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The Impacts of Nutria on Vegetation in Oregon

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ABSTRACT: Nutria have been present in the Pacific Northwest for more than 70 years, and though their dramatic impacts on wetlands in the southeastern U.S. is well documented, the northwestern populations have been little studied. Using paired exclosure plots, nutria herbivory pressure on the native vegetation is shown to be considerable but dependent on species type and disturbance history. In coastal wetland habitats, nutria selectively feed on forbs compared to grasses, lowering their aboveground biomass. This study also shows opposing responses to nutria herbivory for disturbed and undisturbed plots, with nutria lowering total biomass in areas that have not experienced a biomass-clearing disturbance event and thus have diminished competition intensity.

KEY WORDS: competition, disturbance, herbivory, invasive species, *Myocastor coypus*, nutria, Pacific Northwest

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INTRODUCTION

Many critical ecological processes can be altered with the introduction of an invasive herbivore, including succession and the relative importance of competition. Invasive species have been shown to dramatically alter the natural succession of ecosystems after a disturbance (Vitousek and Walker 1989). Herbivory can also play an important role in succession, affecting the establishment and abundance of certain species (Kuijper *et al*. 2004, Wooten 2002), and Veblen *et al.* (1992) specifically linked an invasive herbivore to altered forest structure. Plant species' response to herbivory is variable (Focardi and Tinelli 2005) and not always negative. Though it often results in a decrease in fitness, proof of certain species' ability to overcompensate for herbivory is tenuous (Belsky 1986). Competition is another process that has been shown to affect flora's response to herbivory (Simons and Johnston 1999, Bergelson *et al.* 1996). Studies from the Gulf Coast suggest that nutria (*Myocastor coypus*) can affect large ecosystem processes such as succession and establishment, and they have been shown to affect species disproportionate to their abundance (in the south?) (Taylor and Grace 1995, Fuller *et al*. 1985, but see Chabreck *et al*. 1959 as cited in Fuller *et al*. 1985). Nutria's specific effects in the Northwest have not been adequately studied, however, nor have their effects on succession after a disturbance or in areas of differing competitive intensity.

Nutria

Nutria are large, nocturnal or crepuscular, semi-aquatic rodents (Witmer and Lewis 2001). Argentina, Bolivia, Chile, Brazil, Uruguay, and Paraguay all have native populations, but nutria are a worldwide invasive species, occurring in Europe and Southeast Asia and on every continent except Australia and Antarctica (Carter and Leonard 2002). The average adult nutria weighs more than the native muskrat (*Ondatra zibethica*) and less than the native beaver (*Castor canadensis*) (LeBlanc 1994). Their preferred habitat is freshwater marshes and wetlands with an adequate food supply (LeBlanc 1994). On the coasts of the U.S., they range from freshwater to brackish wetlands, avoiding the totally saltwater environment. Borgnia *et al.* (2000) illustrated that nutria activity is limited to 10 m from the water's edge. Guichon *et al.* (2003*b*) recorded nutria in the water for 99.8% of their feeding observations.

Nutria eat vegetation and consume 25% of their body weight each day (LeBlanc 1994). In their native habitat, nutria selectively forage on hygrophyllic monocotyledons (Guichon *et al*. 2003*b*). Willner *et al*. (1979) published that roots were the most abundant portion of their diet, and in Maryland 88% of it was semi-aquatic plants. Nutria will eat *Eleocharis* spp. and *Hydrocotyle* spp. in freshwater environments and *Scirpus olneyii* in brackish or intermediate areas of the Gulf Coast (Marx *et al*. 2004). Wentz (1971) demonstrated that *Salix* spp. were the largest part of their diet, and *Saggittaria latifolia* and *Polygonum* spp. were selectively foraged in the Willamette Valley of Oregon. Nutria will also eat farm crops such as sugarcane and rice when the crops are close enough to the water (Marx *et al*. 2004, LeBlanc 1994).

