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Spatial connectedness of plant species: potential links for apparent competition via plant diseases

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This study evaluated the reactions of seven common C4 grasses of the tallgrass prairie of the USA Great Plains to the economically important wheat pathogens *Pyrenophora tritici-repentis* and *Gaeumannomyces graminis* var. *tritici* (Ggt) isolated from wheat. The *P. tritici-repentis* isolates (race 1) were pathogenic on all grasses tested, but symptom severity was markedly low. Three of the grass species inoculated with Ggt were highly susceptible, while four species exhibited no symptoms. Because measures of connectedness can provide a proxy for population processes, connectedness was evaluated within and among the seven grass species in representative tallgrass prairie environments for all potential pathogen-sharing patterns. *Andropogon gerardii* was ubiquitous, so all plant species were well connected to it. *Andropogon scoparius* (= *Schizachyrium scoparium*), *Sorghastrum nutans* and *Panicum virgatum* were fairly common but specialized to particular environments. *Bouteloua curtipendula* was uncommon but occurred in all environments, while *Buchloë dactyloides* and *Bouteloua gracilis* were uncommon and only occurred in upland sites. Co-occurrence of plant species was generally not reciprocal in that, for many species pairs, species A rarely occurred without potential exposure to inoculum from species B, while species B commonly occurred without species A. The three grass species susceptible to Ggt may act as sources of inoculum for each other within tallgrass prairie, with the potential to influence fitness, and tallgrass prairie and commercial wheat ecosystems in the Great Plains also have the potential to share both pathogens.

Keywords: agriculture–wildlands interface, biofuel crops, graph theory, networks, pathogen spill-over, switchgrass

Introduction

When the same pathogen genotypes can infect more than one species, connectivity for pathogen populations will generally be enhanced, and the dynamics of host species can be coupled via cross-species infections. The effects of pathogen sharing on host species may be particularly important for community dynamics in response to epidemics if some host species are more tolerant than others and so can act as reservoirs of the shared pathogen (Power & Mitchell, 2004; Malmstrom *et al.*, 2005b; Cobb *et al.*, 2010) and impose apparent competition – i.e. effects similar to competition but based on a shared enemy – by increasing the local inoculum load (Holt, 1977; Alexander & Holt, 1998; Cobb *et al.*, 2010). The connectivity among habitat patches, or, in the case of pathogens, between plant hosts within a landscape, depends upon abiotic attributes of the landscape, the dispersal ability of the pathogen, the behaviour of vectors (if any) and the spatial and temporal proximity of susceptible host tissues (Skelsey *et al.*, 2005; Jeger *et al.*, 2007; Lamour *et al.*, 2007; Harwood *et al.*, 2009; Margosian *et al.*, 2009; Xu *et al.*, 2009; Moslonka-Lefebvre *et al.*, 2011; Garrett, 2012; Meentemeyer *et al.*, 2012; Sutrave *et al.*, 2012). Measurements of connectivity can provide a proxy for population and community processes, as it is sometimes easier to estimate connectivity than it is to directly measure such processes (Minor & Urban, 2007).

The tallgrass prairie of the USA Great Plains encompasses a matrix of dominant C4 perennial grasses interspersed with perennial C3 grasses and forbs (Knapp *et al.*, 1998), a system of particular interest for conservation and restoration. Tallgrass prairie may be a model for the development of new 'low-input high-diversity' bioenergy systems (Tilman *et al.*, 2006) and the use of prairie grasses in monocultures for biofuel production raises new questions about epidemiology in such systems (Crouch *et al.*, 2009; Schrotenboer *et al.*, 2011; Stewart & Cromey, 2011). Agroecosystems dominated by graminoid monocultures of wheat and maize commonly form an interface with tallgrass prairie, and native prairie grasses and crop cultivars can host similar pathogens, potentially influencing pathogen and host population dynamics and evolution (Burdon & Thrall, 2008; Alexander, 2010). The impact on native systems of pathogens originating in agricultural species and associated weed species can be important, as illustrated by the impact of *Barley yellow dwarf virus* (BYDV) on native California grasslands (Malmstrom *et al.*, 2005a,b; Borer *et al.*, 2007), although the impact of species from managed

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systems on natural systems often receives less attention (Blitzer *et al.*, 2012) and requires a careful assessment of cross-infectivity. For example, BYDV was found in three dominant tallgrass prairie grass species in Kansas, but the species (strains) sampled from them did not include the species (strain) of BYDV that was most common in adjacent agricultural systems (Garrett *et al.*, 2004).

The present study focuses on two diseases that potentially could be significant sources of spillover infection into prairie patches from surrounding agricultural lands. Tan spot and take-all are both important wheat diseases that cause significant yield losses in the Great Plains, USA. Ascospores of *Pyrenophora tritici-repentis* (anamorph *Drechslera tritici-repentis*), the causal agent of tan spot, overseason on plant debris, and resulting ascospores disperse by water splash and wind to subsequent wheat crops to initiate disease (Bockus *et al.*, 2010). From foliar lesions caused by ascospores, the polycyclic, conidial stage of the fungus produces new infections. *Pyrenophora tritici-repentis* causes foliar lesions on a wide host range, including wheat and several perennial grasses such as *Andropogon gerardii*, *Koeleria macrantha*, *Thinopyrum ponticum*, *Andropogon scoparius* and *Elymus canadensis* (Krupinsky, 1987, 1992a,b; Krupinsky & Tanaka, 2001). However, the origins of the isolates and range of severity reactions have not been documented. Additionally, isolates obtained from grass hosts may produce disease symptoms on wheat and in some cases are as aggressive as wheat isolates themselves (Krupinsky, 1992a).

