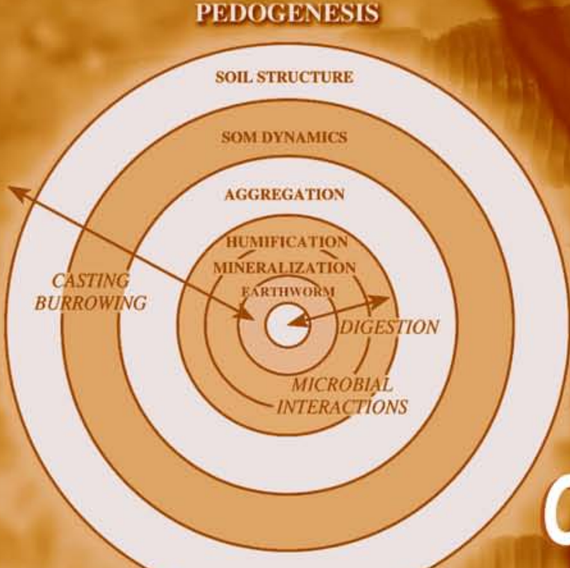
SECOND EDITION

Earthworm Ecology



Edited by

Clive A. Edwards

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Preface

Charles Darwin was the first scientist to bring earthworms to the attention of scientists and the general public, more than a century ago. Darwin noted the importance of earthworms in breaking down dead plant materials, recycling the nutrients they contain, and turning over soil. His book *The Formation of Vegetable Mould through the Action of Worms* (1881) summarized his conclusions on earthworms, which he reached after 40 years of observation and experimental work. In this book, he expressed the opinion that "earthworms have played a most important part in the history of the world." The importance of his personal contributions to our knowledge of the roles and biology of earthworms cannot be stressed enough and led to a great upsurge in research into the morphology, histology, and taxonomy of earthworms in the late 19th and early 20th centuries.

However, it was only in the last 25 years that interest in and research into the ecology and biology of earthworms has peaked. Much of this work was summarized by Edwards and his coauthors in their book *The Biology and Ecology of Earthworms* (first edition 1972, second edition 1977, third edition 1996) and by Lee in his book *Earthworms: Their Ecology and Relationships with Soil and Land Use* (1985). Interest in earthworm ecology and the importance of earthworms to soil formation and fertility has been increasing at an extremely rapid rate and so has research into the subject. This is evidenced by the increases in the number of references cited by the authors of *The Biology and Ecology of Earthworms* in its three editions. In 1972, they cited 565 references; in the second edition (1977), they cited 674; but in the third edition (1996), they cited more than 1500. This probably represented only a third of scientific papers published up to that time.

The first edition of *Earthworm Ecology* (1998) owed its origin to the Fifth International Symposium on Earthworm Ecology, which was held in Columbus, Ohio, in July 1994. At this Symposium, attended by more than 220 scientists from 38 countries, 165 research presentations were made, many of which are published in a special volume of the journal *Soil Biology and Biochemistry.* In the eight sessions that were held at the Columbus Symposium, each opened with an invited review paper of a key topic by a distinguished earthworm scientist and concluded with a final overview of the subject and conclusions by another well-known earthworm scientist. The 16 invited papers were edited to form the eight sections in the first edition of *Earthworm Ecology*, which covered all the major aspects of earthworm ecology, including earthworm diversity, behavior, physiology and general ecology, and the roles of earthworms in nutrient cycling, soil maintenance, plant growth, ecotoxicology, and waste management, with two chapters summarizing research on each topic. Since the first edition of *Earthworm Ecology* was published in 1998, there have been two further Symposia on Earthworm Ecology, in Vigo, Spain, in 1998 and in Cardiff, Wales, in 2002; the number of publications on earthworms has continued to increase rapidly. The first edition was extremely well received by scientists, students, and the general public. In view of the rapidly expanding developments and discoveries in earthworm biology and ecology, it seemed appropriate to update, and revise extensively, the first edition of the book and add new chapters that address the most rapidly developing areas of earthworm research.

This second edition includes extensive revisions of the original chapters as well as additional chapters on the history of earthworm research, mechanisms by which earthworms increase soil fertility and promote plant growth, and the importance of invasions of exotic species of earthworms in North America and other regions of the world; there is a new chapter on vermiculture and vermicomposting in Europe. These changes make this book an even more valuable addition to the publications that summarize the increasing importance of earthworms in natural ecosystems and crop production. It also addresses key issues in earthworm biology and ecology and is an essential key reference work for soil scientists and agronomists as well as those people with a great interest in earthworms.

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About the Editor

Clive Edwards, Ph.D., is recognized as a world authority on earthworms, and his book *Ecology and Biology of Earthworms* is now in its third edition. After graduating from Bristol University and then earning a M.S. and Ph.D. at the University of Wisconsin, U.S.A., Dr. Edwards was appointed to the U.K. Ministry of Agriculture. In 1960 he joined Rothamsted Experimental Station as a Senior Principal Scientific Officer where his work focused on research into the effects of agricultural chemicals on the soil environment. From 1966 to 1968 he was visiting professor at Purdue University, U.S.A. He was appointed as Chair of the Department of Entomology at The Ohio State University, U.S.A. in 1985.

Dr. Edwards has published extensively on soil ecology, environmental toxicology, and sustainable agriculture, and he is currently recognized as a world authority on earthworms. His book *Ecology and Biology of Earthworms* is the first comprehensive book on earthworms since Charles Darwin's *The Formation of Vegetable Mould Through the Action of Worms*, which was published in 1881. In 1996, Professor Edwards' book *Ecology of Earthworms* won a Presidential Citation from the U.S. Soil & Water Conservation Society.

In 2001, Dr. Edwards presented The Ohio State University Distinguished Lecture The Future of Human Populations; Energy, Food and Water Availability in the 21st Century — one of the university's highest honors for a faculty member. His involvement with the British Crop Protection Council has been an outstanding contribution to all the Pests & Diseases Conferences.

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Part I

Introduction

1 The Importance of Earthworms as Key Representatives of the Soil Fauna

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CONTENTS

HISTORY

The great importance of the soil biota in soil pedogenesis and in the maintenance of structure and fertility is not always fully appreciated by physical and chemical soil scientists. Earthworms are arguably the most important components of the soil biota in terms of soil formation and maintenance of soil structure and fertility. Although not numerically dominant, their large size makes them one of the major contributors to invertebrate biomass in soils. Their activities are important for maintaining soil fertility in a variety of ways in forests, grasslands, and agroecosystems.

Aristotle was one of the first people to draw attention to the role of earthworms in turning over the soil; he aptly called them "the Intestines of the Earth." However, it was not until the late 1800s that Charles Darwin, in his definitive work *The Formation of Vegetable Mould through the Action of Worms* (1881), really brought attention to the extreme importance of earthworms in the breakdown of dead plant and animal matter that reaches soils and in the continued turnover and maintenance of

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soil structure, aeration, drainage, and fertility. Before Darwin's book was published, earthworms were commonly considered soil-inhabiting crop pests. His views on the beneficial aspects of earthworms were supported and expanded subsequently by other contemporary scientists such as Muller (1878), Urquhart (1887), and many others. The observations Darwin described were so advanced that it was half a century before many of them were confirmed (see Chapter 2, this volume).

