The Effects Of Exotic Plant And Animal Species On Nature Preserves

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During the age of exploration and colonization, from the 15th to the 20th centuries, travelers and businessmen transferred all kinds of living creatures from their native habitats to other "suitable" homes, sometimes continents away. Insects, fungi, and weedy plants obtained free rides in shipments of grain or on the backs of livestock, then spread from ports and towns into the surrounding countryside. Introductions were made for agricultural and horticultural purposes and, in the case of game species, to improve hunting or fishing. Sailors, hoping to establish dependable supplies of meat, deposited hogs and goats on oceanic islands. The result, worldwide, has been an unprecedented mixing of long-separated flora and fauna, a number of commercial successes, and a great variety of resource management problems (Elton 1958).

Nature reserves are vulnerable to problems with introduced species for several reasons:

1) Preserves often contain sensitive or endemic biotic communities which are easily occupied by invaders and modified by disturbance.
2) Preserve management often restricts most means of artificial population control, such as hunting and pesticide application.
3) Preserves are often remote or roadless, making monitoring and removal of invaders difficult.
4) New preserves often begin with dozens of recent invaders already present and influencing ecosystem structure but without any plans for removing or controlling these species.
5) Parts of a preserve may have been modified by man then suddenly released from human use without any management to correct past damage or change.
6) Species which are vigorous invaders can establish themselves in fields, gardens or game farms outside a preserve and can then invade along roads or over boundaries.

The purpose of this paper is to briefly review the impacts of exotic species in preserve environments.

DEFINITION OF AN EXOTIC:

The first problem for a preserve manager is: What is an exotic species? Invasion and colonization are, after all, natural processes which operate in terrestrial and aquatic ecosystems and continue to influence biotic community structure even when there is no human interference.

In the U.S., preserve managers often designate species present prior to Columbus's arrival as "native" and species brought by European, Asian or African colonists after 1492 as "exotic". Dependence on man is not by itself an indication of exotic status since some native domestic or weedy species have coevolved with agriculture. The manager, therefore, needs to distinguish: 1) native wildland species, usually those taxa in place since the last major climatic or environmental change, 2) "natural" invaders, those taxa which have expanded their ranges without the aid of man, 3) indigenous agricultural or man-dependent species, taxa which have evolved in the region or have long associations with local cultures, 4) exotic agricultural or man-dependent species, taxa which are recent introductions and were not developed in their present form in the region, 5) exotic wildland species, taxa which are indigenous to another region and were introduced by man's activity, either intentionally or accidently. If possible the approximate date of the introduction should also be determined. A nature preserve might designate species as pre-Columbian, pre-preserve (brought in by European settlers) and post-preserve (recent invaders and accidental introductions of park managers).

THE IMPACTS OF EXOTIC SPECIES:

For an exotic species to be successful, it must be a superior competitor in its new environment. Often an exotic is "too superior", reproduces explosively, overruns its potential habitat and causes major modifications in ecosystem composition and function. Since the goal of most nature preserves is to protect the native biota and to preserve examples of functioning natural ecosystems, the abrupt changes induced by exotic invasion are usually considered undesirable.

It is important for the preserve manager to recognize that only a few exotics are likely to become problem species. Most, if not all, of the U.S. National Parks support exotic species, but only some park areas report management difficulties with exotics, and of the hundreds of non-native species present, only a few are mentioned in National Park Service natural resources management plans. In the Great Smoky Mountains National Park for example, there are about 1,500 vascular plant species present, about 400 of which are thought to be of European or Asian origin. Of these, less than 10 are thought to be spreading or otherwise threatening park resources, and only one, kudzu, (*Pueraria lobata*), is presently subject to annual control efforts. A majority of the exotic plants in the park occupy roadsides, lawns or open fields, or are found around abandoned house sites and are thus directly associated with recent man-caused disturbances. When natural successional processes close the canopy over these disturbed sites, few of the exotic plants are strong competitors, and their populations slowly disappear.

The exotic species present in preserves do not always spread into "natural areas" or into undisturbed sites but may concentrate around visitor centers, staff housing areas and along mowed roadsides. From a managerial perspective, a majority of these species are more of an aesthetic intrusion than a biological threat, but they may be considered undesirable because 1) they give the park visitors a false impression of the native biota, 2) they may not be representative of the appropriate "natural or historic scene" and 3) they may inhibit return of native species to disturbed areas. Exotic species which are unable to spread from man-created habitats can also serve as reservoirs for parasites or diseases which infect native species, for example Chinese chestnut.

Successful exotic invaders of natural areas can by contrast influence any process or biological characteristic of a functioning preserve ecosystem. This includes all trophic relationships (herbivore, detritavore, or predator-prey), interspecific competition, primary and secondary succession, nutrient cycling, system productivity, system diversity and system stability. Equally important, but often ignored, are changes in biogeophysical processes, substrate deposition, soil formation and erosion, solar insulation, hydrologic balance and disturbance frequency.

Exotics vary in the type and degree of ecosystem impact, but even a species specific pathogen can affect all major ecosystem components, especially if its host is a community dominant. The balsam woolly aphid (*Adeleges picea*), for example, is an insect accidently imported from Europe that infests only one plant species, the Frasier fir (*Abies fraseri*) in Great Smoky Mountains National Park. The aphid is a virulent pest, killing almost 100% of the mature fir in an infected stand. Since the fir occurs at high elevations where there are only two other important canopy trees, red spruce (*Picea rubens*) and yellow birch (*Betula lutea*), the initial impact of aphid invasion is to remove a high percentage of the trees in mixed spruce-fir stands and to completely topple the ridge top stands of pure fir.