Gaeumannomyces graminis var. *tritici*, the causal agent of take-all disease of wheat, survives in infected roots and crowns, dead or living, and infection occurs when susceptible plant roots come into close contact with these inoculum sources (Bockus *et al.*, 2010). Among turf grasses, most perennials are resistant to take-all, but large brown patches infected by the closely related fungus *G. graminis* var. *avenae* can occur (Sarniguet & Lucas, 1992). Both varieties of *G. graminis* seem to be weakly competitive as saprophytes and in both continuous wheat cropping systems and turfgrass, take-all typically disappears after 6–10 years, apparently as a result of the build-up of antagonistic or competing soil microflora (Sarniguet & Lucas, 1992; Weller *et al.*, 2002).

The first objective of this study was to determine the reactions of seedlings of seven perennial warm-season grass species (Table 1) native to the tallgrass prairie of the Great Plains to inoculation with isolates of tan spot and take-all pathogens collected from wheat. This objective addressed a larger scale of epidemic processes than just within the prairie itself, i.e. the potential for spillover between agriculture and tallgrass prairie. Understanding pathogen impacts at the seedling stage is particularly important in gauging the long-term role of pathogens in governing community structure, because during community assembly (e.g. during recovery from a disturbance), plant populations as they first establish will be dominated by seedlings. Reactions of the seven species were evaluated in controlled experiments to allow direct comparisons of the species' responses.

Table 1 Grass species and cultivars included in a study of responses to tan spot (caused by *Pyrenophora tritici-repentis*) and take-all (caused by *Gaeumannomyces graminis* var. *tritici*) pathogens from wheat

Species	Common name	Cultivar	Source
Andropogon gerardii	Big bluestem	Kaw	Kansas
		Bonilla	North Dakota
Andropogon scoparius	Little bluestem	Cimarron	Kansas
		Aldous	Kansas
Sorghastrum nutans	Indian grass	Cheyenne	Kansas
		Osage	Kansas
Panicum virgatum	Switchgrass	Blackwell	Kansas
		Kanlow	Kansas
Bouteloua curtipendula	Sideoats grama	Pierre	North Dakota
		Haskell	Texas
Bouteloua gracilis	Blue grama	Bad River	North Dakota
Buchloë dactyloides	Buffalo grass	Texaco	Texas
		Cody	North Dakota

The second objective was to determine potential connectedness within and among these seven grass species through analysis of their co-occurrence and abundance in a range of tallgrass prairie environments defined by frequency of burning, presence or absence of grazing, and upland or lowland positions. This objective addressed a smaller scale of epidemic processes, namely that within tallgrass prairie after, for example, a spillover event from neighbouring agricultural lands. This analysis consisted of determining the abundance of the grass species in each of 12 representative tallgrass prairie environments, categorizing the seven grass species in terms of their abundance and degree of environmental specialization, and determining the rates of co-occurrence for each grass species pair. The basic rationale for this was that with passive dispersal via (e.g.) wind or splash dispersal of infective spores, there should be a strong effect of distance between infected and susceptible hosts on transmission rates. Hence, measures of spatial overlap should translate to plausible measures of the opportunity for pathogen transmission among species.

Finally, data from these two objectives were used to evaluate the spatial connectedness of the tallgrass prairie landscape for *G. graminis* var. *tritici* and *P. tritici-repentis* populations, where most dispersal of these two pathogens within prairie probably occurs at rather modest spatial scales because of the nature of their dispersal mechanisms. While the study did not directly test for apparent competition via pathogens in tallgrass prairie, it was hoped to provide a useful context for ongoing analysis of the complex interactions among plants in agriculture, plants in tallgrass prairie, and their shared pathogens.

Materials and methods

Plant species

One to two varieties of each of seven C4 grass species were studied (Table 1). Plant germplasm was supplied by USDA Plant Materials Centers located in the central USA in Kansas, Texas and North Dakota. Whenever possible, varieties obtained from Kansas were included so as to more closely match genotypes in native Kansas prairies and to better represent cultivars used in Kansas prairie restoration, Conservation Reserve Programs, and new types of biofuel production systems. For these purposes, the cultivars of tallgrass prairie plants chosen were generally those subjected to artificial selection for better seed production. (While selection for biofuel traits may alter susceptibility in *Panicum virgatum* to viral infection (Schrotenboer *et al.*, 2011), little is known about the effects of selection for seed production on disease susceptibility.) Wild plants may more commonly reproduce clonally, and artificial selection may deplete genetic variation, but cultivars of *A. gerardii* were found to maintain levels of genetic diversity comparable to those of wild populations (Gustafson *et al.*, 2004). All species are perennial, warm-season members of the Poaceae and common features in the Kansas tallgrass prairie, although *Buchloë dactyloides* and *Bouteloua gracilis* typically dominate in the drier shortgrass prairies of the Great Plains. *Andropogon gerardii*, *Andropogon scoparius* (= *Schizachyrium scoparium*), *Sorghastrum nutans* and *P. virgatum* are four dominant grasses of the tallgrass prairie in the central Great Plains (Freeman, 1998; Towne, 2002). Two hard red winter wheat cultivars, Karl 92 and TAM 105, were selected based on their known reactions to tan spot as moderately resistant and highly susceptible controls, respectively. Wheat cv. Victory was used as a susceptible control in take-all experiments, while take-all-resistant wheat varieties currently do not exist. Although wheat cultivars have different growth rates and optimal temperatures for disease development compared to native grasses, they were nevertheless useful as controls and for comparison purposes because of their convenience and predictability for evaluating inoculum success and disease reactions.