EARTHWORM TAXONOMY

Earthworms belong to the order Oligochaeta, which includes more than 8000 species from about 800 genera. Earthworms are common all over the world in natural forests and grasslands as well as agroecosystems. However, many oligochaetes have an aquatic habit, and there is considerable controversy over earthworm systematics (see Chapters 3 to 5, this volume). Earthworms are found in most regions of the world, except those with extreme climates, such as deserts and areas that are under constant snow and ice. Some genera and species of earthworms, particularly those belonging to the Lumbricidae, are extremely widely distributed and are termed *peregrine*; often, when these species are introduced to new areas, they become dominant over the endemic species. This situation applies to parts of the northern United States and Canada, particularly those areas close to major waterways (see Chapters 3 and 5, this volume).

However, the indigenous earthworm fauna of North America has not been well studied other than by Gates and Reynolds and earlier workers (Chapter 4). Endemic species include those in the Acanthodrilidae, with its most abundant genus *Diplocardia*; members of the Sparganophilidae; and species in the Megascolecidae, of which the most common genus is *Pheretima*. There are very few earthworm taxonomists, which has an impact on earthworm research the world over (see Chapter 4, this volume).

EARTHWORM ECOLOGY

The size of earthworms ranges from a few millimeters to as much as 2 m in length, from 10 mg to nearly a kilogram in weight, and up to 40 mm in diameter. The record was a specimen believed to be a *Microchaetus* sp. that was 7 m long and 75 mm in diameter (Lungström and Reinecke 1969). The larger earthworms are usually found in southern latitudes, such as South America, South Africa, Southeast Asia, Australia, and New Zealand. No other terrestrial invertebrate has such a wide range of sizes between the smallest and the largest individuals (Lee 1985)

Populations of earthworms vary greatly in terms of numbers or biomass and diversity. Populations range from only a few individuals per square meter to more than 1000 per square meter (Lee 1985; Edwards and Bohlen 1996; Lavelle et al. 1999). The size of populations depends on a wide range of factors, including soil type, pH, moisture-holding capacity of the soil, rainfall, and ambient temperatures, but most importantly, on the ready availability of organic matter. This is because interactions between organic matter and microorganisms provide food for earthworms.

Earthworm populations in cultivated land usually do not exceed 100 per square meter or 400 per square meter in grassland, and similar populations to those in grassland are usually found in woodlands, where the availability of organic matter is seldom limiting. Numbers as high as 2000 per square meter have sometimes been recorded, although relatively few earthworms occur in the more acidic mor soils under coniferous forests. Usually, the largest earthworm populations are lumbricids, which seem to be able to survive adverse soil and litter conditions much better than species belonging to many of the other families. The earthworm biomass in most soils exceeds the biomass of all other soil-inhabiting invertebrates. It has been stated that earthworm biomass in a pasture may be ten times that of stock animals that graze on it (see Chapters 6 and 14, this volume).

The diversity of species of earthworms varies greatly between sites and habitats, and there often tend to be species associations in different soil types and habitats. Earthworm communities in soils in temperate countries are dominated by lumbricids and tend to be considerably less diverse than in soils with other earthworm families in warmer latitudes (Lavelle et al. 1999). However, even in the most complex soil systems, the diversity of earthworm species does not seem to be very great, rarely exceeding ten, and there are usually only three to five species in any particular site. There is some evidence that species that fill the same ecological niche do not normally occur in the same degree of abundance at a particular site (Edwards and Lofty 1982a,b; Edwards and Bohlen 1996).

The activity of earthworms differs greatly between seasons in temperate regions, where earthworms are active mainly in the spring and autumn. During the winter, they penetrate deeper into soil, where they are much more protected from the adverse winter cold temperatures. In dry summer periods, they also burrow deeper into soil and sometimes construct cells lined with mucus in which they estivate in a coiled position until environmental conditions become favorable again.

Although cocoons may be produced at almost any time of the year, cocoon production is usually seasonal. In temperate regions, the most cocoons are produced in spring or early summer, with a second, much smaller peak in autumn. Numbers of cocoons range from 1 to 20 per mating, depending on species.

The life cycles of many species of earthworms have not been well studied. There probably is adequate information on about 12 species of temperate lumbricid earthworms, 7 species from Africa (Lavelle et al. 1999), and 20 species of earthworms common in tropical agroecosystems (Barois et al. 1999). Earthworms have potential for very long life cycles of up to 10 to 12 years, although in the field, many species may live only 1 or 2 seasons because of their susceptibility to a wide range of predators (Edwards and Bohlen 1996). Indeed, their potential longevity, combined with their fecundity, means that very large populations could build up rapidly in the absence of predation or adverse environmental conditions. In addition, some species can produce cocoons parthenogenetically without mating, which increases their potential to spread to new sites.

Their moisture and temperature relationships have major effects on their ability to populate new sites. Earthworms lose moisture through their cuticles, so they are very dependent on soil moisture, and their activities are linked closely with rainfall patterns in both temperate and tropical environments. However, for some reason, in periods of intense precipitation, some species may emerge from their burrows, and they are often found in large numbers on the soil surface, where they may die. Cocoon production and the growth of earthworms are correlated positively with temperature, but the cocoon incubation period, percentage hatching, and number of hatchlings produced per cocoon are correlated negatively with temperature (Edwards 1998). Many species cannot survive below 0°C, and most species cannot survive above 30 to 35°C (Edwards 1983). Nevertheless, they have behavioral patterns and resistant cocoons that enable them to survive adverse climate conditions.

EARTHWORMS AND SOIL FERTILITY

Soil Formation

Earthworms are extremely important in soil formation, principally through activities in consuming organic matter, fragmenting it, and mixing it intimately with soil mineral particles to form water-stable aggregates. During feeding, earthworms promote microbial activity by an order of magnitude, which in turn also accelerates the rates of breakdown and stabilization of humic fractions of organic matter. Different species of earthworms do not affect soil formation in the same way because of very different behavior patterns. Some species consume mainly inorganic fractions of soil, whereas others feed almost exclusively on decaying organic matter (see Chapters 8 and 9, this volume). They can deposit their feces as casts either on the soil surface or in their burrows, depending on the species concerned, but all earthworm species contribute in different degrees to the comminution and mixing of the organic and inorganic components of soil and decrease the size of not only organic particles, but also mineral particles (Shrickhande and Pathak 1951; Joshi and Kelkar 1952).

During passage through the earthworm gut, the different kinds of mineral particles become mixed intimately with organic matter and form aggregates, which improve both the drainage and moisture-loading capacity of the soil. These aggregates are usually very water stable and improve many of the desirable characteristics of soils. There have been various suggestions as to the possible ways in which earthworms form aggregates, such as by production of gums (Swaby 1950) or calcium humate (Meyer 1943), by plant residues (Ponomareva 1953), or by means of polysaccharide molecules (Parle 1963). Various authors have estimated that up to 50% of the aggregates in the surface layers of soil are formed by earthworms (Kubiena 1953). Earthworms also contribute in many ways to soil formation, structure, and physical characteristics (see Chapters 10 and 11, this volume).

Turnover of Soil

As Darwin first noted, earthworms move large amounts of soil from the deeper strata to the surface. The amounts moved in this way range from 2 to 250 tons per hectare per annum, equivalent to bringing a layer of soil between 1 mm and 5 cm thick to the surface every year, creating a stone-free layer on the soil surface. In temperate climates, all the upper 15 cm of soil may be turned over every 10 to 20 years (Edwards and Bohlen 1996). However, much larger turnovers have been reported from tropical agroecosystems (Lavelle et al. 1999).

