A TEST OF FEDERALLY THREATENED WATER HOWELLIA (*Howellia aquatilis* Gray) PRESENCE AS AN INDICATOR OF UNFAVORABLE ENVIRONMENTAL CONDITIONS FOR INVASIVE REED CANARYGRASS (*Phalaris arundinacea* L.)

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of LAURA ANN ROBISON find it satisfactory and recommend that it be accepted.

Chair

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A TEST OF FEDERALLY THREATENED WATER HOWELLIA (*Howellia aquatilis* Gray) PRESENCE AS AN INDICATOR OF UNFAVORABLE ENVIRONMENTAL CONDITIONS FOR INVASIVE REED CANARYGRASS (*Phalaris arundinacea* L.)

Abstract

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Reed canarygrass (*Phalaris arundinacea* L.*)* is an invasive perennial grass in North American temperate wetlands. It is an effective competitor due to tall, dense growth that creates deep shade, high responsiveness to eutrophication, and broad ecological amplitude. Attempts to control the species have been unsuccessful.

Reed canarygrass dominates wetland habitats in Turnbull National Wildlife Refuge, near Cheney, Washington. At Turnbull, reed canarygrass occurs in wetlands that also support the federally-listed threatened plant *Howellia aquatilis* Gray. Studies show that reed canarygrass adversely impacts water howellia populations.

We hypothesized that water howellia persists in certain wetlands because habitat conditions are less favorable to reed canarygrass than in other wetlands. To test this hypothesis we located seven wetlands with water howellia and six without howellia that had dominant reed canarygrass stands. We mapped vegetation association and standing crop changes along a hydrological gradient, and recorded site characteristics including soils, aspect, tree and shrub canopy, and coarse woody debris. We also recorded reed canarygrass seed head density, native plant standing crop, and aboveground rooting behavior of reed canarygrass.

Wetlands with water howellia had significantly shorter ($P = 0.0423$) upland-to-wetland gradients, consistent with their smaller average size. In both wetland types, mid-gradient vegetation zones were longer and had higher reed canarygrass biomass than zones nearer the ends of the gradient. Reed canarygrass biomass was not significantly different ($P > 0.34$) between wetland types in any zones, and seed head density was significantly different ($P = 0.0339$) in only one vegetation zone.

Wetlands with water howellia had a significantly greater ($P = 0.0226$) proportion of zones where reed canarygrass production was impaired, most often by coarse woody debris or shrubs. Soil profiles of wetlands with howellia also had significantly ($P \leq 0.03$) more coarse organic soil on the wetland end of the gradient.

Our results did not support the hypothesis, though there were some differences in reed canarygrass performance between wetland types. The persistence of water howellia in some wetlands may be due to more shade-generating canopies and coarse woody debris, or to different ecological or historical characteristics in the smaller basins where it occurs.

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INTRODUCTION

The problem of invasive species

Invasive species are a major threat to global biodiversity, ranking second only to habitat loss in causing extinctions (IUCN 2004). The aggressive proliferation of these species eliminates many native species from their habitats, but invasive species may also degrade ecosystem functionality or change ecosystem characteristics. For example, spotted knapweed (*Centaurea maculosa)* may increase soil erosion by excluding native grasses and their stabilizing roots (Lacey et al. 1989), and the paperbark tree (*Melaleuca quinquenervia*) increases the frequency of fires in invaded systems (Mack et al. 2000).

Invasive species are often closely tied to human activity. Humans have exponentially increased rates of species introductions to novel habitats and continents, both intentionally and unintentionally (Mack et al. 2000). Human activity may also decrease the ability of ecosystems to resist invasion. The fluctuating resource hypothesis of invasibility (Davis et al. 2000) states that systems will be most vulnerable to invasion when resource availability exceeds demand by the plant community. This may occur by enrichment of a limiting resource, disturbance that reduces resident plant biomass or vigor, or a combination of the two. Since human activity often promotes both disturbance and nutrient enrichment, invasive species impacts can be expected to increase as human population and intensive land use increase in the coming century.

Reed canarygrass (*Phalaris arundinacea* L.) is a perennial, cool season grass of wetland habitats in Eurasia and northern North America (Lavergne and Molofsky 2006). The species is widely recognized as invasive and a threat to biodiversity in wetland ecosystems (Apfelbaum and Sams

1987; Lavergne and Molofsky 2006; WSNWCB 2006). It presents a severe threat to local biodiversity because it can exclude not only other plants, but also birds, amphibians, insects, and other species that depend on native plants (Apfelbaum and Sams 1987; Gaston 1998; Green and Galatowitsch 2001; Werner and Zedler 2002).

Characteristics of reed canarygrass that promote invasiveness

Several life history traits may contribute to the high invasive potential of reed canarygrass (hereafter RCG). It grows rapidly, reaching heights of 1-2 meters within a growing season (Weinmann et al. 1984), and often forms dense, shady stands in which few other plant species can survive (Werner and Zedler 2002; Rule 2004). It is well-adapted to nutrient-rich environments because of its high capacity for nutrient uptake, especially nitrogen (Maurer and Zedler 2002). Its potential for biomass productivity is so high that it is used for wastewater treatment (Marten and Heath 1973) and it may be adopted as a biomass energy crop (Hallam et al. 2001). It begins spring growth relatively early in some areas (Maurer and Zedler 2002), although not in the American inland northwest. Growth may resume in the autumn if sufficient moisture is available (Piper 1939).

RCG also has several adaptations that help it withstand disturbance. An extensive underground network of scaly rhizomes allows rapid vegetative growth; this can surpass even other aggressive rhizomatous plants such as quackgrass (Stannard and Crowder 2001). Rhizomes also provide a reserve of energy and nutrients that can be used for culm regeneration following destruction of the rest of the plant by fire, grazing, or other control methods (Stannard and Crowder 2001). RCG can root from the nodes of either intact or cut stems (Hovin et al. 1973). It is also highly resilient after defoliation. Forman (1998) found that at least three defoliations in a season were needed to significantly reduce RCG production, and 100% of the plants survived five defoliations.

Reed canarygrass environmental tolerances and optimums

In addition to its high competitive ability, RCG has a wide environmental tolerance. It is suited to almost all temperate climates, which includes the northern half of the continental United States. Ideal temperatures for photosynthesis were measured as 20°C (68°F) (Marten and Heath 1973). RCG occurs at a wide range of altitudes, from coastal wetlands to mountain meadows (Stannard and Crowder 2001). Its anoxia-tolerant rhizomes allow it to persist in areas with seasonal inundation (Apfelbaum and Sams 1987), surviving up to 49 days of spring flooding. However, RCG is also more tolerant of drought than many cool-season grasses of humid and subhumid habitats (Marten and Heath 1973).

Young RCG plants are suppressed in shady areas (Maurer and Zedler 2002), but established plants may withstand in excess of 81% shade (Forman 1998). Although RCG does not grow in saline soils, it can tolerate pH levels from 4.9 to 8.2 (Marten and Heath 1973). In some cases, vegetative RCG clones that are “subsidized” through a connection to the mother plant can even expand into environments beyond their environmental tolerance (Maurer and Zedler 2002).

Perhaps most worrying is the fact that RCG thrives in habitats impacted by human activity. RCG production increased in wetlands where urban stormwater had increased sedimentation and nutrient input (Maurer et al. 2003; Kercher and Zedler 2004). Stormwater also tends to produce high frequency, short duration flooding. Miller and Zedler (2003) found that RCG production was highest in a high frequency hydroperiod and lowest in a prolonged flooding hydroperiod. However, RCG may also dominate wetlands where water levels become higher or more stable; these wetlands are often dominated by tall, rhizomatous emergents such as *Typha* spp. and RCG (Shapley and Lesica 1997).

Human influence on reed canarygrass in the Pacific Northwest

The high invasiveness of reed canarygrass today may be due to its long-standing importance to humans as a forage grass. Most early studies of RCG focus on its forage potential and environmental tolerances (Piper 1939; Marten and Heath 1973), although there are occasional studies on control of problematic, sediment-trapping RCG in irrigation canals (Hodgson 1968). Studies of RCG invasiveness and its ecological role appear after 1985 (Apfelbaum and Sams 1987; Gillespie and Murn 1992). RCG continues to be an important forage species due to its tolerance to poorly drained areas and repeated grazing (Stannard and Crowder 2001). In many wetlands, cattle grazing supports higher wetland plant diversity by suppressing RCG (Bennington 1972), although the cattle may have negative effects such as decreased water quality (Stannard and Crowder 2001).

There is some debate whether RCG is native to North America and the Pacific Northwest, or whether it was introduced from Europe. Both theories may be correct. There are several RCG botanical specimens from the Pacific Northwest that probably predate Euro-American settlement (Merigliano and Lesica 1998). However, seeds from throughout continental Europe have been introduced to North America (Lavergne and Molofsky 2007), and at least 13 agriculturally improved varieties of RCG have been introduced to the Pacific Northwest for pasture use (Carlson et al. 1996). Recent studies suggest that RCG's invasiveness is due to the wide pool of genetic resources that it gained from repeated introductions in its new range (Lavergne and Molofsky 2007).

Land managers and researchers are increasingly seeking methods to control RCG (Apfelbaum and Sams 1987; Naglich 1994; Stannard and Crowder 2001; Reinhardt and Galatowitsch 2004; Adams and Galatowitsch 2006; Lavergne and Molofsky 2006). Common control methods include tillage, mowing, grazing, herbiciding, burning, shading, and "scalping," which removes the top 12 inches of soil (Stannard and Crowder 2001). However, all of these methods are non-selective and have other drastic ecological impacts. Planting of native species, cover crops, and competitive native woody species have less drastic impacts, but plantings do not perform well unless accompanied by other RCG control methods (Lavergne and Molofsky 2006).

Control of established stands requires large commitments of time, effort, and money, and is seldom permanent, only setting back dominance by RCG. A literature survey by Forman (1998) found no cases of RCG-dominated sites that had been restored to a native community completely free of RCG. In addition, the effectiveness of individual control methods may vary in different areas (Naglich 1994), compounding the difficulty of developing an effective control plan.