Dixon *et al.* (1979) found that temperature and snowfall have a negative effect on weight. Guichon *et al.* (2003*a*) recorded substantial mortalities when there were consecutive days of frost. Willner *et al.* (1979) showed that low temperatures resulted in low mean litter sizes, and that 90% of nutria in the Blackwater Wildlife Refuge were killed by the severe 1976-1977 winter. This dramatic decline was corroborated by Gosling (1989) and Doncastor and Micol (1990).

Nutria Impacts

Nutria are being blamed for a myriad of environmental problems, varying somewhat by region. The possibility of nutria as vectors for diseases has been studied. Dulap and Theis (2002) showed that high percentages of nutria carry *Giardia lamblia*, and Menard *et al.* (2001) examined nutria as a reservoir for *Fasciola hepatica*. Anecdotal information points to nutria having a negative effect on the native muskrat population (Witmer and Lewis 2001), which was an observation reported by muskrat trappers as long ago as the 1950s. In Maryland, nutria foraging is causing a decrease in the habitat for waterfowl, songbirds, and wetland birds (Reshetiloff 2004).

One extreme example of the impact of nutria is highlighted by the aerial surveys done by the Fur and Refuge Division of the Louisiana Department of Wildlife and Fisheries. Starting in 1993, these flights in the southeastern part of the state showed that 60,000 acres were damaged by nutria foraging, and that damage had increased to 100,000 acres by the end of the 1990s (Marx *et al*. 2004). In Maryland, another state heavily affected by nutria, the Pautuxent Wildlife Research Center and Blackwater National Wildlife Refuge (NWR) are also experiencing staggering wetland loss. At the Blackwater NWR, 6 mi^2 of marsh have been lost to open water, and more than half of the remaining marsh has significant damage (PWRC 1999).

Invasive species have been shown to dramatically alter the species composition and abundance of native species in their invaded ecosystem (for overview see Vitousek *et al*. 1997). The specific effects of nutria on vegetation can be widespread and vary in impact (Marx *et al*. 2004, Blair and Langlinais 1960). Much of the important research has come from studies in various Louisiana coastal wetlands. Nutria have been shown to significantly alter the aboveground biomass in exclosure experiments (Ford and Grace 1998, Taylor and Grace 1995, Fuller *et al*. 1985). They also have been shown to influence the species composition in the research areas, both decreasing and increasing species diversity (Taylor and Grace 1995). In some cases, nutria overfeeding has lead to local extinction of species (Gosling 1989, Wentz 1971). Detailed analyses of nutria diets at Argentina lakesides, Louisiana freshwater forested habitats, and wetlands in central Oregon found their diet varied considerably by season and certain species of plant were eaten disproportionately (Guichon *et al*. 2003*b*, Wilsey *et al*. 1991, Wentz 1971). Nutria also significantly lower belowground root production in grazed plots when compared to exclosed ungrazed plots (Ford and Grace 1998).

STUDY SITE

One of the main goals of the Oregon Coast National Wildlife Refuge is to preserve habitat for migratory birds, specifically several subspecies of the Canada goose (*Branta canadensis*). This mission results in preserving many lowland, riverside land parcels and thus is an appropriate place to study the marsh-dwelling nutria. The refuge was also selected as the study site because of the long-term presence of nutria. Further, the refuge's managers were interested and helpful.

Nestucca Bay and Siletz Bay Wildlife Refuges were chosen as study sites for their presence and absence, respectively, of nutria. Nestucca Bay is a tidal marsh that has been turned into pasture through the creation of a berm and a tidal gate, limiting the range in water levels caused by the tide. Nestucca Bay had an established nutria population in 1959 (Wentz 1971) and also had a field that was not going to be used for pasture or harvested throughout the summer of 2005. Siletz Bay, about 20 mi south of Nestucca Bay, is characterized by a tidally influenced slough with a constant influx of fresh water that connects to the Siletz River just to the west of the study plots. It does not contain nutria, but the onsite manager and personal observation confirm that beaver do utilize the area, thus establishing it as a more natural comparison to Nestucca Bay's ecosystem with invasive nutria. Other native fauna likely occurring at both locations include river otters (*Lutra canadensis*), elk (*Cervus canadensis*), and various small rodents.

