Neotyphodium infection and hybridisation as a function of environmental variation

Abstract

Neotyphodium is an asexual, vertically transmitted, obligate fungal endosymbiont infecting cool-season grasses such as Arizona fescue. The relationship between Neotyphodium and several native grass hosts ranges from antagonistic to mutualistic. One theory that may explain how Neotyphodium infection is maintained despite inconsistent mutualistic benefit to the host is the bounded hybrid superiority hypothesis. This hypothesis argues that hybrids are more fit than non-hybrids in response to some environmental stresses. Neotyphodium infects hosts in both hybrid and non-hybrid forms. We tested the possibility of hybrid superiority in depauperate habitats (low soil water and nitrate) by quantifying the types and frequency of host infections (uninfected, hybrid-infected and non-hybrid-infected), and the quality of resources available between three host populations. A second theory, the geographic mosaic theory of coevolution, may also explain different symbiotic outcomes at the population level in response to variation in abiotic and biotic population characters. We provide cursory support for both hypotheses.

Keywords: geographic mosaic theory of coevolution, hybrid, Festuca, Neotyphodium, symbiosis, mutualism, bounded hybrid superiority

Introduction

The geographic mosaic theory of coevolution postulates that low migration rates coupled with unique selection pressures at the population level result in specialised coevolutionary trajectories (Thompson 1999; Thompson & Fernandez 2006). For symbiotic interactions, local selection pressures may cause variation in outcomes. If migration is low or variable between coevolving organisms, then a geographic mosaic results with some populations well-adapted to their symbiont and others maladapted. In addition, differential rates in gene flow as well as variation in interspecific interactions can lead to variable symbiotic outcomes between and within populations (Gomulkiewicz et al. 2003). Previous research by Sullivan & Faeth (2004) found very low gene flow in Neotyphodium spp. among host populations of Arizona fescue. Since F. arizonica (AF) is a long lived facultative host that relies on wind pollination, genotypic mismatching is a plausible expectation. Thus, we predicted that unique infection frequencies, endophyte haplotypes, and plant performance may be associated with key abiotic parameters creating a mosaic of interspecific interactions. Specifically, we predicted that populations with the lowest soil moisture should have the highest infection frequencies if endophyte infection enhances host performance in drought conditions as determined by Morse et al. (2002, 2007). We also expected hybrids to be comparatively more prevalent in depauperate habitats (see below). Regardless of the neutral or negative effects of endophyte infection in Festuca arizonica, host grass populations retain high infection frequencies ranging from 60% to 100% (Schulthess & Faeth 1998).

Arizona fescue can be infected by two ‘forms’ of Neotyphodium, hybrid (H) or nonhybrid (NH). Neotyphodium hybrids result from mutual infection of the host by Neotyphodium sp. and Epichloë species (Schardl et al. 1994; Selosse & Schardl 2007; Tsai et al. 1994). Including the possibility of three infection types, (uninfected, hybrid, or nonhybrid infected) provides an opportunity to investigate the bounded hybrid superiority (BHS) hypothesis (Arnold 2004). Hybridisation infuses new genetic variation thought to be adaptive to the endophyte-host symbiosis (Selosse & Schardl 2007). The BHS hypothesis predicts that hybrids will be favoured, and therefore probably more frequent, in marginal habitats (Brasier et al. 1999; Brasier et al. 1998; Cruzan & Arnold 1993; Ellstrand & Schierenbeck 2006; Rieseberg 1995; Rieseberg et al. 2003) due to the expression of intermediate or mixed parental phenotypes.

To determine whether infection and, in particular, hybrids were correlated with environmental factors at the population level, we selected three F. arizonica (AF) populations and measured the following biotic and abiotic population characters: (1) soil moisture (growing season defined as May (spring) – September

Figure 1 Population percentages for each infection type; E= uninfected hosts, H = hybrid infection hosts, NH = nonhybrid infected hosts.

Figure 2 Average available soil NO3 for summer months 2006 (May through July and August through October 2006) for each Arizona population. Nitrate in mg/L of resin extraction.
Results

All three populations had more E+ than E- plants (Fig. 1); CW = 79.6% E+, BS = 71.4% E+, MD = 73.8% E+. The frequency of H versus NH in each population was significantly different from the a priori expectation of 50:50 for all three populations. Buck Springs and MD had significantly more NH (P=0.01 and P=0.001, respectively) than H infected. Clint’s Well had significantly more H (P=0.04) than NH. Nitrate levels were not significantly different between populations (ANOVA, df = 2, P=0.21) (Fig. 2). Clint’s Well had a significantly lower percent soil moisture than other sites in May of 2006 (ANOVA, df = 2, P=0.051) but not in August (ANOVA, df = 2, P=0.931) (Fig. 3). Clint’s Well and BS did not have significantly different plant heights (data not shown) but plants at MD were significantly taller than at both CW and BS (T-test, df = 2, P=0.00). Only one population produced seeds (MD).

Discussion

As expected all populations contained significantly more E+ than E- plants and had different ratios of H:NH infected plants. Our first prediction that greater infection frequencies would be found at ‘poorer’ habitats was not supported. Although CW did have the lowest soil NO₃, and the lowest springtime moisture levels (May 2006), it did not have significantly more E+ plants than the other populations (ANOVA, df = 4, p = 0.25); all populations possessed more E+ versus E- plants. Since the entire Mogollon Rim area is typified by frequent droughts and ustic (frequently dry) soil regimes, it is not surprising we did not find a significant difference in E+ frequencies between the three populations. If infection does indeed enhance host response to drought, all populations would favour E+ over E-hosts since all populations suffer drought. Perhaps the fitness response of the grass/endophyte interaction to moisture is such that the symbiosis benefits both Neotyphodium and its host during droughts but not under favourable soil moisture availability (favourable to the host) (Faeth & Sullivan 2003). This would fit the model presented by Gomulkiewicz et al. (2003) where fitness interactions can vary from antagonistic, to commensalistic, to mutualistic in time and yet be stable, provided that mutualism is the geometric mean interaction. The fact that the population with the lowest springtime soil moisture and soil NO₃, also had the highest frequency of hybrid Neotyphodium, suggests that hybrids may increase host performance in relatively more stressful habitats. Hybrids were predominant at CW, a marginal habitat in terms of soil moisture (and possibly NO₃) levels at least early in the growing season. This population is only depauperate in these key resources, but it also supports the lowest under-story diversity and abundance (pers. obs.). Thus, these initial data provide preliminary support for the BHS hypothesis as well as the existence of geographic mosaics of interspecific interactions responsive to local selection pressures. This suggests that abiotic or environmental selection pressures determine the type of interaction and favour one endosymbiotic type over the other (H versus NH) at the population level (Emms & Arnold 1997). Clearly, sampling of additional populations to increase sample size and spectrum of environmental conditions and manipulative experiments will be necessary to pinpoint whether infection, and specifically endophyte hybridisation, is a functional response to environmental factors varying at the population level.

REFERENCES


Tsai, H.; Liu, J.; Staben, C.; Christensen, M.; Latch, G.; Siegel, M.; Schardl, C. 1994. Evolutionary diversification of fungal endophytes of tall fescue grass by hybridization with *Epichloë* species. *PNAS* 91: 2542-2546.