Plant culture

Plants were grown in the greenhouse under natural light conditions within an average temperature range of 20–26°C. All plants were grown from seed in plastic 2·5 × 12·5-cm cones (Stuewe and Sons) and fertilized with Peter's 20:20:20 every 2 weeks following emergence. In the tan spot experiment, individual seeds were sown into a 50:50 sterilized soil:sand mix. Ten cones of each cultivar composed a replicate. In the take-all experiment, individual seeds were sown in vermiculite. A replicate consisted of two sets of 10 cones each, placed side by side in vertical rows, where one row was randomly selected for inoculation. In each experiment, four replicates were grown in a randomized complete block design.

Fungal inoculum and disease establishment

Pyrenophora tritici-repentis

Inoculation procedures were based on methods described by Raymond *et al.* (1985). Four different isolates (race 1) of *P. tritici-repentis* collected in Kansas from naturally infected hard red winter wheat were grown on 1/4-strength potato dextrose agar in Petri dishes for *c.* 1 week in the light at room temperature. Mycelial plugs (5 mm) were then removed and inoculated into plates of V8 agar (150 mL V8 juice, 850 mL distilled water, 3·0 g $CaCO_3$ and 15 g agar) and cultured in the dark for 4–5 days at 24°C. Aerial hyphae were flattened around the perimeter with a sterile, bent glass rod and plates were placed at 24°C for 12–24 h in the light followed by 16–24 h in the dark at 18°C. Conidiophores and conidia are produced by *P. tritici-repentis* during light and dark cycles, respectively. Spores were harvested by rinsing plates with distilled water, gently scraping colonies with a bent metal scraper, and pouring the slurry through a layer of cheesecloth. Spore numbers were 8000–10 000 mL^{-1} and were an approximately equal mixture of the four isolates.

Seedlings were grown for 6 weeks prior to inoculation. At inoculation, *c.* 350 000 spores per flat of 100 cones were sprayed on plant surfaces using a De-Vilbiss atomizer at 69 kPa. Plants were then placed into a mist chamber for 48 h at 22 ± 5°C. After misting, plants were again placed in the greenhouse under the same conditions, and leaves two and three were rated for percentage leaf area affected by disease 7 days later.

Gaeumannomyces graminis *var.* tritici

To produce inoculum, 150 mL distilled water were added to 140 g whole oat kernels in 1-L glass jars. Jars were capped with perforated, cotton-plugged lids and shaken to moisten the oats. Jars were autoclaved and allowed to cool in a laminar flow hood. Three to four plugs (5 mm) of mycelium growing on 1/4-strength PDA were buried in the oats and incubated at room temperature. Jars were periodically shaken to prevent kernels and mycelium from clumping. After kernels became blackened by mycelium (2–3 weeks), they were spread out on tarpaulins to air-dry. Dried kernels were stored at 4°C prior to use.

At planting, three inoculated kernels were placed *c.* 2·5 cm below the soil line within inoculated cones, 1·0 cm below the seed. After 6 weeks, each plant was categorized as either 'survived' (no visible symptoms) or 'dead/dying' (substantial necrotic tissue, or more brown than green tissue). Of the plants that survived, roots and crowns were collected and observed for symptoms.

Statistical analyses of host reactions

The mean tan spot severity for each cultivar was compared in an analysis of variance (ANOVA) based on least significant differences (LSD) using SAS software. The percentage mortality caused by take-all infection was calculated for each plant cultivar as: [(percentage of non-inoculated plants that survived) – (percentage of inoculated plants that survived)] / (percentage of non-inoculated plants that survived). This measure was reached as follows. It was assumed that deaths from other factors, and from infection, occurred independently, at instantaneous constant per capita mortality rates of d and d', respectively. Over a given time period (T), the number surviving (N_T) and the overall percentage surviving (s) for inoculated plants are described by

$$N_T = N_0 e^{-(d+d')T}$$

$$s = N_T / N_0 = e^{-(d+d')T}$$

Were there only non-infective deaths, then percentage survival from this cause alone would be expected to be $s' = e^{-dT}$, and were there only infective deaths, percentage survival from infections alone would be $s'' = e^{-d'T}$. Note that $s = s's''$, so $s'' = s/s'$. The percentage mortality from infection, were there no other cause of death, would then be $1 - s'' = \frac{s'}{s'} - s'' = \frac{s' - s}{s'}$.

Analysis of co-occurrence of host species

The co-occurrence of the seven grass species in tallgrass prairie was evaluated using data collected as part of the Long-Term Ecological Research (LTER) Program at Konza Prairie Biological Station (KPBS) in Riley and Geary counties in the Flint Hills of

Kansas, USA (39°05′N, 96°35′W). The plant community structure across environments is represented in an extensive long-term data set maintained as part of the LTER program (Briggs & Knapp, 2001; Silletti & Knapp, 2002; Collins & Smith, 2006); this study used cover data from the KPBS data set PVC02. Experimental treatments representing different land management scenarios have been applied at KPBS at the watershed scale, including different burn frequencies (every 1, 4 or 20 years) and the presence or absence of grazing by bison (*Bos bison*; Hulbert, 1985; Knapp *et al.*, 1998). Each grazing–burning treatment combination was represented by two watersheds, with the exception of the 20-year ungrazed combination for which there was only one watershed available after 2000. The watersheds in the analyses were SPB, 1D, N1B, N1A, 4B, 4A, N4D, N4A, 20B, N20B and N20A; more information about these particular watersheds is available at the KPBS website.

