Low allelopathic potential of an invasive forage grass on native grassland plants: a cause for encouragement?

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Summary

Tall fescue (\textit{Festuca arundinacea} Schreb.), a highly competitive European grass that invades US grasslands, is reportedly allelopathic to many agronomic plants, but its ability to inhibit the germination or growth of native grassland plants is unknown. In three factorial glasshouse experiments, we tested the potential allelopathic effects of endophyte-infected (E\textsuperscript{+}) and uninfected (E\textsuperscript{−}) tall fescue on native grasses and forbs from Midwestern tallgrass prairies. Relative to a water control, at least one extract made from ground seed, or ground whole plant tissue of E\textsuperscript{+} or E\textsuperscript{−} tall fescue reduced the germination of 10 of 11 species in petri dishes. In addition, the emergence of two native grasses in potting soil was lower when sown with E\textsuperscript{+} and E\textsuperscript{−} tall fescue seedlings than when sown with seeds of conspecifics or tall fescue. However, when seeds of 13 prairie species were sown in sterilized, field-collected soil and given water or one of the four tall fescue extracts daily, seedling emergence was lower in one extract relative to water for only one species, and subsequent height growth did not differ among treatments for any species. We conclude that if tall fescue is allelopathic, its inhibitory effects on the germination and seedling growth of native prairie plants are limited, irrespective of endophyte infection. On the other hand, the apparent inability of these plants to detect tall fescue in field soil could hinder prairie restoration efforts if germination near this strong competitor confers fitness consequences. We propose that lack of chemical recognition may be common among resident and recently introduced non-indigenous plants because of temporally limited ecological interactions, and offer a view that challenges the existing allelopathy paradigm. Lastly, we suggest that tall fescue removal will have immediate benefits to the establishment of native grassland plants.

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Zusammenfassung
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Introduction

Invasive, exotic plants possess physiological traits and life history strategies that enable them to exploit ecological opportunities. In most cases, however, their local abundance and geographic range ultimately depend on competitive interactions with other plants. Competition can lead to plant displacement through the usurpation of limiting resources, or by the allelopathic inhibition of germination or growth via phytotoxic chemical release (Fuerst & Putman, 1983; Nilsson, 1994; Zimdahl, 1999; Olson & Wallander, 2002). One fundamental difference between these community-structuring forces is the community response time following the death of a competitor; phytotoxins can persist in the soil or litter layer long after allelopathic plants senesce (Gentle & Duggin, 1997; Blum, Shafer, & Lehman, 1999; Gallet, Nilsson, & Zackrisson, 1999; An, Pratley, & Haig, 2000), thereby reducing the establishment potential of an area, whereas there can be a relatively more rapid utilization of resources following death of a non-allelopathic competitor (Grace, 1999; Edwards, Bourdot, & Crawley, 2000; Jutila & Grace, 2002). In restoration areas, this distinction is not trivial.

Tall fescue (*Festuca arundinacea* Schreb.) was introduced into the United States from Europe in the late 1800s primarily as a forage grass (Buckner, Powell, & Frakes, 1979). One hundred or more tall fescue varieties have since been released (Murphy & Watkins, 2002), including Kentucky-31, which contains the systemic fungal endophyte *Neotyphodium coenophialum* (Morgan-Jones & Gams) Glenn, Bacon, & Hanlin. Grasslands (Kettle, Rich, Kindscher, Pittman, & Fu, 2000; Washburn, Barnes, Rhoades, & Remington, 2002) and other habitats have now been invaded by many of these varieties in the Midwestern, eastern and southern United States (Ball, Pederson, & Lacefield, 1993; Roberts, 2000).

Clay and Holah (1999) found that plant species richness decreased in successional fields harboring endophyte-infected (E⁺) tall fescue but increased when the tall fescue was uninfected (E⁻) (but see Spyreas, Gibson, & Middleton, 2001).
Relative to E– varieties, E+ tall fescue is more drought-tolerant (Arachavaleta, Bacon, Hoveland, & Radcliffe, 1989; West, 1994; Asay, Jensen, & Waldron, 2001), has greater herbivore resistance (Cheplick & Clay, 1988; West, Izekor, Oosterhuis, & Robbins, 1988; Clay, 1996; Siegel et al., 1990) and can be more competitive under many environmental conditions (Marks, Clay, & Cheplick, 1991; Clay, Marks, & Cheplick, 1993; Hill, Belesky, & Stringer, 1998; Vaylay & van Santen, 1999).

