Kentucky 31, Far from Home

Clay and Holah (1) used a cultivar of tall fescue, Kentucky 31 (KY-31), to demonstrate that fungal endophyte symbiosis, by enhancing the competitive dominance of tall fescue, reduced species diversity in successional fields. They then extended these results to conservation biology, predicting that endophyte-driven loss of plant diversity is likely where tall fescue is common and highly infected. I propose, however, that these results should rather be seen as evidence of ecosystem vulnerability to human-induced invasion by an exotic species.

The ecological and economic importance of infected KY-31 in the United States is indisputable (1–4). Associated endophytic fungus makes this cultivar particularly vigorous, highly resistant to herbivores, and tolerant of a wide range of environmental conditions. The cultivar has become a tenacious invader of grasslands throughout much of the eastern United States (3). Since the stock of this ecotype was collected originally from a stand in Menifee County, Kentucky, in 1931 and was released as the cultivar Kentucky 31 in 1943, it has emerged as a model system for studies directing conventional wisdom of endophyte-plant associations worldwide (5).

It is important to recognize, however, that tall fescue is a species originally introduced from Europe, where, although widely distributed, it has not shown competitive dominance in native or man-made ecosystems: In Europe, the species is found only in damp grasslands, river banks, and seashores (6), irrespective of whether it is endophyte infected (7). Rather, tall fescue distribution in Europe is apparently determined by climatic, edaphic, or other environmental factors.

I propose that the lack of genetic diversity of the KY-31 cultivar and of its associated endophytic fungi play a central role in tall fescue’s great success in the United States. The cultivar’s original gene pool represents a single population—and, more important, the genetic diversity of the fungal strain in KY-31 is restricted to the original gene pool, because the fungus is transmitted vertically from the maternal plant to offspring via seeds. If contagious transmission is ruled out, as is usually assumed (1), only one fungal genotype is transmitted to seed progeny throughout the host plant line. Thus, to make generalizations on the importance of fungal endophytes, endophytes in other cultivars and native grass species, and in various environments, must also be examined (5).

The efficiency of highly competitive exotic species is promoted by high ecosystem productivity (8), reduction of species number and the genetic base of cultivars during domestication (9), and the loss of the initial species richness of the ecosystem (10)—all characteristics common in “tall fescue green” areas in the United States, where natural grasslands have largely been fragmented into small patches in an otherwise agricultural landscape (3). Exotic species have long been recognized as “one of the great historical convolutions in the world’s fauna and flora” (11); nor is the idea of central role for microorganisms particularly novel in this context (9, 12). KY-31 provides an example of the potency of a nonpathogenic microorganism strain with a very restricted gene pool in an invaded ecosystem. Determining the general importance of endophytic fungi as a threat to biodiversity, however, will require more comprehensive studies of endophytes and their host plants, encompassing the species and genetic diversity of both endophytes and host plants, the prevalence of contagious spread of fungi, and an emphasis on trophic interactions and habitat fragmentation.

Kari Saikkonen
Section of Ecology
University of Turku
Finland
E-mail: karisaik@utu.fi

Response: Saikkonen suggests that our results, which demonstrated that endophyte-infected (E+) tall fescue (Festuca arundinacea) significantly reduced species richness in experimental plots relative to E− tall fescue (1), constitute evidence of ecosystem vulnerability to human-induced invasion by exotic species rather than a general model for grass-endophyte symbiosis. Clearly, the spread of this and other exotic species in North America has been facilitated by humans. We believe, however, that we have isolated the effects of endophyte infection from other potentially confounding factors, by comparing replicated E+ and E− plots and by holding species identity and gene pool constant.

Saikkonen does not think our results should be extended to tall fescue in its native European range, because it is not as abundant there as in the United States. Few landscapes in Europe, however, have not been altered by human activities; thus, although tall fescue is native to the region, it occurs primarily in non-native habitats, just as in the United States. For a number of European grass species and populations, endophyte infection rates approach 100% (2–4). Would tall fescue and other native grasses be as successful as they are in the absence of endophyte symbiosis? The question cannot be answered without conducting the type of experiment described in our paper.

We do not agree that lack of genetic diversity in KY-31 and its endophyte play a central role in its success. Tall fescue was already widely distributed and highly infected throughout the United States when an ecotype was collected from the wild, propagated, and released as variety KY-31. Although the gene pool of KY-31 may be limited, it is not uniform: tall fescue is obligately outcrossing, is highly variable in morphology and physiology, and exhibits significant genotype × endophyte interactions (5, 6). The endophyte is asexual and exhibits very limited genetic diversity, but that is true throughout its range (7). Recent studies suggest that the endophyte of tall fescue is of hybrid origin (8), as is the hexaploid host. The symbiotic association is, therefore, an amalgamation of multiple plant and fungal genomes.

We suggested that an important factor determining the success of E+ grasses is high concentrations of alkaloid toxins combined with strong grazing pressure (1). The well-documented ecological successes of many native wild E+ grasses is clearly not predicated on being either exotic or inbred (9–11). In the St. Kilda islands of Scotland, infection frequency of red fescue (Festuca rubra) was positively correlated with feral sheep grazing pressure and significantly improved plant survival (12). In China, the native E+ grass Achnatherum inebrians has become the dominant species over vast areas as grazing pressure from cattle has increased in recent years (11).

Saikkonen concludes that exotic species, including microorganisms, have long been recognized as disruptive of native ecosystems. We agree. Our results demonstrate that the effect of an exotic grass on plant biodiversity depends significantly on endophyte infection. To our knowledge, the importance of these symbiotic interactions on grassland community structure has not previously been demonstrated. Extending our study to include
more species, incorporating effects of contagious spread and habitat fragmentation, and considering a wider range of trophic interactions, as Saikkonen suggests, are ambitious and worthwhile goals—but they depend on an affirmative answer to a simple question: Does endophyte infection have any effect on the community? Our study has provided that answer.

Keith Clay
Jenny Holah

References
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