotic	FACU+	white clover
Trisetum canescens	Poaceae	grass	native	NL	tall trisetum
Typha angustifolia	Typhaceae	grass	native	OBL	narrow-leaf cattail
Typha latifolia	Typhaceae	grass	native	OBL	broadleaf cattail
Vaccinium uliginosum	Ericaceae	hard	native	FACW+	bog blueberry
Veronica americana	Scrophulariaceae	herb	native	OBL	American speedwell
Veronica anagallis-aquatica	Scrophulariaceae	herb	native	OBL	water speedwell
Veronica scutellata	Scrophulariaceae	herb	native	OBL	marsh speedwell
Vicia disperma	Fabaceae	herb	native	NL	two-seeded vetch
Vicia hirsuta	Fabaceae	herb	exotic	NL	tiny vetch
Vicia tetrasperma	Fabaceae	herb	exotic	NL	lentil or sparrow vetch
Vicia villosa	Fabaceae	herb	exotic	NL	hairy, winter or woolly vetch

Appendix C. Moth species information

Moth Species	Family	General host	Specific host	Origin
Arctia caja	Arctiidae	herb		native
Cisseps fulvicollis	Arctiidae	grass		native
Clemensia albata	Arctiidae	lichen		native
Grammia nevadensis	Arctiidae	herb		native
Hyphantria cunea	Arctiidae	hard		native
Lophocampa argentata	Arctiidae	conifer		native
Phragmatobia fuliginosa	Arctiidae	herb		native
Pyrrharctia isabella	Arctiidae	herb		native
Spilosoma virginica	Arctiidae	herb		native
Tyria jacobaeae	Arctiidae	herb	*Senecio jacobaea*	exotic
Prionoxystus robiniae	Cossidae	hard		native
Cabera erythemaria	Geometridae	hard	Salix	native
Ceratodalia gueneata	Geometridae	herb		native
Cyclophora dataria	Geometridae	hard	Quercus	native
Cyclophora pendulinaria	Geometridae	hard		native
Eulithis xylina	Geometridae	hard		native
Eupithecia columbiata	Geometridae	hard		native
Eupithecia harveyata	Geometridae			native
Eupithecia misturata	Geometridae	hard		native
Hesperumia sulphuraria	Geometridae	hard		native
Idaea demissaria	Geometridae			
Idaea dimidiata	Geometridae	herb		exotic
Itame colata	Geometridae	hard	Purshia	native
Nematocampa resisteria	Geometridae	hard	Salix	native
Nemoria darwiniata	Geometridae	hard		native
Neoalcis californiaria	Geometridae	hard		native
Orthonama obstipata	Geometridae	herb		native
Pero mizon	Geometridae	hard		native
Protitame matilda	Geometridae	hard	Salix	native
Scopula junctaria	Geometridae	herb		native
Semiothisa curvata	Geometridae	hard	Artemisia	native
Semiothisa denticulata	Geometridae	hard	Rosaceae	native
Semiothisa neptaria	Geometridae	hard	Salix	native
Semiothisa nubiculata	Geometridae			native
Semiothisa signaria	Geometridae	conifer		native
Sicya crocearia	Geometridae	hard		native
Sicya morsicaria	Geometridae	hard	Quercus mistletoe	native
Unknown Eupithecia	Geometridae			
Unknown Xanthorhoe	Geometridae			
Xanthorhoe defensaria	Geometridae	hard		native
Xanthorhoe ferrugata	Geometridae	herb		native
Xanthorhoe munitata	Geometridae			native
Malacosoma californicum	Lasiocampidae	hard		native

Appendix C. Moth species information continued

Moth Species	Family	General host	Specific host	Origin
Malacosoma disstria	Lasiocampidae	hard		native
Phyllodesma americana	Lasiocampidae	hard		native
Orgyia canis	Lymantriidae	hard		native
Acronicta lepusculina	Noctuidae	hard	Salix	native
Acronicta marmorata	Noctuidae	hard	Quercus	native
Adelphagrotis stellaris	Noctuidae	hard		native
Agroperina dubitans	Noctuidae	grass		native
Agroperina lateritia	Noctuidae	grass		native
Agrotis ipsilon	Noctuidae	herb		native
Agrotis vancouverensis	Noctuidae	herb		native
Aletia oxygala	Noctuidae	grass		native
Amphipyra pyramidoides	Noctuidae	hard		native
Amphipyra tragopoginis	Noctuidae	herb		native
Apamea amputatrix	Noctuidae	grass		native
Apamea castanea	Noctuidae	grass		native
Apamea cinefacta	Noctuidae	grass		native
Apamea ophiogramma	Noctuidae	grass		exotic
Archanara alameda	Noctuidae	grass	Typha spp.	native
Archanara oblonga	Noctuidae	grass	Typha spp.	native
Archanara subflava	Noctuidae	grass	Typha spp.	native
Aseptis adnixa	Noctuidae	hard	Oemleria	native
Autographa californica	Noctuidae	herb	Fabaceae	native
Autographa pasiphaea	Noctuidae			native
Bellura obliqua	Noctuidae	grass	Typha spp.	native
Bomolocha palparia	Noctuidae	hard		native
Brachylomia algens	Noctuidae	hard	Salix	native
Caenurgina erechtea	Noctuidae	herb	Fabaceae	native
Caradrina morpheus	Noctuidae	herb	Fabaceae	exotic
Catocala faustina	Noctuidae	hard	Salix	native
Catocala ilia	Noctuidae	hard	Quercus	native
Copablepharon grandis	Noctuidae			native
Cosmia calami	Noctuidae	hard	Quercus	native
Crymodes devastator	Noctuidae	grass		native
Dargida procincta	Noctuidae	grass		native
Diarsia esurialis	Noctuidae	hard		native
Diarsia rosaria	Noctuidae	grass		native
Discestra trifolii	Noctuidae	herb		native
Egira rubica	Noctuidae	hard		native
Eosophoropteryx thyatyroides	Noctuidae	herb	Thalictrum	native
Euxoa messoria	Noctuidae	herb		native
Euxoa septentrionalis	Noctuidae	herb		native
Euxoa tessellata	Noctuidae	herb		native
Feltia herilis	Noctuidae	herb		native
Feltia jaculifera	Noctuidae	herb		native

