

Are horses responsible for introducing non-native plants along trails in the eastern United States?

A final report to the American Endurance Riders Conference (AERC)



December 28, 2006

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Project Summary

Non-native plant species pose a serious ecological and economic threat to managed and natural ecosystems; therefore, there is a great need to identify major sources for the introduction of non-native species and develop management plans to reduce or eliminate their introduction. Horses have been suggested to be an important source for the introduction of non-native plant species along trails, but the data to date has largely been anecdotal. In this study, horse hay, manure and hoof debris samples were collected from 12 to 24 horses at five endurance rides in North Carolina, Kentucky, Illinois, Wisconsin, and Michigan. One sub-sample of each material from each horse was sown in pots and grown under ideal conditions to determine if horse hay, manure and hoof debris samples contained seeds from non-native species. A second sub-sample of each material from each horse was placed back on their respective trail to determine if non-native seeds would germinate and establish on the trails. Vegetation surveys were also conducted along 50 m transects perpendicular to horse and hiking (horses not permitted) trails at three of the five sites to compare species composition of native and non-native plant species. On average, non-native plant species germinated in 5.2% of the hay samples in the pots, but non-native species did not germinate from the manure or hoof debris samples. However, only 3 of the 288 ($\approx 1\%$) hay, manure, and hoof debris plots established on horse trails at the five sites contained native plants at the end of the first growing season and no live plants were observed at the end of the second growing season. Non-native species composition and percent of total plants species did not differ between horse and hiker trails, and non-native plant species were only found within one meters of the trail. The results of this and other studies demonstrate that horse hay and manure contains seeds of non-native plant species, but native and non-native plant species rarely become established on horse trails because of the harsh environmental conditions. Opportunities to reduce the risk of horses introducing non-native plant species in natural and managed ecosystems are discussed.

Introduction

Conservation biologists, natural resource managers, and private landowners are increasingly concerned with the invasion of non-native species in natural ecosystems (Mooney and Drake 1986, Soule 1990, Williamson 1996, Vitousek et al. 1997). Non-native species, also known as alien, non-indigenous, or exotic, are species or strains that become established in natural ecosystems and replace native species. Non-native species pose both economic and ecological concerns. Non-native plants often decrease biodiversity by replacing native plant species and other organisms that depend on the plants. The loss of species diversity makes the ecosystem "unhealthy" or susceptible to degradation (Mooney and Drake 1986, Williamson 1996).

Non-native species also have a pronounced economic impact. Weeds cost the U.S. economy \$32 billion a year by decreasing crop production by 12% (Pimentel et al. 1999), and 73% of the weeds are non-native (Pimental 1993). The costs estimates provided by Pimental and his colleagues excluded costs of (i) producing the herbicides (\$4 billion), (ii) programs to control non-native plant species (\$3 billion), and (iii) environmental and public health damage caused by herbicides (\$9 billion). Pastures for livestock are especially susceptible to invasion by native and non-native weeds, with an estimated 45% of the invading species being non-native plants (Pimentel 1993). Forage production from pastures is a \$10 billion industry in the U.S. and yield losses caused by non-native species total \$1 billion annually (USDA 1998).

Given the large adverse effects non-native species can have on the ecological and economic integrity of ecosystems it is critical to prevent further degradation of natural and managed ecosystems. Sound management plans are needed to quantify modes of invasion of non-native species into ecosystems and identify opportunities to reduce or eliminate their sources of introduction.

Disturbances, particularly unnatural ones, appear to make ecosystems more susceptible to biological invasions (Braithewaite et al. 1989, Binggeli 1996, Adkinson and Jackson 1996). No ecosystem is free from disturbance, and since European settlement, the forest landscape has experienced increased logging, wildfire, road building, and the introduction or accidental release of non-native animals that transport invasive plants and/or their seeds. Trail horses have been accused of being an important cause for the spread of invasive or non-native plant species (Bates 1935, Land 1994). Given that non-native plant species commonly occur in pastures and horses consume pasture grasses and defecate pasture grass waste, it is plausible that horses may be a source for the introduction of non-native species. However, there are few data to support or refute this assertion (but see Campbell and Gibson 2001).

The availability and viability of non-native seeds is a biological bottleneck that may be an important factor restricting the importance of horses introducing non-native plants. Environmental and physical conditions of the trail are additional bottlenecks that may prevent non-native germinated seedlings from establishing and colonizing ecosystems adjacent to horse trails. The objectives of this research project are to: (i) assess the importance of different sources of material (i.e. hay, manure, and hoof debris) by which horses may introduce non-native plant seeds, (ii)

determine if seeds of non-native species introduced by horses can germinate and establish on horse trails, (iii) determine if non-native plant species established on trails colonize into natural ecosystems, and (iv) compare the presence and abundance of invasive plant species along horse trails to other recreation activities that may also be responsible for the spread of non-native species in natural ecosystems. The systematic study will provide valuable data to help land managers mitigate the introduction of non-native plant species by horses, if horses are found to be an important source for non-native species.

Methods

Study Sites and Experimental Design

The study was conducted in five locations along a south – north gradient from North Carolina to Michigan that encompasses two of the American Endurance Ride Conference (AERC) regions (Table 1). The selection of sites was based on logistics, proper experimental controls, financial support, and the author's familiarity with local flora. The large geographic region of riders (15 states and one Canadian province) represented in this study and varied environmental conditions of the study sites make the results highly relevant to policy makers and land managers. The sites were selected to encompass a large geographic region. Twenty horse were selected at each ride, except for the Biltmore Estates ride where 24 horses were sampled, and the AHDRA I ride where only 12 horses were sampled. Horses were selected randomly at each ride.

Table 1. Study site, respective location and AERC region, and the states and provinces from which horses were selected for study.