METHODS

Exclosures are often used to evaluate the effect of an animal's herbivory impact. With nutria, exclosures previously have been used in Louisiana with robust results (Ford and Grace 1998, Taylor and Grace 1995). Our study created 48 study plots, 24 each at Nestucca and Siletz Bays. Half of these plots were fenced (referred to as treatments), and the other 12 (control) plots were not. The control and treatment plots were paired and never more than 3 m from each other. Six of the treatment/control pairs at both Nestucca and Siletz Bays were harvested of all aboveground biomass at the start of the project in mid-May. All 48 plots were harvested of all aboveground biomass in mid-August of the same year.

The treatment plots were fenced below ground with 2-in mesh chickenwire 20 cm (8 in) downward and 5 cm (2 in) outward, and to a height of 60 cm (24 in) above the ground. The fences enclosed a 2×3-m area, creating a 0.5-m buffer around the 1×2-m size of all study plots. All plots were closer than 8 m to the water. The biomass samples collected from each site were sorted into species and placed into a drying oven at 70ºF. Their final weight was recorded after their weight had ceased dropping for more than a day.

Root-core samples were taken in May and August in all plots. In May, we used a borer to create a 2.5-cm-wide, 15-cm-deep core of soil in the center of the plot. The hole was replaced with sand, and in August it was re-cored to measure the root in-growth of the surrounding vegetation (Ford and Grace 1998). The roots were sifted from the dirt or sand for all samples and then dried at 70ºF until a stable weight was obtained.

RESULTS

There was no significant difference between Siletz and Nestucca's May root mass measurements ($p = 0.288$) (Table 1), establishing the sites as similar and acceptable for comparisons. Examinations of Nestucca Bay plots reveal no significant differences in the average root mass, but there is a trend when the harvested sites are examined. Within the harvested plots, the largest average weight switches from May control plots to August treatment plots. The status of the plot as treatment or control had very little predictive power (ANCOVA, $p = 0.717$) within the plots not harvested in May. The effect of nutria herbivory is more pronounced, though not significant (ANCOVA, $p = 0.362$), in the harvested plots.

Diversity was not significantly affected by the herbivory of nutria over the 3 months of the project. Two-way ANOVAs showed no difference between Nestucca and Siletz Bays ($p = 0.319$), nor between treatments and controls ($p = 0.617$). Using May diversity as a covariate, Nestucca Bay treatment and control plots

Table 1. Root mass measurements (g) of Nestucca (with nutria) and Siletz (without nutria) study plots, means are shown with SE. Harvested and nonharvested rows show the differing disturbance history of the plots. Measurements for treatment and control groups were taken in May initially, and at the end of the project in August.

	Root Mass Measurements (g)			
	May Control	May Treatment	August Control	August Treatment
All Nestucca Plots (*n*=12)	0.90 ± .80	0.83 ± .74	0.09 ± .08	0.10 ± .09
Harvested (*n*=6)	1.20 ± .15	1.03 ± .22	0.09 ± .02	0.15 ± .07
Not Harvested (*n*=6)	0.61 ± .11	0.63 ± .10	0.09 ± .03	0.04 ± .02
All Siletz Plots (*n*=12)	1.66 ± .16	1.53 ± .14	0.11 ± .04	0.16 ± .06
Harvested (*n*=6)	1.72 ± .18	1.84 ± .22	0.09 ± .03	0.11 ± .05
Not Harvested (*n*=6)	1.34 ± .27	1.48 ± .16	0.13 ± .07	0.21 ± .10

Table 2. ANOVAs significance tests within treatments and within controls of plot biomasses when divided into forbs and grasses. * denotes p < 0.05 and *n.s.* denotes p > 0.05. Top boxes are the initial conditions of the 6 harvested plots, and bottom box is for all 12 plots. Plot mean biomass for forbs and grasses is also given.