Appendix C. Moth species information continued

Moth Species	Family	General host	Specific host	Origin
Graphiphora haruspica	Noctuidae	hard	Salix	native
Heliothis phloxiphaga	Noctuidae	herb		native
Heliothis zea	Noctuidae	herb		native
Helotropha reniformis	Noctuidae	grass	Cyperaceae	native
Hemeroplanis finitima	Noctuidae			native
Homorthodes communis	Noctuidae	hard	Alnus	native
Idia aemula	Noctuidae	lichen	lichen	native
Idia americalis	Noctuidae	lichen	lichen	native
Lacinipolia cuneata	Noctuidae	hard		native
Lacinipolia patalis	Noctuidae	hard		native
Lacinipolia pensilis	Noctuidae	herb		native
Lacinipolia rectilinea	Noctuidae	herb		native
Lacinipolia stricta	Noctuidae	herb		native
Leucania farcta	Noctuidae	grass		native
Lithacodia albidula	Noctuidae	grass		native
Luperina venosa	Noctuidae	herb		native
Mamestra configurata	Noctuidae	herb		native
Melanchra picta	Noctuidae	herb		native
Melipotis jucunda	Noctuidae	hard	Salix	native
Noctua comes	Noctuidae	herb		exotic
Ochropleura plecta	Noctuidae	hard	Salix	native
Oliga tonsa	Noctuidae			native
Oligia indirecta	Noctuidae	grass	Juncaceae	native
Orthosia hibisci	Noctuidae	hard		native
Palthis angulalis	Noctuidae	hard		native
Papaipema insulidens	Noctuidae	herb	Asteraceae	native
Parabagrotis exertistigma	Noctuidae	herb		native
Peridroma saucia	Noctuidae	herb		native
Perigonica tertia	Noctuidae	hard	Quercus	native
Platyperigea extima	Noctuidae	herb		native
Plusia nichollae	Noctuidae	grass	Cyperaceae	native
Protagrotis obscura	Noctuidae	grass		native
Protorthodes curtica	Noctuidae	herb		native
Protorthodes smithii	Noctuidae			native
Proxenus mindara	Noctuidae	herb		native
Proxenus miranda	Noctuidae	herb	Fabaceae	native
Pseudorthodes irrorata	Noctuidae	hard		native
Schinia meadi	Noctuidae			native
Spaelotis bicava	Noctuidae	hard		native
Spodoptera praefica	Noctuidae	herb		native
Xestia cinerascens	Noctuidae			native
Xestia c-nigrum	Noctuidae	herb		native
Xestia smithii	Noctuidae	hard		native
Xestia xanthographa	Noctuidae	grass		exotic

Appendix C. Moth species information continued

Moth Species	Family	General host	Specific host	Origin
Xylena nupera	Noctuidae	hard		native
Zale lunata	Noctuidae	hard	Salix	native
Zosteropoda hirtipes	Noctuidae	herb		native
Clostera apicalis	Notodontidae	hard	Salix	native
Furcula scolopendrina	Notodontidae	hard	Salix	native
Gluphisia septentrionis	Notodontidae	hard	Salix	native
Nadata gibbosa	Notodontidae	hard		native
Oligocentria semirufescens	Notodontidae	hard		native
Schizura unicornis	Notodontidae	hard		native
Agonopterix alstroemeriana	Oecophoridae	herb	*Conium maculatum*	exotic
Ethmia marmorea	Oecophoridae			native
Unknown Oecophorid	Oecophoridae			
Unknown Ypsolopha	Plutellidae			
Unknown Pterophorid	Pterophoridae			
Achyra rantalis	Pyralidae	herb		native
Chrysoteuchia topiaria	Pyralidae	grass		native
Crambus leachellus	Pyralidae	grass		native
Crambus pascuellus	Pyralidae	grass		native
Crambus plumbifimbriellus	Pyralidae	grass		native
Crambus tutillus	Pyralidae	grass		native
Euchromius ocelleus	Pyralidae	grass		native
Evergestis funalis	Pyralidae	herb		native
Evergestis pallidata	Pyralidae	herb	Brassicaceae	native
Fumibotys fumalis	Pyralidae	herb		native
Herpetogramma pertextalis	Pyralidae			native
Loxostege commixtalis	Pyralidae	herb	Fabaceae	native
Loxostege sticticalis	Pyralidae	herb		native
Nomophila nearctica	Pyralidae			native
Ostrinia penitalis	Pyralidae	herb	Nymphaeaceae	native
Pediasia dorsipunctella	Pyralidae	grass		native
Pediasia trisecta	Pyralidae	grass		native
Petrophilia confusalis	Pyralidae	algae	algae	native
Pima fulvirugella	Pyralidae			native
Prorasea praeia	Pyralidae			native
Saucrobotys fumoferalis	Pyralidae	herb		native
Tehama bonifatella	Pyralidae	grass		native
Udea itysalis	Pyralidae	herb		native
Udea profundalis	Pyralidae	herb		native
Unknown *Pima*	Pyralidae			
Unknown Pyralid	Pyralidae			
Antheraea polyphemus	Saturniidae	hard		native
Hyles lineata	Sphingidae	herb	Onagraceae	native
Paonias excaecatus	Sphingidae	hard		native
Smerinthus cerisyi	Sphingidae	hard	Salix	native

Appendix C. Moth species information continued				
Choristoneura rosaceana	Tortricidae	hard		native
Unknown Tortricid	Tortricidae			

Appendix D. Purple loosestrife and reed canary grass impact study collaborators

Cooperator	Affiliation	City	State
David Ambrose	Clatsop Co. Soil and Water Conservation District	Astoria	OR
Andy Brower	Oregon State University: Zoology	Corvallis	OR
Gary Brown	USDA-APHIS PPQ	Portland	OR
Christine Buhl	Oregon State University: Environmental Science	Corvallis	OR
Tim Butler	Oregon Department of Agriculture	Salem	OR
Scott Carter	Port of Portland: Research Coordinator	Portland	OR
Al Clarke	USFWS-Julia Butler Hansen Wildlife Preserve	Cathlamet	WA
Troy Clark	Friends of Smith and Bybee Lakes	Portland	OR
Eric Coombs	Oregon Department of Agriculture	Salem	OR
Joel David	USFWS-Julia Butler Hansen Wildlife Preserve	Cathlamet	WA
Geoffrey Dorsey	US Army Corps of Engineers	Portland	OR
Jason Fuller	Oregon State University: Entomology	Corvallis	OR
Ralph Garono	Earth Design Consultants	Corvallis	OR
Jessica Gonzales	USFWS-Willapa Bay	Ilwaco	WA
Richard Guadagno	USFWS-Baskett Slough Wildlife Preserve	Rickreal	OR
Paul Hammond	Oregon State University: Zoology	Corvallis	OR
Nancy Hendrickson	Portland Bureau of Environmental Services	Portland	OR
Laurie Hewitt	USDA-APHIS	Union	OR
James Houk	USFWS-Willamette Valley Wildlife Preserves	Corvallis	OR
Douglas Johnson	Oregon State University: Rangeland Resources	Corvallis	OR
Mary Kentula	US EPA	Corvallis	OR
Tom Kollasch	USFWS-Julia Butler Hansen Wildlife Preserve	Cathlamet	WA
Virginia Lesser	Oregon State University: Statistics	Corvallis	OR
Hans Luh	Oregon State University: Forest Science	Corvallis	OR
Margaret Magruder	Lower Columbia River Watershed Council	Clatskanie	OR
Dan McClain	Lower Columbia River Watershed Council	Clatskanie	OR
Peter McEvoy	Oregon State University: Botany and Plant Pathology	Corvallis	OR
Colin Meston	Oregon State University: Environmental Science	Corvallis	OR
Jay Mower	Columbia Slough Watershed Council	Portland	OR
Phil Rossignol	Oregon State University: Fisheries and Wildlife	Corvallis	OR
Emily Roth	Metro Parks and Greenspaces	Portland	OR
Marjo Schat	Oregon State University: Entomology	Corvallis	OR
Kumari Sivam	Tualatin Riverkeepers	Tualatin	OR
Carrie Stevenson	Port of Portland: Wetland Mitigation Specialist	Portland	OR
Elaine Stewart	Metro Parks and Greenspaces	Portland	OR
Bruce Sutherland	Lower Columbia Estuary Project	Portland	OR
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Dennis Wiley	Oregon State Parks-Champoeg	St. Paul	OR
Kirby Winter	USDA-APHIS	Ontario	OR