Cover of each plant species was estimated in eight long-term transects per sampled watershed, four in an upland position in Florence soil (shallow, rocky cherty silty clay loam) and four in a lowland position in Tully soil (relatively deep, non-rocky silty clay loam). Within each transect, five 10-m^2 permanent circular quadrats were evenly spaced 12·5 m apart, and cover estimates taken annually at comparable time of years. There were approximately three estimates of cover for each quadrat in each year; the cover estimates were averaged for each species in each quadrat across the 1999–2003 interval, resulting in one estimate of cover per species per quadrat. Cover of each species in each quadrat was estimated using the following scale (1 = 0–1% cover, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95% and 7 = 95–100%). For these analyses, scale values for each species in each quadrat were converted to the midpoint of the cover class. Quadrat means were averaged to produce a mean within each transect, and this mean was used in statistical analyses.

It is suggested that the spatial pattern of co-occurrence can be used to make inferences about the potential for disease transmission across species within the prairie community. It was assumed in this study that co-occurrence within a quadrat would permit transmission of a pathogen from one species to another, at a much higher rate than transmission among quadrats within a transect, or among transects or separate landscapes. Moreover, given the presence of a focal species in a quadrat, were it to be infected, it was assumed that the probability of transmission to the other species in the quadrat would increase with the average biomass of the other species.

The mean percentage cover for each species in each combination of burning/grazing/slope position was calculated by averaging over the (typically) eight transects per treatment combination. The standard error was calculated by treating a transect as an experimental unit, so the mean cover of each ‘target’ species for each quadrat in which the focal species (the potential source species) occurred was averaged within a transect to yield the transect mean. Within each plant species, an analysis of variance was performed to determine the significance of burn return time, position on slope, presence or absence of grazing, and their interactions, as predictors of percentage cover, treating slope position as a subplot within a split-plot design. Plant species were categorized based on their overall abundance across environments and based on their degree of apparent specialization to particular environments. The conditional mean percentage cover for species A, conditional on the presence of focal species B, was defined as the mean percentage cover for species A considering only those quadrats within which focal species B occurred. The standard error of the conditional mean percentage cover was also calculated by treating a transect as an experimental unit; transects in which the focal species did not occur were not included in analyses. The probability of occurrence of a species, conditional on the presence of a focal species, was also calculated at the quadrat scale based on those quadrats in which the focal species occurred, and then averaged within a transect. A transect was treated as an experimental unit for calculation of the standard error.

Results

Impacts of pathogens upon potential hosts

The *P. tritici-repentis* isolates (race 1) produced lesions on all species and varieties, and were therefore pathogenic to at least some degree on all prairie grasses tested in each of the tan spot experiments (Table 2). This fungus is thus clearly a generalist in terms of the range of host plant species it can use. The difference between severity on moderately resistant and highly susceptible wheat controls was highly significant ($P < 0{\cdot}0001$). When experiments were analysed together, tan spot severity on Karl 92 (moderately resistant) was approximately half that on TAM 105 (highly susceptible; data not shown). Severity of tan spot on the prairie grasses was very low regardless of species or cultivar, and was substantially less than on either of the wheat controls ($P < 0{\cdot}0001$). In the first experiment, percentage leaf area affected by tan spot for the switchgrass cv. Kanlow was 13·7%, the highest rating among all prairie species, but significantly lower than the moderately resistant wheat control. In this experiment the two switchgrass cultivars, Kanlow and Blackwell, had significantly different responses, although the difference between them was small compared to the difference between switchgrass

Table 2 Tan spot severity in grass species inoculated with race 1 isolates of *Pyrenophora tritici-repentis* from wheat

		Tan spot severity (%)[a,b]	
Species	Cultivar	Experiment 1	Experiment 2
Andropogon gerardii	Kaw	0·75	0·01
	Bonilla	3·56	0·15
Andropogon scoparius	Cimarron	0·46	0·25
	Aldous	1·83	0·17
Sorghastrum nutans	Cheyenne	0·39	0·55
	Osage	0·55	0·10
Panicum virgatum	Blackwell	6·39	2·97
	Kanlow	13·7	0·23
Bouteloua curtipendula	Pierre	0·69	1·01
	Haskell	3·48	0·77
Bouteloua gracilis	Bad River	1·29	0·49
Buchloë dactyloides	Texaco	0·60	0·02
	Cody	0·89	0·13
Resistant wheat control	Karl 92	25·9	28·0
Susceptible wheat control	TAM 105	60·0	45·3
LSD ($P < 0{\cdot}05$)	–	5·03	5·03

[a] Percentage leaf area showing symptoms of tan spot.

[b] Values are means of leaves two and three from each plant tested, with 10 plants in each of four replications.

and wheat. There were no other significant differences among mean severities for any of the prairie grasses in either experiment (including Kanlow and Blackwell in experiment 2). Judging from these disease responses, native prairie grass species were highly resistant to this particular pathogen, relative to cultivated wheat.

Gaeumannomyces graminis var. *tritici* either elicited little detectable response or caused severe reductions in the number of survivors (Table 3). The susceptible wheat control (cv. Victory) suffered 91·5% mean mortality across experiments. *Bouteloua curtipendula*, *Bo. gracilis* and *Bu. dactyloides* were all highly susceptible to *G. graminis* var. *tritici* (similar in response to the susceptible wheat control) and mean losses ranged from 90 to 95% per species. Varieties within species did not differ in overall disease response. Thus, some native grasses appeared highly vulnerable at the seedling stage to this pathogen.