In addition, tall fescue is reportedly allelopathic to numerous plants (Peters & Zam, 1981; Smith & Martin, 1994; Chung & Miller, 1995), and E+ tall fescue may be more allelopathic than uninfected conspecifics via the production of organic acids, pyrrolizidine alkaloids and phenolic compounds (Luu, Matches, Nelson, Peters, & Barner, 1989; Springer, 1996; Malinowski, Alloush, & Belesky, 1998, 1999). These studies used agronomic plants, but here we investigate the allelopathic potential of E+ and E– tall fescue on 13 species of graminoid and broad-leaved plants native to tallgrass prairies of the Midwestern United States. We chose these species to provide a taxonomically diverse assemblage of representative species from this community (Table 1; also see Howe, Brown, & Zorn-Arnold, 2002).

In a glasshouse, we tested whether: (i) seedling emergence of two native grasses was inhibited by the presence of seeds or seedlings of E+ and E– tall fescue and (ii) germination and seedling growth of 13 native grassland species was reduced by aqueous extracts of seed or whole plant tissue of E+ and E– tall fescue. Our goal in (ii) was first to maximize the allelopathic potential of tall fescue by measuring the germination response of prairie plants in petri dishes, and then simulate more realistic field conditions by measuring their emergence and height growth in sterilized, field-collected soil. Evidence of tall fescue allelopathy may indicate that prairie restoration efforts would be hindered in areas invaded by tall fescue. However, it is also plausible that lack of germination inhibition by tall fescue could be harmful to prairie plant establishment if germination in the presence of this strong competitor reduces subsequent growth, survival or reproductive output. We argue that germination inhibition following phytochemical exposure could be adaptive, and may not be the result of classic allelopathic interference.

### Materials and methods

#### Tall fescue aqueous extracts

We created separate 75 g fresh wt·t−1 aqueous extracts from seed, and from combined shoot and root tissue of E+ (variety Kentucky-31) and E– (variety Barcel) tall fescue (n = 4 extracts). Seeds were soaked in distilled water (dH2O) at 22 °C for 48 h, ground at high speed for 30 s in a blender and soaked for an additional 24 h. These extracts were then strained through cheesecloth and collected. Whole plant extracts were made similarly, but all shoots and roots from four to six-week old tall fescue were washed in tap water and soaked in dH2O for 24 h prior to blending. Tall fescue tissue

<table>
<thead>
<tr>
<th>Species (family)</th>
<th>Common name</th>
<th>Petri dish</th>
<th>Sterilized soil</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Asclepias tuberosa (Asclepiadaceae)</strong></td>
<td>Butterfly weed</td>
<td>**</td>
<td>0</td>
</tr>
<tr>
<td><strong>Rudbeckia hirta (Asteraceae)</strong></td>
<td>Black-eyed Susan</td>
<td>****</td>
<td>0</td>
</tr>
<tr>
<td><strong>Silene regia (Caryophyllaceae)</strong></td>
<td>Royal catchfly</td>
<td>*</td>
<td>0</td>
</tr>
<tr>
<td><strong>Baptisia leucantha (Fabaceae)</strong></td>
<td>White wild indigo</td>
<td>****</td>
<td>0</td>
</tr>
<tr>
<td><strong>Dalea purpurea (Fabaceae)</strong></td>
<td>Purple prairie clover</td>
<td>****</td>
<td>0</td>
</tr>
<tr>
<td><strong>Desmanthus ilinoensis (Fabaceae)</strong></td>
<td>Illinois bundle flower</td>
<td>***</td>
<td>0</td>
</tr>
<tr>
<td><strong>Monarda fistulosa (Lamiaceae)</strong></td>
<td>Wild bergamot</td>
<td>****</td>
<td>0</td>
</tr>
<tr>
<td><strong>Andropogon gerardii (Poaceae)</strong></td>
<td>Big bluestem</td>
<td>**</td>
<td>0</td>
</tr>
<tr>
<td><strong>Elymus hystrix (Poaceae)</strong></td>
<td>Bottlebrush grass</td>
<td>NA</td>
<td>0</td>
</tr>
<tr>
<td><strong>Elymus virginicus (Poaceae)</strong></td>
<td>Virginia wild rye</td>
<td>NA</td>
<td>0</td>
</tr>
<tr>
<td><strong>Panicum virgatum (Poaceae)</strong></td>
<td>Switchgrass</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td><strong>Sorghastrum nutans (Poaceae)</strong></td>
<td>Indian grass</td>
<td>**</td>
<td>0</td>
</tr>
<tr>
<td><strong>Potentilla arguta (Rosaceae)</strong></td>
<td>Prairie cinquefoil</td>
<td>****</td>
<td>0</td>
</tr>
</tbody>
</table>

