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BIOLOGICAL PROCESSES: RELATIONSHIPS BETWEEN EARTHWORMS AND SOIL TEMPERATURE[†]

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ABSTRACT

Soil fauna play important roles in many soil processes and conditions which relate to agricultural systems. Earthworms are credited with enhancing soil fertility and soil physical properties by their feeding and burrowing activities. Most research on earthworms has focused on the warmer seasons of the year and relatively little is known about earthworm activity and survival during the portion of the year with frozen soils. Earthworms may survive winter by acclimatization, aestivation, or by burrowing to deeper depths where the soil is not frozen. More research is needed on the fate of earthworms in frozen soils. Suggested research areas include: 1) studies designed to determine the effects of freezing temperatures on the survival and behavior of earthworms, 2) studies to determine the effect of freezing and freeze-thaw cycles on the structure and stability of earthworm burrows, and 3) studies to determine the effect of freezing and thawing on the physical integrity of the burrow linings and cast materials.

Introduction

Biological activity of soil fauna involves mounding, mixing, forming macropores, forming and destroying peds of soil and regulating of nutrient cycling (1). Anderson (2) divided soil invertebrates into primarily three classes based on body width: micro- (<100 mm), meso- (<1-2 mm) and macro-fauna (<10 to 20 mm). Microfauna, consisting primarily of Protozoa and Nematoda, are associated with water films and water filled voids and do not alter the structure of soils. Mesofauna consist of enchytraeids, Collembola (insects), and Acarina (mites) and are primarily associated with air filled pores. This group feeds on organic matter and fungal hyphae associated with decomposing organic matter. The macrofauna include isopods, millipedes, earthworms, ants, and other insects. They are considered more important in affecting soil structure through their feeding and burrowing habits than members of the micro- and mesofauna.

Soil structure is modified by burrowing, redistributing plant residue, and depositing feces containing mineral soil. Burrowing is primarily associated with searching for food, activities associated with reproduction, and escaping from unfavorable environmental conditions.

Our objectives in this paper are to discuss some aspects of the response of earthworms to temperature and potential areas of research on earthworms and frozen soils.

It is generally accepted that biological, physical, and chemical processes in the soil are influenced by earthworms. Benefits from the activities of earthworms have been summarized by many authors and include:

1) burrowing and excavation while searching for food, providing living, aestivation, and cocoon deposition sites,
2) lining of the burrows and aestivation sites with mucus and fragments of residue,
3) redistributing residue from the soil surface into the soil matrix,
4) and transporting mineral soil material or ingested plant material to the soil surface or to voids within the soil matrix.

These activities are important in redistributing and incorporating large amounts of residue, increasing water infiltration, altering aggregate stability, increasing soil aeration, increasing plant root distribution, and mixing of soil between layers.

Earthworms are the largest of the soil fauna and may attain lengths of > 1 m and diameters of > 20 mm and weights in excess of 500 gm (3). There are about 3,000 recognized species of earthworms (4) but only 6 to 7 species are important in agricultural systems (5, 6). Species commonly found in row crops in North America are *Aporrectodea tuberculata* (Eisen), *A. turgida* (Eisen), *A. rosea* (Savigny), *A. trapezoidea* (Duges), *Lumbricus terrestris* (Linneaus), *L. rubellus* (Hoffmeister), and *Octolasion tyrtaeum* (Savigny). Population estimates for earthworms in North America range from 8 m^{-2} in Indiana (7) to 2000 m^{-2} in Georgia (8).

Reviews have been published on earthworm ecology and relationships of earthworms to land usage (9, 10, 5, 11, 12). Most research efforts have been directed toward population ecology and the benefits of earthworms in altering physical, biological, and chemical processes within the soil. Ecological studies have been conducted primarily for establishing lethal

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maximal and optimal temperatures for growth and reproduction. However, knowledge about how earthworms respond to stress conditions, such as freezing and freeze-thaw cycles is limited. In a recent review of the literature, only a few references were found pertaining specifically to earthworms and frozen soils. This information dealt with population regulation and none dealt with interactions between earthworms and water or chemical movement in frozen soils.

Response to temperature is species specific and varies according to the developmental stage. Lee (10) summarized data on the lethal and optimal temperatures for several species of earthworms from different geographical areas. His data indicated most species of earthworms have an upper lethal temperature in the range of 25 to 35°C.

Physiological processes and activities, such as development, growth, species composition and abundance of earthworms are entirely or partially temperature dependent. Body temperature of Annelids is about that of their immediate environment (13). Unfavorable environmental conditions are avoided by migrating to depths in soils where moisture and temperature conditions are more favorable (14). Alternatively, earthworms may enter one of three forms of inactivity. All three forms are generally considered a form of aestivation. Although the process of aestivation may vary among species, usually at the onset of aestivation the earthworm ceases to feed, the gut is emptied, and a round cavity lined with mucus is constructed. The worm then proceeds to coil into a compact sphere and remains in this position until aestivation is terminated.