Ecology of water howellia

Water howellia (*Howellia aquatilis* Gray) is an annual aquatic plant that occupies the same wetland habitats as reed canarygrass. It has flaccid, usually branched stems 10-100 cm long, and linear leaves that are 1-5 cm long. Flowers may be produced above or below the water surface (Lesica 1992; Shapley and Lesica 1997). The plants require wetland zones that are flooded from April through July, but dry for seed germination in August or September (Shapley and Lesica 1997). Seedlings are dormant over the winter, but resume growth in spring under as much as 2 meters of water (Lesica 1992).

Water howellia is currently listed by the U. S. Fish and Wildlife Service as a federally threatened species. Although howellia has never been a common plant, it has lost considerable habitat during the past century. Habitat loss is thought to be due to several factors including wetland drainage, alteration or disturbance of wetlands by timber harvest, livestock grazing, and invasive plants, especially RCG (Shelly and Gamon 1996). Within wetlands, RCG has a relatively wide hydrological tolerance, but it grows best in the same seasonally-inundated wetland zones that are optimal for water howellia (Shelly and Gamon 1996), (M. Rule, pers. comm.). RCG has been documented to displace water howellia; this is likely because RCG stands produce denser shade than the relatively open canopies of native communities dominated by *Equisetum fluviatile, Sium suave,* and *Carex vesicaria* (Lesica 1997).

Water howellia seems to occur less often in wetlands with conditions that are favorable for RCG. For example, water howellia is uncommon in wetlands with higher or more stable water levels, likely because these conditions promote tall, rhizomatous emergents such as cattails and RCG. Water howellia is also uncommon in wetlands with high nutrient levels, which promote large rhizomatous species and light-blocking algae (Shapley and Lesica 1997). It seems to be more common in shadier habitats: howellia wetlands on Turnbull National Wildlife Refuge in eastern

Washington tend to have shorelines with high (76-100%) tree cover, made up largely of *Populus tremuloides* (25-50%) and *Pinus ponderosa* (25-50%) (Rush 1998). Water howellia populations may also be common on relatively short, steep basin slopes that increase the shading of wetland zones by upland trees, on slopes with high cover by shrubs such as *Cornus stolonifera,* on north-facing aspects receiving less sunlight, and in shady microhabitats beneath coarse woody debris (M. Rule, pers. comm.). Although a greenhouse study and field observations indicates that water howellia grows best on soils with high organic matter content (Lesica 1992), soil type is not expected to affect the growth of RCG (Carlson et al. 1996).

Hypothesis and study objectives

This study is intended to characterize natural conditions that are unfavorable to reed canarygrass production and dominance. We hypothesized that the persistence of water howellia in some wetlands was primarily due to weaker competition by RCG, and that low performance of RCG was caused by unfavorable environmental conditions. The objectives of our study were to:

1. Compare reed canarygrass standing crop between wetlands with water howellia populations and wetlands without howellia populations.
2. Compare native and naturalized plant standing crop between wetlands with water howellia populations and wetlands without howellia populations.
3. If reed canarygrass standing crop is different between wetland types, characterize environmental conditions that correlate with lower reed canarygrass performance.
4. Interpret results in terms of applications to reed canarygrass control.

METHODS

Site Description

The study area is located within Turnbull National Wildlife Refuge (TNWR), which is managed by the U.S. Fish and Wildlife Service. TNWR is located in eastern Washington about five miles south of Cheney, in the channeled scablands ecoregion. The channeled scablands are a unique geological area that was shaped by massive flood events during a glacial era over 18,000 years ago. Repeated, cyclic failures of ice dams on glacial Lake Missoula released floodwaters that scoured massive channels and deposited debris in eastern Washington and Oregon (USGS 1973). At TNWR, the legacy of the floods is large wetland basins with high hydrologic connectivity, interspersed by rocky ridges (Figure 1). These wetlands are important for local and migrating waterfowl.

Before the refuge was founded in 1937, much of the land was used for agriculture, and many wetlands were drained for pasture or cropping (Bernard 1947; Rule and Curry 1999). Many of these wetlands were planted with reed canarygrass (RCG). Early refuge managers reflooded wetlands, and also planted RCG as a wetland restoration technique (Rule 2004). Cattle grazing was permitted on the refuge until 1994 (Rule and Curry 1999), and RCG was an important forage species (Bennington 1972).

Experimental Design

Thirteen wetlands within the TNWR were selected for vegetation sampling. These included seven wetlands with water howellia populations and six wetlands without water howellia. Wetlands with documented water howellia populations were selected from a refuge list (Rush

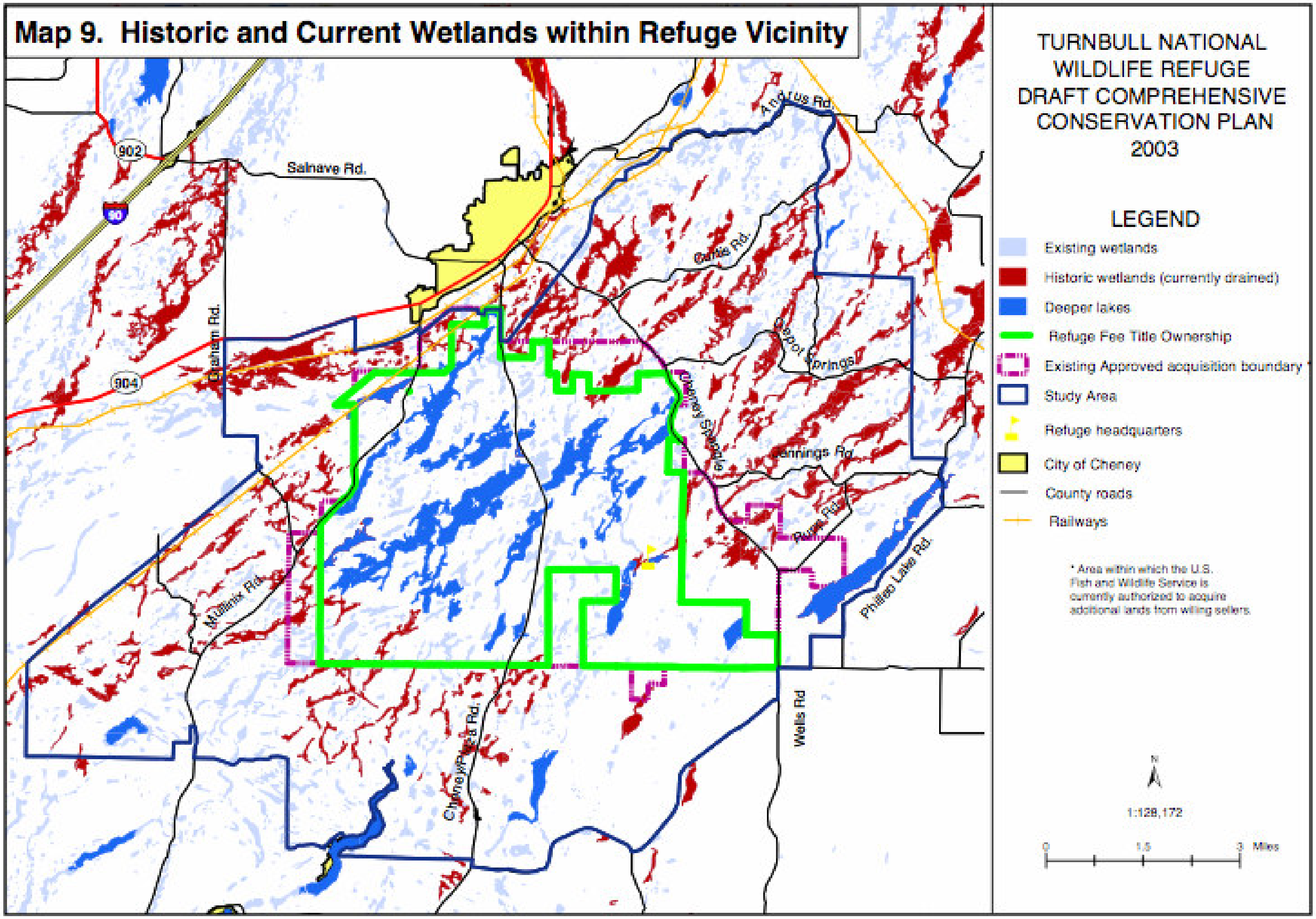

Figure 1. Map of Turnbull National Wildlife Refuge, Spokane County, Washington (USFWS 2005). All sampling sites are located within the refuge.

1998). To select wetlands without howellia and with strong reed canarygrass performance, we used a refuge list of wetlands previously prioritized for RCG control (Rule 2004). Because wetlands supporting water howellia on the refuge are generally relatively small, averaging 4.2 acres (Rush 1998), we attempted to select large water howellia wetlands and small RCG control wetlands from the lists. The RCG control wetland list included only five wetlands that met our size criteria, so a sixth wetland was selected from a topographic map, based on similar basin size, shape, depicted hydrology, and location within the refuge. Our water howellia wetlands and RCG control wetlands averaged 6.0 acres and 13.7 acres, respectively.

We placed four transects within each wetland, each with a different aspect (north, south, east, or west). Transects were drawn on a USGS topographic map prior to visiting the wetland, then located in the field using a global-positioning-system (GPS) unit. Transects were placed perpendicular to the basin contours, along an upland-to-wetland gradient. The transects incorporated the entire ecological amplitude of reed canarygrass, starting one meter upland to the highest RCG plant, and ending at the closest meter division below the lowest RCG plant. On each transect, seven square 0.0625 m^2 plots were placed at intervals of one-sixth of the transect length, and then two plots were added at the midpoints of the outer segments, for a total of nine plots (Figure 2). The higher density of plots near the transect ends was intended to collect more environmental information about the areas where RCG approached, and reached, its ecological limits. All sampling was conducted during October 2006.

Vegetation Zone Classification

We classified each portion of the transect into eight vegetation zones that described hydrology and reed canarygrass productivity (Table 1). The vegetation zones were measured on a line-intercept based upon the distinct vegetation transitions apparent at the site (Figure 2, Figure 3). Sampling plots were classified into the vegetation zone that overlapped their position on the transect. Plots were placed systematically, independently of vegetation zones, but if a vegetation zone had no plot, then a plot was added within it.