Asterisks (*) indicate the number of tall fescue extracts (nmax = 4) with estimates of final germination or seedling emergence number lower than that of water, as determined by 95% confidence interval comparisons (see text for parameter estimates). Estimates for extracts did not exceed that of water for any species. "0" indicates no differential response between water and the extracts; "NA" indicates that the species was not analyzed because of low germination.
had been grown in a glasshouse in a potting soil mixture (1:1:1—Soil:Peat:Perlite) and was given ample tap water every other day. Glasshouse temperatures were 29 (day)/15 (night) °C under ambient light conditions (13.5 h light/10.5 h dark). Percent endophyte infection for the E+ and E− seeds was 58% and 0%, respectively.

**Tall fescue seed and seedling effects**

We tested whether the presence of E+ and E− tall fescue seeds reduced the emergence of two *Elymus* spp. relative to their emergence among conspecific seeds. On 27 March 2002, we separately sowed 25 seeds of E+ and E− tall fescue into 7.5 × 7.5 × 6 cm pots containing our potting soil mixture. To these pots, we added either 25 seeds of Virginia wild rye (*Elymus virginiana* L.) or 25 seeds of Bottlebrush grass (*E. hystrix* L.). As a control, 50 seeds of each *Elymus* spp. were sown in separate pots. All seeds were sown to a depth of 0.5 cm.

We also tested whether tall fescue seedlings affected the emergence of *Elymus* spp. by initially sowing 25 seeds of E+ and E− tall fescue in separate pots. After these seedlings emerged on 3 April 2002, we separately added 25 seeds of each *Elymus* sp. to each of the E+ and E− tall fescue pots and covered them with 0.5 cm of potting soil. Fifty seeds of each *Elymus* spp. were sown as a control. There were 10 replicates of each treatment and these were arranged in a completely random factorial design.

*Elymus* seeds sown in monoculture were stratified in dH$_2$O for one week at 3 °C, whereas those sown with E+ and E− tall fescue were respectively stratified in 75 g l$^{-1}$ E+ and E− seed extracts to simulate a tall fescue seed bank environment. All pots contained 8660 seeds m$^{-2}$. Each pot initially received 40 ml of dH$_2$O or extract and subsequently was given 20–30 ml of solution daily to avoid allelochemical runoff. We used an extract concentration of 25 g l$^{-1}$, which Smith and Martin (1994) report as realistic in mixed pastures containing tall fescue. Extracts were made weekly and were stored at 3 °C. Seedling emergence was recorded twice per week. After 19 days, we measured the lengths of monocot leaves and dicot shoot apexes (i.e., 'height') from the soil surface for the four tallest seedlings in each pot. The experimental design and treatment number were the same as in the petri dish experiment. Glasshouse temperatures were 32/20 °C under ambient light conditions (15 h light/9 h dark).

**Data analysis**

In each of the three experiments, cumulative germination (or seedling emergence) number (G) was modeled using the following logistic equation:

$$G = A[1 + \exp(\beta t - \kappa t)]^{-1},$$

where $A$, $\beta$, and $\kappa$ are parameter estimates of the germination curve asymptote, first day of germination and linear germination rate, respectively, and $t$ equals day. In each experiment, we used 95% confidence intervals to compare the parameter estimates of the control to those containing tall fescue for each species.

