Soil Properties and Exotic Plant Invasions: A Two-way Street

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Abstract

Invasions of exotic plant species have become not only widespread but also a major threat to the health of native ecosystems. In order to manage these invasions, it is important to understand the changes that exotic plants may cause in the environment, and the signs that such changes are taking place. Typically, studies of exotic invasions focus on two issues – the characteristics that render species invasive and communities invasible. Invasiveness is most commonly explained in terms of characteristics of the reproductive and physiological ecology of the plants – seed production and dispersal, tolerance of environmental conditions, etc. Invasibility is commonly related to the species richness, nutrient availability, and the frequencies of anthropogenic and natural disturbance. However, none of these patterns have proven generally true. In addition, only a small fraction (usually about 10%) of established exotic species become pests. The traits which may explain why some new species may become established may not be the same as the traits which allow some of them to become widespread pests. I suggest that one explanation for this transition may be the development of a positive feedback between the plants and the soil that promotes the growth of the exotics at the expense of the natives. Extensive studies of native plant species have demonstrated a variety of mechanisms by which plants alter the soil environment in which they live, making the plant-soil interaction a two-way street.

I have examined the evidence for such feedback processes for two invasive exotic species which have become abundant in eastern deciduous forests, the shrub Japanese barberry (*Berberis thunbergii*) and the annual grass Japanese stiltgrass (*Microstegium vimineum*). Barberry was introduced by the Arnold Arboretum in 1870 for horticultural use. It forms dense clusters of shrubs which in some places coalesce into dense thickets. Stiltgrass appeared in Tennessee in 1917, probably inadvertently introduced. It forms both patches and dense, continuous lawns in closed-canopy forest. Both species are currently found in over 30 states, and are continuing to spread.

I and my colleagues initially documented vegetation and soil properties in three forested areas (Morristown National Historical Park, Allamuchy State Park and Worthingon State Forest) in which heavily infested areas occurred adjacent to uninvaded forest. We found that soils in the invaded sites had strikingly lower amounts of litter on the forest floor, much thinner organic soil horizons, and higher pH values in the mineral soil than did the nearby uninvaded sites. These patterns were also documented across a landscape of adjacent invaded and uninvaded patches. This landscape-level study also suggested that in invaded areas, available nitrate (NO_3^-) was positively correlated with the abundance of the exotics.

We further examined the relationships of plant occurrence and nitrogen dynamics by sampling soils directly beneath barberry clusters, within stiltgrass lawns, and amongst the native Vaccinium stems of the uninvaded areas. These studies corroborated the patterns suggested by the previous results: both extractable nitrate and the net nitrification rate was higher under the exotics than under the native plants.

The patterns of changing soil characteristics can be related to differences between the exotic and native species in a variety of traits. A two-year experiment showed that the decomposition rate of *Berberis* litter is much faster than those of native canopy species (*Quercus alba* and *Betula lenta*); however, *Microstegium* litter decomposes at a rate about equal to *Betula* (*Berberis:* 90% mass loss in 1 year, versus about 30% mass loss for *Quercus* and 40-50% mass loss for *Betula* and *Microstegium*). The *Berberis* also has a much higher standing crop of nitrogen in the biomass than does the understory shrub species that it replaces; this reflects higher N concentrations in leaves, stems and roots. *Microstegium* has relatively low N concentrations in the leaves and culms, but its roots are also rich in N. The two exotic differ strikingly, however, in the amounts of root tissue present: Berberis has large amounts of N-rich fine roots, whereas the Microstegium has a remarkably small root biomass. The two exotic species also have high levels of activity of the enzyme nitrate reductase in

their leaves, unlike the native canopy and understory species; this enzyme is correlated with the ability to utilize nitrate as a source of nitrogen. These results suggest that the high levels of nitrate observed in the soil match an ability of the exotics to utilize this form of the nutrient, unlike the native species. Additional experiments done with plants grown in the greenhouse in previously uninvaded soils show that the microbial community, as indexed by a range of extracellular enzyme activities and also by the profiles of phospholipid fatty acids present in the microbial cell walls, are different under the three species (*Berberis, Microstegium* and the native *Vaccinium pallidum*). Together, these data show that Berberis changes ecosystem-level processes through differences in the nutrient content of its tissues, whereas Microstegium may change these processes by having so little root biomass that the soil volume is essentially unoccupied by active root biomass.

The widespread distribution of these species – virtually all protected natural areas, parks and forests in the New York metropolitan area are invaded, for example – combined with the results of these studies suggest that changes to soil properties and processes may be equally widespread. Thus, feedback processes involving soil-plant interactions may be an important component of the invasiveness of some exotic plant species, and may also contribute to the invasibility of some sites. These changes may, furthermore, cause changes in successional dynamics as native species adapted to low-nitrogen, acidic forest soils are outcompeted by weedy species able to take advantage of the higher amounts of nitrate and the lower acidity.

Acknowledgments

I thank Drs. Peter Kourtev and Weize Huang for their contributions to all aspects of this research. Many students, including Megi Kourtev, Lara Masker, Karin Tekel, Jeff Lambe, and Michelle Hughes, assisted with both field and laboratory studies. The research was supported by the USDA NRICGP.

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