Site/ (Ride name)	Location	AERC Region	States & Provinces represented
Biltmore Estates (Biltmore Estates Challenge)	Asheville, NC	SE	GA, IN, KY, NC, ME, MN, ON, PA, TX, VA
Land Between the Lakes Nat'l Rec. Area (LBL Express)	Golden Pond, KY	SE	MO, KS, KY, TN, IN,
Kickapoo State Rec. Area (AHDRA I)	Oakwood, IL	MW	IL, MI, WI
South Kettle Moraine State Forest (Glacier Trails)	Eagle, WI	MW	IA, IL, MI, WI
Hiawatha National Forest (Grand Island)	Rapid River, MI	MW	IL, MI, WI,

At each ride, a representative sample of hay, or hay substitute, was collected from each owner and the sample was sub-sampled and placed in two labeled bags. A manure sample was collected from the horse paddock, divided into two sub-samples and placed into two labeled bags. Hoof scrapings were collected from all four feet of the horse (except when horses had pads), combined, thoroughly mixed, and divided into two sub-samples (Photo 1). One sub-sample of each material was

placed in a larger labeled bag and transported back to Madison, WI for the pot germination study and the second sub-sample of each tissue from each horse was placed on the trail within 24 hours of sample collection.

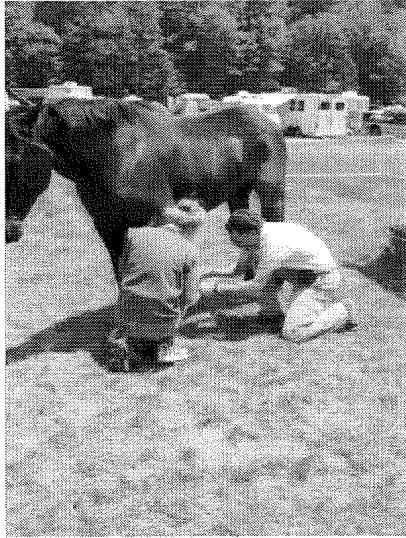


Photo 1. Collection of hoof debris from an endurance horse at the 2006 Biltmore Estates Challenge.

The hay, manure and hoof debris sub-samples for pot germination study were transported back to Madison, Wisconsin and added to 15 liter plastic potting buckets filled with commercial potting soil. The pots were placed outside and watered twice per week with a complete Hogland's nutrient solution to ensure the germinating plants had adequate water and nutrients. Plants were grown to the end of August 2005, and each germinated plant was identified by species and classified as native or non-native (United States Congress, Office of Technology Assessment 1993). Other sources used to identify non-native plant

species included Lorenzi and Jeffrey (1987), Royer and Dickinson (1999), Czarapata (2005), and USDA (1971).

The second sub-sample of hay, manure, and hoof debris was placed in a 50 cm diameter plot located every meter along each transect at five random locations on the trail designated for horses (Figure 2). The start and end point of each transect was marked with a large plastic stake driven flush to the ground so the transect could be re-located. At the end of the 2005 growing season each plot was surveyed and each germinated plant was identified by species and status (native or non-native).



Photo 2a-c (left to right). (a) A transect containing the hay, manure, and hoof debris samples collected from 20 horses participating in the Land Between the Lakes (LBL) Express endurance ride in 2005, (b) close-up of a hay sub-samples placed on the trail, and (c) close up of a manure sub-sampled placed on the trail.

The trails transects were re-surveyed in summer 2006 to verify 2005 results. In addition, ancillary data were collected to help explain why germination and establishment rates were so low. To test the hypothesis that resource(s) limitation were limiting the successful establishment of plant species, soil water holding capacity (θ , percent by volume), soil bulk density (BD, mass per unit volume), and fraction of incoming photosynthetic active radiation, or visible light (F_{IPAR}) were measured at each of the five transect locations at the five study sites. Photosynthetic active radiation was measured simultaneously outside the forest along a nearby road and in the middle of transects using sunfleck ceptometer (Decagon Devices, Pullman, WA) equipped with 40 integrated sensors that measure visible light (400 – 700 nm) used by plants in photosynthesis. Field measurements and data analysis followed Gower et al. (1999). Soil bulk density was measured for 0-20 cm depth at a random location along each of the five transects using standard method (Elliott et al. 1999). Soil water holding capacity was indirectly estimated from soil texture analysis. A 5 cm diameter core (0 – 20 cm depth) was collected at a random location along each of the five transects and soil texture was measured in the laboratory using the hygrometer technique (Bouyoucos 1962).

To answer the third objective, 0.25 x 0.25 m vegetation survey plots were established along a transect that was perpendicular to the same horse trail where sub-samples were placed. Plots were established at 0.25, 0.5, 1.0, 2.5, 5.0, 10.0, 15.0, 25.0, 37.5 and 50.0 meters from the trail. Five transects were established at each study site. At three study sites (Land Between the Lakes National Recreation Area, KY; Kickapoo State Recreation Area, IL; and Southern Kettle Moraine State Forest, WI) five additional transects were established on trails open to hikers but closed to horses. The KY, IL and WI sites were the only study sites where horse and non-horse trails were close to each other and the vegetation and soil surrounding the trail systems were similar.



Photo 3 a-b (left to right). Photo of the mixed white pine – hardwood forest along the red trail at the Biltmore Estates Challenge ride where a 50 m transect was surveyed for native and non-native plant species, and (b) example of a survey plot with understory vegetation.

RESULTS

Non-native plant species only occurred in pots that contained hay samples. Non-native plants comprised 4, 13, 2, 2, and 5 % of the total plants in the hay pots from the Biltmore Estates, Land Between the Lakes, AHDRA I, Glacier Trails and Grand Island rides, respectively (Figure 1). Table 2 summarizes the non-native species that germinated from hay samples in the pots. A complete list of the species present in hay, manure, and hoof debris samples is provided in Appendix 1.