Soil Aeration and Drainage

Earthworms also affect soil structure in other ways. Some species make permanent burrows, whereas others move randomly through the soil, leaving cracks and crevices of different sizes. Both sorts of burrows are important in maintaining soil aeration, drainage, and porosity. Moreover, earthworm burrows are usually lined with a protein-based mucus that helps stabilize these channels, and many of the species with permanent burrows cast their feces around the lining of the burrows, with the cast material usually containing more plant nutrients in a readily available form than the surrounding soil.

There is good evidence that earthworm activity increases both the porosity and the air-to-soil volume (Wollny 1890; Hopp 1974; Edwards and Lofty 1977). Burrows are also important in improving soil drainage, particularly because those of some species, such as *Lumbricus terrestris* L., penetrate deep into soil in permanent burrows (Edwards and Lofty 1978, 1982a,b) and can even pass through layers of clay. The burrows and pores also increase the infiltration rate greatly (Slater and Hopp 1947; Teotia et al. 1950; Carter et al. 1982), and there are numerous reports of water penetrating the surface soil between two and ten times faster when earthworms were present than when they were not (Stockdill 1966; Wilkinson 1975; Tisdall 1978). These effects on infiltration can be of two kinds. The first is the presence of large surface-opening holes that are not usually taken into account by soil scientists when conventional models of infiltration are developed (Edwards and Lofty 1982a). Second, the crevices also created by earthworms, but which are smaller, not only increase infiltration, but also aid in water retention (see Chapters 10 and 11, this volume).

Finally, earthworm activity makes a significant contribution to soil aeration (Stockli 1928; Kretzschmar 1978) by creating channels, particularly in heavy soils, that allow air to penetrate into deeper layers of soil, minimizing the incidence of anaerobic layers.

Organic Matter Breakdown and Incorporation into Soil

Although all species of earthworms contribute to the breakdown of plant-derived organic matter, they differ greatly in the ways in which they break down organic matter and incorporate it into the soil. Their activities can be of three kinds, each associated with a different group of species. Some species are limited mainly to the plant-litter layer on the soil surface, decaying organic matter or wood, and seldom penetrate soil more than superficially. The main role of these species seems to be comminution of the organic matter into fine particles, which facilitates microbial activity.

Other species live just below the soil surface most of the year, except when the weather is very cold or very dry; do not have permanent burrows; and ingest both organic matter and inorganic materials. These species produce organically enriched soil materials in the form of casts, which they deposit either randomly in the surface layers of soil or as distinct casts on the soil surface.

Finally, there are the truly soil-inhabiting species with permanent burrows that penetrate deep into the soil. These species feed primarily on organic matter but also ingest considerable quantities of inorganic materials and mix these thoroughly through the soil profile. These last species are of primary importance in pedogenesis. All species depend on consuming organic matter in some form and play an important role in the final stages of organic matter decomposition, which is humification into complex amorphous colloids containing phenolic materials, probably by promoting microbial activity.

There is little doubt that, in many ecosystems, earthworms are the key organisms in the breakdown of plant organic matter. Populations of earthworms usually expand in relation to the availability of organic matter; in many temperate and even tropical forests, it seems that earthworms have the capacity to consume the total annual litter fall. Such a total turnover has been calculated for an English mixed woodland (Satchell 1967), an English apple orchard (Raw 1962), a tropical forest in Nigeria (Madge 1965), and an oak forest in Japan (Sugi and Tanaka 1978); it seems likely that similar calculations would be valid for other sites (Edwards and Bohlen 1996). There is current speculation that invasions of lumbricids into North American forests are changing them dramatically and having an impact on rates of organic matter turnover and soil cover (see Chapters 5, 8, 9, and 13, this volume).

Nutrient Availability

During feeding by earthworms, the carbon:nitrogen ratio in the organic matter falls progressively; moreover, most of the nitrogen is converted into the ammonium or nitrate form. At the same time, the other nutrients, phosphorus and potassium, are converted into a form available to plants. Soils that have poor populations of earthworms often develop a structure with a mat of decomposed organic matter at the soil surface (Kubiena 1953); this can also occur in grassland and is common on poor upland grasslands in temperate countries and in New Zealand in areas where earthworms have not yet been introduced (Stockdill 1966) (see Chapters 6 and 14, this volume).

EFFECTS OF AGRICULTURE ON EARTHWORMS

Earthworm populations are affected greatly by many of the main agricultural practices; in particular, cultivations, fertilizers, pesticides, and crop rotations exert major effects on earthworm activities and communities.

Cultivations have considerable effects on earthworm communities, particularly those species with deep burrows. A single cultivation does not have any drastic effects on earthworm populations other than by mechanical damage, destruction of permanent burrows, and exposure to bird predators. However, repeated heavy cultivations progressively diminish earthworm populations. No till (direct drill) and a variety of conservation tillage practices, such as ridge tillage and shallow plow, favor the buildup of larger earthworm populations that are limited only by the availability of food (Edwards and Lofty 1982a; Edwards and Bohlen 1996).

Fertilizers can be either organic or inorganic, including a broad range of organic manures from sources such as cattle, pigs, poultry, sewage wastes, and wastes from industries such as those involving a brewery, paper pulp, or frozen potatoes. These materials are major factors in the buildup of large field earthworm populations; when such organic wastes are added to agricultural land, earthworm populations may double or triple in a single season. Some liquid manures that have not aged or composted can have temporary adverse effects on earthworm populations when applied to soils as slurries because of their ammonia and salt contents, but these effects are usually short term.

Many inorganic fertilizers also contribute indirectly to the buildup of earthworm populations because of increased crop yields and hence increased amounts of crop residues added to the soil. However, earthworms are very sensitive to ammonia, and ammonia-based fertilizers often have adverse effects on earthworm populations, especially when these fertilizers are applied annually over several seasons (Edwards and Lofty 1982b).

Pesticides, which include insecticides, herbicides, fungicides, and nematicides, are used extensively on agricultural land in developed countries. It is often assumed that many pesticides are toxic to earthworms or have harmful effects on them. However, most herbicides have few direct effects on earthworms, although the triazine herbicides are slightly toxic. However, herbicides have drastic indirect effects on earthworms through their influence on the availability of organic matter (Edwards and Thompson 1973). Most fungicides have few effects on earthworms, with the exception of the carbamate-based fungicides, such as benomyl, which are very toxic. Of the insecticides in current use, only the organophosphate, phorate, and most carbamate-based compounds such as carbaryl, carbofuran, and methiocarb, and the avermectins are toxic to earthworms (Edwards 1984a, b). Of more than 200 pesticides reviewed by Edwards and Bohlen (1992), fewer than 20 were seriously toxic to earthworms (see Chapters 16 and 17, this volume).

Crop rotations have been progressively decreasing in industrialized agriculture. There has been relatively little work on the effects of crop rotations on earthworm problems. In general, the inclusion of crops such as cereals that leave considerable organic residues encourage the buildup of earthworm populations more than do legumes, which decompose quite rapidly. Root crops, for which most of the crop is removed, discourage the buildup of earthworm populations (Edwards and Bohlen 1996).