The most noticeable effects on species other than fir are physical. The dead fir knock over other trees and create canopy gaps making the forest vulnerable to further windfall. The light opening initiates a succession which varies with the location but is often dominated by head-high blackberry bushes (*Rubus* spp.). Shade-tolerant herbs, including the Smokies' endemic Rugel's ragwort (*Senecio rugelia*), decline in the understory while light-tolerant ferns and grasses increase. The fallen trees temporarily remain in thick, tangled piles which become a fire hazard when dry due to the relatively slow decay rates at high elevations (1,500 to 2,000m). (Hay et al. 1978, Eager 1978, Johnson 1977.) The same type of system effects have occurred as a result of the chestnut blight, and, in that case, the loss of a major mast (autumn fruits) producer has influenced the movements, habitat preferences and probably the population densities of large animals such as black bear (*Ursus americana*).

Exotic Plant Species, Competition and Displacement of Native Species

Among the ecosystem effects of exotic plant species, competition with and displacement of native species are the most frequent complaints of preserve managers. These impacts may be moderate; a few individuals of the exotic scattered through a native plant community; or in the case of a very aggressive species such as the kudzu (*Pueraria lobata*), the impacts may be so great that community composition is completely altered. At Cumberland Gap National Historic Park (Kentucky-Tennessee-Virginia), state maintenance crews planted kudzu on road-cuts in order to quickly establish vegetation cover and prevent soil erosion. Decades later, the kudzu not only still dominates the steep banks but is slowly displacing adjoining forest. The kudzu affects all the strata of the forest - tree canopy, shrub layer and herb layer - and prevents native successional species from occupying open habitats. Tree species such as sumac (*Rhus* spp.), pines (*Pinus* spp.) and tulip tree (*Liriodendron tulipifera*), which normally invade open sites and old fields, cannot survive under the dense layer of kudzu leaves. Thus the banks remain in a perpetual "exotic dis-climax" (Butler et al. 1981).

Thomas (1980), in a series of experimental manipulations of exotic plants growing in the temperate deciduous forests and marshes of Theodore Roosevelt Island (District of Columbia), found that growth rates of the exotics differed both between species and in different habitats. Japanese honeysuckle (*Lonicera japonica*) in a cleared understory habitat, added the greatest annual biomass increment followed by English ivy (*Hedera helix*) in upland sites. The ivy was the only species that was fairly evenly distributed among all the available habitats. In plot-weeding experiments, where all the plants of a particular exotic were removed from a study plot but other species were left, Thomas (1980) found that the ivy had a greater influence on native herbs than on woody plants, whereas the opposite was true for Japanese honeysuckle. The overall impact of both vine species, however, was "to destroy the (indigenous) forest".

Exotic plants may decrease or increase the total biomass or productivity of a site and often decrease the plant species diversity. A kudzu-dominated slope at Cumberland Gap National Historic Park, for example, supports from 0 to 5 native woody plant species. A normal forest stand in the area would support from 10 to 28. Where the Cajeput tree, (*Melaleuca quinquenervia*) has invaded wet prairie or marshes in south Florida (including Everglades National Park and Big Cypress National Preserve) plant species diversity may decrease from 60% to 80%. The Australian pine (*Casuarina equisetifolia*) so thoroughly inhibits native species in the Everglades that groves of this exotic tree have almost no understory (Austin 1978; author's observations).

In addition to direct competition effects, exotic plants may influence geochemical and geophysical conditions and processes. The Austrailian pine, growing on beaches and dunes in Everglades National Park, excludes native plants that stabilize dunes thereby causing excessive washing away of unstable substrates and accelerated beach erosion (Austin 1978). Some exotics, by contrast, tend to slow erosion (not necessarily an undesirable effect) and may function as soil "builders". Kudzu not only fixes nitrogen, but the thick mats of vines protect the soil surface and deposit organic matter. Unfortunately, native species are not able to reoccupy these "improved" sites.

Plants may change the nutrient balance in the soil or produce allelopathic chemicals which retard other species. Conifers, in dense plantations, can acidify soils due to the high organic acid content in their litter and can slowly change soil structure, increasing the depth of the organic horizon. Exotic ice plants in Channel Islands National Park salinize the soil, making it too high in sodium for native plants to reoccupy sites cleared of these succulent herbs (Nick Whelan, personal communication).

One effect of exotic plants, important in arid regions, is the lowering of the water table. Tamarisk (*Tamarix* spp.) is now a high-priority management problem in U.S. southwestern parks including Death Valley National Monument, Grand Canyon National Park and Big Bend National Park. The deep-rooted tamarisk invades water courses and springs where it displaces native plants both by competition for space and by depleting available water. Once the tamarisk population is well entrenched, surficial water sources such as small marshes dry up, and springs cease to run. This, in turn, eliminates drinking water for wildlife and important, if limited, aquatic habitats. Animal species affected vary from desert bighorn sheep (*Ovis canadensis nelsonii*) and migratory waterfowl to microscopic aquatic invertebrates (U.S. National Park Service 1976).

Exotic plants in aquatic systems are notorious for closing waterways. Not only can species such as water hyacinth fill lakes and ponds, but they can affect ecosystem function by modifying gas exchange, nutrient cycling and even, through shading, water temperature.

An interesting effect of some exotic plants is modification of disturbance regimes. Mature stands of peppertree (*Schinus terebinthifolius*) are highly fire resistant, largely due to lack of fuel in the understory. Managers in Everglades National Park have found that fire is not only a poor tool for controlling this tenacious South American native but that unlike native terrestrial plant communities, *Schinus* stands retard fire spread (Koepp 1979). The opposite, increased fire frequency or intensity, is also a potential effect of exotic encroachment. Exotic plants may also modify erosion rates thus increasing the susceptability of communities to storm damage, especially on barrier islands and floodplains.