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites

Plant Species	AB	BB	BS	BW	CP	EE	FB	FC	FI	HL	II	JB
Agropyron intermedium							7.40					
Agropyron repens	2.83											
Agrostis capillaris					1.03							
Agrostis exarata			0.23									
Agrostis longiligula	4.03											
Agrostis stolonifera			0.17	1.33		0.73			0.03		3.97	
Aira caryophyllea	1.07				1.00							
Alisma plantago-aquatica									0.70		1.33	
Alnus rubra					0.67							
Alopecurus pratensis	12.50				47.83							
Amelanchier alnifolia					4.33							
Anthoxanthum odoratum	3.33											
Asclepias fascicularis												
Aster subspicatus											1.10	
Athyrium filix-femina			0.17									
Azolla mexicana												1.33
Beckmannia syzigachne												
Bidens cernua			2.40						2.07		4.67	
Bidens frondosa			0.07									
Brodiaea congesta					0.30							
Brodiaea elegans					0.20							
Bromus mollis						14.50						
Bromus sitchensis					1.57							
Bromus sp.					0.57							
Callitriche heterophylla											0.50	
Camissia quamash												
Carex aperta									5.23		5.03	
Carex aquatilis		3.63										
Carex densa	0.17			0.07	3.00	1.17						
Carex obnupta	2.17			1.67								
Carex ovalis	5.57				0.50	0.67						
Carex scoparia					0.33							
Carex sp.												
Carex stipata												
Carex tumulicola					3.73	0.50						
Carex unilateralis					1.83	1.00						
Centaurium erythraea	7.17				0.60	2.27						
Chenopodium sp.												
Cicuta douglasii				0.83								
Cirsium arvense		1.20	2.90		0.50		2.57					
Cirsium vulgare	0.50		1.50		1.33	1.50	0.17					
Conium maculatum							3.17					
Cornus stolonifera												

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites continued

Plant Species	AB	BB	BS	BW	CP	EE	FB	FC	FI	HL	II	JB
Crataegus douglasii	0.10		1.83			0.57						
Crataegus monogyna	4.57				0.83							
Cyperus strigosus												
Daucus carota	2.23		0.03		0.57	0.20						
Deschampsia cespitosa									4.13		2.17	
Dipsacus fullonum						1.67						
Downingia elegans						1.00						
Elaeagnus angustifolia												
Elatine triandra									3.80		0.57	
Eleocharis acicularis									2.37			
Eleocharis ovata			1.23									
Eleocharis palustris			0.50	7.50					27.90		0.67	
Elodea nuttallii									0.17		0.13	
Epilobium angustifolium		0.30										
Epilobium ciliatum			12.50						3.43		1.10	
Epilobium denisflorum					0.33							
Epilobium hirsutum												
Epilobium sp.							0.63					
Equisetum arvense												
Equisetum telemateia												
Fauria crista-galli											0.83	
Festuca arundinacea					0.50							
Fraxinus latifolia	0.17	0.10				4.27						
Galium aparine			0.33		5.00	0.13		0.07				
Galium parisiense					0.37							
Galium trifidium	0.07	0.70	0.70	0.30			0.07				1.30	
Geranium dissectum	0.27				0.33							
Gnaphalium uliginosum	0.27		0.67		0.30	0.67						
Gnaphlium stramineum												
Grindelia integrifolia	0.10											
Heracleum lanatum			1.33									
Holcus lanatus	7.83		1.77		1.17	16.77						
Hordeum brachyanthemum	0.17		0.10									
Hypericum perforatum	0.17		0.03		0.33	0.10						
Hypochaeris radicata	10.80					3.27						
Impatiens capensis												
Iris pseudacorus							0.50				1.17	
Iva axillaris							0.83					
Juncus acuminatus									0.73			
Juncus articulatus												
Juncus balticus												
Juncus effusus			17.67		2.83	0.17						
Juncus ensifolius			0.67			1.17						
Juncus nevadensis												

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites continued

Plant Species	AB	BB	BS	BW	CP	EE	FB	FC	FI	HL	II	JB
Juncus oxymeris									6.03		5.67	
Juncus patens												
Juncus sp.	1.47				0.17							
Juncus tenuis	6.43					4.83						
Lathyrus angulatus	3.60											
Lathyrus palustris											0.50	
Leersia oryzoides												
Lemna minor			3.57				11.67					2.97
Lepidium latifolium							5.97					
Leucanthemum vulgare	1.23					0.33						
Lilaeopsis occidentalis									1.73			
Lotus corniculatus												
Lotus denticulatus	3.10											
Lotus purshiana	0.37				0.23							
Lotus uliginosus		0.33										
Ludwigia palustris			0.43			1.00				0.27		
Lupinus polyphyllus	3.00											
Lycopus americanus												
Lycopus uniflorus												
Lysimachia nummularia												
Lythrum salicaria			0.17				22.60		12.83	91.67	1.67	
Melilotus alba							0.17					
Mentha arvensis						1.00					2.67	
Mentha piperita				0.33								
Mentha pulegium				0.80								
Mimulus guttatus									3.93		2.20	
Myosotis discolor	0.43		0.53	0.63	0.37	0.80						
Myosotis scorpioides									2.80		10.90	
Nepeta cataria												
Oenanthe sarmentosa					0.07					0.93	7.57	
Parentuccellia viscosa	0.73		0.23			3.70						
Phalaris arundinacea	3.50	87.43	6.83	53.80	0.83	18.83	1.67	94.67	1.67		7.17	66.07
Phleum pratense			0.57									
Plagiobothrys figuratus						0.03						
Plantago lanceolata	4.93				0.33	0.13						
Plantago major												
Poa sp.	1.63											
Polygonum hydropiper									4.73		0.67	
Polygonum hydropiperoides			0.23				3.17			0.67		1.33
Polygonum persicaria												2.00
Populus balsamifera												
Potentilla pacifica									2.57		3.17	
Prunella vulgaris	0.93											
Quercus garryana					1.17							