EARTHWORMS AS INDICATORS OF SOIL QUALITY AND HEALTH

There has been considerable interest in the concept of maintaining soil quality and health. There has been considerable discussion on defining these terms and on identifying appropriate physical, chemical, and biological indicators of soil quality. One definition is "the ability of a soil to sustain biological productivity, maintain environmental quality and promote plant, animal and human health" (Doran and Parkin 1996). Soil is a heterogeneous mixture of abiotic and living components, including a very complex range of soil-inhabiting organisms. The basic functions of soils depend on their structural and functional integrity and the impacts of disturbances on management on these functions.

A wide range of indicators of soil quality and health criteria has been suggested, but it is becoming increasingly clear that it is essential that the indicators must include biological components because soil is a dynamic entity (Blair et al. 1996). It is difficult to use microbial indicators of soil quality and health as much as desired because of a lack of simple methodologics that can be used in the field by relatively untrained workers.

Soil microinvertebrates have been suggested as possible indicators of quality and health (Linden et al. 1994), but sampling microarthropod or nematode populations is difficult, so their identification and utility as suitable indicators is a complex problem. There is a consensus among soil ecologists and most farmers that earthworms may be one of the best indicators available of soil quality (Doube and Schmidt 1997). They are easy to sample and identify and, as the discussions in this book illustrate, are important indicators of both soil health and soil quality (see Chapters 2 and 6, this volume).

EARTHWORMS AND SOIL POLLUTION

There has been increasing interest in the use of earthworms as organisms to assess the environmental effects of soil pollution. Three Conferences on Earthworm Ecotoxicology (1991, U.K.; 1997, the

Netherlands; 2001, Denmark) were each attended by more than 100 scientists and provide good evidence of this interest. Standardized testing protocols have been developed by such national and international organizations as the Organization for Economic Cooperation and Development and the European Union (Edwards 1983, 1984b). Many aspects of earthworm ecotoxicology are reviewed in Chapters 16 and 17 of this volume.

EARTHWORM IMMIGRATIONS

Interest has increased greatly in migrations of earthworms across regions and continents. Peregrine earthworms, especially lumbricids, are invading soils across the world, particularly into agricultural soils, but more recently into forest soils. These issues are discussed extensively in Chapters 5 and 13 of this volume.

NEED FOR EARTHWORM RESEARCH

Although the number of publications on earthworm biology and ecology is increasing rapidly, there still seems an urgent need for greatly expanded research, particularly on some aspects of earthworm activity.

There still is inadequate knowledge of the basic biology and ecology of even some of the more common species of lumbricoids. Very few studies have addressed the problems of the detailed interrelationships among earthworms, microorganisms, and decaying organic matter and its incorporation into soil (see Chapters 2 and 12, this volume). There is good empirical evidence that introduction of earthworms together with organic matter into impoverished soil, with addition of organic matter and adjustment of pH, can increase soil fertility greatly, but there is little knowledge of the mechanism of such increases or even the best ways of introducing earthworms.

Most important is the worldwide lack of knowledge of the geographic distribution of earthworms and populations of the different species. Until more is known of the fundamental biology and ecology and the activities of the many different species and their role in maintaining soil structure and fertility, it is impossible to assess their potential role in soil improvement. These problems are particularly acute in North America, where there are few earthworm specialists, and taxonomic research is extremely sparse.

CONCLUSIONS

This second edition of *Earthworm Ecology* appears only 5 years after the first edition; it has been revised extensively, and four new chapters on important issues have been added. The reasons for creating a second edition so soon were partially because of rapid developments in earthworm biology and ecology and, to some extent, because of the great reception of the first edition by scientists and the public. It is hoped that this new edition will find a ready audience, and that it will encourage further interest in earthworms.

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2 How Earthworms Affect Plant Growth: Burrowing into the Mechanisms

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EFFECTS OF EARTHWORM ON PLANTS: THE HISTORY

The importance of earthworms for soils, plant growth, and society has undergone various phases, from profound recognition to utter ignorance and disdain. They were highly regarded as promoters of soil fertility during the Egyptian empire (Minnich 1977), and early philosophers such as Aristotle considered them beneficial animals, calling them the "earth's entrails" (or intestines) (Kevan 1985). From antiquity to Darwin's time, however, not much information is available on earthworms (see review by Kevan 1985); throughout much of the 17th up to the beginning of the 20th century, earthworms were considered garden pests that needed elimination from soils (Minnich 1977; Brown et al. 2004).

Probably the earliest and best-known report of the potential benefits of earthworms to soils is the much-quoted letter of Rev. Gilbert White to the Hon. Daines Barrington, written on May 20, 1777. This letter also provided some first hints of the mechanisms by which earthworms affect plant growth. White (1789) wrote:

> Dear Sir — … Earthworms, though in appearance a small and despicable link in the chain of Nature, yet, if lost, would make a lamentable chasm. For to say nothing of half the birds, and some quadrupeds which are almost entirely supported by them, worms seem to be the great promoters of vegetation, which would proceed but lamely without them, by boring, perforating, and loosening the soil, and rendering it pervious to rains and the fibers of plants, by drawing straws and stalks of leaves and twigs into it; and most of all, by throwing up such infinite numbers of lumps of earth called worm-casts, which, being their excrement, is a fine manure for grain and grass … Gardeners and farmers express their detestation of worms; the former because they render their walks unsightly, and make them much work; and the latter because, as they think, worms eat their green corn. But these men would find that the earth without worms would soon become cold, hard-bound, and void of fermentation, and consequently sterile; and, besides, in favour of worms, it should be hinted that green corn, plants, and flowers, are not so much injured by them as by many species of *coleoptera* (scarabs), and *Tipulidae* (long-legs) in their larva, or grub-state; and by unnoticed myriads of small and shell-less snails, called slugs, which silently and imperceptibly make amazing havoc in the field and garden.

It was not until almost a century later that Darwin (1881), in his book *The Formation of Vegetable Mold Through the Action of Worms*, firmly established the benefits of earthworms to soils. Other authors (Hensen 1877, 1882; Müller 1878, 1884; Wollny 1890) supported the positive role of earthworms in soil processes and plant growth, and Wollny (1890) was the first actually to quantify this relationship. Despite initial skepticism about the reports of Darwin and Hensen (Wollny 1882a), he became convinced that earthworms were important for plant production when his experiment showed increased yields of 12 species of plants, ranging from negligible amounts up to 733% (rape), by adding earthworms (Wollny 1890). However, he continued to warn about the generalization of these results to field situations.

From the early 20th century to the present, the number of experiments increased, and the intervals between them decreased, so that there are presently more than 120 papers published on the effects of earthworms on plant production. The aim of most of these investigations was to answer the following questions:

- Do earthworms affect plant growth (positively or negatively), and if so, by how much?
- Which plants are affected most (positively or negatively)?
- Which earthworm species are most efficient at promoting plant growth?