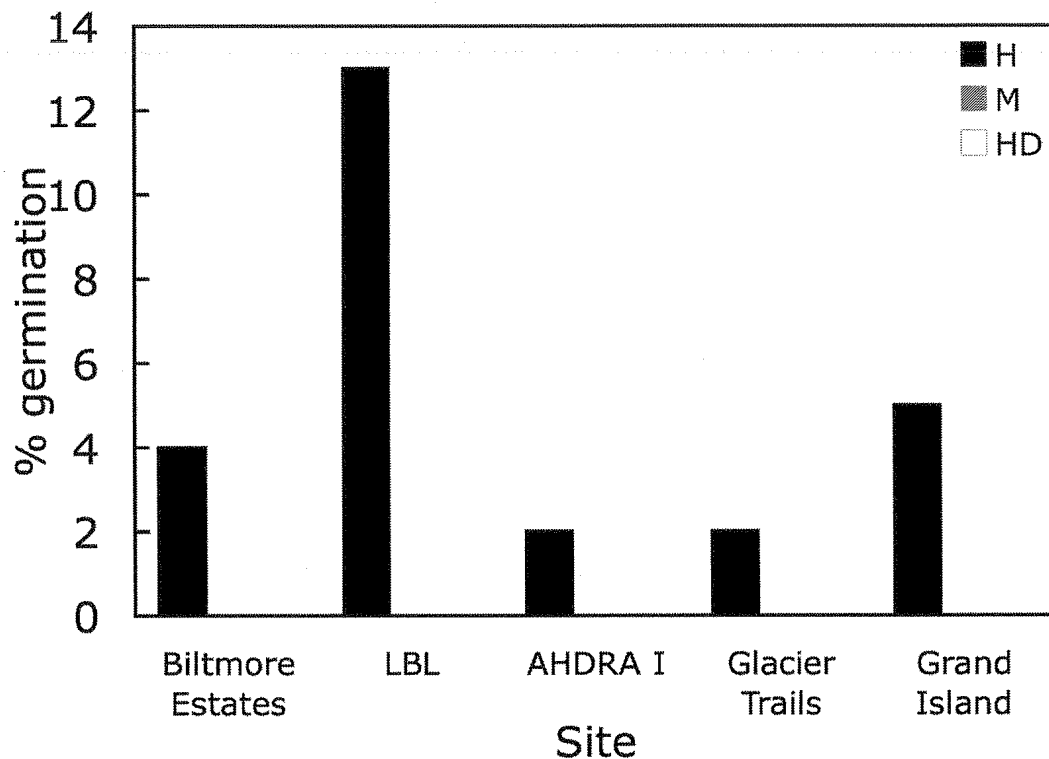


Figure 1. Percent of germinated plants in the pots that were non-native species. Values are based on the 26, 20, 20, 20, and 12 samples of hay, manure, and hoof debris collected at the Biltmore Estates, land Between the Lakes (LBL), Arabian Horse Distance Rider Association I (AHDRA), Glacier Trails, and Grand Island rides, respectively.

Table 2. Summary of non-native plant species that germinated from hay samples. Names include scientific name and (common name).

AERC ride	Non-native species
Biltmore Estates	<i>Digitaria</i> spp. (crabgrass), <i>Agropyron repens</i> (quackgrass), <i>Setaria</i> spp. (foxtail)
LBL Express	<i>Digitaria</i> spp. (crabgrass), <i>Rosa multiflora</i> (multiflora rosa), <i>Agropyron repens</i> (quackgrass), <i>Chenopodium album</i> (lambsquarter)
AHDRA I	<i>Agropyron repens</i> (quackgrass), <i>Polygonum pennsylvanicum</i> (smartweed)
Glacier Trails	<i>Cirsium arvense</i> (Canadian thistle)
Grand Island	<i>Cirsium arvense</i> (Canadian thistle), <i>Potentilla</i> spp. (cinquefoil)

The germination and establishment of native and non-native plants on the trail was extremely low. Based on survey of the five transects on the trail at each site in late summer 2005, only one hay plot at Biltmore Estates and two hay plots at Land Between the Lakes contained plants, and the plants at both sites were native grasses (Photo 4 and Figure 2). In other words, 3.8, 10, 0, 0, and 0% of the hay plots on the trails at Biltmore Estates, Land Between the Lakes, AHDRA I, Glacier Trails, and Grand Island sites, respectively, contained plants in 2005, and no plants grew in the manure and hoof debris plots. A resurvey of transects in 2006 revealed no plants were alive in any plots (data not shown).

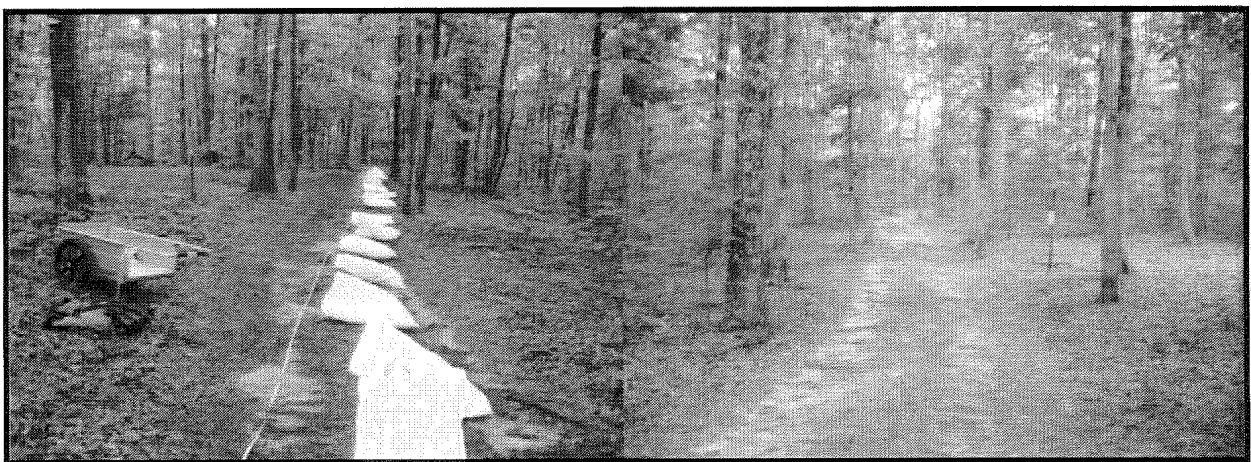


Photo 4 a-b (left to right). Photo of one of the five transects established at the Land Between the Lakes, and (b) the upper part of the same transect in summer 2005.