May Plots (*n*=6)	**Mean Biomass (g)**	**May Control Forbs**	**May Treatment Forbs**
		167.55	143.67
May Control Grasses	433.57	*n.s.*	
May Treatment Grasses	463.19		*

August Plots (*n*=12)	**Mean Biomass (g)**	**August Control Forbs**	**August Treatment Forbs**
		256.48	377.5
August Control Grasses	420.55	*	
August Treatment Grasses	389.51		*n.s.*

are not different (p = 0.895), and May diversities are not a useful predictor of August diversities (p = 0.580). Two-way ANCOVA of site and treatment/control using May diversity as the covariate yields no significant differences in any of the variables. The R^2 for this test is 0.15; there is a lot of variation in the plot diversities that is not being captured in this test.

Cursory tests of the biomasses of the plots showed no significant effect of nutria herbivory pressure. Two-way ANOVA of site (Siletz Bay or Nestucca Bay) and treatment/control shows no significance of either variable (p = 0.570 and p = 0.990, respectively). At Siletz Bay, there was significantly less biomass in August compared to May (two-way ANCOVA, p > 0.001), but there were no differences in treatment or control status (two-way ANCOVA, p > 0.896), showing that native herbivores are not having a significant impact on the wetland vegetation.

Personal observations and previous studies (Guichon et al. 2003*b*, Ford and Grace 1998, Wentz 1971) show that nutria selectively eat particular species. When the biomass measurements are partitioned into grasses (including sedges and rushes) and forbs, some very important differences come to light. In the May data, one-way ANOVAs show there were significantly more grasses in the treatment plots (p = 0.008), and no differences in the control plots (p = 0.054) (Table 2). In August, however, there were significantly less forbs in the control plots (p = 0.029) and no difference within the treatment plots (p = 0.92). Forbs in the treatment plots have become more equal to grasses, and in the control plots they have become less equal to grasses.

A plot's condition as harvested or nonharvested in May also predicts differing reactions to nutria herbivory. In the 6 plots that were harvested, two-way ANOVAs of type (forb or grass) and status (treatment or control) variables show that type (p = 0.178) is by far more important than whether it was within a fence or without (p = 0.529) (Figure 1). The opposite is true in the 6 plots not harvested in May. Here, the status of the plot as treatment or control is most significant (p = 0.077) and the type is much less (p = 0.492).

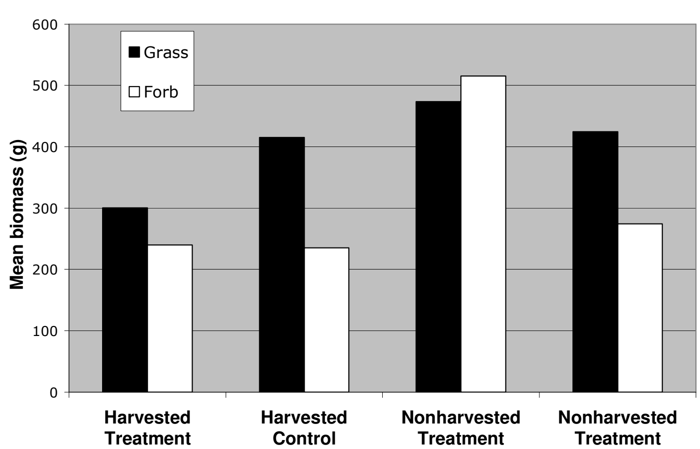

Figure 1. Mean biomass of grasses compared to forbs in harvested and nonharvested control and treatment groups.