Spatial patterns of co-occurrence

The cover of some grass species exhibited substantial differences between environments (Fig. 1), although *A. gerardii* clearly dominated the community, with the highest mean percentage cover in every environment. *Andropogon scoparius* and *S. nutans* had the next highest mean cover overall, with *A. scoparius* at its most abundant in ungrazed sites with more frequent burning and *S. nutans* at its most abundant in annually burned sites and lowland grazed sites. *Panicum virgatum* had the next highest mean cover overall, and was more abundant in lowland ungrazed sites than elsewhere. For these four most abundant species, burn return time, slope position and grazing all had a significant ($P < 0·05$) influence, as main effects or in interactions, on percentage cover. *Bouteloua curtipendula* generally had low mean cover but was present in all 12 environments; only slope position had a significant ($P < 0·05$) influence on percentage cover for this species. *Bouteloua gracilis*, on the other hand, was uncommon in general and absent from the lowland sites. Similarly, *Bu. dactyloides* was present only in upland grazed sites. For these last two species, slope position and the interaction between slope position and grazing had significant ($P < 0·05$) effects on percentage cover. The seven grass species were grouped into five classes based on these patterns of distribution (Table 4).

It has been suggested that when pathogen dispersal tends to be over short distances, the mean local (within-quadrat) percentage cover of a host species A, calculated only in quadrats where a focal host species B occurs, is a measure of how potentially connected the two species are (Fig. 2). The conditional mean cover of *A. gerardii* was lowest for sites in which *Bu. dactyloides* occurred, but even there it had a mean cover of 25% and so it could be a substantial source of inoculum for any of the grasses. The conditional mean cover of *A. scoparius* was the second highest overall and was particularly high (17%) in sites where *Bo. gracilis* occurred. The conditional mean cover of *S. nutans* was the third highest overall and was particularly low (2·7%) where *Bu. dactyloides* occurred. The conditional mean cover of *P. virgatum* was fourth highest overall, with lower cover where *Bo. gracilis* (0·75%) and *Bu. dactyloides* (0·83%) occurred. The conditional mean cover of *Bo. curtipendula* was fifth highest overall and was fairly uniform across the occurrence of other species. The profile of the conditional mean cover of *Bo. gracilis* and *Bu. dactyloides* was similar, with a particularly high mean cover for *Bu. dactyloides* conditional on its own occurrence. Mean cover in the presence of *A. gerardii* gives a general measure of mean cover because *A. gerardii* was ubiquitous.

The probability that one particular host species ('species A') occurs, given that another particular host species ('species B') occurs, provides an alternative measure of the connectedness between species pairs (Table 5). *Andropogon gerardii* was present whenever any of the other grass species were present and this was also essentially true for *S. nutans*. *Andropogon scoparius* was also common, but there were some locations in which most other species occurred in its absence. Although cover of *Bo. curtipendula* was low relative to the more dominant grasses, it was distributed fairly uniformly and so was present at least 75% of the time when any of the other grasses were present, and it was almost always present when *Bo. gracilis* was present. This relationship was not reciprocal; *Bo. curtipendula* grew in the absence of *Bo. gracilis* 81% of the time. *Bouteloua gracilis* was

Table 3 Mortality of grass species inoculated with the take-all pathogen (*Gaeumannomyces graminis* var. *tritici*) isolated from wheat

		Percentage mortality to take-all[a]		
Species	Cultivar	Experiment 1	Experiment 2	Phenotype[b]
Andropogon gerardii	Kaw	0·00	10·00	R
	Bonilla	0·00	0·00	R
Andropogon scoparius	Cimarron	2·00	0·00	R
	Aldous	0·00	0·00	R
Sorghastrum nutans	Cheyenne	2·38	0·00	R
	Osage	0·00	0·00	R
Panicum virgatum	Blackwell	2·56	0·00	R
	Kanlow	0·00	0·00	R
Bouteloua curtipendula	Pierre	100	87·1	S
	Haskell	94·8	88·7	S
Bouteloua gracilis	Bad River	95·1	84·8	S
Buchloë dactyloides	Texaco	97·9	91·7	S
	Cody	97·4	87·5	S
Susc. wheat control	Victory	97·0	86·1	S

R, resistant; S, susceptible.

[a] Percentage mortality to take-all compared to non-inoculated plants, calculated for each plant cultivar as: [(percentage of non-inoculated plants that survived) − (percentage of inoculated plants that survived)] / (percentage of non-inoculated plants that survived).

[b] Plants were deemed susceptible if percentage mortality was high (>84%).