Edwards and Lofty (9) discuss three forms of inactivity. *Quiescent:* earthworms respond directly to unfavorable conditions, with activity resuming as soon as conditions become favorable. *Facultative diapause:* response caused by adverse environmental conditions, with activity resuming at a certain critical time after conditions become favorable. *Obligatory diapause:* response occurs at a predicted time of the year independent of current environmental conditions, this form, while independent of current condition, is triggered by a sequence of environmental changes or internal mechanisms.

Earthworms are generally hermaphroditic, with separate testes and ovaries. Sperm cells are exchanged between copulating individuals and are stored in spermathecae for subsequent fertilization of the ova. After copulation is complete, the worms separate and each clitellum produces a secretion which hardens over its outer surface. The worm then moves backwards drawing the secretion over its anterior end. These secretions containing the eggs harden and form a tough resistant structure (cocoon) around the eggs. It is important to note that a cocoon is merely a shell protecting developing embryos.

Cocoons are usually deposited in the top 10 cm of the soil (15) and thus would be exposed to freezing temperatures. Differences in frost tolerance are considerable between species. Holmstrup et al. (16) compared the frost tolerance of lumbricid earthworm cocoons in –1, –5, and –10°C temperatures. Of the species studied, most appeared able to withstand a mild degree of frost and were able to tolerate exposure to –1°C. Greater mortality occurred at the lower temperatures; but, this may have been caused by the lack of an acclimatization period or the rapid lowering of the temperature. In this study, cocoons were removed from 15°C rearing conditions and immediately subjected to colder temperatures.

Immature and adult earthworms are vulnerable to temperatures below 0°C. Hopp (17) compared survival of earthworms in different cropping systems. In continuous and rotation corn, a sharp decrease in the number of earthworms occurred at the time of the first intense freeze. Numbers of earthworms in a grain-and-sod rotation remained stable. He concluded that the decrease in numbers was prevented by insulative protection of the ground surface in the late fall. Unfortunately, these data are reported as "total earthworms" and the effect on specific species is unknown.

Earthworms move in the soil matrix in search of food, to escape adverse environmental conditions, and to colonize new areas. Lee (10) described three types of burrows. The first type is usually inhabited by earthworms that feed and cast on the surface of the soil. The burrows are usually orientated vertically, permanently inhabited, and extend down in the underlying soil horizons. Earthworms inhabiting this type of burrow usually escape adverse environmental conditions by migrating downward in the soil. The second type of burrow is usually orientated horizontally, temporarily inhabited, and does not extend downward into the soil. The third type of burrow is more or less vertical and formed by earthworms that live near the soil surface. This type of burrow is usually used as a refuge when unfavorable conditions exist at the soil surface. Often these burrows terminate in mucus-lined chambers.

Infiltration of water is usually two to ten times faster in soils having earthworms compared to soils without earthworms (10). Tunnel orientation, continuity, diameter, length, casting placement, microrelief around the burrow opening, surface sealing, and whether the burrow is occupied may alter infiltration rates (12). Interactions between freezing or freeze-thaw cycles and earthworm burrows have not been investigated.

Recommendations for future research

Advances in our understanding of earthworms and their importance in farming systems depend upon a complete understanding of how earthworms relate to environmental stress conditions that exist throughout the yearly cycle. In general, it is assumed that all activity, including growth and reproduction cease at some threshold temperature. At lower temperatures, earthworms become dormant and no longer contribute to soil processes such as fertility and infiltration. Thus, we have identified several areas that should be considered for future research; they are:

1. Investigations are needed to understand the effects of freezing temperatures on the survival and behavior of earthworms. It is generally accepted that earthworms respond to unfavorable environmental conditions by either entering some form of dormancy or retreating to greater depths in the soil, thereby avoiding the stress. Neither the factor(s) which actually triggers these responses nor the mechanisms involved in the prevention of freezing injury are known. Research is also needed to understand how different life stages (cocoons, immatures, and adults) respond to temperature levels and if preconditioning is necessary for survival. Since earthworms move within the soil matrix, research is needed to determine the rate of movement particularly in those cases in which the existing burrows have been destroyed by activities such as tillage.
2. Research is also needed to determine the effect of freezing, as well as freeze-thaw cycles, on the continuity and permeability of earthworm burrows. Specifically, research is needed to determine if the burrows remain open and if they are important in the drainage of water from early spring rains or snow melts.
3. Studies are also needed to determine the effect of freezing and freeze-thaw cycles on aggregate stability of the burrow lining and cast materials, both those placed at the soil surface, as well as, those below the soil surface. Since cast stabilities are affected by food sources and soil types, these investigations need to be determined over a broad range of environmental conditions and food types to understand the effects of the freezing and/or freeze-thaw cycles on the water stability of the earthworm casts.

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