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites continued

Plant Species	AB	BB	BS	BW	CP	EE	FB	FC	FI	HL	II	JB
Ranunculus orthorhynchus											0.50	
Ranunculus repens												
Ribes aureum							0.17					
Rorippa curvisiliqua			0.10									
Rosa elegans			1.10	3.00								
Rosa nutkanana					3.00							
Rosa pisocarpa	0.33					1.83						
Rubus discolor	6.17	0.17	4.77		4.17	1.17		0.33				
Rubus laciniatus					0.50	3.40						
Rubus ursinus					2.50	1.00						
Rumex acetosella			0.50		0.33	0.17						
Rumex crispus			0.70									
Sagittaria latifolia									0.17	0.50	13.50	
Salix lucida var. lasiandra			0.43						1.60		0.50	
Salix scouleriana												
Salix sessilifolia									0.17			
Salix sitchensis			1.17	2.50								
Sambucus racemosa												
Scirpus acutus							7.67		1.30			
Scirpus americanus							1.07		0.10			
Scirpus microcarpus									21.10		18.50	
Senecio jacobaea	0.50											
Setaria viridis												
Sium suave									1.33		3.07	
Solanum dulcamara			5.23	0.50	0.17		1.60	0.50		0.07		
Solidago canadensis												
Sonchus asper							0.13					
Sphaerophysa salsula												
Spiraea douglasii	2.50											
Stachys rigida												
Stellaria borealis			0.30			0.13						
Toxicodendron diversilobum					0.33							
Trifolium arvense												
Trifolium incarnatum	4.17											
Trifolium repens						0.13						
Trisetum canescens			1.73									
Typha angustifolia									0.33			
Typha latifolia			10.47	0.57	0.33	0.03	28.07					
Veronica americana			13.83						0.50		0.07	
Veronica anagallis-aquatica												
Veronica scutellata				0.77		0.23						
Vicia hirsuta					5.03							
Vicia tetrasperma			3.33		5.90	8.87						
Vicia villosa			0.43		0.33	1.73						

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites continued

Plant Species	JF	KW	MS	PI	PN	PP	PS	RL	RR	SM	UM	WI
Agropyron intermedium												
Agropyron repens												
Agrostis capillaris						8.17						
Agrostis exarata						0.17		1.73				
Agrostis longiligula												
Agrostis stolonifera	0.40	0.40	1.13	1.17		12.93		0.50				1.37
Aira caryophyllea												
Alisma plantago-aquatica	0.13			6.07				1.17				0.67
Alnus rubra			0.50			1.17		0.33				
Alopecurus pratensis		0.30										
Amelanchier alnifolia												
Anthoxanthum odoratum												
Asclepias fascicularis	0.43											
Aster subspicatus		0.33										
Athyrium filix-femina												
Azolla mexicana			0.50									
Beckmannia syzigachne	0.80			0.90								
Bidens cernua				10.60								0.33
Bidens frondosa			0.23			0.57					0.23	
Brodiaea congesta												
Brodiaea elegans												
Bromus mollis												
Bromus sitchensis												
Bromus sp.					0.73							
Callitriche heterophylla			1.93	3.73								
Camissia quamash	0.37											
Carex aperta				2.43								
Carex aquatilis	3.57						1.50					
Carex densa	7.03	4.60	0.10									
Carex obnupta	0.57	27.83										0.90
Carex ovalis												
Carex scoparia	7.40	1.27	0.17			0.90		1.27				
Carex sp.							1.93					
Carex stipata	1.37					0.20		0.33				
Carex tumulicola												
Carex unilateralis	1.87	1.23										
Centaurium erythraea					0.30	2.30						
Chenopodium sp.											1.83	
Cicuta douglasii												
Cirsium arvense		0.67	3.83		0.13	0.07	0.53	6.07			16.50	
Cirsium vulgare		0.67	0.67		0.20			0.80				
Conium maculatum												
Cornus stolonifera			1.83									
Crataegus douglasii	0.17											

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites continued

Plant Species	JF	KW	MS	PI	PN	PP	PS	RL	RR	SM	UM	WI
Crataegus monogyna		0.83										
Cyperus strigosus								0.17				
Daucus carota						2.37						
Deschampsia cespitosa		22.90		0.97								1.10
Dipsacus fullonum		4.07	3.60				0.83					
Downingia elegans												
Elaeagnus angustifolia											0.50	
Elatine triandra				0.40								
Eleocharis acicularis												
Eleocharis ovata			3.67			0.50		5.17				
Eleocharis palustris	10.93			16.70	3.30			2.33	5.93			23.10
Elodea nuttallii				0.67								
Epilobium angustifolium												
Epilobium ciliatum	1.70	0.33	0.77	2.60	0.27	0.47	0.03	0.70				2.37
Epilobium denisflorum											1.67	
Epilobium hirsutum									3.83		0.43	
Epilobium sp.												
Equisetum arvense					0.67	6.17		2.33				
Equisetum telemateia			2.67									
Fauria crista-galli												
Festuca arundinacea												
Fraxinus latifolia	2.83	1.00	0.67									
Galium aparine			1.63									
Galium parisiense												
Galium trifidium	1.37	0.90					0.07					
Geranium dissectum						0.33						
Gnaphalium uliginosum					0.10			0.70				
Gnaphlium stramineum					0.20							
Grindelia integrifolia												
Heracleum lanatum												
Holcus lanatus		1.67	0.47			3.43		0.07				
Hordeum brachyanthemum	0.60	0.17										
Hypericum perforatum					0.67	1.57						
Hypochaeris radicata						1.80		0.17				
Impatiens capensis		0.10	2.90									
Iris pseudacorus												
Iva axillaris												
Juncus acuminatus						5.10		3.33				1.13
Juncus articulatus					1.10	4.37		3.53				
Juncus balticus									6.67			
Juncus effusus	0.83	2.90	14.03		7.00	1.17		3.17				
Juncus ensifolius						1.93						
Juncus nevadensis		0.50										
Juncus oxymeris	0.83			0.83								4.03