However, despite the abundant literature on the responses of plants to earthworms and the identification of a number of soil, environmental, or earthworm factors associated with particular plant responses, rarely has the question of how these effects occur (i.e., what the mechanisms behind the observed effects are) been addressed properly (Blakemore and Temple-Smith 1995; Edwards and Bohlen 1996; Brussaard 1999). In most papers, mechanisms were alluded to only briefly, and in several instances, the possible reasons for the observed effects of earthworms were not even mentioned. Furthermore, the proposed mechanism often cannot be confirmed or validated. The reason for this apparent lack of focus on the mechanisms behind the effects of earthworms on plants may be partly because of the following:

- The predominant paradigms driving agricultural development from Liebig (1840) up to the "green revolution" period (ending in the 1970s), with research focusing mainly on alleviating physical and chemical constraints to plant production through the use of artificial inorganic inputs and improved (often hybrid) crop varieties (Sánchez 1994)
- Production (yield-oriented) research that has concentrated mainly on aboveground plant responses and rarely has studied changes in root growth, morphology, distribution, and the belowground interactions (e.g., of earthworms with microorganisms)
- Inadequate experimental designs or insufficient criteria on parameters measured to assess the possible mechanisms involved
- The very complex nature of indirect and direct biological interactions that occur in soils, particularly between earthworms, soil properties and processes, and other organisms in soils

Earthworms and Plant Production in the Tropics

Many aspects of the effects and management of earthworms in tropical agroecosystems were reviewed by Lavelle et al. (1999). In particular, Brown et al. (1999) summarized the results of 28 experiments in the greenhouse and at the field level that identified the various soil properties and processes affected by earthworm activities and their impacts on plant production. The experiments were done in 8 tropical countries and involved at least 34 earthworm species and 19 plant species and were tested in 23 soil types belonging to 8 soil groups. An analysis of 246 studies of the effects of earthworms on plant shoot production (Figure 2.1) and 88 studies of the effects of earthworms on grain yields demonstrated clearly that earthworms usually have positive effects on plant growth (75% of all studies resulted in plant growth increases) and biomass. A mean 57% increase was observed in plant shoot mass, and a 36% increase was found for grain yields. Important negative effects occurred only rarely, usually because of some dysfunction in the soil created or induced by earthworm activities. They also observed that root production, contrary to that of the aboveground parts, was usually affected less by earthworm activity, possibly because of difficulties in studying this parameter or because plants growing in more healthy soils (presumably the case in earthworm-worked soils) tend to invest more energy in growing the aboveground plant parts, producing fewer roots per unit shoot biomass, resulting in higher shoot:root ratios.

The factors that seemed to affect the ultimate responses of plants to earthworms were the following:

- The part of the plant harvested, with greater effects of earthworms on biomass (positive) of shoots than grains and with the smallest effects on root growth.
- The species of plant involved, with greater effects of earthworms on the shoot growth of perennial plants (trees and bushes) and larger effects on yields of gramineous grain crops compared with legumes.
- The species of earthworms involved, with the pantropical endogeic species *Pontoscolex corethrurus* producing the greatest yield increases and the widespread Indian Dichogastrini

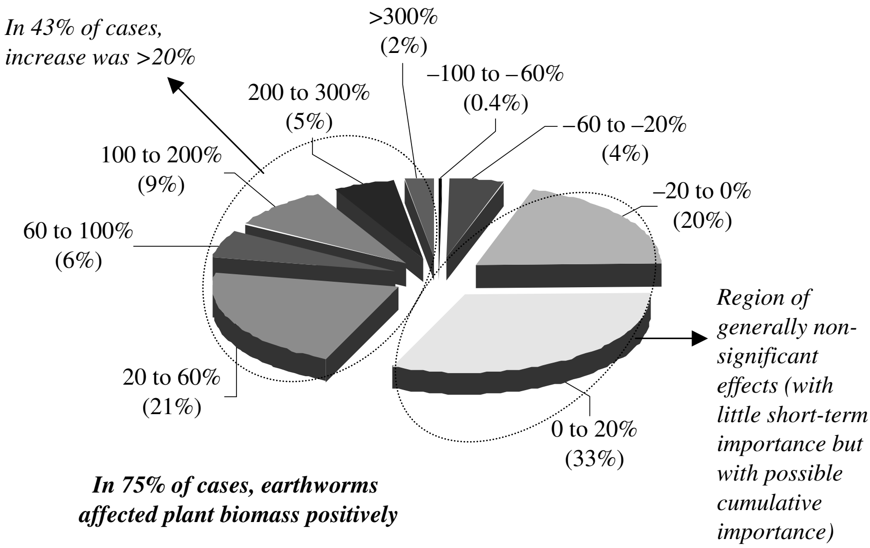

FIGURE 2.1 Effects of tropical earthworm species on plant shoot production. Each slice of the pie indicates a range of shoot biomass increase due to earthworms (e.g., 0 to 20%), and the percentage of cases where that range of increase was observed (values in parentheses). The chart was built using 246 data points (cases) taken from a total of 28 experiments involving at least 34 earthworm and 19 plant species tested in 23 soil types belonging to 8 great groups. (Modified from Brown et al., 1999.)

species *Drawida willsii* and West African species *Millsonia anomala* and various small eudrilids all having a good potential for introduction and management into soils.

- The earthworm biomass introduced or present in the soil, with higher yields usually occurring in response to greater earthworm biomass in a curvilinear relationship (moderate yield increases of 20 to 40% occurred with earthworm biomass values above 17 g m^{-2} and over 40% of grain production increases occurred with earthworm biomasses above 32 g m^{-2}).
- Earthworm survival. In both pot and field trials, the mortality of introduced earthworms was often high, particularly when the species was not adapted properly to the soil used or when few or no organic residues were applied (survival was greater when organic residues were present).
- The presence of organic residues on the soil surface, with greater effects on plant yields when such residues were present.
- The timescale of the measurements (i.e., the duration of the experiment), usually with positive cumulative increases in plant biomass because of earthworm activities with time, although occasionally (depending on the soil type or earthworm and plant species) the cumulative effects on plant biomass observed were negative.
- The spatial scale of the experiment (i.e., pot vs. field experiments), with effects on yield usually greater at the pot scale for any given plant and earthworm combination.
- The natural richness of the soil used in the experiment, with greater benefits on productivity in poorer soils (low percentage carbon content, coarser textures) than in richer soils (more carbon, clayey texture) with earthworms producing higher yields in moderately acid soils (pH between 5.6 and 7.0) than in strongly acid soils ($pH < 5.6$) or alkaline soils ($pH > 7.0$).

Different combinations of earthworm species, soil types and conditions, plant species, and various imposed human or environmental constraints may alter the potential effects of the earthworms on soil properties and plant growth. Thus, pinpointing the exact reasons for mechanisms of a specific plant response to earthworms in an experiment is not easy; more often than not, several mechanisms rather than a single mechanism are probably operating simultaneously.

The main aim of this chapter is to seek and identify possible mechanisms by which earthworms can promote or suppress plant growth. Furthermore, we dig further into some of these mechanisms and provide both conceptual diagrams of how they may be functioning and a few case studies dealing with each of the seven main mechanisms we propose. Finally, we end with some suggestions on how advancement will occur in this biologically complex area of research. Our basic premise is that through better understanding of the ways by which earthworms affect plant growth and production, plant and soil management techniques and practices can be adapted, improved, or implemented to prevent the occurrence of negative effects of earthworms on soils and plants and to maximize their positive effects on crops for the benefit of farmers, gardeners, ranchers, foresters, and other land users.