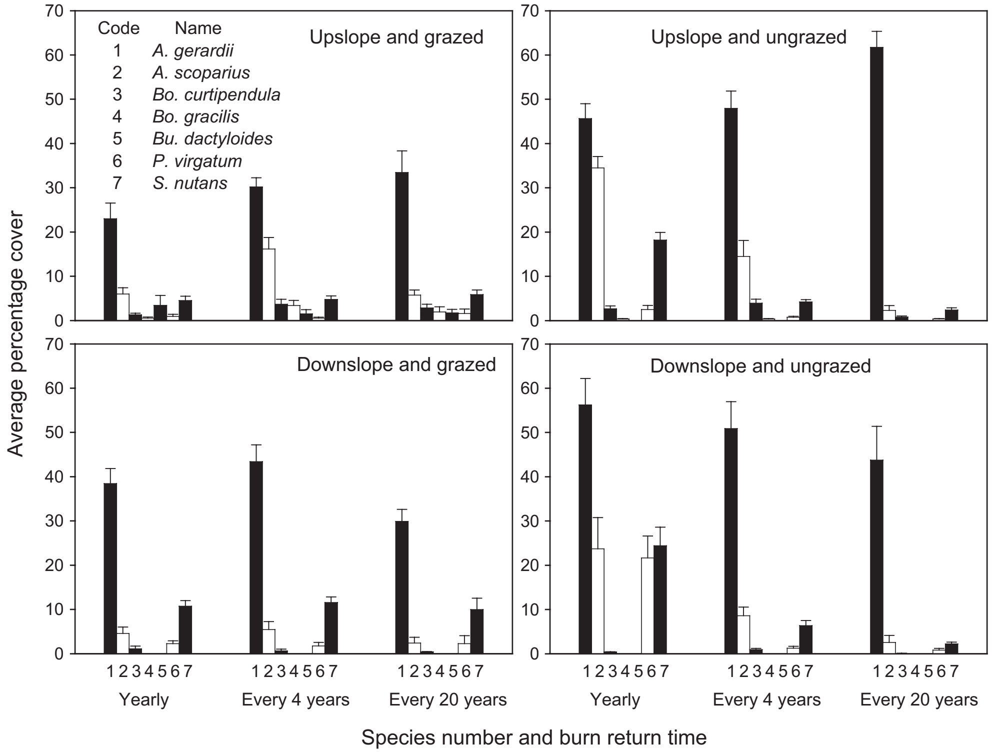

Figure 1 Mean cover of seven grass species (Table 1) in each of 12 environments at Konza Prairie Biological Station, Kansas, USA. Standard errors are indicated.

Table 4 General classes of host abundance, degree of environmental specialization and conditional probability of occurrence, and the classification in these groupings of seven tallgrass prairie grass species based on data from Konza Prairie Biological Station, Kansas, USA

Abundance[a]	Environmental specialization[b]	Conditional probability of occurrence[c]	Host species of this type[d]
High	Low	High	*Andropogon gerardii*
Intermediate	Intermediate	High	*Sorghastrum nutans* *Andropogon scoparius*
Intermediate	Intermediate	Intermediate	*Panicum virgatum*
Low	Low	High	*Bouteloua curtipendula*
Low	High	Low	*Bouteloua gracilis* *Buchloë dactyloides*

[a] Overall percentage cover as illustrated in Figure 1.

[b] Degree of variation in percentage cover across environments, as illustrated in Figure 1.

[c] The overall probability of occurrence of species A when a particular focal grass species B is present, as summarized in Table 5.

[d] Host species that match particular combinations of the three characterizations.

present more than 19% of the time only for *Bu. dactyloides*, for which it was present 75% of the time. This relationship was also not reciprocal, *Bu. dactyloides* being present only 19% of the time when *Bo. gracilis* was present. *Panicum virgatum* was intermediate, being present a minimum of 26% of the time for *Bu. dactyloides* and being present around 50% of the time for most other species.

Discussion

The relationship between the spatial co-occurrence of species, and shared pathogens, under the assumption that some degree of spatial intimacy is required for cross-species infection, can be conceptualized in different ways. First, in some cases, pathogens can inflict modest damage on a host without being a prime determinant of its local abundance or spatial distribution. If, in this case, two host species do not overlap in space, then there will be little or no opportunity for cross-species transmission. If, by contrast, there is substantial overlap, the opportunity for cross-species transmission may be common, and the prevalence of a pathogen in one host (particularly a rare species) could be substantially enhanced by its spatial overlap with alternative hosts. This could be important for ongoing coevolutionary dynamics between hosts and pathogens, and also could set the stage for epidemics, following disturbance.

A second, more subtle, possibility arises when pathogens have devastating impacts on some hosts but not others. In this case, resistant hosts should persist locally,

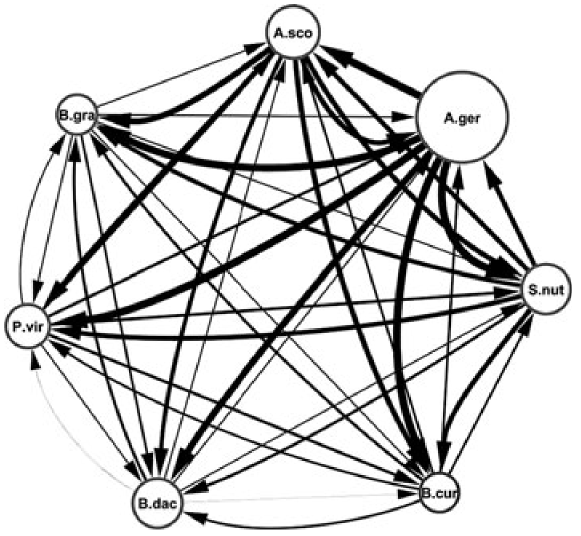

Figure 2 Graph indicating the relative mean cover of each grass species studied (Table 1) where present (size of node), and the relative mean cover of each grass species when each focal grass species was present (weight of directed arrow), based on populations at Konza Prairie Biological Station, Kansas, USA. These results are based on all the watersheds included in the analyses reported here. For example, *Andropogon gerardii* ('A.ger') had the highest mean cover, as indicated by its large circle, and its cover was similar when associated with each of the other species, as indicated by similarly weighted arrows pointing to them. By contrast, *Buchloë dactyloides* ('B.dac') had lower mean cover, as indicated by its smaller circle, and had differing levels of cover when associated with different species, as indicated by the different weightings of arrows leading from it to other species. Higher mean cover indicates greater connectedness between the two species. Conditional occurrence was defined at the scale of 10 m^2 quadrats. 'A.sco' = *Andropogon scoparius*; 'B.cur' = *Bouteloua curtipendula*; 'B.gra' = *Bouteloua gracilis*; 'P.vir' = *Panicum virgatum*; 'S.nut' = *Sorghastrum nutans*.

but vulnerable hosts should tend to disappear, at spatial scales defined by the domain of spread of infective spores from resistant, infected hosts. In this case, the absence of current connectedness (as measured in terms of present-day overlap) may reflect past strong apparent competition that is no longer present because the opportunity for cross-infection has disappeared because of the strength of the interaction.