The reason for classifying plots into vegetation zones was to remove the confounding influence of variable reed canarygrass production along the upland-to-wetland gradient. On each transect, standing crop consistently resembles a bell curve, with peak biomass and seed head density near the center. Therefore, in our analysis, comparisons of reed canarygrass performance between wetlands were conducted for each zone separately.

Vegetation Sampling

At each 0.0625 m^2 plot, all aboveground biomass for the current year (standing crop) was harvested and oven-dried for 24 hours at 70°C (158°F), then separated and weighed by species. The number of reed canarygrass seed heads in each plot was also recorded. In addition, we recorded whether reed canarygrass plants in the plot were rooting at stem nodes or forming root mats, and whether any reed canarygrass plants had been grazed. (Cattle grazing no longer occurs on the refuge, but elk, deer, moose and waterfowl may graze RCG).

Table 1. Definitions of the eight vegetation zone categories.

Vegetation Zone Classification	***Abbreviation***	***Definition***
Upland	UPL	No reed canarygrass is present Dry soils and no hydrology
Upland-Subordinate RCG	US	Reed canarygrass makes up less than 50% of vegetation Vegetation is short, often less than one foot tall Seed heads are rare or absent
Upland-Lower-Stature RCG	UL	Reed canarygrass makes up over 50% of vegetation Vegetation is visibly shorter than Tall-RCG zone Seed heads occasional but less prominent
Tall RCG	T	Reed canarygrass makes up over 50% of vegetation Plants are relatively tall and upright Seed heads are common, and often relatively large
Wetland-Lower-Stature RCG	WL	Reed canarygrass makes up over 50% of vegetation Vegetation is visibly shorter than Tall-RCG zone Seed heads occasional but less prominent
Wetland-Subordinate RCG	WS	Reed canarygrass makes up less than 50% of vegetation Vegetation is short, often less than one foot tall Seed heads are rare or absent
Wetland	WET	No reed canarygrass is present Wet soils and wetland hydrology
Impaired-RCG	IMP	An environmental factor that impairs reed canarygrass growth is present (e.g. tree overhang)

The zones were assigned in the field based on distinct vegetation transitions apparent on the transects (Figure 2, Figure 3). Favorable hydrological conditions for water howellia occur in the Upland-Lower-Stature-RCG and Tall-RCG zones.

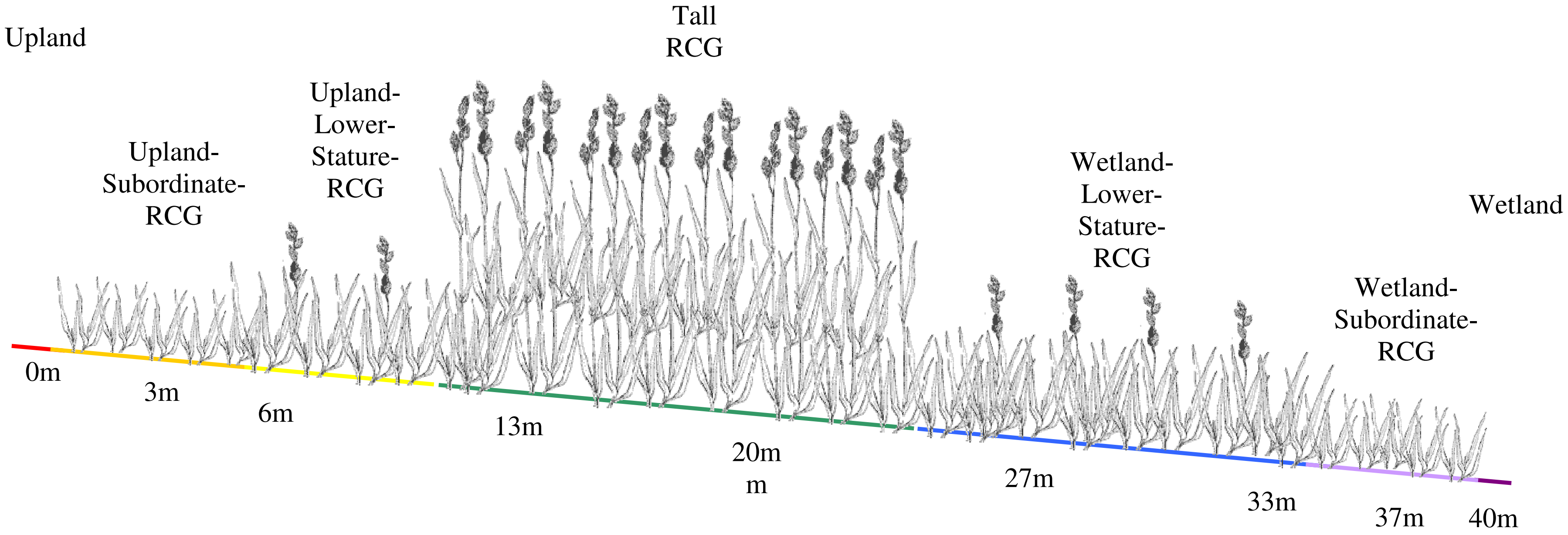

Figure 2. Diagram of an upland-to-wetland gradient with sampling transect and plots. Vegetation zones are spaced according to average proportions recorded in reed canarygrass control wetlands. Other plant species were present, but are not depicted on this figure. Favorable hydrological conditions for water howellia occur in the Upland-Lower-Stature-RCG and Tall-RCG zones.

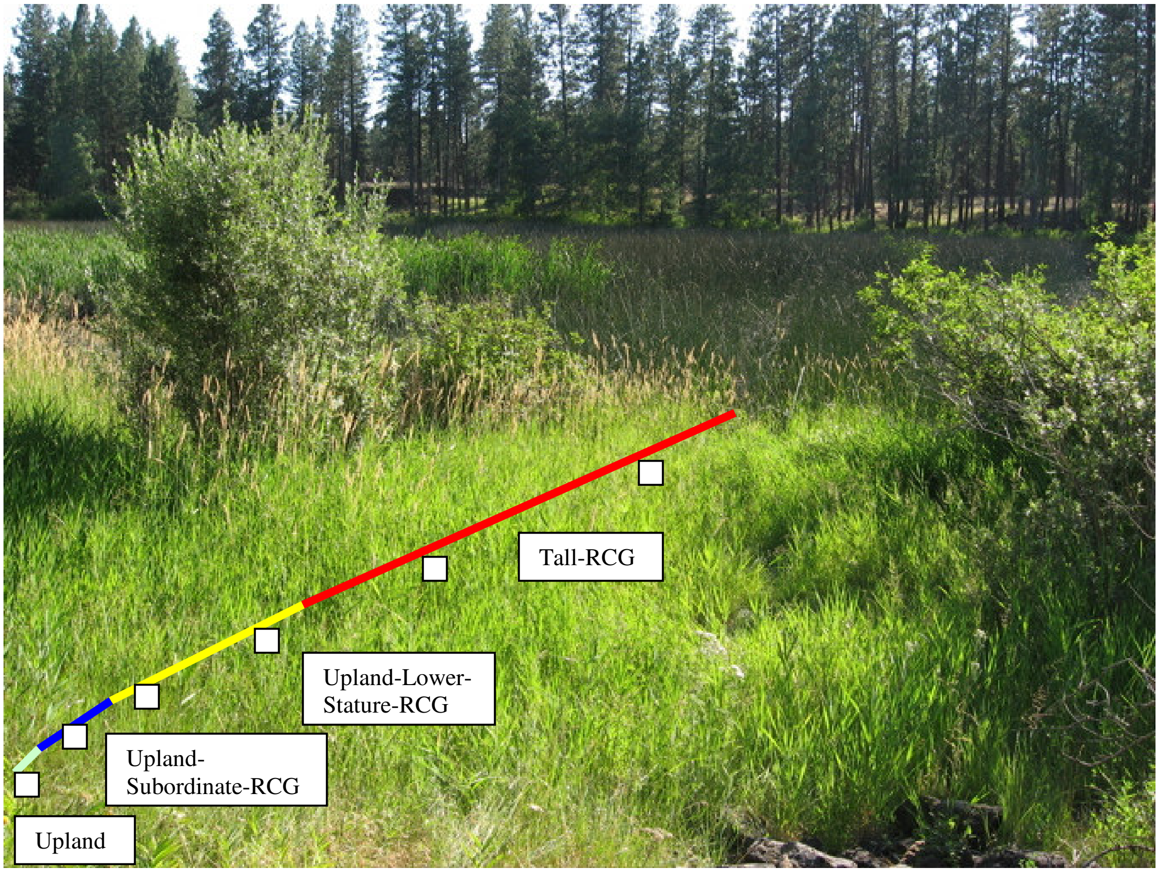

Figure 3. Example transect placed along an upland-to-wetland gradient in the study area. Different colors represent different vegetation zones, and squares represent hypothetical sampling plots. Vegetation zones below the Tall-RCG zone on the gradient are not visible in this photo. This wetland follows a common pattern of upland zones dominated by upland grasses and forbs, middle zones dominated by reed canarygrass, and wetland zones dominated by *Typha latifolia.*

Soil Sampling

As an indirect measure of hydrology, soils at each plot were evaluated for soil color and texture. After clipping biomass in each 0.0625 m^2 plot, a 12-cm diameter, 12-cm deep soil sample was removed using a drain spade, examined, and replaced. Soil vertical structure was recorded by classifying each centimeter as mineral soil, ash, fine organic matter, coarse organic matter, or coarse litter. Soil color was recorded using a Munsell moist soil color book (Munsell Color 1975).

Statistical Analysis

We used a split plot, mixed model analysis of variance (ANOVA) to compare averages for response variables on transects between water howellia wetlands and RCG control wetlands. Comparisons were done for each vegetation zone individually, and were run using SAS statistical software (SAS Institute, Inc. 2002). Fixed effects in the model were *wetland type* (water howellia type, RCG control type), *transect aspect* (north, south, east, west), and an *interaction* term. Individual wetlands were analyzed as a random effect. If the data set for a response variable failed a Shapiro-Wilk W test for normality, the data set was transformed and rechecked for normality. We used an arcsine-square root transformation for proportion data, and a logarithm (x + 1) transformation for all other data. We set $P < 0.10$ as our threshold for statistical significance to accommodate the high variability of field data without controlled conditions. In a very few cases, the transformed data did not meet normality assumptions; we tested these data for significant differences using a non-parametric Wilcoxon rank sum test.

