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An Experimental Study on the Effects of Earthworms on the Ecological Success of Fern Gametophytes

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The successful establishment and maintenance of pteridophyte populations requires the co-occurrence of both the gametophyte and the sporophyte life history phases. Yet, most studies of pteridophyte ecology consider only the sporophyte stage (eg. Grime, 1985). While there are a few studies of gametophyte ecology (eg., Cousens, 1988; Duckett, 1985), there is little knowledge of the factors that limit the distribution and abundance of gametophytes.

One factor relevant to the gametophyte phase is the earthworm. Modern families of earthworms likely radiated in soils characteristic of angiosperm forests (Satchell, 1983; Bouche, 1983; Piearce, 1989). Lovis (1977) suggests that the modern "polypodiaceous" ferns radiated in response to ecological changes brought about by the radiation of the angiosperms. Modern genera of earthworms and leptosporangiate ferns evolved during the Tertiary in communities dominated by angiosperms (Lovis, 1977; Bouche, 1983).

Earthworms are known to be involved in dispersal of both the seeds of spermatophytes (McRill & Sagar, 1973) and the spores of pteridophytes (Hamilton, 1988). Earthworms may play a particularly important role in bringing buried seeds and spores to the surface and placing them in improved sites for germination (Grant, 1983). Earthworms naturally till the soil, providing increased aeration, increased porosity and a more even distribution of soil nutrients. They also positively influence soil nutrient content by acting as a first step in the decomposition of detritus, and cause an increase in the numbers and diversity among microbial populations in the soil, thereby increasing the rate of decomposition, and increasing nutrient turnover rates (Lee, 1985). Earthworms prey on small pieces of vegetation, fungi, algae, and even other earthworms (Darwin, 1881; Lavelle, 1983; Lee, 1985). The green, surface dwelling gametophytes characteristic of modern ferns would likely make excellent prey for earthworms. As earthworms have been shown to be influential in the gametophyte habitat, an experiment was undertaken to determine if the presence of earthworms influences the germination of spores, gametophyte establishment, and/or gametophyte reproductive success.

MATERIALS AND METHODS

Fertile fronds of *Deparia acrostichoides* (Sw.) Kato [= *Athyrium thelypteriodes* (Michx.) Desv.] were collected in October 1987 at Long Run, in The Wayne National Forest, near Glouster, Ohio (T11N R14W sec. 11 Corning, Ohio Quadrangle: 82 deg. 4′ 30″ W. 39 deg. 32′ 30″ N). The earthworm *Lumbricus terrestris* (L.) was collected from a mown lawn on the campus of Ohio

University. This species was collected as it is not only common in local woods, but the species, and the genus, are one of the most common of temperate earthworms (Lee, 1983).

Earthworms were placed in a 45 cm × 43 cm × 13 cm plastic tub with wet potting soil for six months. This allowed for a generation of worms of a size class appropriate for this study (approximately 2 mm in diameter × 5 cm in length). Fifteen fertile fronds of *D. acrostichoides* were dried and mixed by hand with 2.25 kg of potting soil. Forty 5 cm diameter plastic pots were then filled with the soil. Pots were divided into two groups of twenty, with each group placed into a plastic flat filled with tap water to a depth of 1 cm. The twenty pots in one flat were each inoculated with 2 earthworms. Flats were covered with a clear plastic lid, and placed in an east-facing window on May 7, 1988. Pots were checked for the presence of gametophytes and/or sporophytes 19 times between May 7, 1988, and January 10, 1989 (a period of 250 days).

Results

Initially, all pots became infested with fungi. However, after 48 days, fungi were not observed on the soil containing worms. Fungi were always observable on soils lacking earthworms. Algae were observed on the worm-free soils after 62 days, and were present until the end of the experiment. Arthropods could be observed on the worm-free soil after 113 days. Algae were never observed on the soil containing worms, and arthropods did not appear until the final observation date of January 10, 1989.

With the exception of a single plant appearing 30 days after initiation of the experiment (which died within 18 days), gametophytes did not appear on worm-free soil until day 107. In contrast, gametophtyes first appeared on soils with worms after 22 days, and continued to appear on soil with earthworms until they were present in 18 of the 20 pots. Gametophytes were never present in more than 5 of the 20 pots of soil lacking earthworms (Figure 1).

Sporophytes were produced only on soils inoculated with earthworms. The first of these was observed after day 113. There were 3 pots with sporophytes by the end of the experiment (Fig. 1). In total 7 sporophytes were produced, although by the end of the experiment only 3 survived. Mortality of sporophytes was observed to be due to burial, presumably through the action of earthworms. There was never any evidence of gametophyte burial.

Discussion

Spore germination and the establishment and reproductive success of gametophytes were enhanced by the presence of earthworms. There was no evidence that earthworms destroy gametophytes, but they apparently bury young sporophytes. The two questions raised by this investigation are: 1) How do earthworms change the soil to cause it to be more favorable to gametophytes and 2) Why are sporophytes buried, but not gametophytes?