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites continued

Plant Species	JF	KW	MS	PI	PN	PP	PS	RL	RR	SM	UM	WI
Juncus patens		5.00										
Juncus sp.												
Juncus tenuis	1.47											
Lathyrus angulatus												
Lathyrus palustris												
Leersia oryzoides			0.10	0.17		0.50					0.83	
Lemna minor		0.33						0.17				
Lepidium latifolium										0.77	0.67	
Leucanthemum vulgare		0.07										
Lilaeopsis occidentalis												
Lotus corniculatus			0.90		4.00	0.83						3.17
Lotus denticulatus												
Lotus purshiana					1.37	8.73		9.67				
Lotus uliginosus		1.40										
Ludwigia palustris				1.00	17.67			6.83				
Lupinus polyphyllus								4.67				
Lycopus americanus						0.73						
Lycopus uniflorus								1.57				
Lysimachia nummularia					0.87							
Lythrum salicaria				1.00	19.50	13.83		14.07	65.67	83.83	5.83	47.23
Melilotus alba						1.00						
Mentha arvensis	3.57											
Mentha piperita												
Mentha pulegium	1.13											
Mimulus guttatus				10.97								8.47
Myosotis discolor	4.47	1.43			1.33	0.17		0.30				
Myosotis scorpioides				3.17								2.93
Nepeta cataria											0.70	
Oenanthe sarmentosa	30.57			1.17								
Parentuccellia viscosa					0.33	3.13		0.73				
Phalaris arundinacea	2.10	2.80	8.50	6.57	7.03	1.47	78.03	8.10			4.40	3.40
Phleum pratense												
Plagiobothrys figuratus												
Plantago lanceolata						0.17						
Plantago major						0.10						
Poa sp.												
Polygonum hydropiper				8.17								
Polygonum hydropiperoides					0.30	2.67						1.03
Polygonum persicaria												
Populus balsamifera					1.03	0.50		0.67				
Potentilla pacifica												
Prunella vulgaris												
Quercus garryana												
Ranunculus orthorhynchus												

Appendix E. Mean percent cover of vascular plant species within the 24 wetland field sites continued

Plant Species	JF	KW	MS	PI	PN	PP	PS	RL	RR	SM	UM	WI
Ranunculus repens			0.83									
Ribes aureum												
Rorippa curvisiliqua		0.10										
Rosa elegans	5.37											
Rosa nutkanana												
Rosa pisocarpa		3.23	0.83									
Rubus discolor			2.00		16.50	2.27	4.50	0.67				
Rubus laciniatus												
Rubus ursinus		0.17						3.33				
Rumex acetosella	2.87	0.07				0.17						
Rumex crispus												
Sagittaria latifolia				3.00				7.17				1.40
Salix lucida var. lasiandra			0.33			2.67		2.00				0.43
Salix scouleriana			5.00			2.43		2.00				
Salix sessilifolia					1.20	0.33						
Salix sitchensis			0.33					1.17				
Sambucus racemosa			0.33									
Scirpus acutus				1.17					0.27	6.33	17.93	
Scirpus americanus				7.33					8.17			2.33
Scirpus microcarpus			1.73	14.40		1.83		0.47				1.93
Senecio jacobaea								0.83				
Setaria viridis					1.63							
Sium suave												
Solanum dulcamara	3.83	2.17	3.40		0.07					0.20	1.67	
Solidago canadensis					0.33	0.27		3.57				
Sonchus asper			0.17			0.17			7.67			
Sphaerophysa salsula											0.20	
Spiraea douglasii		0.83	11.67		0.17							
Stachys rigida	0.63											
Stellaria borealis												
Toxicodendron diversilobum												
Trifolium arvense					1.83	4.90		0.07				
Trifolium incarnatum						0.50						
Trifolium repens												
Trisetum canescens												
Typha angustifolia											16.33	
Typha latifolia	0.83	3.27			0.07	1.23		1.33	6.80	3.33	28.00	
Veronica americana	1.33		14.10	1.77				0.33				0.93
Veronica anagallis-aquatica											0.33	
Veronica scutellata	3.37				0.57							
Vicia hirsuta							12.43					
Vicia tetrasperma		0.20	0.87									
Vicia villosa						0.57						

Appendix F. Abundance of moths sampled at 20 wetland field sites

Apache Bluff

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala	1	1			1			1			1		5
Caenurgina erechtea							1						1
Caradrina morpheus				1									1
Choristoneura rosaceana				1	1								2
Chrysoteuchia topiaria					2			6					8
Clemensia albata								1					1
Crambus plumbifimbriellus								1					1
Crambus tutillus					1								1
Crymodes devastator										1			1
Diarsia rosaria									1				1
Euchromius ocelleus									1	2	2		5
Eupithecia misturata		1											1
Feltia jaculifera										1			1
Malacosoma californicum								1	2				3
Noctua comes				1									1
Phyllodesma americana							1						1
Spilosoma virginica								1					1
Unknown Tortricid				2	1		2	2					7
Grand Total	1	2	0	5	6	0	4	13	4	4	3	0	42

Bird Blind

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala	2	1					1				2		6
Caenurgina erechtea							2			1	3		6
Chrysoteuchia topiaria							4						4
Cisseps fulvicollis												1	1
Crymodes devastator		1											1
Diarsia rosaria	1												1
Euchromius ocelleus							1			1			2
Ochropleura plecta	1	1	1									1	4
Ostrinia penitalis				1	2								3
Pero mizon											1		1
Spilosoma virginica				1	1								2
Tehama bonifatella	2									1			3
Xestia xanthographa											1	1	2
Grand Total	6	3	1	2	3	0	8	0	0	3	7	3	36

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Baskett Slough

Month sampled	**May**			**June**			**July**			**August**			**Total**
Sample number	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	
Moth species													
Achyra rantalis												1	**1**
Agroperina dubitans							2		1				**3**
Agrotis vancouverensis							1	1	1				**3**
Aletia oxygala	3		6	14	3	8	7	1	6	10	10	21	**89**
Antheraea polyphemus				1									**1**
Archanara oblonga										3	3	1	**7**
Caenurgina erechtea									1		1	1	**3**
Catocala ilia											1		**1**
Chrysoteuchia topiaria							3		4				**7**
Crymodes devastator							2	4	2	5	5	7	**25**
Cyclophora pendulinaria										1			**1**
Dargida procincta								1					**1**
Diarsia rosaria										1	8		**9**
Euchromius ocelleus				14	3		203	65	80		4	16	**385**
Helotropha reniformis							1						**1**
Idaea dimidiata							1		1				**2**
Leucania farcta	1					1	1	1			2	1	**7**
Luperina venosa							1						**1**
Nematocampa resisteria										1			**1**
Papaipema insulidens											1		**1**
Pero mizon											1		**1**
Prionoxystus robiniae				1									**1**
Pyrrharctia isabella									1				**1**
Semiothisa denticulata							1						**1**
Smerinthus cerisyi				1		1	1						**3**
Spilosoma virginica	2	1	1										**4**
Unknown Pterophorid									1				**1**
Xanthorhoe defensaria										1			**1**
Grand Total	6	1	7	31	6	10	224	73	98	22	36	48	562