In addition, we used a two-way ANOVA to analyze final germination number in the petri dish experiment. We tested whether the presence of E+ and E− tall fescue seeds reduced the emergence of two *Elymus* spp. relative to their emergence among conspecific seeds. On 27 March 2002, we separately sowed 25 seeds of E+ and E− tall fescue into 7.5 × 7.5 × 6 cm pots containing our potting soil mixture. To these pots, we added either 25 seeds of Virginia wild rye (*Elymus virginiana* L.) or 25 seeds of Bottlebrush grass (*E. hystrix* L.). As a control, 50 seeds of each *Elymus* spp. were sown in separate pots. All seeds were sown to a depth of 0.5 cm.

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**Petri dish experiment**

Fifteen hundred seeds of 13 tallgrass prairie species (*Table 1*) were stratified at 3 °C for one week in separate ziplock bags that contained a paper towel and 15 ml of dH$_2$O or one of the four tall fescue extracts. For each species, 50 seeds were then placed into each of thirty, 10 cm diameter polystyrene petri dishes containing Fisherbrand course filter paper. Six ml of dH$_2$O (control) or extract were added to each dish and these were placed in a glasshouse between 3 and 5 April 2002. Germination was recorded twice per week for 19 days. During the first ten days, 5 ml of dH$_2$O or extract was added twice to each dish when the filter paper began to dry, and dH$_2$O was added to all dishes on day 14. The glasshouse conditions were the same as those previously described. *Elymus* spp. were deleted from the analysis because they did not germinate. This factorial experiment was arranged in a completely randomized block design with six replicates per treatment combination.

**Sterilized, field-collected soil experiment**

On 20 June 2002, we tested whether the seedling emergence and height growth of the 13 prairie plant species differed between dH$_2$O (control) and the four tall fescue extracts. Fifty unstratified seeds of each species were separately sown in 9 × 9 × 7 cm pots to a depth of 0.5 cm in sterilized, field-collected soil (Drummer, Fine-silty, mixed, superactive mesic Typic Endoaquoll). Seed density was 5660 seeds m$^{-2}$. Each pot initially received 40 ml of dH$_2$O or extract and subsequently was given 20–30 ml of solution daily to avoid allelochemical runoff. We used an extract concentration of 25 g l$^{-1}$, which Smith and Martin (1994) report as realistic in mixed pastures containing tall fescue. Extracts were made weekly and were stored at 3 °C. Seedling emergence was recorded twice per week. After 19 days, we measured the lengths of monocot leaves and dicot shoot apexes (i.e., 'height') from the soil surface for the four tallest seedlings in each pot. The experimental design and treatment number were the same as in the petri dish experiment. Glasshouse temperatures were 32/20 °C under ambient light conditions (15 h light/9 h dark).
experiment, and final seedling emergence and height in the sterilized field soil experiment, with species and aqueous medium (i.e., dH2O and extracts) as fixed factors and block as a random effect. Because a significant species × aqueous medium interaction in the petri dish experiment explained only 2.5% of the model’s variation, linear contrasts were used to assess whether germination number differed between: (1) water and extracts, (2) whole plant and seed extracts, and (3) E+ and E− extracts. Tukey-Kramer adjustments were used for all factor level comparisons to control for comparisonwise error rates ($\alpha = 0.05$). Because tall fescue varieties differed, we could not distinguish this effect from an endophyte effect (see Peters & Zam, 1981). All statistical tests and estimates of germination and emergence parameters were performed in the Statistical Analysis System (SAS, 2001).

Results

The seedling emergence of each Elymus spp. in potting soil did not differ for seeds simultaneously sown with E+ or E− tall fescue seeds and those sown with conspecifics (Fig. 1). However, sowing seeds of each Elymus spp. in the presence of E+ and E− tall fescue seedlings reduced their emergence relative to those sown in monoculture (Fig. 1). The estimated emergence rates and first day of emergence did not differ among treatments for either Elymus spp., and level of endophyte infection did not affect any germination parameters.