THE MECHANISMS BY WHICH EARTHWORMS AFFECT PLANT GROWTH: A CONCEPTUAL BACKGROUND

Types and Modes of Interaction

The effects of earthworms on soils can take three main forms: effects on biological, physical, or chemical soil properties and processes. Furthermore, because earthworms share the soil environment with roots, their effects on plant growth and root development can be either direct or indirect. Thus, the mechanisms of how earthworms influence plant productivity can be divided into three main types: physical, chemical, and biological. These can operate either directly or indirectly. *Indirect effects* mean that the plant is affected by earthworm activities through changes in the physical, chemical, or biological soil or rooting environment produced by earthworms; the *direct mode* of action means that the earthworms or their activities lead to direct changes in root growth and productivity.

Spatial and Temporal Scales of Earthworm Action

The soil volume affected by earthworm activities has been termed the *drilosphere* (Lavelle 1988); it constitutes one of the main soil functional domains (Beare et al. 1995; Lavelle 2002) that have significance in regulating major soil processes and functions, such as structure, organic matter (OM) decomposition, nutrient cycling, microbial and invertebrate populations, and plant growth. Because earthworm burrows and casts may outlive the earthworms themselves, and regulate the soil as an environment for other organisms (including plant roots) by controlling its physical structure, nutrient fluxes, and energetic status (resource availability), they have been termed *ecosystem engineers* (Jones et al. 1994; Lavelle et al. 1997).

It is important to note that the drilosphere and the engineering effects of earthworms are very variable and depend on biological factors such as the type of vegetation and the characteristics and composition of the earthworm community at a particular location (species, abundance, biomass, age structure, ecological strategy) and abiotic regulating factors, including climate, soil type, and imposed anthropic (management) factors.

Furthermore, the earthworm drilosphere is a dynamic zone of action that is constantly changing in both space and time as the earthworms ingest and reingest soil, burrow, and cast at different rates and in different locations in the soil. Therefore, the drilosphere can affect soil functions (including plant productivity) at different spatiotemporal scales, manifesting its effects at levels that range from the earthworm gut up to the soil profile (Lavelle 1997); these ideas are explored in Chapter 12.

The effects of earthworms on plants in a given situation and the mechanisms involved are difficult to assess because, although earthworms and their structures (burrows, casts) are often easily identifiable or separable from the edaphosphere and their sphere of influence on the soil (drilosphere) can be measured and quantified physically, chemically, and biologically under controlled conditions, the drilosphere is connected with the rest of the soil system. This means that it can interact profoundly with other soil organisms and functional domains (e.g., rhizosphere, porosphere, aggregatusphere, detritusphere, mermycosphere, termitosphere) (Brown et al. 2000). This interconnectedness becomes even more evident as in attempts to separate the mechanisms responsible for plant responses to earthworms in any given situation, soil type, or area.

Why Focus on Effects of Earthworms on Plant Roots?

Roots, as sensitive sensors of the soil environment and the producers of many signals that ultimately control plant shoot growth (Aiken and Smucker 1996), are the primary and immediate receivers of the contributions of earthworms to soil functions. By controlling nutrient and water supply to the shoots, it is the biomass, density, distribution, and activity (growth rate and longevity) of roots within the soil profile that will largely determine plant productivity (Brown and Scott 1984). Thus, it is the response of roots to earthworm activity that usually controls the overall plant response.

A simple conceptual model connecting the physical, chemical, and biological effects of earthworms on soils with their potential effects on plant root or shoot growth and nutrition is provided in Figure 2.2. The interdependence of earthworm physical activities (production of casts and burrows) and earthworm physiological activities (excretions, secretions, and tissue death) in interactions with soil properties such as organic matter (soil OM, root and residue inputs), microbial populations, and plant production is evident. The effects of chemical substances on soil properties and processes are based on the selection by earthworms of particular soil particles and organic matter, the different nutrient compositions of their feces compared with uningested soil, cutaneous mucus secretion, and excretion of metabolic products. Biological effects on soils are caused primarily by interactions of earthworms with the rhizosphere and soil microorganisms, depending especially on feeding and digestive habits of the earthworms; the physical effects are associated mainly with the structural properties of the drilosphere.

The following sections in this chapter explore the various ways in which earthworms can directly and indirectly affect plant growth, and we propose seven main mechanisms by which this is achieved. The focus is mainly on roots, although we recognize that indirect interactions with the aboveground plant parts and other organisms (both above- and belowground) may also be important (Wurst and Jones 2003). Given that the latter subject is a very recent field of study and that few results are available, we will limit the discussion primarily to belowground interactions and processes.

THE SEVEN MAIN MECHANISMS BY WHICH EARTHWORMS AFFECT PLANTS

We define the seven main mechanisms by which earthworms affect plant growth as follows (see details in Table 2.1):

1. Dispersal and changes in populations and activity of beneficial microorganisms
2. Changes in populations and impacts of plant pests, parasites, and pathogens
3. Production of plant growth-regulating (PGR) and plant growth-influencing (PGI) substances
4. Root abrasion and ingestion of living plant parts by earthworms
5. Interactions of earthworms with seeds
6. Changes in soil structure caused by earthworms
7. Changes in nutrient spatiotemporal availability caused by earthworms

Mechanisms 1 to 5 are mainly biological, operating indirectly (1 and 2) or directly (3 to 5); the last two (6 and 7) are indirect physical (6) or chemical (7) mechanisms.

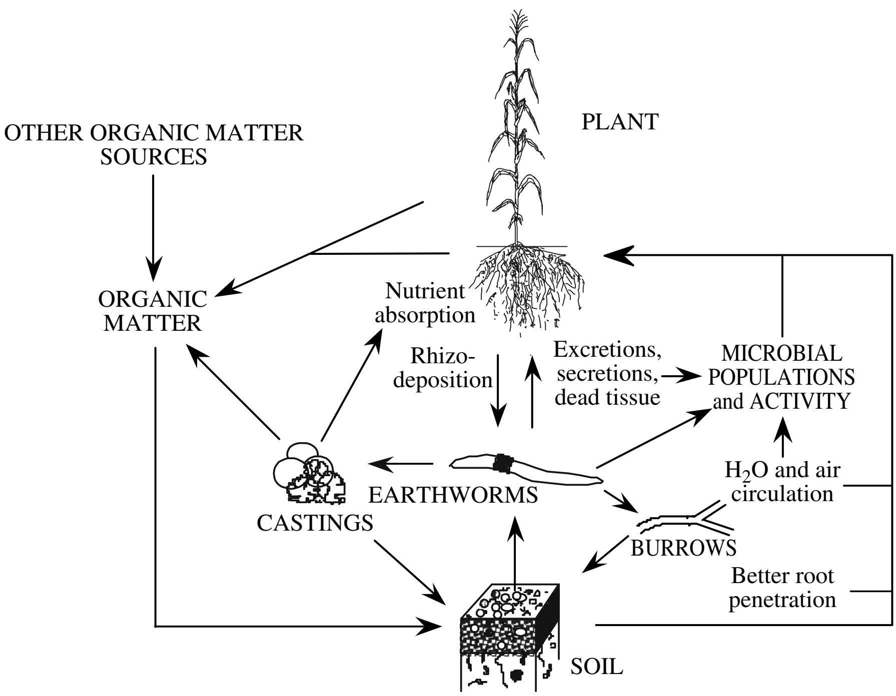

FIGURE 2.2 Simplified conceptual model connecting the physical, chemical, and biological earthworm effects on soils with their potential effects on plant growth and nutrition. (Modified from Cuendet and Bieri, 1999; Syers and Springett, 1983.)