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Boardwalk

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Agroperina dubitans							1						1
Agrotis ipsilon			1										1
Aletia oxygala	1	2	2	4	3	3	4		6	3	5	2	35
Amphipyra tragopoginis										1			1
Arctia caja									1				1
Bomolocha palparia									1				1
Ceratodalia gueneata									1				1
Chrysoteuchia topiaria							3		2			1	6
Cisseps fulvicollis		1											1
Clemensia albata							1						1
Clostera apicalis		2					1				1		4
Crymodes devastator								1		1	1	2	5
Diarsia rosaria	1										1		2
Euchromius ocelleus							1		2	2	16	1	22
Eulithis xylina							2						2
Fumibotys fumalis							2						2
Furcula scolopendrina		1											1
Graphiphora haruspica						1	1	1					3
Idaea dimidiata							3		3				6
Leucania farcta												1	1
Lithacodia albidula							3	1	3				7
Nadata gibbosa									1				1
Parabagrotis exertistigma					1								1
Perigonica tertia	1												1
Plusia nichollae			1										1
Prionoxystus robiniae							1						1
Protitame matilda									1				1
Schizura unicornis							1						1
Scopula junctaria							1		1				2
Unknown Eupithecia										1			1
Unknown Tortricid	1						3		1				5
Xanthorhoe defensaria								1					1
Xanthorhoe munitata												1	1
Zosteropoda hirtipes								1					1
Grand Total	4	6	4	4	4	4	28	5	23	8	24	8	122

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Champoeg Park

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Acronicta marmorata							2						2
Aletia oxygala			1	1	1	1	1	2		15	6	13	41
Caenurgina erechtea							3					1	4
Ceratodalia gueneata							1						1
Choristoneura rosaceana							5						5
Chrysoteuchia topiaria							2	1	2				5
Clemensia albata							1	2	1				4
Cosmia calami							2				1		3
Crambus pascuellus						1							1
Crambus plumbifimbriellus								1	1				2
Crambus tutillus	1		1										2
Crymodes devastator										2	1		3
Cyclophora dataria							3		1				4
Eosophoropteryx thyatyroides							1						1
Euchromius ocelleus	1					1	20	5	11	10	2	13	63
Idaea dimidiata					1		4		3				8
Idia americalis							1						1
Leucania farcta							1	1	1				3
Lithacodia albidula					1	3	1	1					6
Malacosoma californicum									1				1
Proxenus miranda					3	2	1						6
Semiothisa neptaria										1			1
Tehama bonifatella		1											1
Tyria jacobaeae		1											1
Unknown Pterophorid												1	1
Unknown Tortricid					2			3	2				7
Unknown Ypsolopha					1								1
Xestia xanthographa										1		3	4
Grand Total	2	2	2	1	9	8	49	16	23	29	10	31	182

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

EE Wilson

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Agroperina dubitans				1		1							2
Agrotis vancouverensis	1				1		1						3
Aletia oxygala			1	1		6		1		2	11	4	26
Autographa califomica	1												1
Autographa pasiphaea											1		1
Caenurgina erechtea							1	1	1				3
Ceratodalia gueneata											1		1
Chrysoteuchia topiaria						1	1	4	1				7
Clemensia albata							1						1
Crambus pascuellus				1									1
Crymodes devastator											2		2
Cyclophora pendulinaria										1			1
Diarsia rosaria											2		2
Euchromius ocelleus				2	1	2	14	12	10		12	3	56
Eulithis xylina							1		1				2
Eupithecia harveyata			1										1
Eupithecia misturata										1			1
Fumibotys fumalis							2						2
Heliothis phloxiphaga	1												1
Hesperumia sulphuraria								1					1
Idaea dimidiata							1	1					2
Lacinipolia cuneata			2										2
Lacinipolia patalis		1											1
Lacinipolia rectilinea											2		2
Lithacodia albidula	3		1	4	4	2		1					15
Lophocampa argentata									1				1
Luperina venosa						1							1
Malacosoma californicum								3	1				4
Phyllodesma americana	1						1						2
Prionoxystus robiniae								1					1
Proxenus miranda				1		1							2
Scopula junctaria								1	1				2
Semiothisa neptaria		1							1				2
Sicya crocearia					1								1
Smerinthus cerisyi							1						1
Tyria jacobaeae	1		2	2									5
Unknown Tortricid				1		2	2						5
Xestia cinerascens												1	1
Xestia smithii									1				1
Grand Total	8	2	7	13	7	16	26	26	18	4	31	8	166

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Fort Boise

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala												1	1
Archanara alameda									1			7	8
Archanara oblonga								1					1
Archanara subflava							3	6	1	4	2	3	19
Bellura obliqua						1							1
Caenurgina erechtea												1	1
Copablepharon grandis												2	2
Leucania farcta												1	1
Lithacodia albidula									1				1
Loxostege commixtalis						1							1
Loxostege sticticalis												1	1
Nematocampa resisteria									1			2	3
Orgyia canis												2	2
Ostrinia penitalis						2							2
Pediasia trisecta										11	1	2	14
Peridroma saucia									1				1
Petrophilia confusalis				1	1	2	28	4	3	6	7	52	104
Proxenus mindara							1	4	2	1	1	2	11
Pyrrharctia isabella					1								1
Semiothisa curvata												1	1
Semiothisa neptaria						1							1
Smerinthus cerisyi		2	1										3
Spilosoma virginica				2	6	4						2	14
Unknown Oecophorid					1					2		9	12
Unknown Tortricid						2							2
Xanthorhoe munitata							1						1
Xestia c-nigrum										1			1
Grand Total	0	2	1	3	9	13	33	15	10	25	11	88	210

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Fanno Creek

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala	1			3		7	3	2	2	1	1	1	21
Apamea ophiogramma							6	3					9
Autographa californica												1	1
Chrysoteuchia topiaria				3	1		1	3					8
Crambus plumbifimbriellus							7		4				11
Diarsia rosaria												3	3
Euchromius ocelleus							2						2
Heliothis phloxiphaga							1						1
Helotropha reniformis												1	1
Lacinipolia patalis						1							1
Leucania farcta							2	2				1	5
Lithacodia albidula				1			3	1	2				7
Malacosoma californicum									3				3
Pero mizon							1						1
Pseudorthodes irrorata									1				1
Sicya crocearia									1				1
Spilosoma virginica		1											1
Tyria jacobaeae	1												1
Unknown Pima		1											1
Unknown Tortricid		1			1	1							3
Xestia xanthographa												1	1
Grand Total	2	3	0	7	2	9	26	11	13	1	1	8	83

