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Environmental heterogeneity, fungal parasitism and the demography of the grass Stipa leucotricha

Abstract This study investigated the demographic consequences of fungal infection of a perennial grass, Stipa leucotricha. The rate of parasitism of this grass by the host-specific, systemic fungus Atkinsonella texensis varies over short distances. Infection was frequent (57% of plants) in “mottes” (clusters of woody plants) but rarer in adjacent open grasslands (9%). To test the hypothesis that the relative performance of infected and uninfected plants differed in the two habitats, infected and uninfected genotypes were collected from mottes in a central Texas population, propagated in the greenhouse and then transplanted into the same site in replicate plots within mottes, at the edges of mottes, and in open grassy areas. Demographic data were recorded for 30 months over three growing seasons. Plants were observed to lose and gain infection. Infection had no significant effect on plant survival, tiller number or dry mass although infected plants tended to be larger. Uninfected plants had a significantly higher probability of setting seed but there were no differences in seed production by reproductive plants. There were significant effects of planting environment on all of these measures. Motte edges were most favorable for S. leucotricha transplants while motte interiors were least favorable and open areas were intermediate. There was no evidence of habitat x infection interactions; therefore the fungal infection had similar effects in different habitats. The high frequency of infection in motte habitats is best explained by more efficient contagious spread there. The favorability of motte edges for plant growth is substantially offset by higher infection rates at the edges of mottes.

Key words Demography · Environmental heterogeneity · Fungal parasitism · Reciprocal transplant · Stipa leucotricha

Introduction

Populations of plants and other sessile organisms may experience very different environments over small spatial scales. Indeed, patchy environments, as continuous gradients or as mosaics, are probably the rule for plant populations (Fowler 1988c). This patchiness can have important effects on demographic parameters and the dynamics of populations (e.g., Quinn 1975; Grant and Antonovics 1978; Levin and Clay 1984), population genetic structure (Antonovics 1968; Stewart and Schoen 1987; Linhart 1988), and interactions of plant populations with other plant, animal, and microbial species (Crawley 1983; Burdon 1987; Fowler 1988c; Allen and Allen 1990; Louda et al. 1990).

A common type of patchiness occurs in landscapes where vegetation dominated by woody plants meets herbaceous vegetation, as occurs at woodland margins and in savannas. One or a few trees can affect light intensity, soil properties, and the composition of the surrounding vegetation (Parker and Muller 1982; Koop and Walker 1985; Archer et al. 1988; Belsky et al. 1989; Stuart-Hill and Tainton 1989). Interactions with herbivores and pathogens may also vary over short distances between adjacent wooded and open habitats. For example, Collinge and Louda (1988) found that rates of insect herbivory on Cardamine cordifolia were significantly higher in open sunny sites than in neighboring shaded sites (see also Huffaker and Kennett 1959; Lincoln and Mooney 1983). Similarly, Jarosz and Burdon (1988) found that wild barley, Hordeum leporinum, was more frequently infected by scald, Rynchosporium secalis, under trees than in neighboring open areas (see also Burdon et al. 1989). Such spatial variation in biotic interactions may restrict the distributions of many plant species even though they
are physiologically capable of growing in a wider range of habitats.

In this study we investigated the effects of environmental heterogeneity and fungal infection on the demography of the perennial grass Stipa leucotricha. This grass grows in several distinct habitats created by clusters of woody plants ("mottes") in central Texas grasslands. These habitats differ in the frequency of infection of the host grass Stipa leucotricha by the fungus Atkinsonella texensis, as well as in herbaceous vegetation, light, and so on. The primary objective of this study was to test the hypothesis that the effect of fungal infection is conditional on environment, i.e. that infected and uninfected plants differ in their response to environmental heterogeneity. To do this we experimentally determined (1) how the survival, growth, and fecundity of Stipa leucotricha vary among habitats, (2) how infection alters the same traits, and (3) whether there are interactions between habitat type and fungal infection such that the impact of disease varies with environment. Multi-species interactions that vary as a function of environmental heterogeneity are potentially important in many plant populations but have rarely been investigated experimentally in natural communities.

Materials and methods

Study organisms

Stipa leucotricha Trin. and Rupr. (Texas wintergrass, Texas speargrass; henceforth referred to as Stipa) is a caespitose perennial grass found in grasslands, prairies, and brushy areas of Oklahoma and Texas south to Coahuila and Nuevo Leon (Correll and Johnston 1970). On the eastern Edwards Plateau in central Texas, where this study was conducted, juniper (Juniperus ashei Buchh.) and other woody plants often grow in discrete clusters (mottes) scattered throughout a grassland matrix (Fowler 1988a, 1990). Stipa is abundant at the edges of and inside mottes, but also occurs in adjacent open grassland, where it is usually less abundant and shorter in stature (N. Fowler, personal observation). Active growing periods occur in the spring (when it flowers) and in the fall. Flowering culms produce a terminal panicle of 5-25 chasmogamous spikelets, each containing a single flower and seed, and a smaller number of cleistogamous flowers and seeds at the lowest nodes, surrounded by the leaf sheaths, called axillary cleistogenes (Dyksterhuis 1945).