Exotic plants may influence native fauna by changing plant community structure and therefore animal habitat factors such as amount of cover and availability of nest sites. Austrailian pine in Everglades National Park has interfered with the nesting of rare or endangered species such as sea turtles and the American crocodile (*Crocodilus acutus*) (Austin 1978). Exotics may be preferred food items, attracting native animals, as is the case with white tailed deer browsing Japanese honeysuckle, or exotics may be unpalatable and may reduce the available forage.

Exotic Carnivores, Population Reduction and Extinction of Native Species

Among the ecosystem effects of exotic carnivores, population reduction and extinction of native species are usually the most important. Although any type of exotic species may eventually cause the extinction of a native species, some introduced predators have wrought major changes, particularly to island faunas, within very short spans of time.

Iverson (1978), for instance, documented a complete extirpation of the Caicos Island iguana (*Cyclura carinata*) on Pine Cay (not a preserve) in the British West Indies in only three years. In 1973, the 350 ha island supported about 5,500 iguanas. With the construction of a hotel complex, the number of feral cats greatly increased, and domestic dogs began to range across the island. Both species started preying on lizards, and by 1978 no iguanas were left.

In 1872, four male and five female Indian mongooses (*Herpestes griseus*) were introduced to Jamaica as a control agent for black and brown rats, also aliens in the West Indies. The mongoose was primarily responsible for the extinction of the Jamaican iguana (*Cyclura collei*) and the galliwasp skink (*Diploglossus occiduus*) and the decimation of the Jamaican coney (*Geocapromys brownii brownii*), a small skink (*Mabuya spilonotus*) and a tree snake (*Alsophisater ater*). Mongooses have spread to a number of other Caribbean islands and are a potential threat to faunal conservation in any island preserve. In 1952, two pairs of mongooses were liberated on 182 ha Buck Island, one of the few terrestrial areas in the largely marine Buck Island Reef National Monument (Virgin Islands). The mongooses extirpated an endangered lizard, *Ameiva polops*. The U.S. Fish and Wildlife Service has tried unsuccessfully for 10 years to eliminate the mongooses. An attempted reintroduction of the lizard also failed, presumably due to mongoose predation (Lewis 1953, Mittermeier 1972, Nellis et al. 1978).

Exotic carnivores may serve as competitors with native species. Moyle (1976) comments that in California native populations of trout often decline following the introduction of exotic trout, an effect presumably due to competition. In the Great Smoky Mountains National Park (GRSM), the introduced western rainbow trout (*Salmo gairdneri*) and, to a lesser extent, the European brown trout (*Salmo trutta*) have been implicated in the slow disappearance of the park's only native salmonid, the brook trout (*Salvelinus fontinalis*). From 1900 to 1975, brook trout range in GRSM declined from an estimated 680 km of stream to 197 km. Although competition is difficult to prove in the field, Moore et al. (1981) removed the rainbow trout from several stream sections where both rainbow and brook trout occurred. As the removal continued for three years, the standing crop (kg/ha) of brook trout increased by 21% to 89% in three streams and decreased slightly in a third. The total trout standing crop, averaging 116 kg/ha before the removal, did not return to this level after partial elimination of the rainbows but remained in the 60 to 80 kg range. These results imply that the invading rainbows do depress and can potentially eliminate the native trout populations. The rainbows may also, as has been suggested by fisheries biologists and anglers, increase the weight and size of fish available to sport fishermen.

Competition from either exotic plants or animals may result in the decline of an endangered or endemic species. Competition from mosquito-fish (*Gambusia affinis*) may have contributed to the decline of a number of endemic pupfishes (*Cyprinadon* spp.) in California (Moyle 1976). Exotics may also hybridize with native species, thus eliminating unique gene pools.

Exotic Herbivores, Reduction or Removal of Native Vegetation

The most important impact of exotic herbivores is the reduction or removal of native vegetation. Herbivores may also compete with native grazers and can cause major changes in ecosystem structure including reduced system productivity and diversity, as well as soil erosion. The most influential exotic herbivores are usually insects and ungulates such as bovids (cattle), equids (horses) and cervids (deer). Exotic birds and fishes which are herbivorous or omnivorous are more likely to adversely impact native biota through competition than through over-grazing.

The feral goat (*Capra hircus*), a problem species in dozens of preserves, causes a full range of undesirable ecosystem changes. In Hawaii Volcanoes National Park, where goats have browsed and grazed native vegetation for more than 150 years, the U.S. National Park Service evaluated their impact by constructing several goat exclosures -- fenced study plots which goats cannot enter. In the "pali" area of the park where the heaviest goat concentrations are found, an exclosure constructed in 1969 originally contained only exotic species, principally grasses. After three years of goat exclusion, several native species made up half the ground cover within the goat-free zone. A great surprise for scientists was the appearance of a previously undescribed plant species, a broadleaf legume, *Canavalia kanensis*. Presumably, the goats had long ago eradicated all the *Canavalia* plants, leaving only dormant seeds in the soil (Baker and Reese 1972, Mueller-Dombois 1979).

Spatz and Mueller-Dombois (1972) investigated koa tree (*Acacia koa*) reproduction outside and inside these same exclosures and found that goats cropped koa sprouts to 10 cm height. Goat browsing and trampling injured stems and roots, fostering the production of suckers, probably much denser than in the natural pre-goat state. These results imply: 1) that goats could eventually extirpate even the browse-resistant koa and 2) that if goats are removed, the koa population would initially produce more than the normal number of sapling sized stems. Baker and Reese (1972) list 19 plant species native to Hawaii Volcanoes National Park which are thought to be rare due to grazing pressure from feral pigs, cattle and goats. In 1972, 12 were endangered, in some cases existing as "a few tens of individuals", and one was thought to be extinct. Coblentz (1977, 1978) reports severe alteration of vegetation on Santa Catalina Island (California). Goat-free areas had 50% more vegetative cover and three times greater herbaceous productivity (in a dry year).