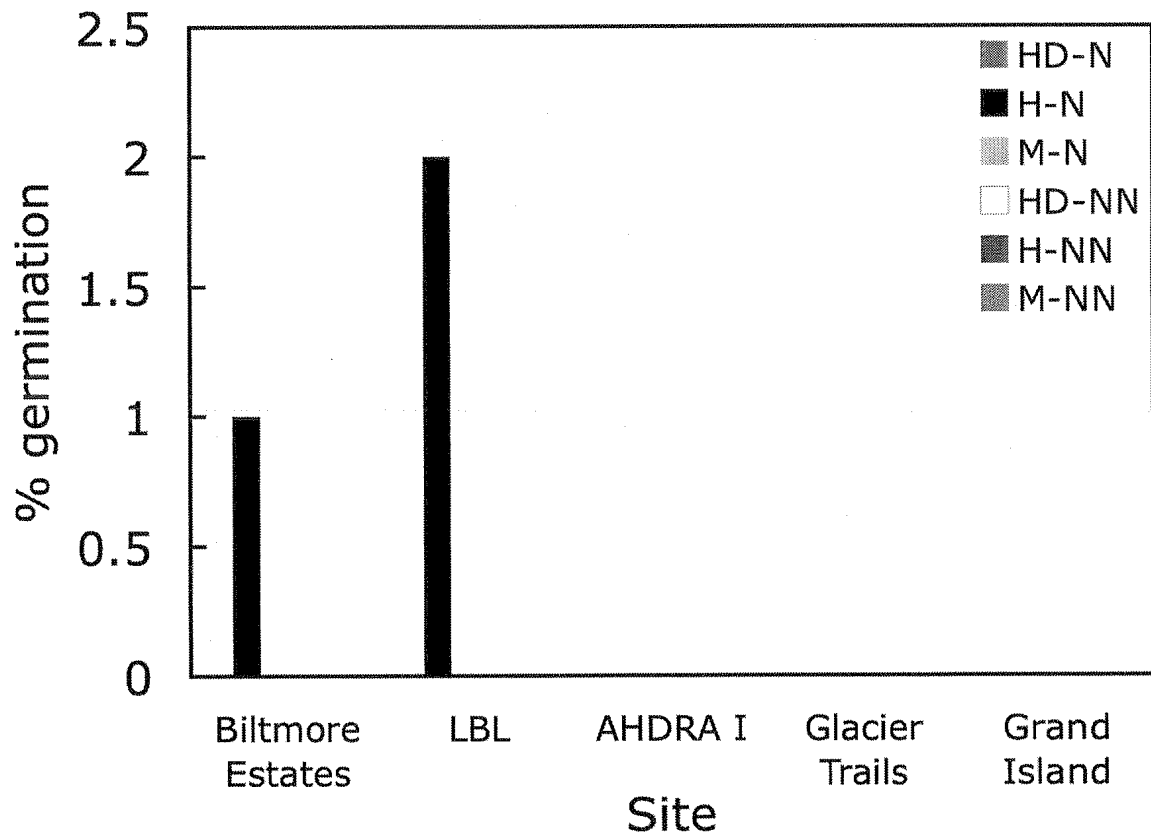


Figure 2. Percent of all (hay, manure and hoof debris) plots at each study site that contained germinated native and non-native plants. Legend is as follows: hay = H, manure = M, hoof debris = HD, native = N and non-native = NN.

Vegetation composition of transects perpendicular to the trail was dominated by native species along the horse trails (94 – 98%) and hiking trails where horses are prohibited (93 – 99%) (Figure 3). Non-native species composition did not differ significantly ($P > 0.05$) between horse and hiking (i.e. non-horse) trails, and ranged from 1 – 7 % for hiking trails and 2 – 6 % for horses trails. These data indicate that non-native plant species were established at approximately a similar rate for trails that allowed and prohibited horses. Non-native plants were always found within 1 meter of the trail, suggesting the plants were not getting established in adjacent ecosystems we sampled in this study.

