Density-Dependent Parasitism of the Soil-Borne Nematode *Criconemella xenoplax* by the Nematophagous Fungus *Hirsutella rhossiliensis*

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Abstract. Spatial sampling was used to investigate temporal density-dependent parasitism of the plant-parasitic nematode *Criconemella xenoplax* by *Hirsutella rhossiliensis* in three peach orchards on eight sample dates. The patches of soil in which the nematode and fungus interacted were assumed to possess similar density-dependent dynamics and to be small, independent, and asynchronous. Furthermore, sampling of separate patches was assumed to provide similar information with respect to density dependence as would temporal (repeated) sampling of the same patch. Percent parasitism was dependent on the number of *C. xenoplax*/100 cm³ soil (P = 0.0001). The slope was unaffected by orchard or date but ranged from 0.0001 to 0.0043 depending on distance from the irrigation furrow. The relative shallowness of the slope and the large variation in percent parasitism not explained by nematode density suggest that *H. rhossiliensis* is a weak regulator of *C. xenoplax* population density.

Introduction

The probability of a host being attacked by a parasite is often thought to be dependent on host density [1, 3]. When hosts are rare, encounters between hosts and parasites are unlikely, and the parasite has little effect on host population density. When hosts are abundant, parasite reproduction or aggregation results in temporal or spatial increases in density. As parasite density increases, encounters become frequent, and the parasite can limit host population growth. Density-dependent suppression of hosts by parasites is defined as regulation [4]. Determination of the nature of regulation increases understanding of the parasite’s potential to suppress the host population and provides information on the stability of host and parasite numbers [1–4].

Regulation of soil-borne nematodes by fungal and bacterial parasites is poorly understood. Linford et al. [15] implied that nematode-trapping fungi regulated the plant-parasitic nematode, *Meloidogyne* sp., but parasitism was not quantified. Subsequently, Cooke [7] showed that parasitism of nematodes by nematode-trapping fungi was unrelated to host numbers. Perry [16] included regulation by obligate fungal parasites in a model describing the population dynamics of the plant-parasitic nematode *Heterodera avenae*. Density-dependent para-
sitism was suggested in the interaction of the nematode *Meloidogyne* sp. and the bacterial parasite *Pasteuria penetrans* in sugarcane fields [18] and in the interaction of the nematode *Cironemella xenoplax* and unidentified fungi in vineyards [5]. Gray [9] described strong regulation of bacterial-feeding nematodes by fungal parasites, but the system involved activated sludge and not soil. The liquid nature of the system permitted sampling through time of an apparently uniformly distributed, well-defined population.

The soil-borne nematode *Cironemella xenoplax* Raski (Luc and Raski) is a serious pest of peach trees and other *Prunus* spp. All stages other than the egg are vermiform and motile in the soil (movement probably limited to less than 5 mm/day) and feed only on host roots. Generations overlap, and the age structure is stable throughout the year in California peach orchards (H. Ferris, unpublished data). The life cycle requires about 30 days at 20°C [19]. One hundred *C. xenoplax*/100 cm³ soil is considered the "economic injury level"; if populations are above this level, pesticide treatment is recommended.

The fungus *Hirsutella rhossiliensis* Minter and Brady parasitizes and is frequently associated with *C. xenoplax* [10]. All vermiform stages of the nematode are susceptible to the fungus. *H. rhossiliensis* produces nonmotile spores that adhere to and initiate infection of passing nematodes. At 20–25°C, the fungus kills the nematode within 72 hours and sporulates from the cadaver shortly thereafter [11]. Parasitized nematodes disappear from soil in about 15 days, but the rate of degradation varies with soil temperature and nematode life stage [13]. The relative density of *H. rhossiliensis* spores is highly correlated with the number of *H. rhossiliensis*-parasitized *C. xenoplax* in peach orchard soils (T. M. McInnis and B. A. Jaffee, unpublished data). The fungus parasitizes certain species of nematodes other than *C. xenoplax* but has no saprophytic activity in the presence of other soil organisms [12].

Our unpublished observations suggest that the level of parasitism of *C. xenoplax* by *H. rhossiliensis* depends on nematode population density. Because the presence or absence of density-dependent parasitism could affect the utility of this fungus as a biological control agent [2], we would like to determine if and how parasitism is affected by host nematode density.

The most direct way to detect and characterize temporal density-dependent parasitism within a population is to quantify parasitism and host density through time. Because of extremely limited mobility of soil nematodes and fungal parasites, the volume of soil (patch) occupied by interacting nematodes and fungi is probably limited. We assume that these patches are approximately 700 cm³ (the volume collected by our sampling tool). Repeated sampling of these small patches is difficult because soil sampling is destructive and a significant portion of the patch and population is removed or at least disturbed with each sample.

In this study, we used spatial sampling to make inferences on temporal density-dependent parasitism of *C. xenoplax* by *H. rhossiliensis*. We assumed that (1) a peach orchard contained many similar but independent and asynchronous populations of *C. xenoplax*, (2) these populations occurred in patches of 700 cm³ of soil, and (3) samples from separate populations collected at one time in the same area provided similar data as would samples from one population collected through time.