The heavy removal of vegetative cover by goats in turn influences the fauna of a preserve and may indirectly cause a decline in the populations of many native animal species including the rare or endangered. MacFarland (1974 a,b) considered goats to be a major competitor with the endemic giant tortoises in Galapogos National Park, although Gould and Swingland (1980) found that goats on Aldabra Island were browsers and the giant tortoise (*Geochelone gigantea*) was primarily a grazer. Since in the later investigation the goats had alread created a browse line,·6 m above the ground, it remains to be seen if the tortoises, which cannot climb up in shrubs, would browse more if there were more woody shoots available near the ground and may indirectly cause a decline in the populations of many native animal species. Yocum (1967) considers the feral goat a primary competitor of the nene (*Branta sandvicensis*), an endangered Hawaiian bird, and Coblentz (1978) credits goat-induced vegetative alterations with limiting the distribution or populations of several species of snake (*Thamnophis* sp., *Crotalus* sp., and *Lampropeltus* sp.), an endemic race of quail (*Lophorttyzx californicus*), the channel island fox (*Urocyon litoralis*) and two species of mice (*Peromyscus* sp. and *Reithrodontomys* sp.) on Santa Catalina Island. Trampling and cover removal can modify soil structure and initiate severe erosion. This may affect organisms dwelling in litter as well as seed germination patterns.

Not all non-native herbivores that severely disturb park resources are domestic species. The mountain goat (*Oreamnos americanus*) was introduced to what would eventually be Olympic National Park (Washington) in the late 1920's. It is important to note that this species is indigenous to the Cascade Mountain Range just 150 km to the east of the Olympic Penensula. Under portection in Olympic National Park, the introduced goat population expanded to an estimated 700 individuals which remained concentrated in high alpine areas and overgrazed the very erosion-sensitive alpine tundra. The goats utilize endemic plants, reduce cover and, through trampling and wallowing, initiate severe slope erosion. Soil bulk density may be increased from .5 g/cc to 2.0 g/cc on goat-trampled sites (Olmstead 1979, Hutchins and Stevens, 1981). The National Park Service was, at the time of this writing, in the process of returning the goats to their native range.

An herbivorous insect which utilizes several species may, like the ungulates just discussed, cause major modification in forest or grassland structure. The gypsy moth (*Porthetria dispar*), originally introduced to the U.S. as a potential silk producer, repeatedly defoliates oak (*Quercus* sp.) mixed hardwood forests, eventually killing older or less-vigorous trees. At Morristown National Historic Park (New Jersey), surveys conducted in 1971 found that the gypsy moth had killed about 10,000 oaks on less than 500 ha. Two species of oak, the white and the red (*Quercus alba* and *Q. rubra*) were more sensitive to defoliation than other tree species. Mortality varied from approximately 30% to 70% in different areas of the park.

Ehrenfeld (1979) quantified the replacement of the trees killed at Morristown by gypsy moths and found that black birch (*Betula lenta*), beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) were far more important than the decimated oaks. Yet, in Morristown National Historic Park, the forest itself will not be destroyed nor will it be replaced by species foreign to the present mature community. Unlike some of the examples of goat invasion, the physiognomy of the community will not be greatly modified. Insect infestations only result in soil erosion in extreme cases and are less likely than ungulate overpopulation to remove rare plant species (author's observations). An adverse impact, common after insect outbreaks, is an unnatural accumulation of fuel and an increased probability of fire. Ungulate overgrazing, by contrast, may so diminish fire fuels that fire frequency greatly decreases.

The final major type of exotic animal is the omnivore, swine and rats being the most common. Looking specifically at wild and feral swine, we find a variety of impacts related to foraging and other behaviors. Wild swine graze the shoots and harvest the fruits of plants. Hogs also consume carrion and prey on a great variety of animals including mollusks, earthworms, rodents, insects, insect larvae and salamanders. One of the most devasting of hog behaviors is rooting, turning over the leaf litter and surface soil in search of invertebrates, plant roots and rodent seed caches. Wallowing in small springs, streams or muddy spots (presumably a thermoregulatory behavior) does not directly remove any resources but causes trampling around water sources and local bacterial contamination. Males tusk trees, shredding the bark and scarring the cambium.

Bratton (1974, 1975) quantified the direct impacts of non-native wild boar in very heavily-utilized, grey beech forest, in Great Smoky Mountains National Park. Since the wild boar had not occupied the whole park but were slowly extending their range from west to east, she could sample both rooted and unrooted sites with matching elevations, topographic positions, and dominant species. In 1973, the most heavily disturbed sites had 2% to 5% of the expected herbaceous cover. Although all the plant species thought to be originally present were still found somewhere on the hog-occupied ridge tops, the diversity of a .1 ha plot could be decreased by 50% and 1 in 2 plots averaged 2.0 species instead of the expected 6.0.

Bratton (1974) also compiled a list of common wildflowers observed to be trampled, uprooted, or consumed by hogs. Some of the species such as an endemic mint, *Stachys clingmanii*, have been listed as endangered by the states or have very local distributions. Two of the park's wood lilies (*Lilium* spp.) are considered rare and the bulbs of the whole genus are selectively eaten by hogs.