The grass is frequently infected by the fungal parasite A. texensis (Diehl) Leuchtmann and Clay (Diehl 1950; Leuchtmann and Clay 1989). This host-specific fungus forms systemic infections by growing epiphytically on meristems, leaf primordia and developing inflorescences (Leuchtmann and Clay 1989). Panicles of chasmogamous flowers are aborted in infected plants although the axillary cleistogenes may still be produced. Instead of chasmogamous flowers a fungal fruiting body (stroma) is produced. The transfer of conidia between stromata on different plants results in the production of meiotic ascospores, which can contagiously infect new hosts (Leuchtmann and Clay 1989). The exact mechanism of contagious spread is not known but in the related A. hypoxylon ascospores are apparently washed into leaf axils (K. Clay, personal observation). Stipa plants are sometimes observed with both aborted, stroma-bearing inflorescences and normal, seed-bearing inflorescences. Microscopic examinations have indicated that the fungus is absent rather than asymptomatic in normal inflorescences on infected plants (K. Clay, personal observation).

Local distribution and infection frequency

To quantify infection rates of Stipa by A. texensis in mottes and in open grassland areas, a series of 30 m transects was run in different sites in spring 1983. Three sites typical of Stipa habitat were selected. The Pedernales Falls State Park site, in Blanco Co., Texas, 80 km west of Austin, was the driest site and had the lowest proportion of area in mottes. The Gill Ranch site, in Travis Co., 15 km west of Austin, had a greater proportion of area in mottes. The Johnny Moore Road site, Travis Co. (near Austin), was a mosaic of open grassy areas, mottes, and scattered stands of honey mesquite (Prosopis glandulosa Torr.). The number of transects through each habitat in each site is given in Table 1. Every 30 cm along each transect, the nearest Stipa plant was scored as nonflowering (and therefore of unknown infection status), as uninfected (possessing uninfected inflorescences), or as infected (possessing aborted inflorescences). If no plants occurred within 15 cm of the point, a blank was recorded. No plants were scored twice.

Reciprocal transplant experiment

To determine the separate and joint effects of fungal infection and habitat on Stipa performance a reciprocal transplant experiment was conducted. Flowering plants were dug up from Pedernales Falls State Park in spring 1984. The site was a typical mosaic of mottes and open grassy areas (see Fowler 1984, 1988b). At least 25 plants per infection class were collected. Plants were collected sufficiently far apart to insure that each was a different genotype. Due to the rarity and small size of infected plants in open areas, we were able to collect both infected and uninfected plants only from within mottes.

Plants were potted in a standard soil mix (2:1:1 sterile topsoil: perlite: peat) and maintained in a greenhouse. In spring 1985 plants were divided into ramets (clones) two to three tillers in size. Each ramet (henceforth referred to as a plant) was planted in the same soil mix in a plastic tube (Ray Leach "Conetainer", Canby, Ore., USA). Deaths of some plants resulted in an unbalanced number of ramets per genotype and of genotypes per origin. Therefore genotype was not included in the statistical analyses.

Plants were transplanted into a site at Pedernales Falls State Park adjacent to the collection site in December 1985. Four transects were located, each extending from a plot inside a large motte to a plot in an adjacent open grassy area. A third plot (the "edge" plot) was situated along each transect just inside the edge of the motte canopy. The distances between adjacent plots along a transect varied from 3 to 10 m. In each motte and edge plot, the canopy was entirely composed of Juniperus ashei, except in one motte plot where Diospyros texana Scheele was also present. Holes of similar depth and diameter to the plastic tubes were dug in a grid (15 cm spacing between rows and columns) in each of the 12 plots. A total of 218 individual plants propagated from infected and uninfected motte plants were transplanted in December 1985. There were more plants of infected than uninfected origin (138 versus 80) due to differences in original size and hence survival rates in the greenhouse. Plants were randomly assigned to plots and transects so that each plot and transect received approximately equal numbers of individuals from each origin. Each transplant was ringed with a red plastic-coated wire and its grid location and initial tiller number was recorded.

Light level, air temperature, and relative humidity were measured at each of the 12 experimental plots. Soil characteristics were not measured although they may have affected plant performance. While temperatures and humidities were very similar among plots, plots at the edge and inside mottes received only 25% and 20% respectively of the average photosynthetic photon flux density (PPFD) received by plots in the open, as measured by a LiCor Li-1095A sensor at ground level when the sun was unobscured by clouds. Motte plots were shaded all day. Edge plots were shaded