In analyzing most measurements, we found that aspect did not significantly affect our response variables. Therefore, we conducted a second analysis, pooling data from all plots within a wetland for each vegetation zone. This analysis used a mixed model ANOVA with a fixed effect of *wetland type* and a random effect of individual wetlands. Normality tests and transformations were done in the same way as above with $P < 0.10$ for statistical significance.

RESULTS

Length of Vegetation Zones

The total length of the upland-to-wetland transects was significantly longer in reed canarygrass (RCG) control wetlands compared to water howellia wetlands (P = 0.0423). Average lengths were 41.1 m and 23.7 m, respectively. Within the transects, most vegetation zones were approximately twice as long in RCG control wetlands as in water howellia wetlands (Figure 4). However, the zone lengths were only significantly different for the Upland-Subordinate-RCG zone (P = 0.0625). Zones in the middle of the transect tended to be longer than zones near the ends (Figure 2). The longest zones were the Tall-RCG zone, which averaged 8.0 m, and the Wetland-Lower-Stature-RCG zone, which averaged 11.0 m.

Impaired-RCG zones were defined as zones with an environmental factor that hampered RCG production, so that performance could not be explained by water availability alone. These zones were not present on all transects, or in all wetlands. In our data set, Impaired-RCG zones were caused by coarse woody debris, shrubs (*Cornus stolonifera* or *Salix* sp.), tree canopies (*Pinus ponderosa* or *Populus tremuloides*), and shallow or exposed rock (Table 2). Water howellia wetlands had significantly higher (P = 0.0943) average lengths of Impaired-RCG zones per wetland. This difference was due to both higher frequency of Impaired-RCG zones in howellia type wetlands (n=15) compared to RCG control wetlands (n=4), and a tendency toward longer Impaired-RCG zones in water howellia wetlands. Types of Impaired-RCG zones also varied between wetland types. For example, shrubs and tree canopy overhang occurred in 67% of Impaired-RCG zones in water howellia wetlands, but were never recorded in RCG control wetlands.

Proportion of Vegetation Zones

The proportion of the transect occupied by each vegetation zone was calculated by dividing the length of the zone by the length of the total transect. Average proportions of zones were similar between RCG control wetlands and water howellia wetlands (Figure 5), with only three zones significantly different between the wetland types. Not surprisingly, on the shorter transects in water howellia wetlands, the fixed-length Upland and Wetland zones had significantly higher proportions (P = 0.0137, P = 0.0355 respectively). More significantly, the proportion of Impaired-RCG zones was significantly higher (P = 0.0226) in water howellia wetlands (5.8%) compared to RCG control wetlands (0.9%). The proportions of the other zones tended to be similar to the lengths of the zones, with the largest proportions in the middle of the transect. The largest proportions were the Tall-RCG zone at 27.2% and the Wetland-Lower-Stature-RCG zone at 25.7%.

Reed Canarygrass Standing Crop

Reed canarygrass aboveground standing crop did not differ significantly between wetland types in any vegetation zone (Figure 6). Biomass data formed a rough bell curve, with the highest biomass in the Tall-RCG zone, totaling 553 g/m^2. However, the bell curve was skewed toward the wetland end of the gradient. For example, biomass was sharply different between the two lower-stature RCG zones on either side of the Tall-RCG zone: the Upland-Lower-Stature-RCG zone produced only 286.6 g/m^2 while the Wetland-Lower-Stature-RCG zone produced 515.6 g/m^2.

Reed canarygrass seed head density was also similar between wetland types (Figure 7). Like RCG biomass, seed head density formed a bell curve along the gradient that peaked in the Tall-RCG zone (66 heads/m^2), and was skewed toward the wetland end. However, head density was significantly different between wetland types in one vegetation zone. In the Wetland-Subordinate-RCG zone, seed head density was significantly higher ($P = 0.0339$) in RCG control wetlands (16.6 heads/m^2) compared to water howellia wetlands (5.4 heads/m^2). RCG standing crop and seed head density had a strong positive correlation ($R^2 = 0.9019$, Figure 12).

RCG rooting behavior and RCG grazing were similar between wetland types, with only one significant difference: RCG plants in the Wetland-Subordinate-RCG zone were significantly more likely ($P = 0.0965$) to root at nodes in RCG control wetlands (41%) compared to water howellia wetlands (19%). In both wetland types, rooting and grazing activity peaked in the Wetland-Lower-Stature-RCG zone. This zone had much higher frequencies for rooting at nodes (81%), root mat formation (38%), and grazing (38%) than adjacent zones. Table 3 summarizes RCG standing crop and environmental conditions in each vegetation zone.

Native Vegetation Standing Crop

Native and naturalized aboveground standing crop along the gradient followed a general pattern in all wetlands sampled. The upland end of the transect was dominated by upland grasses such as *Bromus* spp., wet meadow grasses such as *Poa pratensis* and *Agrostis* spp., forbs such as *Achillea millefolium* and *Medicago lupulina,* and occasional shrubs such as *Symphoricarpos alba* and *Cornus stolonifera.* The middle of the transect had high RCG biomass and relatively low biomass of species such as *Juncus balticus, Carex vesicaria,* and *Poa pratensis.* The wetland end of the transect was dominated by either *Scirpus acutus* or *Typha latifolia,* with *Sparganium eurycarpum* and *Eleocharis* spp. as subordinates. Water howellia wetlands had significantly higher ($P = 0.0639$) biomass of *Sparganium eurycarpum* (48.2 g/m^2) than RCG control wetlands (5.4 g/m^2) in the Wetland-Subordinate-RCG zone (Table 4), but no other significant differences in species composition were recorded. The most abundant species in each vegetation zone are listed in Table 4.

Native and naturalized standing crop did not differ significantly between wetland types in most vegetation zones (Figure 8). In the Impaired-RCG zone, however, native and naturalized biomass was significantly higher in water howellia wetlands (15.2 g/m^2) than in RCG control wetlands (0.0 g/m^2), ($P = 0.0737$). Small plants did occur in the Impaired-RCG zones of RCG control wetlands (Figure 9), but their biomass was negligible at our measurement scale. Native and naturalized biomass was much higher in the Wetland-Subordinate-RCG (274 g/m^2) and Wetland zones (318 g/m^2) than in other vegetation zones. This biomass consisted almost entirely of *Scirpus acutus* and *Typha latifolia* (Table 4). Native and naturalized species biomass and RCG biomass were negatively correlated ($R^2 = 0.7339$, Figure 12).

The average number of native and naturalized species occurrences in the 0.0625 m^2 sampling plot did not differ significantly between wetland types in any vegetation zone (Figure 9). Species occurrences were lowest in the zones with high RCG performance. For example, the Tall-RCG zone averaged 1.1 non-RCG species per 0.0625 m^2 plot. However, species occurrences were only slightly higher in the Wetland-Subordinate-RCG zone (1.6 species/plot) and Wetland zone (1.3 species/plot). Species occurrences were highest in the Upland (3.5 species/plot) and Upland-Subordinate-RCG zones (3.5 species/plot).

Total Standing Crop

Total aboveground standing crop of all plant species did not differ significantly between wetland types in most vegetation zones (Figure 10). However, in the Upland zone, total biomass was significantly higher in RCG control wetlands (239 g/m^2) than in water howellia wetlands (172 g/m^2), ($P < 0.10$, Wilcoxon test). In addition, differences in total biomass in the Wetland-Subordinate-RCG zone approached significance ($P = 0.1024$). Like previous biomass profiles, standing crop formed a rough bell curve. However, this curve was centered over the Wetland-Lower-Stature-RCG zone rather than the Tall-RCG zone, largely due to high native productivity on the wetland end of the gradient. The highest total biomass values occurred in the Tall-RCG zone (596.7 g/m^2) and Wetland-Lower-Stature-RCG zone (519.4 g/m^2). Species occurrences were not strongly correlated with RCG biomass, RCG seed head density, or native biomass (all $R^2 < 0.35$), but were negatively correlated with total biomass ($R^2 = 0.6452$, Figure 13).

Soil Characteristics

Soil characteristics along the upland-to-wetland gradient followed a relatively consistent pattern in all the sampled wetlands. Soil color was highly consistent along the upland-to-wetland gradient, and typically showed the same color values throughout the transect. Most chroma, or color intensity, readings were low values of 1 or 2, which can indicate wetland conditions (USACE 1987). Soil vertical structure, which recorded the depths and relative positions of soil types, changed from almost completely mineral soil in the upland zones to large percentages of coarse organic and fine organic material in the wetland zones (Table 3).

Water howellia wetlands consistently had more coarse-organic soil than RCG control wetlands (Figure 11). This was the only soil type with significant differences between wetland types in our data set. In the three wettest vegetation zones (Wetland-Lower-Stature-RCG, Wetland-Subordinate-RCG, and Wetland), water howellia wetlands had significantly more coarse-organic soil within their 12-cm deep soil profiles ($P \leq 0.0264$). All three of these zones averaged 4.9 cm of coarse-organic soil in water howellia wetlands, but 2.9 cm, 2.5 cm, and 1.9 cm, respectively, in RCG control wetlands. Coarse-organic soil was also significantly different between aspects in the Wetland-Subordinate-RCG and Wetland zones ($P \leq 0.0747$), with the most coarse-organic soil on north-facing transects (Table 5).

DISCUSSION

Comparison of Reed Canarygrass Performance

Our hypothesis that wetlands with water howellia would have lower performance by reed canarygrass (RCG) was primarily tested by our vegetation zone and biomass measurements. We found no significant ecological differences for vegetation zone length or vegetation zone proportion on the general upland-to-wetland gradient. This suggests that if the performance of RCG varies between wetland types, these differences are not expressed in the distribution of RCG along the gradient. Impaired-RCG zones, which were characterized by some additional environmental or ecological factor, will be discussed below.