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Horseshoe Lake

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Agroperina dubitans							1						**1**
Aletia oxygala				7	6	11	1			9	10	2	**46**
Cabera erythemaria										1			**1**
Chrysoteuchia topiaria				1			2	4	5				**12**
Crambus plumbifimbriellus									1				**1**
Crymodes devastator							4	2	1	5	4	1	**17**
Diarsia rosaria	1									1			**2**
Euchromius ocelleus						2	20	11	11	4	24		**72**
Eupithecia misturata				1									**1**
Helotropha reniformis							3	1					**4**
Idaea dimidiata				1		1			1				**3**
Malacosoma californicum							2	2	6				**10**
Nomophila nearctica								1		3			**4**
Orthonama obstipata						1							**1**
Petrophilia confusalis				6	2	1	7	1	3		2		**22**
Semiothisa signaria					1								**1**
Spilosoma virginica	6	1		3	1		1						**12**
Unknown Tortricid				1									**1**
Grand Total	7	1	0	20	10	16	41	22	28	23	40	3	211

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Jackson Bottom

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala		2			1		1	1	1	1			7
Chrysoteuchia topiaria				1									1
Cisseps fulvicollis											1		1
Crambus plumbifimbriellus								1					1
Crymodes devastator									1	6			7
Euchromius ocelleus				2				4				1	7
Eulithis xylina							1						1
Helotropha reniformis							1						1
Lithacodia albidula						3		1					4
Loxostege commixtalis							1						1
Malacosoma californicum								2	6				8
Petrophilia confusalis									1				1
Pyrrharctia isabella					1								1
Semiothisa neptaria	1									1			2
Spilosoma virginica	2			1									3
Unknown Tortricid				2				2					4
Grand Total	3	2	0	6	2	3	4	11	9	8	1	1	50

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Jackson Fraizer

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Agroperina dubitans									2				2
Agrotis vancouverensis									1				1
Aletia oxygala			3	2	1	2	2		1		1	1	13
Arctia caja							1		2		2		5
Brachylomia algens							1						1
Choristoneura rosaceana							2						2
Chrysoteuchia topiaria									1				1
Cisseps fulvicollis		1									1		2
Crymodes devastator										1	1		2
Diarsia rosaria										1	2		3
Euchromius ocelleus									4		15	1	20
Eulithis xylina									2				2
Fumibotys fumalis							1	1					2
Helotropha reniformis							1						1
Idaea dimidiata							2		1				3
Lacinipolia rectilinea											1		1
Leucania farcta					1								1
Malacosoma californicum							2		3				5
Pero mizon											1		1
Phyllodesma americana								1	1				2
Plusia nichollae							1						1
Smerinthus cerisyi								1					1
Spilosoma virginica								1					1
Unknown Tortricid	2		2			2	2	1	2				11
Xanthorhoe ferrugata							1						1
Zosteropoda hirtipes							1						1
Grand Total	2	1	5	2	2	4	17	5	20	2	24	2	86

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Knez Wetland

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Agrotis ipsilon	1												1
Aletia oxygala	2		2	3	1	3	1	2	2				16
Choristoneura rosaceana				2	1								3
Chrysoteuchia topiaria		1		1									2
Cisseps fulvicollis		1	1										2
Crymodes devastator									1				1
Dargida procincta			1					1					2
Euchromius ocelleus							1				5		6
Helotropha reniformis										1			1
Leucania farcta												1	1
Malacosoma californicum									3				3
Unknown Tortricid				2	3								5
Xestia xanthographa												2	2
Grand Total	3	2	4	8	5	3	2	3	6	1	5	3	45

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Minthorn Springs

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala	1	1		2		1	1						6
Apamea castanea									1				1
Choristoneura rosaceana					2								2
Chrysoteuchia topiaria				1	1								2
Crambus plumbifimbriellus							1		1	1			3
Diarsia rosaria												1	1
Euchromius ocelleus	4									1			5
Eupithecia misturata				1									1
Furcula scolopendrina	1												1
Graphiphora haruspica						1							1
Helotropha reniformis	1												1
Idaea dimidiata				1									1
Lacinipolia rectilinea	1												1
Malacosoma californicum					1								1
Ochropleura plecta	2	2	1	1	1	1							8
Papaipema insulidens	1												1
Pediasia trisecta	1												1
Petrophilia confusalis							1						1
Smerinthus cerisyi	1												1
Spilosoma virginica	1			1									2
Unknown Pterophorid	1												1
Unknown Tortricid				2	1								3
Xanthorhoe ferrugata												1	1
Xanthorhoe munitata										1			1
Xylena nupera				1									1
Grand Total	15	3	1	10	6	3	3	0	2	3	0	2	48

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Prison North

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Agrotis ipsilon	1									1			2
Aletia oxygala	1	1	1	10	4	1	1	2		18	2		41
Apamea ophiogramma						1							1
Cabera erythemaria									1				1
Caenurgina erechtea				1			1		1				3
Caradrina morpheus				1									1
Chrysoteuchia topiaria							2	5	2				9
Crambus pascuellus						1							1
Crambus plumbifimbriellus							2						2
Crymodes devastator								1		3			4
Euchromius ocelleus					1								1
Fumibotys fumalis									1				1
Gluphisia septentrionis			1										1
Helotropha reniformis							3			2			5
Idaea dimidiata						1							1
Lithacodia albidula				6	2		2	5	2				17
Loxostege commixtalis					1					1			2
Malacosoma californicum								3	2				5
Melipotis jucunda			1										1
Noctua comes											2		2
Nomophila nearctica										1			1
Ochropleura plecta	2				3			1		2			8
Oligocentria semirufescens							1						1
Ostrinia penitalis					1								1
Petrophilia confusalis					1								1
Scopula junctaria										3			3
Semiothisa neptaria							6	1	4	1	4		16
Spilosoma virginica		1	1	3						2	1		8
Tehama bonifatella	1												1
Udea profundalis									1				1
Unknown Tortricid					1								1
Xestia xanthographa											2		2
Grand Total	5	2	4	21	14	4	18	18	14	34	11		145

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Pickle Pond

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Agrotis ipsilon				1									1
Aletia oxygala	1	1	2	4	2	1					1	1	13
Caenurgina erechtea				8	2	4		2		1		2	19
Chrysoteuchia topiaria					1			2	1				4
Cisseps fulvicollis					1								1
Crambus leachellus										3	2	1	6
Crambus pascuellus				4				2	2				8
Crambus plumbifimbriellus				2				2	2				6
Crymodes devastator				1				2		1		1	5
Euchromius ocelleus					1			2	1		1		5
Eupithecia harveyata									1				1
Idia aemula								1		1			2
Idia americalis					2								2
Leucania farcta			1	1									2
Lithacodia albidula				2									2
Malacosoma californicum								1	1				2
Ochropleura plecta	3												3
Petrophilia confusalis										1			1
Semiothisa neptaria					1			2	1		3		7
Sicya crocearia									1				1
Spilosoma virginica				2									2
Tyria jacobaeae			1										1
Unknown Pterophorid								1					1
Unknown Tortricid				1	4					1	1		7
Xestia xanthographa												1	1
Grand Total	4	1	4	26	14	5		17	10	8	8	6	103