Ten of 11 species in the petri dish experiment had lower estimates of final germination number in at least one tall fescue extract when compared with water (Table 1), and estimates in extracts did not exceed those in water for any species. The estimated first day of germination was lower in water relative to all extracts for two of 11 species, but no water-to-extract comparisons of germination rate differed for any species.

The aqueous medium affected final germination number (two-way ANOVA; Fig. 2a; $F_{4,220} = 93.61; p<0.0001$). Using linear contrasts, we found that germination was higher in water than in all tall fescue extracts ($F_{1,220} = 336.94; p<0.0001$), was higher in whole plant extracts compared with seed extracts ($F_{1,220} = 30.97; p<0.0001$), but did not

![Figure 1](image1.png)

**Figure 1.** Final number of emerged seedlings of: (a) *Elymus virginicus* and (b) *Elymus hystrix* when sown in the presence of seeds or seedlings of E+ and E− tall fescue, or when sown in monoculture (C). Means±95% confidence intervals are given.

![Figure 2](image2.png)

**Figure 2.** Final (a) germination and (b) seedling emergence number of prairie plant species in the petri dish ($n=11$ species) and sterilized soil experiment ($n=13$ species). "Tissue" and "Seed" treatments were respectively given aqueous extracts made from whole plants or seeds of tall fescue. Means±95% confidence intervals are given.
differ between the level of endophyte infection \( (F_{1,220} = 1.48; p = 0.2253) \). There was also a sign-
ificant species × aqueous medium interaction \( (F_{4,312} = 4.43; p < 0.0001) \); also see Table 1), but this explained only 2.5% of the variation in our model.

The final number of emerged seedlings in pots containing sterilized field soil was higher in the control relative to one extract for *Panicum virgatum* L. only (Table 1). No water-to-extract comparisons of emergence parameters differed for any other species. No differences were found between extracts and water in the final number of emerged seedlings (Fig. 2b; two-way ANOVA; \( F_{4,312} = 1.11; p = 0.3534 \)) and in final seedling height (\( F_{4,312} = 0.60; p = 0.6631 \)), nor were significant species × aqueous medium interactions found for these factors (\( p > 0.05 \)).

**Discussion**

**Tall fescue allelopathy**

In this study, we tested whether tall fescue can inhibit the germination and subsequent growth of a diverse assemblage of native tallgrass prairie plants. The success of an invading plant can be strongly influenced by its allelopathic effects on other plants (Goslee, Peters, & Beck, 2001; Ridenour & Callaway, 2001), and we found that seedling emergence of both *Elymus* spp. was reduced in the presence of high density E+ and E− tall fescue seedlings. Malinowski et al. (1998) suggested that tall fescue, particularly varieties infected with *N. coenophialum*, can modify the rhizosphere by releasing phenolics, a family of compounds known for their allelopathic activity (Blum, 1998; An et al., 2000). In petri dishes, tall fescue extracts reduced the germination of all but one of the prairie plants, and specific responses to these differed among species. These results suggest that allelopathy by tall fescue could lead to shifts in prairie plant composition if species-specific responses occur in the field.

Our initial experiments were designed to max-
imize the allelopathic potential of tall fescue and provide evidence that its seedlings, and seed and tissue extracts can inhibit the germination and emergence of plants native to Midwestern tallgrass prairies. However, Inderjit and Weston (2000) suggested that conclusions from laboratory studies using potting soil may be spurious because allelo-
chemical movement and degradation can differ between artificial and field soil, and because of poor corroboration with empirical field observations (also see Inderjit, 2001). Moreover, Stowe (1979) criticized petri dish experiments by noting that presumed allelopathic responses could be nothing more than the inhibition of germination due to osmotic potential differentials between aqueous extracts and water.