1. Dispersal and Changes in Populations and Activities of Beneficial Microorganisms

Large populations of beneficial (plant growth promoting [PGP]) microorganisms such as saphrophytic and mycorrhizal fungi, actinomycetes (e.g., *Frankia*), bacteria, and microinvertebrates, such as protozoa and microbivore (fungivorous, bacteriophagous, predatory omnivorous and entomophathogenic) nematodes inhabit the soil. Nevertheless, because of their limited ability to disperse within the soil and the soil environmental and nutritional limitations to their activities, a large proportion of soil microorganisms are inactive at any given time, waiting for suitable conditions to promote higher levels of activity (Lavelle 1997). Invertebrate activities, such as earthworm burrowing and casting, promote soil mixing and bring microorganisms into contact with inaccessible soil resources, stimulating both their populations and their activity. The earthworm gut also provides an ideal environment for enhanced activity levels or multiplication of some microorganisms; others may be digested or their activity levels reduced by passage through the earthworm gut (Brown et al. 2000). The complex resulting effects of earthworms on microbial communities in soils (activity, populations, diversity) depend on the reactions of microorganisms to passage through the earthworm gut and the ability of microorganisms to utilize the drilosphere. Thus, earthworms may affect microbial populations (beneficial, facultatively pathogenic, and adverse species) directly, by feeding and digestive processes or indirectly by burrowing and casting activities, which change root growth and development and the soil environment, thereby making it more or less favorable to the development of microorganisms (Figure 2.3). Furthermore, as earthworms move through the soil matrix, they may disperse microorganisms, both superficially (on the earthworm body) or via ingestion-egestion (in casts).

The ability of earthworms to disperse microorganisms or stimulate microbial activity and increase microbial populations depends greatly on the earthworm's spatial range of activity, food requirements and sources, and behavior. Epigeic, litter feeding, and dwelling species of earthworms are much more

TABLE 2.1
The Seven Main Mechanisms by Which Earthworms Affect Plant (Mostly Root) Growth either Directly or Indirectly through Physicochemical or Biological Changes to the Soil Environment

	Mechanism Category (Type)		
Mechanism Mode	**Biological**	**Physical**	**Chemical**
Indirect (mediated through changes in the rooting environment, or via interactions with organisms that affect root growth and production)	**1. Dispersal or changes in populations and activity of beneficial microorganisms** (plant growth promoting rhizobacteria, N_2 fixing root symbionts, saprophytic and mycorrhizal fungi, microbial biocontrol agents, microbivorous and entomopathogenic nematodes, protozoa) **2. Effects of earthworms on populations of plant pests, parasites, and pathogens** (increase or decrease in populations and incidence of plant-parasitic nematodes, phytopathogenic fungi and bacteria, plant viruses?, shoot- and root-feeding insects) **3. Production of plant growth promoting/regulating substances** (hormones, vitamins, humic matter, auxins, cytokinins, gibberellins, ethylene, microbially induced and/or excreted by earthworms.	**6. Changes in soil structure caused by earthworms** (pore and aggregate size distribution and associated processes, including aeration, water retention, hydraulic conductivity, infiltration, erosion, runnoff, aggregate and crust formation and breakdown, compaction/soil slumping and decompaction/soil loosening)	**7. Changes in nutrient spatiotemperal availability caused by earthworms** (release or immobilization of different plant nutrients, leaching, denitrification, volatilization, OM mineralization, protection and/or humification, chelation of metals, pH changes)
Direct (earthworm activities that influence root growth/production in a direct manner)	**4. Root abbrasion and ingestion of living plant parts by earthworms** (feeding and/or ingestion by earthworms of living roots or plant shoots, and direct damage to growing roots) **5. Interactions between earthworms and seeds** (ingestion, digestion, burial, dispersal, changes in germination rates and potential)		

likely to affect microorganisms in the litter layer and the roots growing through the organic matter/humus (O/H) horizons and the soil surface-litter interface compared with the endogeic (soil-dwelling) geophagous (soil-feeding) earthworm species, which tend to have a greater effect on microorganisms living within the soil. Anecic, litter-burying species of earthworms, which create deep vertical burrows and surface middens (small mounds of leaves blocking the entrance of vertically oriented burrows connected to the soil surface) can have a major influence on microorganisms (fungi, bacteria, actinomycetes) and micro-, meso-, and macroinvertebrates (protozoa, nematodes, mites, springtails, enchytraeids, millipedes, isopods, other earthworms) in surface litter communities (Brown 1995; Anderson and Bohlen 1998; Maraun et al. 1999). However, their effects on the microbial communities living within the soil are probably less than those of endogeic species because of their decreased soil-burrowing activities as they tend to build more permanent burrow systems. Nevertheless, anecic earthworm species (and large endogeic species) often have burrows that reach depths of more than 2 m, which can represent important pathways of microbial dispersal and hot spots of microbial and root growth activity compared with that in the surrounding soil matrix (Bhatnagar 1975; Ehlers et al. 1983).

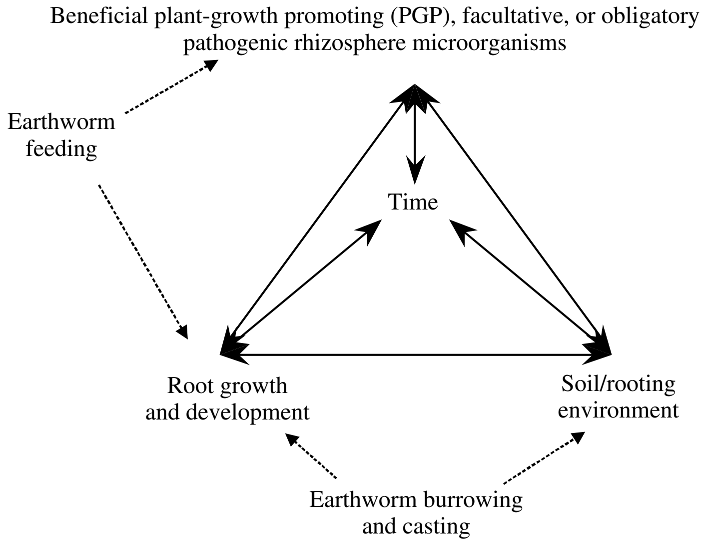

FIGURE 2.3 Interactions among beneficial, facultative and obligatory plant-pathogenic rhizosphere microorganisms, earthworms, plant roots and the abiotic root environment, determining plant root growth and development (note: this is a modified version of the classic "plant disease triangle" taught in plant pathology).

It has often been suggested that earthworms tend to promote changes in the microbial community toward a bacterial-based trophic chain. Actually, phospholipid fatty acid (PLFA) methyl esters analyses of earthworm-worked soils indicated that Gram-negative bacteria seem to be favored compared with Gram-positive bacteria (Clapperton et al. 2001; Enami et al. 2001). Lumbricid earthworms also increase bacterial-to-fungal ratios (Clapperton et al. 2001), although when a plant-pathogenic fungus was inoculated into the soils, earthworms decreased this ratio, implying that they may also increase the soil fungal biomass. Nevertheless, several species of fungi have been shown to be ingested preferentially by the earthworm *Lumbricus terrestris* (Moody et al. 1995; Cooke 1983; Moody et al. 1995; Bonkowski et al. 2000), and Edwards and Fletcher (1988) reported that fungi were a major food source for earthworms. This implies that earthworms (particularly the litter-burying or fragmenting anecic and epigeic species) may impose some selection pressures on fungal populations in both litter and soils. Bacterial-to-fungal ratios in soils are also often greater in earthworm-worked soils because bioturbation tends to affect fungal populations negatively more than those of bacteria (Hendrix et al. 1986).