This work was followed by Howe et al. (1981) who analyzed hog stomach contents. They verified that wild boar were indeed eating showy wildflowers such as spring beauties (*Claytonia* spp.), violets (*Viola* spp.), and trillium (*Trillium erectum*). Remains of mollusks, rodents, and salamanders, including the endemic red-cheeked salamander (*Plethodont jordanii*), were separated from other ingested materials. Singer (1981) then surveyed salamander and rodent densities in rooted and unrooted beech forest. Salamanders were present in rooted sites but did not display a normal distribution on the forest floor. Red-backed voles (*Clethrionomys gapperi*) and shrews (*Blarina brevicauda*) were common in hog-free stands but absent in the rooted sites. These differences cannot be attributed solely to predation. Singer (1981) reports major habitat disturbance at his rodent trap sites, including 87% reduction in herb cover, an 88% increase in bare ground, and a 36% decrease in leaf litter depth. Hogs had moved 77% of all logs and branches in the rooted stands thus displacing important salamander cover.

Much of the ecosystem disturbance caused by hogs is a result of mechanical effects, rather than direct removal of biotic material. Hogs do eat starchy tree roots, particularly of pines (*Pinus* spp.), but most of the apparent damage to trees is the result of tusking or rooting for other food items. Hogs uproot tree seedlings and stimulate root sprouting in beech (*Fagus grandifolia*). Huff (1977) found an average of 26 root sprouts less than 40 cm tall per $100m^2$ in rooted plots and only 1 per $100m^2$ in similar unrooted sites. Since the rooting in grey beech forest is for vernal herbs, much of the summer flora is accidentally disrupted without utilization. Fern rhizomes (*Athyrium felix-femina* and *Dryopteris intermedia*) are turned out of the soil and die by dessication.

Rooting and wallowing initiate surface-soil erosion and siltation of water sources. Singer (1981) found that turning of leaf litter reduced its weight (3,095 kg/ha in unrooted sites versus 1,830 kg/ha in rooted sites) and accelerated decomposition. After rooting, Co, P, Mg, Mn, and Cu were reduced in all soil horizons. Frank Singer and Wayne Swank (unpublished data) have, through a lysimeter study, found a release of nitrates into ground water.

An understudied but important aspect of wild boar interactions with other species is competition. Wild boar utilize some of the same food sources as black bears (*Ursus americana*) and must share one limited resource, the fall mast crop (fruit of *Quercus*, *Carya*, *Juglans*, and *Vitus* spp.).

Wild boar can potentially affect all terrestrial and aquatic elements of park ecosystems, but the magnitude and specific nature of these changes as well as the rates of recovery will vary according to the community type. Baron (1976) found that most communities on Horn Island, Gulf Islands National Seashore (Mississippi), recovered in less than 6 months after hog rooting, and hogs were far less devastating than the major hurricanes that occasionally inundate the islands. Bratton found that exclosure plots in heavily-rooted beech forest in the Great Smoky Mountains National Park regained most of their cover within 3 years but did not regain a full complement of native species. Sites in beech forest show almost no regeneration the first season after spring rooting, but sites on the open and more successional grassy balds do (Bratton 1975, 1977).

In closing this discussion of exotic effects, we need to note that not all their important impacts are necessarily ecological. One of the primary impacts of the demise of the Frasier fir, for instance, has been aesthetic. The fir has been an important component of the landscape in the center of Great Smoky Mountains National Park, and fir stands have lined the major high elevation automobile touring road and the heavily-used Appalachian trail. The dead or dying firs, visible to millions of visitors, fall across roads and trails and surround several major scenic overlooks including a mountain-top observation tower. Local newspaper columnists have already lamented the situation, and the neighboring Blue Ridge Parkway has prepared a pamphlet to help answer tourists' questions about "all those dead trees" (Smathers 1978).

Both exotic plants and animals can damage archeological and historic resources as well as park facilities and developments. Burros in Grand Canyon National Park made trails through ancient agave roasting pits into rock shelters occupied by Anasazi Indians around 1100 a.d. Heavy concentrations of dung have changed soil chemistry and introduced new pollen to rock-shelter deposits. Burro trampling has fragmented artifacts and altered the stratigraphy of the sites (data of R.L. Euler in National Park Service 1980).

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sort is required before effective control strategies can be designed and implemented. The two studies and their objectives were as follows:

> *Seed bank and seedling establishment*—The objective of this study was to characterize the smooth brome seed bank at a tallgrass prairie remnant and then to examine how readily smooth brome seedlings become established in unbroken prairie under a variety of germination environments.
>
> *Growth of smooth brome individuals*—The objective of this study was to compare growth characteristics of smooth brome individuals at an upland site and a lowland site. Smooth brome invades both upland and lowland sites in prairie remnants.

METHODS

Seed Bank and Seedling Establishment

We conducted this experiment at Makoce Washte Prairie, a 16-ha tallgrass prairie remnant owned by The Nature Conservancy and located in Minnehaha County, in eastern South Dakota. This remnant, bounded on three sides (north, east, south) by fencerows and on the fourth side (west) by a roadside ditch, shows the typical pattern of smooth brome invasion. Portions of the remnant not invaded by smooth brome are dominated by big bluestem (*Andropogon gerardii* Vit.). Grass species that occur less frequently include Kentucky bluegrass (*Poa pratensis* L.), little bluestem (*Schizachryium scoparium* Michx.), and switchgrass (*Panicum virgatum* L.). Forb species that occur commonly include Missouri goldenrod (*Solidago missouriensis* Nutt.), white sage (*Artemisia ludoviciana* Nutt.), and stiff-leaved sunflower (*Helianthus rigidus* [Cass.] Desf.). Smooth brome rings the remnant in a strip that varies in width from less than 2 m to more than 30 m. Smooth brome appears to grow most vigorously where there are substantial deposits of soil blown in from surrounding agricultural fields, as is the case at the fencerows. Each year smooth brome individuals growing at the fencerows produce large numbers of flowering culms.