Reed canarygrass aboveground standing crop and seed head density were also highly similar between wetland types in our data set. However, these measurements showed one significant difference: RCG seed head density was higher in the Wetland-Subordinate-RCG zone of RCG control wetlands. This single difference may be due to random error, an ecological difference in only this zone, or ecological differences in multiple zones but detected only in one zone with low variation. The observation that RCG plants rooted at nodes more frequently in this zone in RCG control wetlands suggests an ecological explanation. However, it would be interesting to repeat the study with a larger sample size and higher statistical power. Regardless, we cannot conclude that RCG performance varies between RCG control and water howellia wetland types.

Impaired-RCG Vegetation Zones

However, Impaired-RCG zones showed several significant differences between wetland types in our data set. We found that water howellia wetlands have significantly longer average length, larger average proportion, and higher native biomass for Impaired-RCG zones. In addition, tree and shrub overhang appears to be more common in water howellia wetlands. Because there are few apparent differences in RCG standing crop and distribution between wetland types, Impaired-RCG zones are likely highly important in water howellia persistence. Howellia requires hydrological conditions that occur in the Upland-Lower-Stature-RCG and Tall-RCG zones (M. Rule, pers. comm.), but RCG production in these zones is likely too high for howellia survival. If an Impaired-RCG zone occurs at this hydrological level, however, water howellia could survive in a microhabitat too shady for dense RCG growth (M. Rule, pers. comm.).

Characterization of Reed Canarygrass Ecology

In general, RCG aboveground standing crop and seed head density along the upland-to-wetland gradient formed bell curves. However, productivity was unexpectedly high on the wetland side of the curve, especially in the Wetland-Lower-Stature-RCG zone. This may be due to different rooting behavior by RCG plants in this zone: plants were more likely to root at stem nodes and form dense mats of vegetation than in any other zone (Table 3). This growth form was low to the ground and appeared less productive than it actually was when measured.

Vegetation zone and native biomass data suggest that RCG is a competitive dominant in our study wetlands. In both wetland types, vegetation zone proportions showed that RCG was the dominant species (Tall or Lower-Stature category) 75% of the time and a subordinate species only 25% of the time in its upland-to-wetland ecological range (all zones except for Upland, Wetland, and Impaired-RCG). Native biomass data also illustrated the effectiveness of RCG at excluding other species. Both native species biomass and species occurrences were lowest in the vegetation zones with the highest RCG performance. However, species occurrences were also suppressed in highly productive wetland zones dominated by *Scirpus* and *Typha.* This may illustrate a general ability of highly productive, tall species to outcompete other species, as described in Keddy (2004). Low wetland diversity may also reflect that fewer species can survive in this stressful environment.

Our RCG standing crop values seem to be consistent with other studies of reed canarygrass in Turnbull National Wildlife Refuge (TNWR) and the surrounding area. In 1972, Bennington recorded RCG aboveground standing crop on TNWR in the center of large, dense reed canarygrass swards, which are likely equivalent to the Tall-RCG zone of this study. This study documented 759 g/m^2 in ungrazed areas and 531 g/m^2 in one-year grazing exclosures, while our average RCG aboveground biomass for Tall-RCG zones was 553 g/m^2. Our lower average may reflect a wider selection of wetland sites in our study: Bennington was studying grazing effects on RCG biomass and may have chosen a highly productive area. It may also reflect year-to-year variation in RCG productivity under differing climatic conditions.

Wetland Size and Correlated Effects

Our data showed a clear trend toward larger sized reed canarygrass (RCG) control wetlands compared to water howellia wetlands, apparent in the significantly longer upland-to-wetland transect length (41.2 m versus 23.7 m) and the larger average acreage of these wetlands (13.6 acres versus 6.0 acres). However, it is uncertain whether the size correlation is due to an ecological difference or sampling bias. Our data set does not show strong evidence for a direct effect of wetland size on RCG production. RCG biomass did not correlate strongly with wetland acreage ($R^2 < 0.22$) or transect length ($R^2 < 0.12$), nor did total biomass correlate strongly with wetland acreage ($R^2 < 0.30$) or transect length ($R^2 < 0.38$).

However, basin size has almost certainly indirectly influenced the ecology of these wetlands. Historically, larger basins were likely more attractive for agricultural conversion. In our data set, five of six RCG control wetlands had been drained or partially drained, while only one of seven water howellia wetlands had been drained (USDA, SCS 1968). During agricultural development, many drained wetlands in this region were planted with RCG for livestock forage. Drainage would likely eliminate any resident howellia populations, and it could promote the establishment of dense RCG stands that resisted colonization by other species, even after the restoration of natural hydrology. Agricultural use could also promote alteration of adjacent upland areas, such as brush removal. Alternatively, larger basins may have been a higher priority for RCG control activities, if large infestations prompt more attention, or if large basins allow efficient treatment.

Basin size may also correlate with higher hydrological connectivity. As highly scoured lava beds, wetland basins on TNWR may have natural subterranean connectivity between surface waters. Smaller basins may be more likely to be isolated from natural connections. In addition, ditches remain in and between many wetlands on TNWR, although water control gates maintain high water levels in these channels and the adjacent wetlands during much of the year. These ditches appear to be more common in larger wetlands (Robison, pers. obs. 2006). We speculate that small, isolated wetland basins may have higher year-to-year hydrological variability because they lack the stabilizing influence of the extensive surface water connections apparent in the larger wetlands. High variability may reduce dominance by highly productive rhizomatous emergents such as RCG, *Typha latifolia,* and *Scirpus acutus* (Shapley and Lesica 1997). Less stable water levels may also promote water howellia persistence if hydrological zones can shift up or down the wetland gradient. For example, if a particularly wet year caused flooding in an Upland-Subordinate-RCG zone that was typical of a Tall-RCG zone, this area would provide favorable hydrology for water howellia in a microhabitat with no dense RCG growth (M. Rule, pers. comm.).

Potential for Ecological Differences Between Wetland Types

Although we cannot conclude that RCG performance and distribution along the upland-to-wetland gradient is different between wetland types, some measurements suggest that some ecological differences do exist between wetland types. The significantly thicker layers of coarse-organic soil in water howellia wetlands is particularly striking. These soils may produce better conditions for howellia than other types of substrate, or some environmental factor may be promoting both water howellia persistence and organic matter accumulation. Although draining and tillage of wetland soils is known to reduce organic matter content, the long interval since wetlands were reflooded makes it unlikely that differences from drainage persist today.

Howellia wetlands may have more coarse-organic soil due to increased organic matter inputs or to decreased decomposition rates. The greater frequency of deciduous *Populus tremuloides* trees around water howellia wetlands is one possible source of increased organic matter inputs. Decomposition rates of organic matter are lowest in areas with low temperatures and long inundations. We found that high organic matter accumulation occurred not just in water howellia wetlands, but also on north-facing aspects, which intercept less solar radiation. This suggests that water howellia wetlands may be cooler and wetter than RCG control wetlands. Temperatures could be reduced by shade-casting trees and shrubs, and smaller basins which would be disproportionately shaded by adjacent upland trees. As a third explanation, high organic matter content may reflect low rates of mineral sediment accumulation. Mineral sediments could come from surface runoff or surface water flow, which would be more important in wetlands with high hydrologic connectivity.

The higher standing crop of *Sparganium eurycarpum* (burreed) in water howellia wetlands may also suggest environmental or ecological differences between wetland types. One potential driver would be higher shade levels, although shade differences have not been measured in this study. Burreed may have a higher shade tolerance than RCG: the USDA NRCS PLANTS database classifies RCG as "intolerant" of shading, while *S. eurycarpum* is classified "intermediate" (USDA, NRCS 2007). In a study of other environmental conditions, Wolin and Mackeigan (2005) found that burreed performance was highest under treatments of standing water and high to moderate nutrient levels.

Implications for Reed Canarygrass Management

The general trend of our study showed few differences in the performance and distribution of RCG between wetland types, but significantly more Impaired-RCG zones in water howellia wetlands. Therefore, in this data set it appears that the presence of shading canopies and coarse woody debris are the most important difference between wetland types. Promotion of Impaired-RCG zones, such as coarse woody debris installation or native shrub and tree planting, could create microhabitats for successful water howellia growth. The effects of created Impaired-RCG zones conditions on water howellia performance could be a productive topic for a future experiment.

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Table 2. Impaired-RCG vegetation zones in the data set.

Wetland	**Transect**	**Length (meters)**	**Environmental Factor**			
			Coarse Woody Debris	Shrub Overhang	Canopy Overhang	Rock
Reed canarygrass control wetlands						
East Tritt	4	1	X			
McDowell A	3	2				X
Palmer North	2	5.8	X			
Palmer North	3	0.8	X			
Water howellia wetlands						
30 Acre	1	2.3	X			
Hale NE	1	1.2		X		
Hale NE	1	0.8		X		
Hale NE	3	1.8	X			
Lower Turnbull	3	10.9			X	
Lower Turnbull	3	2.5	X	X	X	
Lower Turnbull	3	6.6	X		X	
Howellia B North	1	2.6		X		
Howellia B North	2	2		X		
Howellia B North	2	7			X	
Howellia B North	4	2.2		X		
Turnbull South	1	2.8			X	
Turnbull South	1	1.5	X			
Howellia B South	1	2.2	X			X
Howellia B South	2	2.6	X			

Table 3. Reed canarygrass standing crop and environmental characteristics within vegetation zones.