DISCUSSION

The impact of herbivory on root productivity is not fully understood. Many greenhouse experiments show a decrease in root growth with increased herbivory (Smith and Schowalter 2001), but field experiments are rare. Grasses have been shown to react positively to belowground herbivory (Bardgett *et al*. 1999) and not at all to aboveground herbivory (McNaughton *et al*. 1998), which might be masking decreased root growth by the forbs in the plots. Harvested plots have a larger difference in aboveground forb and grass weights than nonharvested plots, and root mass impact of nutria is most pronounced in these harvested plots.

When total biomasses are considered, the variability in plots and the disproportionate contribution of grass species such as *Juncus balticus* and *Phalaris arundinacea* to the final dry biomass drown out the herbivory effect of nutria. The selective pressure of nutria herbivory on forbs becomes evident when plots are grouped by species type. When nutria herbivory pressure is removed, forbs increase in total biomass, and in places where nutria forage, they detrimentally affect forbs and not grasses.

The debate about plant response to herbivory has attracted the attention and drawn the output of many scientists. Although plant overcompensation due to herbivory has been claimed in many instances, it is a difficult reaction to capture (Belsky 1986). When the variable of competition is added, herbivory responses become even more particular and varied (Millet *et al*. 2005, Ohgushi 2005). In this experiment, the comparison of harvested to nonharvested plots highlights the varying effect of competition when coupled with the pressure of herbivory from an invasive species. Disturbances have been shown to reduce competition (Lenssen *et al*. 2004, Wilson and Tilman 1993), therefore the simulated aboveground biomass clearing disturbance event effectively reduces the competition within those plots. Figure 1 illustrates that in plots that have undergone a disturbance event, nutria herbivory pressure selectively decreases forbs but does not affect the recovery of grasses. In contrast, flora in nonharvested plots do not have an essentially non-competitive slate to recover from, and here is where nutria are lowering the aboveground biomass of both grasses and forbs alike. These responses to herbivory and competition are in line with those predicted by the Compensatory Continuum Hypothesis (Machinski and Whitham 1989), where only plants with high nutrient availability and without competition are able to overcompensate for herbivory. Nutria had a bigger impact on forbs in plots that are already stressed by an aboveground biomass clearance event, and had a greater overall effect on biomass where competition is an important force.

Phalaris arundinacea is a large invasive grass present in many coastal Oregon wetlands. It creates monotypic stands and can dominate wetlands (Foster and Wetzel 2005) and is a concern to land managers in this area. The impact of invasive nutria on invasive *P. arundinacea* is not known but could be affecting the grass in several ways. Many studies championing the enemy-release hypothesis have shown that native herbivores give invasive plants a competitive advantage over the native plants on which they forage (Dietz *et al*. 2004). Siemann and Rogers (2003) show how the competitive ability of an invasive plant can be limited by invasive herbivores from the plant's native range. In Nestucca Bay, it appears that nutria herbivory is exacerbating the abundance of *P. arundinacea* because control plots contained greater than ⅓ more biomass of the species than treatment plots after being fenced for the 3 months of the project. It is possible that by eliminating nutria herbivory, the native vegetation would be better able to re-establish, but there is not enough initial information from the May plots to corroborate this suggestion.

CONCLUSION

Nutria are having important consequences for the wetlands of the Pacific Northwest region, in addition to the Gulf Coast and mid-Atlantic regions. In the short time span of this project, the negative impact of nutria herbivory on the wetland forbs is evident. The large effect of herbivory in plots with more competition shows that site history as well as the plant community structure influence its response to browsing. The combination of these nutria effects on forbs and more competitive areas could lead to altered paths of succession on the coastal wetlands and to local rarity or extinction of some species.

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LITERATURE CITED

BARDGETT, R. D., C. S. DENTON, AND R. COOK. 1999. Below-ground herbivory promotes soil nutrient transfer and root growth in grassland. Ecol. Letters 2:357-360.

BELSKY, A. J. 1986. Does herbivory benefit plants? A review of the evidence. Amer. Nat. 127(6):870-892.