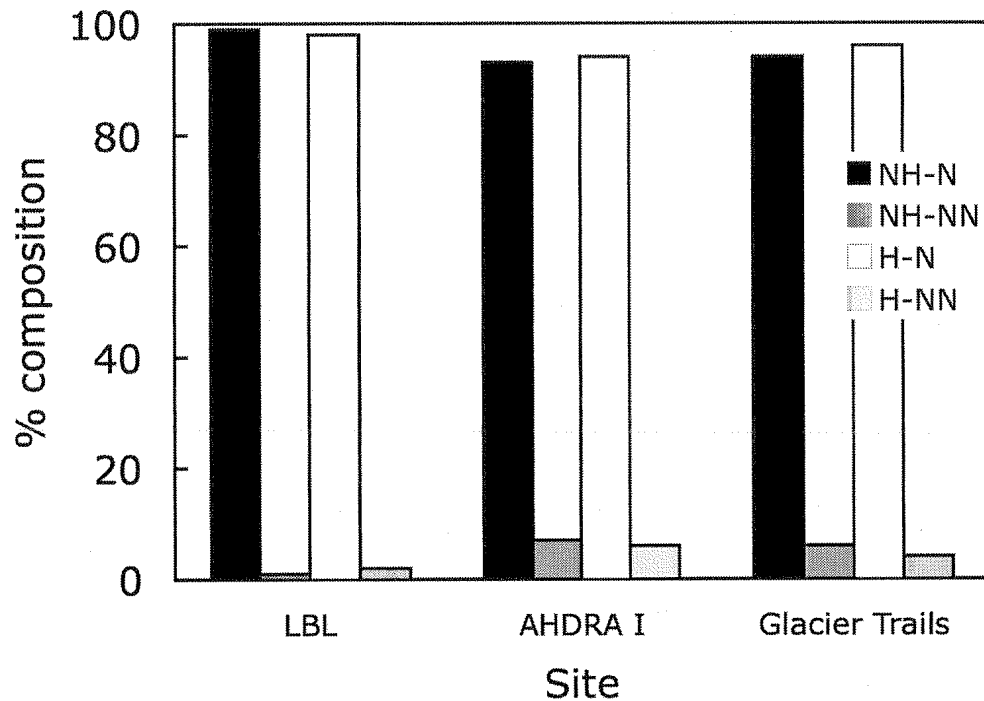


Figure 3. Comparison of the percent composition of native (N) and non-native (NN) plant species observed for the five transects perpendicular to trails where horses are prohibited (NH = no horse) and allowed (H = horses allowed). All values are based on the average of all plots along the 50 m transect that was perpendicular to the trail.

DISCUSSION

Are horses important sources of non-native plants?

Non-native plants are a serious economic and ecological threat to natural ecosystems and therefore it is important to determine the major sources for the introduction of non-native species, and identify management opportunities to reduce or eliminate their introduction. This study examined the role of horses as a source for non-native plants in five study areas that spanned a broad geographic and environmental gradient in the eastern United States.

Figure 4 depicts the various bottlenecks or constraints that prevent horses from spreading non-native plant species. Major horse-related sources of seed introduction include forage, manure and hoof debris. It is also conceivable that seeds could be transported on the horse's coat, but this source has not received attention and could be easily remedied. The results from the pot germination experiment demonstrated hay was the primary source of non-native seeds in this study. Non-native plants comprised 2-13% of the total number of plants germinated and averaged 5.2% of total plants germinated for the five study sites. The absence of non-native viable non-native seeds in horse manure is consistent with the preliminary findings reported by Dominican University of California scientists.

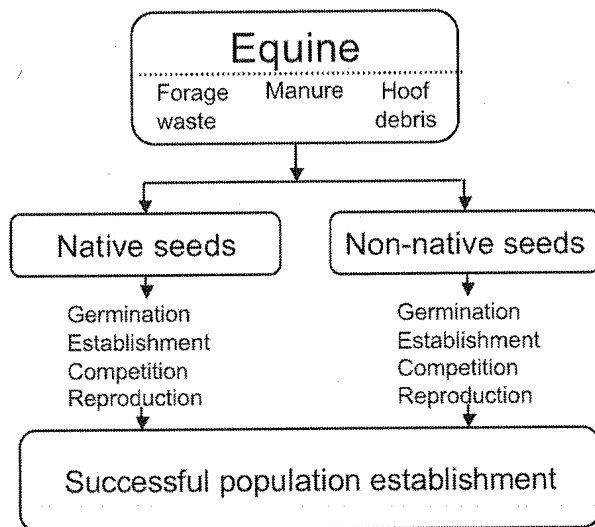


Figure 4. Conceptual model illustrating the pathways that horses may be responsible for the introduction of seeds of non-native plants and the bottlenecks that restrict the successful establishment of non-native plant population.

Conversely, Campbell and Gibson (2001) reported that non-native species comprised 15% of all plant species that germinated from horse dung in a study in southern Illinois. It is worth noting that the Campbell and Gibson study collected horse manure from the trail without any knowledge of its source(s) (i.e. was it from the same horse, the same group of horses, unrelated horses), while in this study the samples were all independent and encompassed a large geographic region. Earlier studies reported that non-native seeds are passed through the horse's digestive system (Harmon and Kiem 1934, Benninger-Truax et al. 1992), but there was no attempt to determine if the seeds were viable. The mastication and digestion of viable weed seed in the equine digestive system reduces seed viability by 98% (Cash et al. 2006).

Although non-native plant species were present in hay samples, and germinated in the pots, the results from the trail were strikingly different. Of the 288 hay, manure and hoof debris samples placed on the trails, only three plots contained living vegetation at the end of the first growing season, and the three plants were not non-native species. Furthermore no live plants were observed at the end of the second growing season. Campbell and Gibson (2001) reported horse dung-treated plots contained 3 non-native species out of 25 species observed on horse trails in southern Illinois. The three non-native species they observed included two common forage species – lespedeza and white clover – and crabgrass.

The 1% germination and establishment rate observed for the transect plots on the horse trails illustrates the difficult physical and environmental conditions seedlings experience during the critical germination and establishment phase. Why do plants have such a low success rate of becoming established on horse trails? It is difficult to determine whether germination or establishment was the bottleneck for plant survival in this study because transects were surveyed only once per year in 2005 and 2006. Causes of seed mortality during the germination phase include (i) predation by vertebrates, invertebrates, fungi and bacteria, (ii) inadequate reserves in the seed caused by physiological aging, and (iii) alteration of the seed by

organisms that passed the seed. Seeds at the surface of soil are very susceptible to loss of storage reserves because of warm soil temperatures and desiccation (Roberts 1988, Mohler 2001). Seed predation seems less likely as a viable explanation because we did observe modest germination of seeds when samples were sown in pots. The period of plant establishment, defined here as the stage between germination and the production of the first true leaf, is thought to be the major bottleneck for some species (Boutin and Harper 1991). Causes for seedling mortality include exhaustion of seed reserves, improper environmental conditions such as drought, seedling disturbance, seedling herbivory, or defects of seedlings. Several of these factors may explain the extremely low germination and/or survival rate of the samples placed on the trail. Unlike agroecosystems, horse trails represent a highly disturbed system. The physical disturbance of the soil of heavily used horse trails undoubtedly makes it difficult for plants to become established.