In our simulation of field conditions, seedling emergence for one of 13 species in sterilized field soil was lower in only one tall fescue extract, and final height did not differ among treatments for any species. We believe the latter findings signify a low allelopathic potential of tall fescue on the prairie plants tested, particularly since lack of runoff in this experiment would tend to concen-
trate allelochemicals. Also, because phenolic acid-utilizing bacteria can break down phenolic allelo-
chemicals (Blum, Staman, Flint, & Shafer, 2000), reductions in the microbial community via soil sterilization may have contributed to allelochemical build-up.

**The shifting allelopathy paradigm**

Lack of prairie plant emergence and growth inhibition by tall fescue extracts in field-collected soil may be encouraging, but we urge interpretative caution. Suppose there was a fitness advantage for a seed to recognize chemicals from a strong, nearby competitor such as tall fescue and remain dormant. Germination in this case would reduce subsequent growth, survival or reproductive output relative to those that germinated near less competitive species. It may therefore be evolutionarily advantageous for seeds to possess biochemical recognition systems for compounds released by potential competitors, but developmental time for these may be limited, particularly with respect to recently introduced species with novel chemistries.

Rabotnov (1982) suggested that coevolutionary allelopathic processes may occur, and hypothesized that relative to introduced plants, those that have long been sympatric are most likely to develop resistance to allelochemicals from neighboring plants (i.e., few inhibitory effects; also see Callaway & Aschehoug, 2000; Mallik & Pellissier, 2000; Bias, Vepachedu, Gilroy, Callaway, & Vivanco, 2003). This may be the case, but if reductions in germination are instead viewed in terms of chemical recognition by recipient plants, we predict exactly the opposite—germination inhibition should generally be highest among species with a shared evolutionary history, and lack of germination inhibition is likely to be most prevalent among
native plants and those that have been recently introduced.

This “biochemical recognition hypothesis”, proposed in similar form by Preston and Baldwin (1999), challenges the allelopathy paradigm, which has traditionally viewed a reduction in germination in the presence of another plant’s chemicals as a form of interference (Lambers, Chapin III, & Pons, 1998). Here, we state that germination inhibition following phytochemical exposure could be adaptive, and may not be the result of classic allelopathic interference. This viable alternative is supported by cases where leachates from known allelopathic plants do not affect the germination of allopatric species or those of recent contact but inhibit the germination of historically sympatric species (Preston, Betts, & Baldwin, 2002, this study). Systems in which plants are most likely to develop a biochemical recognition of neighbors are those where the turnover time of aboveground shoots or whole plants is generally shorter than the longevity of the resident seed bank (e.g., deserts, grasslands, chaparrals). If operational, this hypothesis suggests that native plants may not only be displaced through direct resource exploitation by invasive non-indigenous plants, but could also experience seed bank depletion by naively germinating (and consequently suffering fitness reductions) near these novel, strong competitors. We propose that lack of chemical recognition may be common among resident and recently introduced non-indigenous plants because of temporally limited ecological interactions.

Prairie restoration

Tall fescue has invaded numerous habitats throughout the eastern, southern and Midwestern United States, including grasslands (Kettle et al., 2000; Washburn et al., 2002). Our results suggest that this invasiveness may not be the result of allelopathy. In addition, the apparent low allelopathic potential of this strong competitor on many species from distinct functional groups indicates that its removal, followed by the reseeding of native species, will likely result in the quick establishment of many tallgrass prairie plants. Successful removal of tall fescue and the subsequent increases in grassland plant diversity can be accomplished with herbicides and fire management (Washburn & Barnes, 2000; Washburn et al., 2002), but repeated treatments may be necessary because of tall fescue recruitment from local seed dispersal or a soil seed bank.

Conclusions

Our petri dish and potting soil experiments demonstrate a potential for tall fescue to inhibit the germination and seedling emergence of native prairie plants. However, we believe the nearly complete lack of emergence and growth inhibition by E+ and E− tall fescue extracts in sterilized, field-collected soil indicates that its allelopathic potential on these plants is low. Failure to recognize the presence of tall fescue may confer fitness consequences to seeds that germinate near this strong competitor, and could be the result of poorly developed biochemical recognition systems for chemicals released by tall fescue. If tall fescue’s allelopathic potential in the field is low, the prognosis for quick establishment of native species following the removal of tall fescue is good.

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References