BERGELSON, J., T. JUENGER, AND M. J. CRAWLEY. 1996. Regrowth following herbivory in *Ipomopsis aggregeta*: compensation but not over-compensation. Amer. Nat. 148(4):744-755.

BLAIR, R. M., AND M. J. LANGLINAIS. 1960. Nutria and swamp rabbit damage on *Taxodium distichum* seedlings. J. For. 58: 388-389.

BORGNIA, M., M. L. GALANTE, AND M. H. CASSINI. 2000. Diet of the coypu (nutria, *Myocastor coypus*) in agro-systems of the Argentina pampas. J. Wildl. Manage. 64:354-361.

CARTER, J., AND B. LEONARD. 2002. A review of the literature on the worldwide distribution, spread of, and efforts to eradicate the coypu (*Myocastor coypu*). Wildl. Soc. Bull. 30:162-175.

DIETZ, H., L. R. WIRTH, AND H. BUSCHMANN. 2004. Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahé, Seychelles. Biol. Invas. 6(4):511-521.

DIXON, K. R., G. R. WILLNER, J. A. CHAPMAN, W. C. LANE, AND D. PURSLEY. 1979. Effects of trapping and weather on body weights of feral nutria in Maryland. J. Appl. Ecol. 16(1):69-76.

DONCASTER, C. P., AND T. MICOL. 1990. Response by coypus to catastrophic events of cold and flooding. Holarct. Ecol. 13:98-104.

DULAP, B. G., AND M. L. THEIS. 2002. Giardia in beaver *Castor canadensis* and nutria *Myocastor coypu* from east Texas. J. Parasit. 88(6):1254-1258.

FOCARDI, S., AND A. TINELLI. 2005. Herbivory in a Mediterranean forest: browsing impact and plant competition. Acta Oecol. 28:239-247.

FORD, M. A., AND J. B. GRACE. 1998. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation, and soil elevation changes in a coastal marsh. J. Ecol. 86(6):974-982.

FOSTER, R. D., AND P. R. WETZEL. 2005. Invading monotypic stands of *Phalaris arundinacea*: a test of fire, herbicide, and woody and herbaceous native plant groups. Restor. Ecol. 13(2):318-324.

FULLER, D. A., C. E. SASSER, W. B. JOHNSON, AND J. G. GOSSELINK. 1985. The effects of herbivory on vegetation on islands in Atchafalaya Bay, Louisiana. Wetlands 4:105-114.

GOSLING, L. M. 1989. Extinction to order. New Scientist 121: 44-49.

GUICHON, M. L., V. B. BENITEZ, A. ABBA, M. BORGNIA, AND M. H. CASSINI. 2003*a*. Foraging behavior of coypus (*Myocastor coypus*): why do coypus consume aquatic plants? Acta Oecol. 24:241-246.

GUICHON, M. L., C. P. DONCASTER, AND M. H. CASSINI. 2003*b*. Population structure of coypus (*Myocastor coypus*) in their region of origin and comparison with introduced populations. J. Zool. Soc. Lond. 261:265-272.

KUIJPER, D. P. J., D. J. NIJHOFF, AND J. P. BAKKER. 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. Oecol. 141:452-459.

LEBLANC, D. J. 1994. Nutria. Pp. B71-B80 *in:* S. E. Hygnstrom, R. M. Timm, and G. E. Larson (Eds.), Prevention and Control of Wildlife Damage. Nebraska Coop. Extension Service, Lincoln, NE.

LENSSEN, J. P. M., H. M. VAN DER STEEG, AND H. KRONS. 2004. Does disturbance favor weak competitors? Mechanisms of changing plant abundance after flooding. J. Vegetat. Sci. 15:305-315.

MACHINSKI, J., AND T. G. WHITHAM. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. Amer. Nat. 134(1):1-19.

MARX, J., E. MOUTON, AND G. LINSCOMBE. 2004. Nutria harvest distribution 2003-2004 and a survey of nutria herbivory damage in coastal Louisiana in 2004. Fur and Refuge Div., Louisiana Dept. of Wildlife and Fisheries. 45 pp.