Environmental conditions of horse trails also adversely affect plant germination and establishment. Light is the most important environmental cue that promotes the germination of dormant seeds in the soil (Mohler 2001). Plant germination responds to visible light in the red wavelength – the same wavelength that plants use to drive photosynthesis. Light passing through a heavy overstory canopy is depleted in the red wavelength, and as a result the germination of shade intolerant species is inhibited (Gorski 1975). Moreover, adequate light is required by seedlings to drive photosynthesis and produce the carbohydrates needed to promote plant growth. Many of the non-native weedy plants are extremely shade intolerant – that is to say they require modest to full sunlight (Fenner 1978). The average fraction of incoming visible light reaching the soil surface was less than 0.1 at four of the five sites (Figure 5a). Except for the Grand Island site, the light levels measured were considerably below the requirements for shade intolerant weed species.

A second factor that may have contributed to the poor germination and establishment of plants on the trails is water availability. Young emerging seedlings are especially susceptible to desiccation and drought (Mohler 2001). The bulk density, or mass per unit volume of soil, was greater than 1.6 g/cm^3 – a value that as a general rule of thumb will impede the growth of fine roots of most plants (Figure 5b). Soil compaction also decreases water infiltration in the soil, thereby decreasing water available for plant uptake (Landsberg and Gower 1997). Soil water holding capacity was lowest at the Grand Island site because of the large fraction of the soil particles were sand (Figure 5c).

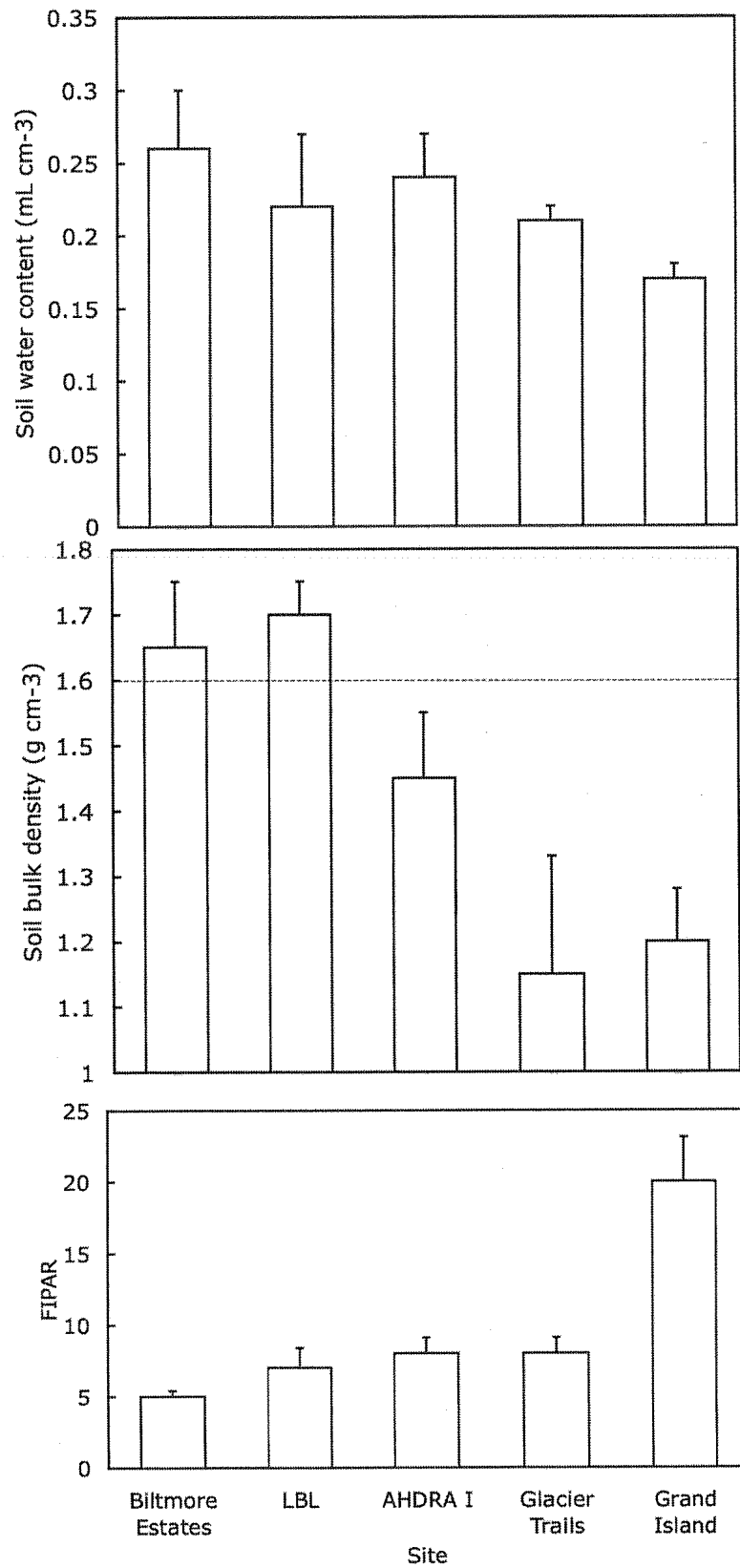


Figure 5 a-c (bottom to top). Average (a) fraction of incident photosynthetic active radiation or visible light at the soil surface, (b) soil bulk density and (c) soil water holding capacity (% by volume) for the five transects at each study site.