Understanding how pathogens may act as hidden players in the dynamics of prairie plant communities is still largely terra incognita. The patterns reported here provide initial steps towards understanding the role of some important fungal pathogens in the structure and dynamics of a number of key prairie grasses. *Pyrenophora tritici-repentis* and *G. graminis* var. *tritici* provide examples of two distinct patterns of pathogen effects and host specificity: the former is a pathogen with slight to modest effects shared among several species, whereas the latter is a pathogen with dramatic effects but shared among a more limited set of species. Other pathogen species have also been reported as associated with two or more of the grass species studied here (Farr & Rossman, 2010), though in many cases it is unclear whether the same pathogen populations infect multiple host species.

Pyrenophora tritici-repentis isolates from wheat were pathogenic on all prairie grasses tested, but only with small discrete lesions, even under the highly disease-conducive abiotic conditions of the experiment. Therefore, the aggressiveness of race 1 wheat isolates appears limited on these prairie grass hosts. This is apparently the first report of pathogenicity of *P. tritici-repentis* on *S. nutans*, *P. virgatum*, *Bo. curtipendula*, *Bo. gracilis* and *Bu. dactyloides*; pathogenicity on *A. gerardii* and *A. scoparius* was reported previously (Krupinsky, 1992b) and the present results corroborate this association. *Pyrenophora tritici-repentis* isolates representing a range of aggressiveness can be present on grass hosts (Krupinsky, 1992a) and, in some cases, levels of aggressiveness have been found similar to those reported for wheat isolates (Krupinsky, 1992b). At least eight races of *P. tritici-repentis* have been described on wheat differentials (Andrie *et al.*, 2007). Additionally, highly resistant wheat cultivars can support both saprophytic growth and substantial ascospore production of the pathogen (Summerell &

Table 5 Conditional probability of occurrence of each grass species A, given the presence of each focal grass species B, based on populations at Konza Prairie Biological Station, Kansas, USA

	Probability of occurrence of each potentially competing species A, given focal species B is present (±SE)						
Focal species B	*Andropogon gerardii*	*Andropogon scoparius*	*Bouteloua curtipendula*	*Bouteloua gracilis*	*Buchloë dactyloides*	*Panicum virgatum*	*Sorghastrum nutans*
A. gerardii	1	0·84 ± 0·03	0·76 ± 0·03	0·19 ± 0·03	0·06 ± 0·02	0·49 ± 0·03	0·99 ± 0·00
A. scoparius	1·00 ± 0·00	1	0·81 ± 0·03	0·19 ± 0·03	0·05 ± 0·02	0·49 ± 0·04	0·99 ± 0·00
B. curtipendula	1·00 ± 0·00	0·91 ± 0·02	1	0·19 ± 0·04	0·05 ± 0·02	0·50 ± 0·04	0·99 ± 0·00
B. gracilis	1·00 ± 0·00	0·96 ± 0·02	0·97 ± 0·03	1	0·19 ± 0·05	0·36 ± 0·06	0·98 ± 0·01
B. dactyloides	1·00 ± 0·00	0·88 ± 0·08	0·87 ± 0·10	0·75 ± 0·11	1	0·26 ± 0·11	0·97 ± 0·03
P. virgatum	1·00 ± 0·00	0·82 ± 0·04	0·75 ± 0·04	0·18 ± 0·04	0·07 ± 0·02	1	1·00 ± 0·00
S. nutans	1·00 ± 0·00	0·85 ± 0·03	0·76 ± 0·03	0·19 ± 0·03	0·06 ± 0·02	0·49 ± 0·03	1

These results are based on all the watersheds included in the analyses reported here. A higher probability of occurrence indicates greater connectedness between the two species. Conditional occurrence was defined at the scale of 10-m^2 quadrats.

Burgess, 1988). Highly resistant prairie grasses could, therefore, still potentially serve as inoculum sources. Indeed, if a prairie grass species can become infected and not suffer as a result, dying grass tissues could provide a saprophytic resource base, and the pathogen could be a significant weapon of indirect competition with more vulnerable grass species. Although some previous reports of pathogens present in tallgrass prairies have not included *P. tritici-repentis*, the pathogen has been isolated from *A. gerardii* and *A. scoparius*, two of the dominant grasses of the tallgrass prairie (Tiffany *et al.*, 1990; Mitchell *et al.*, 2002). For *P. tritici-repentis*, dilution of susceptible wheat plants by even moderately resistant wheat plants in cultivar mixtures had a substantial effect for reduced disease severity (Cox *et al.*, 2004). The effects of host diversity may vary with environment (e.g. Garrett *et al.*, 2009), so are not necessarily consistent across tallgrass prairie environments. Interactions with other microorganisms may also influence epidemics; for example, rust fungi are common on grasses at Konza Prairie Biological Station (K. A. Garrett & S. P. Dendy, Kansas State University, USA, unpublished data) and have been shown to facilitate reproduction in *P. tritici-repentis* under some conditions (Al-Naimi *et al.*, 2005).