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Prison South

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala				1	1		1		1		6	1	11
Apamea ophiogramma							1						1
Caenurgina erechtea							1			4	1		6
Choristoneura rosaceana				1									1
Chrysoteuchia topiaria							2	2	2				6
Cisseps fulvicollis				1									1
Crambus leachellus											1		1
Crymodes devastator										2	1		3
Diarsia rosaria												1	1
Euchromius ocelleus					2							3	5
Fumibotys fumalis												1	1
Lithacodia albidula					1	1							2
Malacosoma californicum								1	2				3
Nomophila nearctica										2		1	3
Ochropleura plecta		1											1
Ostrinia penitalis								1					1
Semiothisa neptaria				1									1
Spilosoma virginica										1			1
Udea profundalis										1			1
Xestia xanthographa										1		1	2
Grand Total		1		4	4	1	5	4	5	11	9	8	52

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Ramsey Lake

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Achyra rantalis												1	1
Agroperina dubitans								1	2				3
Aletia oxygala	4	4	3	5	4	4	3		1	10	1	3	42
Apamea ophiogramma					1								1
Cabera erythemaria												1	1
Caenurgina erechtea				1						1		3	5
Choristoneura rosaceana										1		1	2
Chrysoteuchia topiaria				2					1				3
Crambus plumbifimbriellus									1				1
Crymodes devastator										2		1	3
Diarsia esurialis								1					1
Diarsia rosaria									2				2
Euchromius ocelleus					1					1			2
Eupithecia harveyata	1												1
Helotropha reniformis							2	2					4
Homorthodes communis										1			1
Leucania farcta						1							1
Lithacodia albidula				1			1	1					3
Malacosoma californicum								1	8				9
Melipotis jucunda	1												1
Nomophila nearctica										1			1
Ochropleura plecta										1			1
Ostrinia penitalis				1									1
Parabagrotis exertistigma				1									1
Protorthodes smithii			1										1
Proxenus miranda								1					1
Semiothisa neptaria	1						4			4	1	1	11
Spilosoma virginica				4								1	5
Tehama bonifatella	1		1							1			3
Unknown Tortricid							2						2
Zosteropoda hirtipes				1									1
Grand Total	8	4	5	16	6	5	12	7	15	23	2	12	115

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Rand Road

Month sampled	May			June			July			August			Total
Sample number	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	
Moth species													
Agroperina lateritia				1									**1**
Aletia oxygala	3		2	2	1	3				3	5	3	**22**
Apamea cinefacta		1											**1**
Autographa californica	1												**1**
Chrysoteuchia topiaria						1							**1**
Crymodes devastator				1				1	2		1		**5**
Euxoa messoria											2		**2**
Euxoa tessellata											1		**1**
Heliothis zea											1		**1**
Hyphantria cunea						1							**1**
Idaea demissaria			1										**1**
Leucania farcta						1				1	1	3	**6**
Mamestra configurata				1									**1**
Ochropleura plecta						1							**1**
Parabagrotis exertistigma			2										**2**
Pediasia dorsipunctella	2												**2**
Pediasia trisecta											1		**1**
Peridroma saucia						1				1	2	3	**7**
Phragmatobia fuliginosa												1	**1**
Prionoxystus robiniae					1	1	1						**3**
Prorasea praeia			1										**1**
Protorthodes curtica											1		**1**
Pyrrharctia isabella		1											**1**
Schinia meadi						1							**1**
Spilosoma virginica					2	3							**5**
Unknown Pterophorid	2												**2**
Unknown Pyralid									1				**1**
Unknown Tortricid											1		**1**
Unknown Xanthorhoe			3										**3**
Xestia c-nigrum					1	3				7	15	20	**46**
Zale lunata	1												**1**
Grand Total	9	2	9	5	5	16	1	1	3	12	31	30	124

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Simplot Marsh

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Acronicta lepusculina											2		**2**
Agonopterix alstroemeriana				2									**2**
Aletia oxygala				1							1		**2**
Caenurgina erechtea						1				1			**2**
Catocala faustina										1			**1**
Choristoneura rosaceana							1						**1**
Euxoa messoria										2			**2**
Helotropha reniformis							1						**1**
Lacinipolia pensilis				1									**1**
Leucania farcta											1		**1**
Loxostege commixtalis											1		**1**
Loxostege sticticalis										1	1		**2**
Pediasia trisecta				2		3				9	6		**20**
Petrophilia confusalis				1	2	7	23	5	26				**64**
Proxenus mindara											1		**1**
Pyrrharctia isabella				1									**1**
Saucrobotys fumoferalis										1			**1**
Semiothisa curvata											1		**1**
Spilosoma virginica				1	1	1					1		**4**
Spodoptera praefica				2									**2**
Tehama bonifatella								1		43	17	7	**68**
Unknown Oecophorid				2	2	2			2				**8**
Unknown Pyralid				2			1						**3**
Unknown Tortricid					2	9							**11**
Xylena nupera			1										**1**
Grand Total			1	15	7	23	26	6	28	58	32	7	203

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Umatilla

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Aletia oxygala	1	2	1						5				9
Apamea cinefacta											1		1
Archanara subflava							1						1
Autographa californica					1								1
Caradrina morpheus			1	1									2
Crymodes devastator				1		2			3				6
Discestra trifolii			2										2
Egira rubica										1			1
Euxoa messoria	1					2							3
Euxoa septentrionalis					1								1
Evergestis funalis		1											1
Grammia nevadensis							1						1
Heliothis zea									1				1
Itame colata	1	4	21										26
Leucania farcta									4			1	5
Loxostege commixtalis	1	1				1							3
Loxostege sticticalis			1			3							4
Melanchra picta				1									1
Melipotis jucunda			1										1
Orthosia hibisci										10	4		14
Parabagrotis exertistigma			1							1			2
Pediasia trisecta									1				1
Pero mizon			1										1
Phragmatobia fuliginosa								1					1
Pima fulvirugella			7										7
Platyperigea extima			3		3								6
Prorasea praeia										1			1
Protagrotis obscura			1										1
Protorthodes curtica							1						1
Proxenus mindara				1						3			4
Schinia meadi			1										1
Semiothisa curvata	1	3	3		1				1	1			10
Semiothisa denticulata				1									1
Semiothisa nubiculata		2		1	2								5
Spaelotis bicava												1	1
Spilosoma virginica		1	3	1					1	1		1	8
Udea profundalis				1								1	2

Appendix F. Abundance of moths sampled at 20 wetland field sites continued

Umatilla continued

Month sampled	May			June			July			August			Total
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	
Moth species													
Unknown Eupithecia				1									1
Unknown Oecophorid					2								2
Unknown Pterophorid			1		1								2
Unknown Pyralid							1						1
Unknown Tortricid	1	2	1		1								5
Xestia c-nigrum	1	2	2						5			1	11
Grand Total	7	18	51	9	12	8	4	1	21	18	5	5	159