We assessed the smooth brome seed bank in litter along nine 50-m transects that began at and were perpendicular to the remnant boundary. Transects originated at the remnant boundary and extended inward from all four sides, two each from the east, south, and west, and three from the north. Transect locations were determined arbitrarily and each transect crossed the smooth brome invasion front at some point. On April 7, 1993, litter material was scraped from a total of fifty-four 0.1-m^2 plots located at 10-m intervals along the transects, beginning at the remnant boundary. Twenty-three of the plots were located in the smooth brome strip and 31 were in "true" prairie ahead of the invasion front. Samples were taken to the laboratory, air dried, and then tested for smooth brome seed germination in germination trays placed in a greenhouse under natural photoperiod. Litter samples were evenly scattered over Perlite and then covered by a thin layer of sterile soil. Germination was monitored daily for three weeks. Smooth brome seedlings were identified by comparing them to seedlings known to be smooth brome and by examining the florets from which seedlings had emerged.

To examine seedling establishment potential in unbroken prairie vegetation, under conditions of burning and no burning and in the presence of added surficial soil, we arbitrarily marked 30 point locations 1–3 m ahead of invading smooth brome fronts where smooth brome apparently was absent. On April 24, 1993, four 0.1-m^2 plots were situated at each of these point locations, oriented in northeast, southeast, southwest, and northwest directions from the point. Each plot was separated from adjacent plots by a distance of 10 cm. Fifteen of the four-plot complexes were located in portions of the prairie that had been burned in May 1992, and 15 were located in portions of the prairie that had not been burned since 1988. The vegetation of each plot was clipped to about 10 cm, and the four plots of each complex were treated as follows: (1) the southeast plot received 150 g of heat-treated, dry silt and clay collected from the soil surface at the prairie perimeter and scattered evenly over the plot; (2) the northeast plot received 1 g of smooth brome seed and then 150 g of heat-treated, dry silt and soil, both scattered evenly over the plot; (3) the southwest plot received 1 g of smooth brome seed; (4) the northwest plot received no smooth brome seed and no soil and acted as a control. Prior to the experiment, smooth brome seed was field-collected in January and tested for viability using the germination test described previously. Five 1-g samples produced an average of 177 ± 4 (SE) seedlings during the 3-week germination period. During the growing season, each plot was monitored monthly for smooth brome germination and then, on October 20, 1993, examined for the purpose of counting smooth brome seedlings.

Growth of Smooth Brome Individuals

We used transplanted smooth brome individuals to examine differences in vegetative growth at an upland site and a lowland site at Makoce Washte Prairie. Both sites were located in flat portions of the smooth brome strip and supported mostly smooth brome vegetation. On April 14, 1993, each of two 5-m x 7-m sites was treated with glyphosate, which killed all potentially competing vegetation. On April 29, 1993, 35 individual smooth brome plants, grown in 1-gallon pots in a greenhouse from field-collected seed, were transplanted to each site. Average tiller numbers for transplanted individuals were 2.46 ± 0.14 (SE) and 2.51 ± 0.10 for the upland and lowland sites, respectively. Individuals were randomly assigned to points in a 5 x 7 grid at the interior of each site. Spacing between individual plants was about 40 cm, leaving a buffer strip of approximately 2 m at the border of each site. At 2-week intervals, during the months of May, June, and July, numbers of tillers and flowering culms were counted for each plant at each site. At the end of the growing season, on October 20, 1993, each of the plants was dug out of the soil and transported to the laboratory. Soil was carefully washed away from the roots and rhizomes and dry weights of aboveground biomass, roots, stem bases, and rhizomes were determined. In addition, the number of tillers was counted and the total length of rhizomes was determined. Soil cores, 1.6 cm in diameter and 30 cm deep, were taken from the centers and corners of each site three times during the growing season and were used to characterize bulk density and to make gravimetric determinations of percent soil moisture. Eighteen additional 30-cm soil cores were taken from scattered locations across each site. Eleven of these cores were used to make hydrometric (American Society for Testing and Materials 1981) determinations of soil texture, and the other seven were sent to the South Dakota State University Soil Testing Laboratory, where pH, soluble salts, percent organic matter, nitrate nitrogen, available phosphorus, and potassium were determined.

Statistical Analysis

We used the Mann-Whitney *U*-test to test for significant differences in mean numbers of germinating seeds in litter samples taken from the smooth brome strip and from the true prairie ahead of the invasion front. We used the repeated measures ANOVA to test for season-long differences in tiller numbers between the upland and lowland sites and used the unpaired, two-tailed Student's *t*-test to test for significant differences between end-of-season means in plant and soil characteristics between the two sites. When assumptions of the *t*-test were not met, we used the Mann-Whitney *U*-test. Percentage data were subjected to arcsine transformation before analysis. Means were considered to be different if $P < 0.05$.

RESULTS AND DISCUSSION

Seed Bank and Seedling Establishment

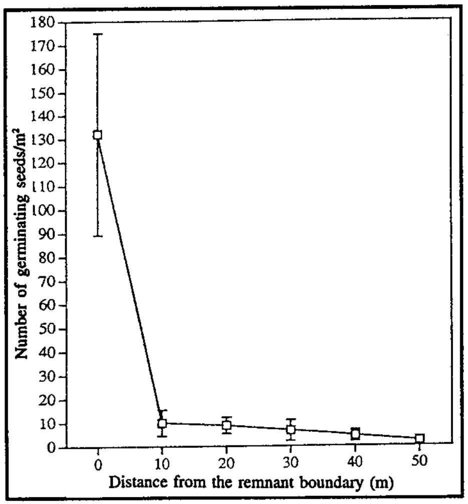

Figure 1. Smooth brome seed bank at Makoce Washte Prairie in relation to distance from the remnant boundary. Data points are of means with standard error bars.