Of the seven grasses inoculated with *G. graminis* var. *tritici*, *Bo. curtipendula*, *Bo. gracilis* and *Bu. dactyloides* were all highly susceptible and generally died shortly after emergence. It is intriguing that these are some of the grass species which seem to be most specialized in their habitat requirements in tallgrass prairie. One hypothesis that could be examined in future work is that this habitat restriction in part reflects heavy losses to infection of seedlings attempting to colonize areas not currently occupied. Even apparent non-hosts might actually support ectotrophic pathogens such as *G. graminis* var. *tritici* at low levels and so serve as an inoculum source for more susceptible plant species (Asher & Shipton, 1981). Take-all, or the presence of *G. graminis* var. *tritici*, has apparently not been reported in tallgrass prairie, although this may be the result of the general lack of study of pathogens on established prairie plants, rather than the unimportance of the association. *Gaeumannomyces graminis* var. *tritici* may not necessarily be a particularly important pathogen in intact natural ecosystems because, as a saprophyte, it is a weak competitor in the presence of other soil microflora (Weller *et al.*, 2002) and natural ecosystems may support a greater diversity of microflora than agroecosystems (Gilbert, 2002). Additionally, the tallgrass prairie is dominated by long-lived perennial grasses that commonly reproduce clonally and less commonly by seed (Benson & Hartnett, 2006). Therefore, seedlings that may be susceptible to take-all are relatively rare in a matrix of older plants. It is hypothesized here that severely disturbed prairie and newly planted sites that feature perennial grasses – including restored prairie, Conservation Reserve Program sites, biofuel systems and hay meadows – may be prone to take-all epidemics (Asher & Shipton, 1981), because of the importance of seedling establishment.

Several patterns of co-occurrence of hosts were found for the seven grass species at KPBS. First, one host species, *A. gerardii*, was by far the most abundant throughout all environments at KPBS and could be a source of inoculum for any species sharing a pathogen. Indeed, the abundance, lack of environmental specialization, and high percentage cover of *A. gerardii* suggest ample connectedness of habitats suitable for *P. tritici-repentis* and other pathogen populations throughout the KPBS landscape. This grass species could be dubbed a 'keystone host' in terms of its potential to govern pathogen dynamics across an entire landscape, although these dynamics under natural field conditions are yet to be studied. The discussion of patterns of co-occurrence of the grass species in the following paragraphs is based on the assumption that connectedness for pathogen populations is strengthened by abundance, co-occurrence and proximity of host species within and among environments (but note the cautionary thought above about how past strong interactions may lead to the absence of spatial co-occurrence at present).

The impact of host-plant connectedness for pathogens depends in part on the nature of pathogen dispersal. For example, the strong dominance of *A. gerardii* is important when considering the impact on plant communities of the common rust pathogen of *A. gerardii* (Barnes *et al.*, 2005). This rust fungus relies on much less abundant dicot alternate hosts for sexual reproduction, but is wind-dispersed and so is adapted for long-distance dispersal. The two pathogens considered in this study have more restricted dispersal than do rust fungi. The dispersal gradient for *P. tritici-repentis*, despite bearing wind-dispersed conidia from foliar lesions during the secondary disease cycle, is relatively steep, with much of the inoculum limited to 3·6–5·4 m from the source (Sone *et al.*, 1994). On the other hand, pathogens that only disperse across short distances may be more detrimental to perennials because of local inoculum build-up; pathogen species with inoculum moving greater distances are more likely to move away from infected plants, leading to lower nearby inoculum densities, especially when hosts are surrounded by non-hosts.

Shared pathogens or other enemies can have important effects on interactions between species (Holt, 1977, 1984; Grosholz, 1992; Gilbert *et al.*, 2001), especially when spillover of inoculum from a more tolerant host occurs (Power & Mitchell, 2004). The effects of the presence of one plant species on the soil community may impact another; for example, soil in which the annual legume *Chamaecrista fasciculta* had grown was less supportive of the development of *A. gerardii* than was soil in which *A. gerardii* had grown (Holah & Alexander, 1999). Apparent competition is understandably difficult to study under natural conditions in complex natural communities, particularly because it tends to disappear if some species are locally excluded because of it, but evidence for it has been found, for example, via shared insect herbivores for tropical tree species (Morris *et al.*, 2004) and among hosts of *Phytophthora ramorum*

(Cobb *et al.*, 2010). Seven common grass species of tallgrass prairie were studied here, but other species may also play a role in epidemics, particularly for a pathogen that includes unrelated host species in its life cycle (Barnes *et al.*, 2005). Temporal variation may also influence connectivity and apparent competition, but for long-lived perennials such as these tallgrass prairie species, such effects may be integrated over several years.

Andropogon scoparius, *S. nutans* and *P. virgatum* demonstrated another type of pattern of occurrence. All three were abundant in some environments and rare in others. Because of this pattern, other host species could escape inoculum spread from this type of host if they were present in certain environments, assuming inoculum dispersal was somewhat limited. *Bouteloua curtipendula* exhibited a third type of distribution: it was present in low numbers in all environments and so could act as an inoculum source to any other species. *Bouteloua gracilis* and *Bu. dactyloides* followed a fourth type of distribution. Both were present only in upland sites, so that other host species sharing a common pathogen with limited dispersal might completely escape inoculum from these species in lowland sites. *Bouteloua curtipendula* was usually present where *Bo. gracilis* grew but also was present in many quadrats without *Bo. gracilis*; that is, *Bo. gracilis* cannot generally escape inoculum from *Bo. curtipendula*, but *Bo. curtipendula* could generally escape inoculum from *Bo. gracilis*. The pattern for *Bo. gracilis* and *Bu. dactyloides* was similar, with *Bo. gracilis* more readily escaping inoculum from *Bu. dactyloides*. These last three species were those found susceptible to *G. graminis* var. *tritici*. Future studies of the genetic and spatial structure of populations of plant pathogens associated with hosts in agriculture and prairie (Ali & Francl, 2003; Crouch & Beirn, 2009; Saleh *et al.*, 2010), combined with reciprocal inoculation studies and studies of the distribution of resistance genes in wild grass populations (Gustafson *et al.*, 2003; Rouse *et al.*, 2011), will help to clarify the rate of pathogen movement among host species and its impact. Ultimately, a clearer model of these interactions may inform recommendations for landscape structures to enhance both tallgrass prairie conservation and restoration, and disease management in conventional and new biofuel agricultural systems.

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