	Upland	Upland-Subordinate-RCG	Upland-Lower-Stature-RCG	Tall RCG	Wetland-Lower-Stature-RCG	Wetland-Subordinate-RCG	Wetland	Impaired-RCG
Length (meters)	1	2.4	**5.3 RCG** **2.6 WH**	8	11	3.6	0.8	**0.4 RCG** **1.7 WH**
Proportion of Entire Transect	**3.4% RCG** **5.9% WH**	9.1%	13%	27%	26%	13%	4.0%	**0.9% RCG** **5.8% WH**
RCG Biomass (grams / m^2)	0	59.6	286	553	516	92.4	0	190
RCG Head Density (grams / m^2)	0	9.7	13.5	66.1	44.5	**16.6 RCG** **5.4 WH**	0	10.0
Percent of plots with RCG rooting at nodes	NA	1.2%	3.3%	52%	81%	**41% RCG** **19% WH**	NA	25%
Percent of plots with RCG forming root mats	NA	0%	0%	6.5%	38%	6.5%	NA	12%
Percent of plots with Grazed RCG	NA	0%	2.9%	7.6%	38%	6.6%	NA	6.3%
Mineral-type soil (cm in 12cm vertical profile)	10.1	10.1	9.4	5.2	2.4	1.7	0.9	5.3
Coarse-organic-type soil (cm in 12cm vertical profile)	0.1	0	0.4	2.4	**2.9 RCG** **4.9 WH**	**2.5 RCG** **4.9 WH**	**1.9 RCG** **4.9 WH**	1.7

*If values are significantly different between the two wetland types, averages for both types are presented. RCG = reed canarygrass control wetlands, WH = water howellia wetlands. For definitions of vegetation zones, please see Table 1.

Table 4. Reed canarygrass standing crop and native standing crop within vegetation zones.

	Upland	Upland-Subordinate-RCG	Upland-Lower-Stature-RCG	Tall RCG	Wetland-Lower-Stature-RCG	Wetland-Subordinate-RCG	Wetland	Impaired-RCG
RCG Biomass (grams / m^2)	0	59.6	287	553	516	92.4	0	190.2
RCG Head Density (heads / m^2)	0	9.7	13.5	66.1	44.5	**16.6 RCG** **5.4 WH**	0	10
Native Biomass (grams / m^2)	174	125	77.8	42.3	50.9	318	274	**0.0 RCG** **15.2 WH**
Native species per $0.0625m^2$ plot	3.4	3.5	2.1	1.1	1.1	1.6	1.3	0.8
Most abundant species (grams / m^2)	*Poa/Agrostis* 107	*Poa/Agrostis* 62.4	RCG 287	RCG 553	RCG 516	*Scirpus acutus* 142	*Scirpus acutus* 197	RCG 190
Second-abundant species (grams / m^2)	*Bromus* spp. 19.2	RCG 59.6	*Poa/Agrostis* 33.6	*Juncus balticus* 19.2	*Scirpus acutus* 22.4	RCG 92.4	*Typha latifolia* 44.8	*Symphoricarpos alba* 3.2
Third-abundant species (grams / m^2)	*Symphoricarpos alba* 16.0	*Juncus balticus* 33.6	*Juncus balticus* 24.0	*Carex vesicaria* 6.4	*Juncus balticus* 8.0	*Typha latifolia* 87.1	*Sparganium eurycarpum* 22.4	*Poa/Agrostis* 0.3
Sparganium eurycarpum biomass (grams / m^2)	0	0	0	0.6	4.4	**5.4 RCG** **48.2 WH**	21.0	0

*If values are significantly different between the two wetland types, averages for both types are presented. RCG = reed canarygrass control wetlands, WH = water howellia wetlands. For definitions of vegetation zones, please see Table 1.

Table 5. Coarse-organic soil in vertical profile within vegetation zones.

Vegetation Zone	**P value Wetland Type**	**P value Aspect**	**Coarse-Organic Soil in Vertical Profile (cm)**			
			North facing	South facing	East facing	West Facing
Upland	0.6039	0.5699	0.08			
Upland-Subordinate-RCG	0.4131	0.6118	0.02			
Upland-Lower-Stature-RCG	0.4677	0.2709	0.43			
Tall-RCG	0.5963	**0.0780**	3.63	1.51	2.81	3.15
Wetland-Lower-Stature RCG	**0.0234**	0.2296	3.05 RCG 4.96 WH			
Wetland-Subordinate-RCG	**0.0198**	**0.0009**	3.62 RCG 7.29 WH	2.22 RCG 4.05 WH	0.25 RCG 2.92 WH	3.61 RCG 5.60 WH
Wetland	**0.0113**	**0.0747**	2.50 RCG 8.20 WH	1.80 RCG 2.42 WH	0.33 RCG 4.80 WH	3.40 RCG 4.20 WH
Impaired-RCG	0.1193	NA	1.68			

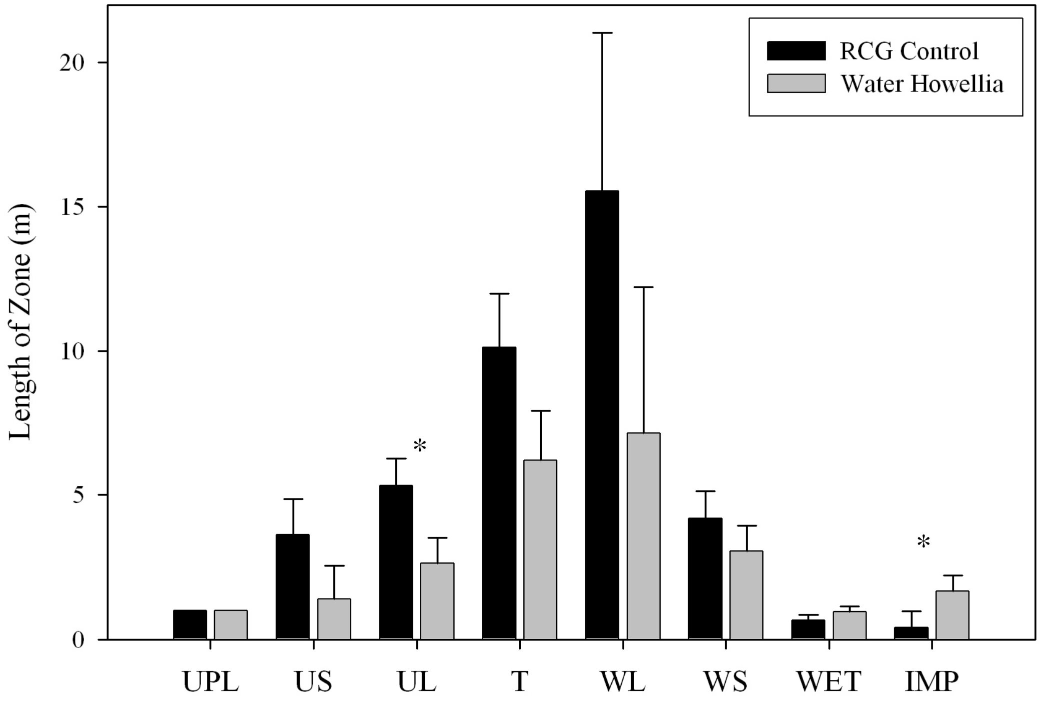

Figure 4. Mean vegetation zone length (± SE) for reed canarygrass control wetlands and water howellia wetlands. Asterisks indicate significant differences between wetland types. For abbreviations of vegetation zones, please see Table 1.

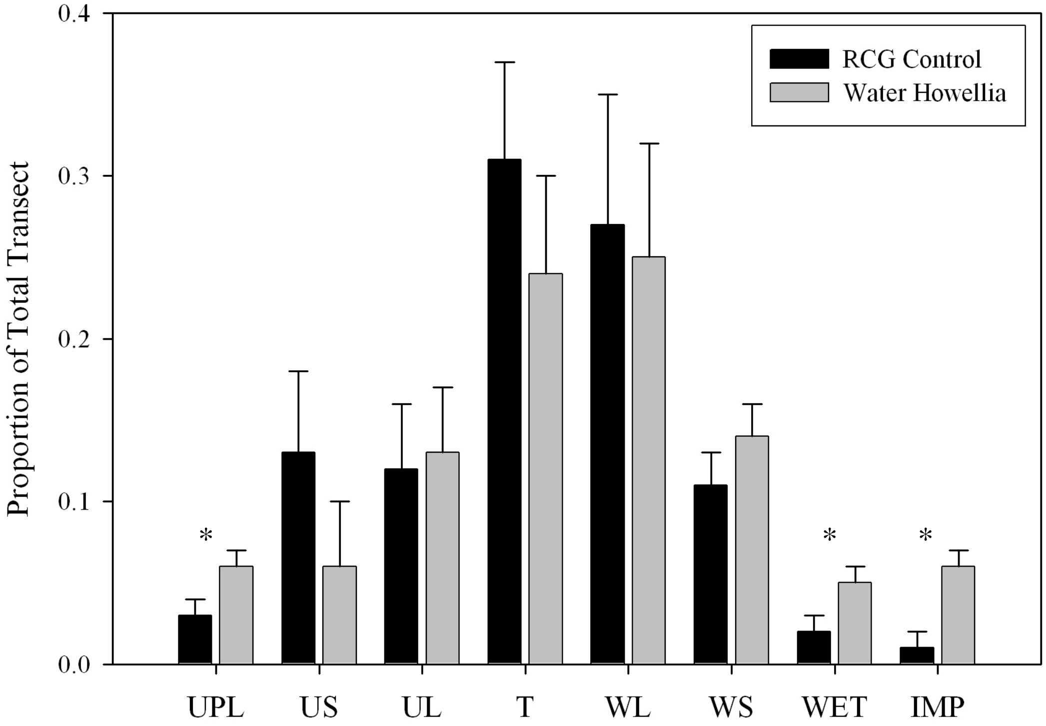

Figure 5. Mean vegetation zone proportion (± SE) for reed canarygrass control wetlands and water howellia wetlands. Asterisks indicate significant differences between wetland types. For abbreviations of vegetation zones, please see Table 1.