A total of 147 smooth brome seeds germinated from the fifty-four 0.1-m^2 plots. An average of 132 ± 43 (SE) viable seeds/m^2 of smooth brome occurred at the remnant boundary, 10 ± 6 seeds/m^2 occurred at 10 m into the remnant, and only 2 ± 2 seeds/m^2 occurred at 50 m into the remnant (Figure 1). The litter of the 23 plots in the smooth brome strip had significantly more smooth brome seeds than did the litter of the 31 plots in true prairie ahead of invasion front (smooth brome strip, $\bar{X} = 57 \pm 21$; prairie, $\bar{X} = 6 \pm 2$; $P = 0.0028$). In the prairie portions of the transects, most of the smooth brome seeds occurred in plots close to the invasion front (Table 1). Nine of the 31 true prairie sampling plots had viable smooth brome seeds, averaging 19 ± 5 seeds/m^2.

Because most of the smooth brome flowering culms at Makoce Washte Prairie are produced at the remnant boundary, the seed bank profile (Figure 1) demonstrates that smooth brome seed undergoes little horizontal displacement. Even so, seed dispersion dynamics do result in the location of at least some smooth brome seeds ahead of the invasion front, where they could, potentially, germinate and become established as seedlings.

In the seedling establishment experiment, some seed germination was observed but no smooth brome tillers were established from seed. At the end of the growing season, a few of the plots had small numbers of smooth brome tillers, but an examination of underground plant parts revealed that these tillers had grown from previously existing rhizomes. The treatment in which smooth brome seed was added to burned plots and then covered with a layer of soil provided optimal conditions for germination, especially since the growing season was one of the wettest on record (mean May–July precipitation for 1964–1992 at Sioux Falls, South Dakota, 16 km distant from the remnant, was 231 mm; May–July 1993 precipitation was 573 mm; source: U.S. Weather Bureau, Sioux Falls, South Dakota). Although some seeds germinated, apparently the roots of the small brome seedlings were not able to penetrate the thatch or were not able to compete effectively with established plants. A number of workers have previously demonstrated that seedling establishment in unbroken swards of grass vegetation is difficult (Snaydon and Howe 1986, Fowler 1988, McConnaughay and Bazazz 1991, Potvin 1993). Seedling establishment in small gaps produced by animal disturbances is more likely (Laycock 1958, Platt 1975, Foster and Stubbendieck 1980, Huntly and Inouye

Table 1. Number of smooth brome seeds (individuals/m^2) germinating from litter sampled at varying distances ahead of the smooth brome invasion front. N = sample size; $\bar{X}$ = mean; SE = standard error. For smooth brome strip, mean smooth brome seed density = 57 + 21 individuals/m^2.

Distance from Invasion Front (m)[a]	Number of Individuals N	 $\bar{X}$	 SE
0–10	9	13	5
11–20	9	4	3
21–30	5	0	—
31–40	5	2	2
41–50	3	0	—

[a] Distance values are given as ranges because locations of sampling plots relative to the the invasion front varied from transect to transect.

1988, Gibson 1989, Hobbs 1991, Benedix and Seastedt 1993). The question of whether or not smooth brome seedlings become established in small disturbance gaps at Makoce Washte Prairie remains to be addressed. Also unknown is whether smooth brome seedling establishment occurs in undisturbed prairie during the fall.

Growth of Smooth Brome Individuals

Twenty-two of 35 individuals transplanted into the lowland site survived to the end of the growing season, while 30 of 35 individuals survived at the upland site. Lower survival in the lowland plants probably was the result of heavy rains early in the growing season, which produced standing water and water-logged soil.

Tillers were produced from transplanted plants throughout the growing season at both lowland and upland sites (Figure 2). Typically, smooth brome shows two episodes of tiller growth, a smaller one in the spring and a larger one after anthesis (Lamp 1952). Apparently, the unusual absence of an extended hot and dry period during the middle of the growing season enabled smooth brome individuals to produce at least some tillers all season long. This response undoubtedly enhances the competitive ability of smooth brome. Season-long tiller numbers were greater at the lowland site than at the upland site (repeated measures ANOVA, $F_{1,50} = 9.61$, $P = 0.0032$). Most of this difference occurred at the end of the growing season (Figure 2; repeated measures ANOVA interaction between site and time during growing season, $F_{6,300} = 13.64$, $P = 0.0001$).

At the end of the growing season, mean total length of rhizomes, weight of all rhizomes, rhizome weight/length, and tiller weight/number of tillers in smooth brome individuals did not differ between the lowland and upland sites (Table 2). The last two variables are measures of individual rhizome thickness and individual tiller size, respectively. However, mean total number of tillers, weight of all tillers, and weight of all roots and stem bases were significantly greater at the lowland site, while mean rhizome length/tiller was significantly greater at the upland site.

Individual smooth brome plants grew more vigorously at the lowland site, as evidenced by the larger number and greater weight of tillers and the greater weight of roots and stem bases (Table 2). However, even though total rhizome length and weight did not differ at the two sites, rhizome length/tiller was greater at the upland site. This is potentially important because tillers regularly are produced along and from the end of rhizomes, and an increase in this ratio may indicate a more rapid rate of horizontal vegetative expansion. Currently, there is much interest in plant species that are able to adapt foraging strategies to the quality and distribution of resources in their environment (Sutherland and Stillman 1988, Campbell et al. 1991). It is possible that smooth brome is another species capable of using different foraging strategies.