Caution should be exercised when interpreting the presence of non-native species along horse trails. Non-native plant species are common to horse trails (Campbell and Gibson 2001, this study), but that does not necessarily infer horses were responsible. For example, non-native species composition and the ratio of non-native:total species composition did not differ between trails open and closed to horse at the three sites examined in this study. Other scientists have reported that the number of exotic plant species is greater along trails than adjacent ecosystems (Hall and Kruss 1989, Parendes and Jones 2000, Tyser and Worley 1992, Benninger-Truax et al. 1992, Adkinson and Jackson 1996). Possible explanations for this pattern include greater resource availability, especially light, in response to gaps in the canopy. Understory plant diversity has been linked to a number of resources including soil water and nutrients (Robertson et al. 1998, Robertson et al. 1993) and light availability (Chazdon et al. 1996, Nicotra et al. 1999). Also, openings in forest canopies increase the number of vegetation strata, which in turn, increases the number and species of birds – key transporters of plant seeds.

Non-Native Plant Classification

When comparing the results of studies quantifying whether horse introduce non-native plant species it is important to consider the source(s) of the classification of plants as non-native plants, and the practicality of the classification. For example, Campbell and Gibson (2001) classified *Poa pratensis*, *Trifolium repens*, and *Kummerowia striata* as an exotic species. *Poa pratensis* L., Kentucky bluegrass, is a perennial, cool-season, sod-forming grass native to Europe, but it is used throughout the U.S. for lawns, golf courses, pastures, and erosion control. *Trifolium repens*, white clover, a herbaceous perennial legume, is native to Europe, North Africa and west Asia, but is a valued forage crop for livestock. *Kummerowia striata*, lespedeza, a perennial legume native to East Asia, and Korea, is commonly used as a forage crop land stabilization cover crop. Campbell and Gibson (2001) used Mohlenbrock (1986) as their source for classifying species as non-native. Two of the sources used in this study (Czarapata 2005, USDA 1971) do not consider the above species non-native. Many grass and clover species are not native to the United States, but their importance and widespread use as forage crops and lawn and recreation field crops raises questions about what constitutes a non-native species.

Management Opportunities to Further Reduce the Risk of Horses Spreading Non-Native Plants

It is important to acknowledge that the results from this study may not be representative for other geographic regions in the United States, or for other types of horse activities. Additional research is needed to determine if the results from this study are representative for other regions and equine activities. One study is ongoing in California (<http://www.dominican.edu/dominicannews/weeds/index.html>).

Despite the extremely low germination and establishment rates of plants on the horse trails, the presence of non-native seed in the hay samples suggests horses pose a threat, albeit small, for the introduction of non-native plant species. Proper disposal of unused or spoiled hay would lessen the likelihood that seeds from

non-native plants get established. Waste in the compost piles could be incinerated or allowed to decompose in a designated area to avoid the spread of seeds.

Estimates for the time it takes for seeds to pass through a horse's digestive tract range from 48 – 72 hours (Alexander 1946, Vander Noot et al. 1967, Cash et al. 2006). Cash et al. (2006) conducted a horse feeding trial where feed was dosed with known quantities of leafy spurge, spotted knapweed, Persian dandelion, wild oat, curly dock and quackgrass – all non-native weeds – and alfalfa. Total passage of viable weed seeds through 72 hours ranged from 0 to 2% for weeds species to over 10% for alfalfa. These data suggest that horses should be placed on certified weed-free hay or hay substitute for three to four days prior to travel to avoid transporting non-native seeds in forage and manure. Given the extremely low viability of the seeds passing through horses, and the low germination and establishment rate of seeds in manure and hay (Campbell and Gibson 2001, this study), judicious disposal of waste seems more prudent.

CONCLUSIONS

Non-native seeds in the hay and manure samples obtained from endurance horses germinated under ideal growing conditions and comprised 2-13% of the total plants identified in the pots. However, less than 1% of the plots established on the horse trail contained live plant at the end of the first growing season, and no live plants were observed in the plots at the end of the second growing season. Understory species composition and fraction of non-native:total species did not differ between trails open and closed to horses at three of the study sites. Collectively, these data suggest horses are not important source for the introduction of non-native plants.

ACKNOWLEDGEMENTS

The American Endurance Ride Conference provided the financial support for the study. The author is grateful to all the riders that agreed to participate in the study.

References

- Adkinson, G.P., M.T. Jackson. 1996. Changes in ground layer vegetation near trails in Midwestern U.S. forests. *Natural Areas Journal* 16:14-23.
- Alexander, F. 1946. The rate of passage of food residues through the digestive tract of the horse. *Journal of Comparative Pathology* 56:266-268.
- Bates, G.H. 1935. The vegetation of footpaths, sidewalks, cart-tracks, and gateways. *Journal of Ecology* 23:463-487.