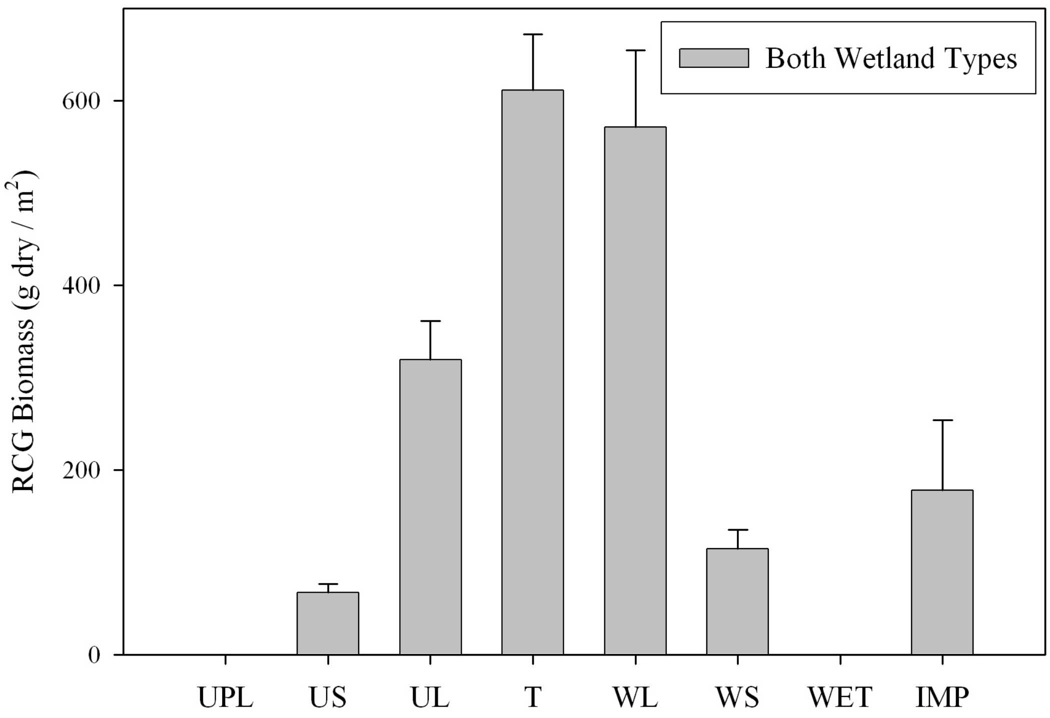

Figure 6. Mean reed canarygrass standing crop (+ SE) in each vegetation zone. There were no significant differences between wetland types, so average biomass for all wetlands is presented. For abbreviations of vegetation zones, please see Table 1.

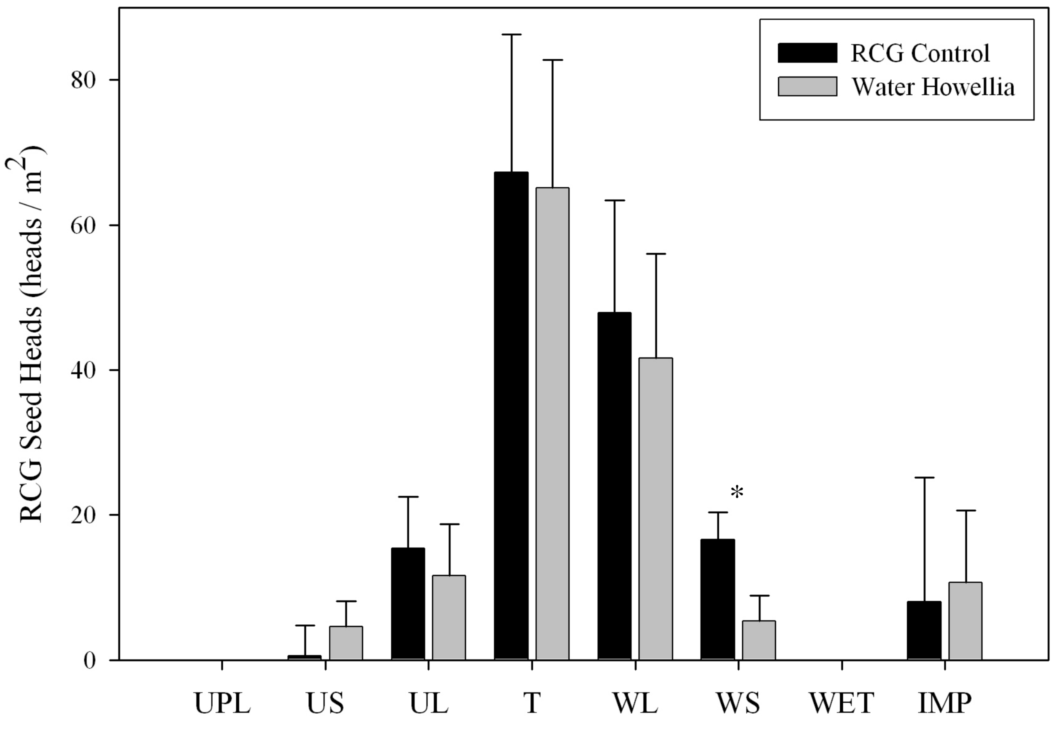

Figure 7. Mean reed canarygrass seed head density (+ SE) for vegetation zones in reed canarygrass control wetlands and water howellia wetlands. Asterisks indicate significant differences between wetland types. For abbreviations of vegetation zones, please see Table 1.

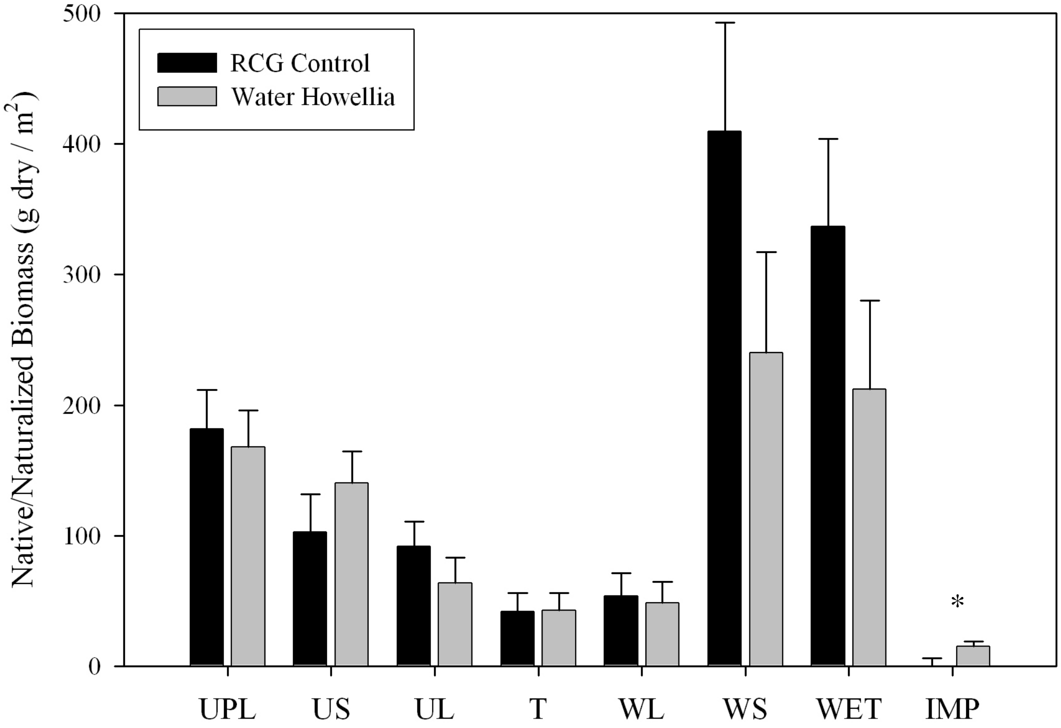

Figure 8. Mean native and naturalized standing crop (± SE) for vegetation zones in reed canarygrass control wetlands and water howellia wetlands. Significant differences between wetland types are indicated by an asterisk. For abbreviations of vegetation zones, see Table 1.

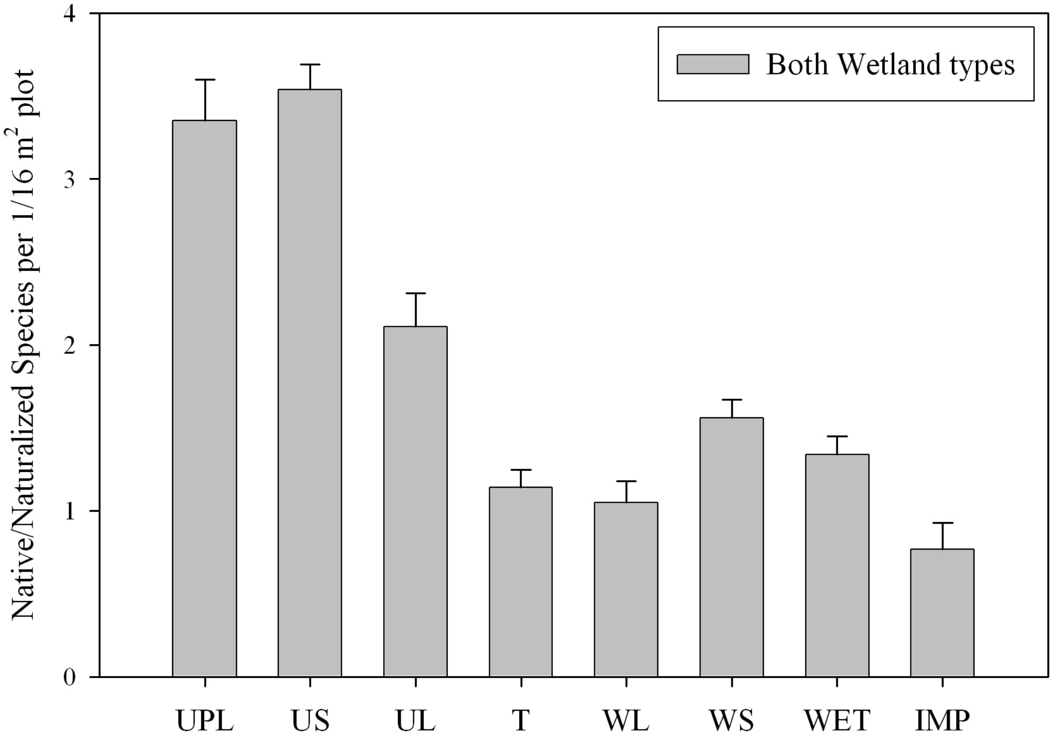

Figure 9. Mean native and naturalized species occurrences per 0.0625 m^2 sampling plot (± SE) in vegetation zones. There were no significant differences between wetland types, so average biomass for all wetlands is presented. For abbreviations of vegetation zones, please see Table 1.