Further investigations addressing specifically the beneficial effects of

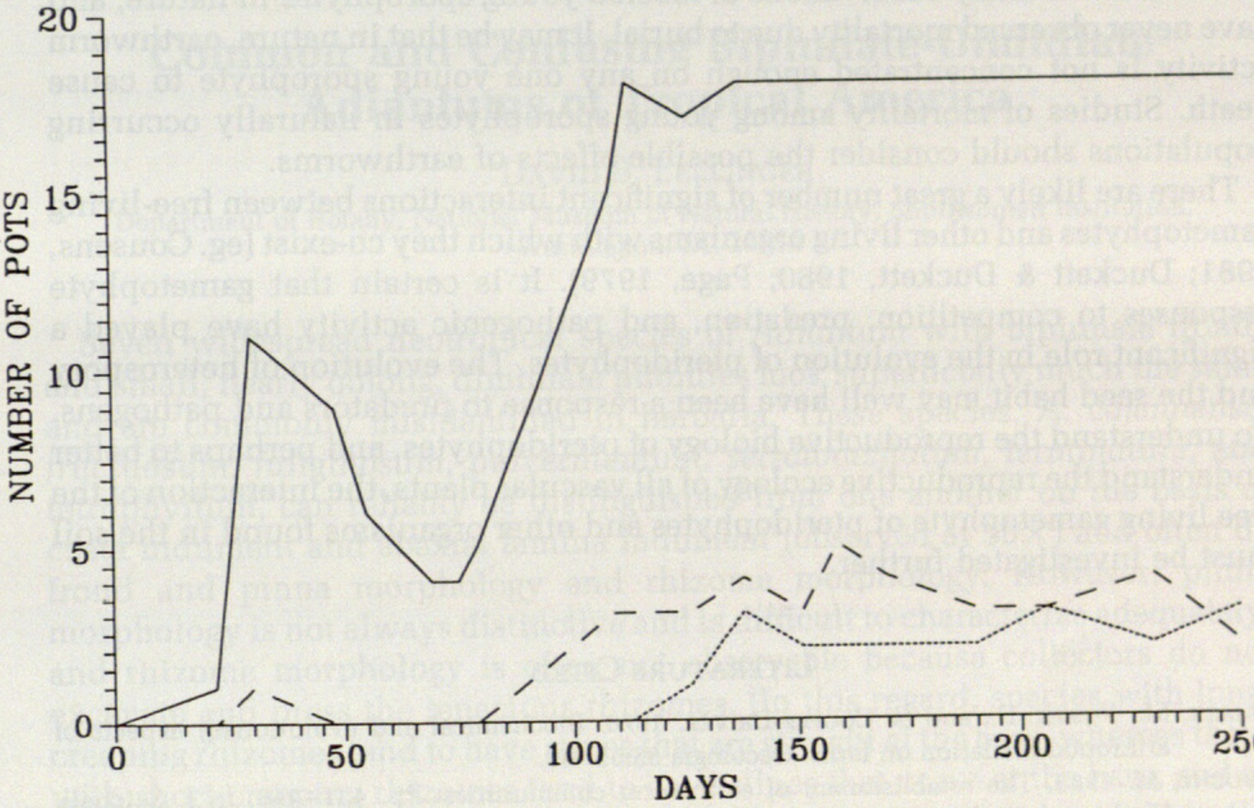

FIG. 1. Number of pots with gametophytes and number of pots with sporophytes versus time. Solid line is gametophytes in pots inoculated with earthworms; dashed line is gametophytes in pots without earthworms; dotted line is sporophytes in pots inoculated with earthworms. Sporophytes did not appear in pots without earthworms.

earthworms on gametophyte populations are needed. Our observations suggest that earthworms reduce the activity of potential pathogens and competitors such as algae, fungi and arthropods in soils, which could cause a more favorable environment for gametophytes. We have no data regarding the effect of differences in soil nutrient content, aeration, and other physical properties known to be influenced by the presence of earthworms. Biotic and abiotic effects of earthworms on the gametophyte environment need further investigation.

There seems to be no reason as to why only sporophytes would be buried. Earthworm predation may potentially be a great threat to gametophyte success, for which gametophytes have evolved some response. There is documentation of chemical defense compounds in the tissue of the sporophytes of many pteridophyte species (eg. Cooper-Driver, 1985; Balick et al., 1978). There is also evidence that chemical defenses in pteridophytes are effective on earthworms (Piearce, 1989; Satchell & Lowe, 1967). It is possible that chemical defenses were selected for, and are most effective in, the gametophyte phase of pteridophyte life histories.

Earthworms are known to be attracted to roots (Lee, 1985). The negative effect of earthworm activity on young sporophytes may be due to the presence of roots.

We have made many observations of labeled young sporophytes in nature, and have never observed mortality due to burial. It may be that in nature, earthworm activity is not concentrated enough on any one young sporophyte to cause death. Studies of mortality among young sporophytes in naturally occurring populations should consider the possible effects of earthworms.

There are likely a great number of significant interactions between free-living gametophytes and other living organisms with which they co-exist (eg. Cousens, 1981; Duckett & Duckett, 1980; Page, 1979). It is certain that gametophyte responses to competition, predation, and pathogenic activity have played a significant role in the evolution of pteridophytes. The evolution of heterospory and the seed habit may well have been a response to predators and pathogens. To understand the reproductive biology of pteridophytes, and perhaps to better understand the reproductive ecology of all vascular plants, the interaction of the free living gametophyte of pteridophytes and other organisms found in the soil must be investigated further.

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