Mean soil bulk density, soluble salts, percent organic matter, nitrate nitrogen, and phosphorus did not differ between the lowland and upland sites (Table 3). However, soil texture was significantly finer, percent soil moisture greater, pH higher, and potassium lower at the lowland site. The differences in pH and potassium probably are unimportant, because the difference in pH was small and the concentrations of potassium probably were not limiting. The differences in soil texture and soil moisture are of greater interest. Fine-textured soils are able to store more water, and this water may support plant growth during later times of low rainfall (Barnes and

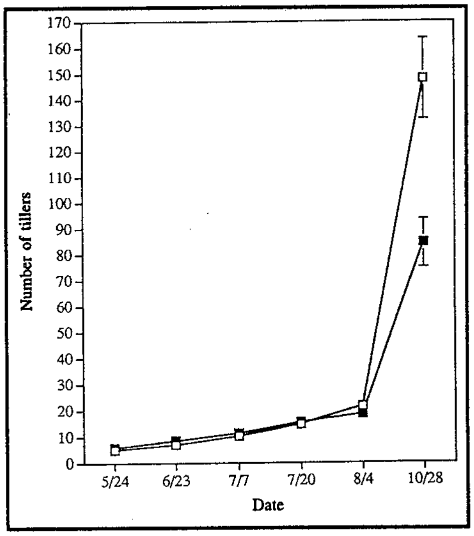

Figure 2. Production of tillers by individual smooth brome plants during the 1993 growing season. Open squares = lowland site, closed squares = upland site. Data points are of means with standard error bars.

Table 2. Characteristics of individual smooth brome plants growing at a lowland site and an upland site. N = 22 for plants growing in the lowland site and N = 30 for plants growing in the upland site.

Plant Characteristic	*Lowland* $\bar{X}$ ± SE	*Upland* $\bar{X}$ ± SE	*t*	*P*
No. of tillers	147.9 ± 15.5	84.3 ± 9.3	–3.71	0.0005
Weight of all tillers (g)	10.91 ± 1.23	6.30 ± 0.83	–3.22	0.0022
Tiller weight/ tiller no. (mg/ind.)	73.5 ± 3.6	72.8 ± 4.6	–0.11	0.9134
Wt. of all roots and stem bases (g)	8.36 ± 1.25	3.56 ± 0.44	–4.07	0.0002
Length of all rhizomes (cm)	165.3 ± 21.0	189.1 ± 18.2	0.85	0.3972
Weight of all rhizomes (g)	1.04 ± 0.21	1.18 ± 0.19	0.48	0.6323
Rhizome weight/ rhiz. length (mg/cm)	5.57 ± 0.67	5.68 ± 0.51	0.13	0.8980
Total rhizome length/ tiller no. (cm/ind.)	1.16 ± 0.14	2.52 ± 0.24	4.41	0.0001

Table 3. Soil characteristics at lowland and upland smooth brome transplantation sites.

Soil Characteristic	Lowland $\bar{X}$ ± SE	Upland $\bar{X}$ ± SE	N	t	P
Texture (% silt and clay)	80.0 ± 2.3	67.1 ± 2.5	11	3.77	0.0012
Moisture (% water)	43.7 ± 2.6	31.2 ± 1.4	15	4.28	0.0002
Bulk density (g cm^{-3})	0.58 ± 0.05	0.58 ± 0.09	15	–0.02	0.9134
pH	6.6 ± 0.6	6.2 ± 0.0	7	-5.85	0.0001
Soluble salts (mmhos cm^{-1})	1.04 ± 0.06	0.90 ± 0.07	7	-1.55	0.1473
Organic matter (%)	5.6 ± 0.2	5.5 ± 0.3	7	–0.21	0.8405
Nitrate nitrogen (ppm)	2.39 ± 0.53	1.89 ± 0.46	7	–0.71	0.4914
Phosphorus (ppm)	17.0 ± 1.4	15.1 ± 1.0	7	-1.12	0.2834
Potassium (ppm)	299 ± 18	399 ± 23	7	3.50	0.0044

Harrison 1982). Greater soil moisture may explain, at least in part, the greater vigor of plants at the lowland site (Knapp et al. 1993). Soil moisture and texture, acting separately or interacting in some way, may also have influenced rates of horizontal expansion at the two sites. For example, at the upland site, lower soil moisture may have stimulated rhizome elongation, and coarser soil may have enhanced the ability of rhizomes to penetrate the soil.

CONCLUSIONS

The results of these studies lead to the following conclusions about smooth brome seedling establishment and vegetative growth at Makoce Washte Prairie, Minnehaha County, South Dakota. First, this prairie remnant has a smooth brome seed bank, part of which exists ahead of the invasion front as well. Second, seedling establishment in unbroken true prairie portions of this remnant is probably a rare occurrence. Third, smooth brome individuals grow better (i.e., produce more above- and below-ground biomass) at lowland sites than at upland sites. These differences in growth might be related to differences in soil moisture, soil texture, or both. Fourth, rates of horizontal spread possibly are greater at upland sites than at lowland sites.

It is important to note that these conclusions are preliminary and not necessarily generalizable to tallgrass prairie remnants at other locations. Controlled and replicated studies at several locations are required to confirm these conclusions. Should they be confirmed by other studies, these conclusions will be helpful in designing and implementing effective strategies for controlling smooth brome. For example, knowledge that smooth brome vegetative growth is limited by available soil moisture might lead a manager to schedule burns for dry years.

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