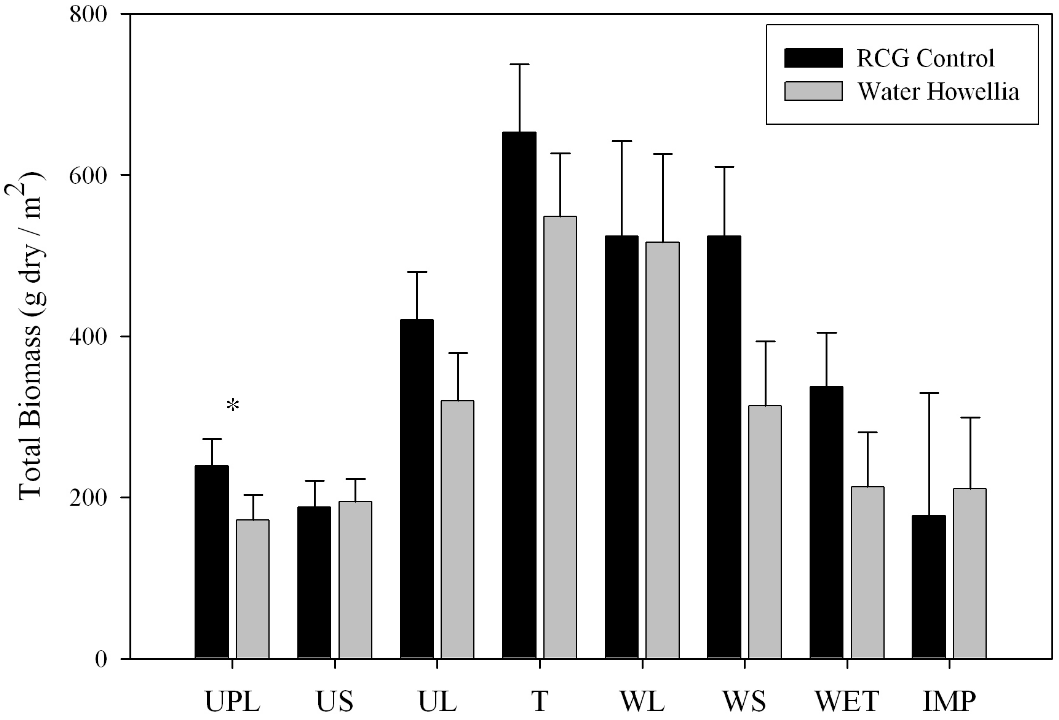

Figure 10. Mean total standing crop (± SE) for vegetation zones in reed canarygrass control wetlands and water howellia wetlands. Significant differences between wetland types are indicated by an asterisk. For abbreviations of vegetation zones, please see Table 1.

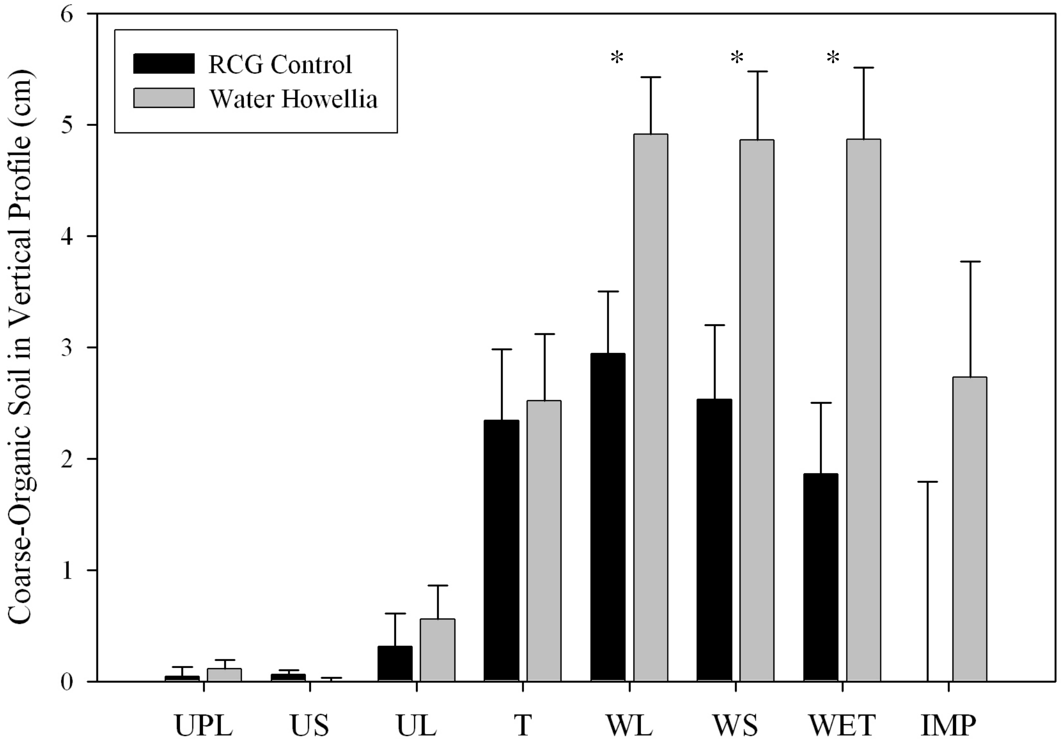

Figure 11. Mean coarse-organic type soil content (± SE) in vertical soil profiles for vegetation zones in reed canarygrass control wetlands and water howellia wetlands. Significant differences are indicated by an asterisk. For abbreviations of vegetation zones, please see Table 1.

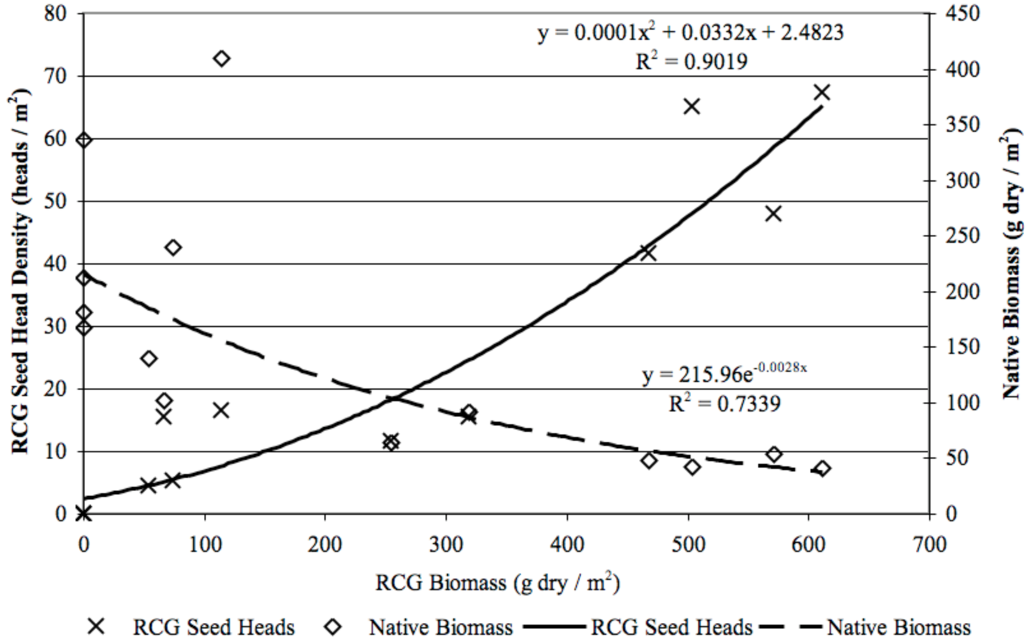

Figure 12. Positive polynomial correlation between reed canarygrass biomass and seed head density, with a negative exponential correlation between reed canarygrass biomass and native biomass. The correlation test was applied to average values in each vegetation zone for both wetland types for each variable.

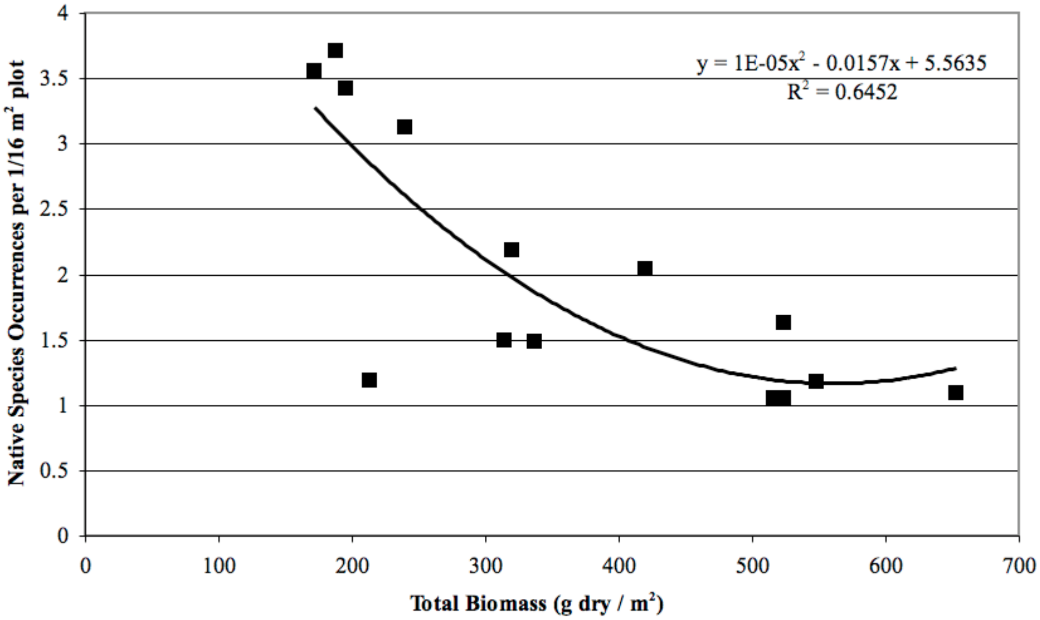

Figure 13. Negative polynomial correlation between total biomass and number of native species occurrences per 0.0625 m^2 sampling plot. The correlation test was applied to average values in each vegetation zone for both wetland types for both variables.