MCNAUGHTON, S. J., F. F. BANYIKWA, AND M. M. MCNAUGHTON. 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology 79(2):587-592.

MENARD, A., A. AGOULON, M. L'HOSTIS, D. RONDELAUD, S. COLLARD, AND A. CHAUVIN. 2001. *Myocastor coypu* as a reservoir host of *Fasciola hepatica* in France. Vet. Res. (Paris) 32(5):499-508.

MILLETT, J., P. MILLARD, A. J. HESTER, AND A. J. S. MCDONALD. 2005. Do competition and herbivory alter the internal nitrogen dynamics of birch seedlings? New Phytol. 168:413-422.

OHGUSHI, T. 2005. Indirect interaction web: herbivore-induced effects through trait change in plants. Ann. Rev. Evol. Syst. 36:81-105.

PWRC. 1999. South American nutria destroy marshes. Fact Sheet 1999-01, Patuxent Wildlife Research Center, Biological Resources Div., USGS, Dept. of the Interior. 1 p.

RESHETILOFF, K. 2004. Some victories in nutria battle. P. 20 in Refuge Update, Vol. 1 No. 1 Jan/Feb), National Wildlife Refuge System, U.S. Fish & Wildlife Service, Arlington, VA.

SIEMANN, E., AND W. E. ROGERS. 2003. Increased competitive ability of an invasive tree maybe limited by an invasive beetle. Ecol. Applic. 13(6):1503-1507.

SIMONS, A. M., AND M. O. JOHNSTON. 1999. The cost of compensation. Amer. Nat. 153(6):683-687.

SMITH, J. P., AND T. D. SCHOWALTER. 2001. Aphid-induced reduction of shoot and root growth in douglas-fir seedlings. Ecol. Entomol. 26(4):411-416.

TAYLOR, K. L., AND J. B. GRACE. 1995. The effects of vertebrate herbivory on plant community structure in the coastal marshes of the Pearl River, Louisiana, USA. Wetlands 15(1):68-73.

VEBLEN, T., M. MERMOZ, C. MARTIN, AND T. KITZBERGER. 1992. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. Conserv. Biol. 6(1):71-83.

VITOUSEK, P. M., C. M. D'ANTONIA, L. L. LOOPE, M. REJMANEK, AND R. WESTBROOK. 1997. Introduced species: a significant component of human caused global change. NZ J. Ecol. 21:1-16.

VITOUSEK, P. M., AND L. R. WALKER. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecol. Monogr. 59:247-265.

WENTZ, W. A. 1971. The impact of nutria (*Myocastor coypus*) on marsh vegetation in the Willamette Valley, Oregon. M.S. thesis, Oregon State University, Corvallis. 41 pp.

WILLNER, G. R., J. A. CHAPMAN, AND D. PURSLEY. 1979. Reproduction, physiological responses, food habits, and abundance of nutria in Maryland marshes. Wildl. Monogr. 65:1-43.

WILSEY, B. J., R. H. CHABRECK, AND R. G. LINSCOMBE. 1991. Spatial and seasonal variation in nutria (*Myocaster coypus*) diets in forested wetlands of Louisiana. Wetlands 11:263-278.

WILSON, S. D., AND D. TILMAN. 1993. Plant competition and resource availability in response to disturbance and fertilization. Ecology 74(2):599-611.

WITMER, G. W., AND J. C. LEWIS. 2001. Introduced wildlife of Oregon and Washington. Pp. 423-443 *in*: D. Johnson and T. O'Neil (Managing Directors), Wildlife Habitat Relationships in Oregon and Washington. Oregon State Univ. Press, Corvallis, OR.

WOOTEN, J. T. 2002. Mechanisms of successional dynamics: consumers and the rise and fall of species dominance. Ecol. Res. 17:249-260.