- Benninger-Truaz, M.C., J.L. Vankat, and R.L. Schaefer. 1992. Trail corridors as habitat and conduits for movement of plant species in Rocky Mountain National park, Colorado, USA. *Landscape Ecology* 6:269-278.
- Binggeli, P. 1996. A taxonomic, biogeographical, and ecological overview of invasive woody plants. *Journal of Vegetation Science* 7:121-124
- Boutin, C. and J.L. Harper. 1991. A comparative study of the population dynamics of five species of *Veronica* in natural habitats. *Journal of Ecology* 79:199-221.
- Bouyoucos, G.J. 1962. Hydrometer method improved for making particle size analyses of soils. *Agronomy Journal* 54:464-465.
- Braithewaite, R.W., W.M. Lonsdale, and J.A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biological Conservation* 48:189-210.
- Campbell, J.E. and D.J. Gibson. 2001. The effect of seeds of exotic species transported via horse dung on vegetation along trail corridors. *Plant Ecology* 157:23-35.
- Cash, D., L. Barney, and S. Gagnon. 2006.
<http://www.animalrangeextension.montana.edu/articles/forage/horses-weeds.htm>
- Chazdon, R.L., R.W. Pearcy, D.W. Less, and N. Fetcher. 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. Pp 5-55 in S.S. Mulkey, R.L. Chazdon, and A.P. Smith (eds). *Tropical forest plant ecophysiology*. Chapman Hall, New York, New York.
- Corbin, J.D. and C.M. D'Antonio. 2004 Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85:1273-1283.
- Czarapata, E.J. 2005. *Invasive plants of the upper Midwest: an illustrated guide to their identification and control*. The University of Wisconsin Press, Madison, WI. 215 p.
- Elliott ET, Heil JW, Kelly EF, Monger HC (1999) Soil structural and other physical properties. In: *Standard Soil Methods for Long-Term Ecological Research* (eds Robertson GP, Coleman DC, Bledsoe CS & Sollins P), pp. 74-85. Oxford University Press, New York, Oxford.
- Fenner, M. 1978. Susceptibility to shade in seedlings of colonizing and closed turf species. *New Phytologist* 81:739-744.
- Gorski, T. 1975. Germination of seeds in the shadow of plants. *Physiologia Plantarum* 34:342-346.
- Gower, S.T., C.J. Kucharik, and J.M. Norman. 1999. Direct and indirect estimation of leaf area index, f(PAR), and net primary production of terrestrial ecosystems. *Remote Sensing of the Environment* 70:29-51.
- Hall, C.N. and F.R. Kuss. 1989. Vegetation alteration along trails in Shenandoah National Park, Virginia. *Biological Conservation* 48:211-227.
- Harmon, G.W. and F.D. Kiem. 1934. The percentage and viability of weed seeds recovered in the feces of farm animals and their longevity when buried in manure. *Journal of the American Society of Agronomy*

- Heady, H.F. 1954. Viable seed recovered from fecal pellets of sheep and deer. *Journal of Wildlife Management*. 7:259-261.
- Land, F. 1994. Troubled trails. *Western Horsemen*. April: 6-9.
- Landsberg, J.J., and S.T. Gower. 1997. Applications of physiological ecology to forest management. Pp. 19-50. Academic Press, New York
- Liebman, M., C.L. Mohler, and C.P. Staver. 2001. *Ecological Management of Agricultural Weeds*. Cambridge University Press, New York, NY. 532 p..
- Lorenzi, H.J. and L.S. Jeffery. 1987. *Weeds of the United States and their control*. Van Nostrand Reinhold Company Inc., New York, NY. 355 p.
- Mohler, C.L. 2001. Weed life history: identifying vulnerabilities. Pp. 40-98. In Liebman, M., C.L. Mohler, and C.P. Staver (Eds.). *Ecological Management of Agricultural Weeds*. Cambridge University Press, New York, NY. 532 p
- Mooney, H.A. and J. Drake. 1986. *The ecology of biological invasions in North America and Hawaii*. Springer-Verlag. New York.
- Nicotra, A.B., R.L. Chazdon, and S.B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908-1926.
- Parendes, L.A. and J.A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and stream in the H.J. Andrews Experimental Forest, Oregon. *Conservation Biology*. 14(1): 64-75.
- Pimentel, D. 1993. Habitat factors in new pest invasions. Pp 165-181. In K.C. Kim, B.A. McPherson (eds.) *Evolution of Insect pests – Patterns of Variation*. New York, NY. John Wiley & Sons.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 1999. Environmental and economic costs associated with non-indigenous species in the United States. *BioScience* 50:53-65.
- Roberts, E.H. 1988. Seed aging: the genome and its expression. Pp. 465-498, In *Senescence and Aging in Plants*, L.D. Nooden and A.C. Leopold (eds.). Academic Press, San Diego, CA.
- Robertson, G.P., M.A. Hutson, F.C. Evans, and J.M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* 69:1517-1524.
- Robertson, G.P., J.R. Crum, and B.G. Ellis. 1993. The spatial variability of soil resources following long-term disturbance. *Oecologia* 96:451-456.
- Royer, F. and R. Dickson. 1999. *Weeds of Canada and the Northern United States*. The University of Alberta Press, Edmonton, Alberta, Canada. 434 p.
- Soule, M.E. 1990. The onslaught of alien species, and other challenges in the coming decades. *Conservation Biology* 4:233-239.
- Tyser, R.W. and C.A. Worley 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.) *Conservation Biology* 6:681-689.
- United States Department of Agriculture. 1998. *Agricultural statistics*. Department of Agriculture, Washington, D.C.
- United States Department of Agriculture. 1971. *Common Weeds of the United States*. Dover Publications, Inc. New York, NY. 463 p.

- United States Congress, Office of Technology Assessment. 1993. Harmful non-indigenous species in the United States OTA-F-565. United States Government Printing Office. Washington, DC.
- Vander Noot, G.W., L.D. Symons, R.K. Lydman, P.V. Fonnesbeck. 1967. Rate of passage of various feedstuffs through the digestive tract of horses. *Journal of Animal Science* 26:1309-1311.
- Vitousek, P.M. 1988. Diversity and biological invasions of oceanic islands. Pp. 181-189. In E.O. Wilson and F.M. Peters (eds.) *Biodiversity*. National Academic Press. Washington DC.
- Vitousek, P.M., H.A. Mooney, J. Lubchenco, and J.M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277:494-499.
- Williamson, M. 1996. *Biological Invasions*. Chapman and Hall. London, UK.