The rhizosphere, a less-than-0.5-mm soil layer surrounding plant roots, is rich in microorganisms, with species that are beneficial or adverse to root growth. Several earthworm species (especially some endogeics) seem to feed mainly in the rhizosphere (James and Seastedt 1986; Rovira et al. 1987; Robertson et al. 1994; Hirth et al. 1998). Activity of lumbricid earthworms has been reported in the rhizosphere of a temperate pasture (Carpenter 1985) and of wheat (Doube and Brown 1998), and feeding in the rhizosphere was inferred from radio- (^{14}C) or stable isotope (^{15}N, ^{13}C) analyses of the tissues of earthworms (*L. terrestris* and *P. corethrurus*) living in soils under various plants (wheat, maize, *Brachiaria decumbens*, and sugarcane) (Spain et al. 1990; Spain and Le Feuvre 1997; Cortez and Bouché 1992; Brown 1999). There are also records of earthworms feeding on living and dead root tissues (see mechanism 4), but the role of root tissues and their derivatives (rhizodeposition) in earthworm diets remains little understood (Brown et al. 2000). Earthworm feeding or movement in or around the rhizosphere can have important consequences for associated microbial and faunal communities (activity, populations, diversity) and thus, indirectly, on plant productivity (Figure 2.3).

FIGURE 2.4 Stimulation of *Eugenia stipitata* (arazá) growth and root mycorrhizal colonization 120 days after inoculating tree nursery bags (filled with 2 parts soil and 1 part composted sawdust) with five (0.35 g total wet weight) or ten (0.7 g) individuals of the pantropical geophagous endogeic earthworm species *P. corethrurus*. (Ydrago 1994; Photograph P. Lavelle.)

Dispersal of mycorrhizal propagules (hyphae, infected root fragments, spores) has been reported by various authors (McIlveen and Cole 1976; Rabatin and Stinner 1988; Ponge 1991; Reddell and Spain 1991a; Gange 1993; Lee et al. 1996; Cavenden et al. 2003), and although some hyphae and spores may be digested, many are still infective after passage through the earthworm gut (Reddell and Spain 1991a; Gange 1993). Mycorrhizal dispersal and deposition of earthworm casts in the rhizosphere may benefit root colonization by fungi, aid plant establishment in early successional stages, and contribute to the heterogeneous nature of mycorrhizal distribution in soil communities (Gange 1993). For example, the pantropical geophagous endogeic earthworm species *P. corethrurus* increased colonization of roots by arbuscular mycorrhizae in various tropical tree seedlings (Ydrogo et al. 1994; Figure 2.4) and a pasture grass (Brown et al. 2000), also increasing plant biomass on several occasions. The actinomycete *Frankia* and ectomycorrhizae were also shown to be dispersed by *P. corethrurus* (Reddell and Spain 1991b; Reddell et al. unpublished), although the effects of this on plant productivity are little known. Nevertheless, soil bioturbation and feeding in the rhizosphere by earthworms may break up extramatrical hyphae and the hartig net, thereby reducing root colonization by these root symbionts, hence providing potential benefits to the plants (Pattinson et al. 1997; Brown et al. 2000; Tuffen et al. 2002).

Plant growth-promoting rhizobacteria (PGPR) such as *Enterobacter cloacae*, *Azotobacter*, *Azospirillum*, *Acinetobacter*, *Bacillus,* and *Pseudomonas* spp. may also be dispersed and their populations or activity increased in the drilosphere (Bhat et al. 1960; Kozlovskaya and Zdhannikhova 1961; Kozlovskaya and Zaguralskaya 1966; Bhatnagar 1975; Loquet et al. 1977; Hand and Hayes 1983; Savalgi and Savalgi 1991; Pederson and Hendriksen 1993). The metabolites released by these microorganisms may be particularly important to the potential plant responses (mechanism 3). Dispersal of these and other microorganisms such as biocontrol bacteria (e.g., *Pseudomonas corrugata*) and fungi (e.g., *Gliocladium virens*, *Trichoderma harzianum*) that colonize the rhizosphere and prevent root diseases needs further investigation. The dispersal of various symbiotic N_2-fixing rhizobacteria that nodulate legume roots (e.g., *Rhizobium trifolii* in clover; Doube et al. 1994a) also needs further research (Stephens et al. 1994e; Stephens and Davoren 1994; Singer et al. 1999). These microorganisms all have an inability to spread actively and rapidly through the soil and colonize plant roots extensively, so earthworms may act as important dispersal vectors for them (Rouelle 1983; Stephens et al. 1993b; Doube et al. 1994b).

Populations and activity of several groups of beneficial soil organisms important in plant litter decomposition and nutrient mineralization processes in soils (e.g., microfauna, mesofauna, and macroinvertebrates) may be affected by earthworms (Brown 1995). For instance, protozoa may be part of earthworm nutrition (Miles 1963; Flack and Hartenstein 1984; Bonkowski and Schaefer 1997), but many protozoan cysts can survive passage through the earthworm gut and can hatch, become more active, and reproduce rapidly in earthworm casts and earthworm-worked soils (Shaw and Pawluk 1986; Barois 1987; Winding et al. 1997; Binet et al. 1998).

Earthworm casts may benefit bacteriophagic nematode populations preferentially over those of other nematode trophic groups (Roessner 1981, 1986; Senapati 1992), but the total numbers of free-living nematodes in earthworm-worked soils may be reduced (e.g., Alphei et al. 1996; Dominguez et al. 2003) or increased (Winding et al. 1997), depending on the situation. Populations of other organisms, such as enchytraeids and various micro- and macroarthropods, may also be increased (e.g., in anecic earthworm middens) or decreased because of changes in microbial populations and food resources in earthworm-worked soils (Brown 1995). However, most of the consequences to plant growth of changes in the populations and activity of micro and macroinvertebrates in earthworm middens, castings, and earthworm-worked soils are unknown and deserve much more attention.

2. Changes in Populations and Impacts of Plant Pests, Parasites, and Pathogens

As with beneficial microorganisms, earthworm feeding, burrowing, casting, and dispersing activities can alter the distribution of populations of plant pathogens such as viruses, bacteria, fungi, parasitic nematodes, or insect pests in soils. Furthermore, by making plants more or less susceptible to these pests, parasites, and pathogens, earthworms can affect root health (Brown 1995). These relationships are illustrated in a modified version of the classic "plant-disease triangle" (Figure 2.3) in which plant root growth and development are shown as a function of the interactions between a favorable environment for both roots and pathogens and the presence or activity of "virulent" of "infective" plant pathogens. The result of these interactions (i.e., plant health status) may therefore be influenced directly or indirectly by earthworm activities.

Earthworms are known to transport and consume a wide variety of plant pathogenic fungi and bacteria and plant-parasitic nematodes (Brown 1995). If populations of these organisms are reduced either directly by transit through the earthworm gut or indirectly via changes in the soil environment, then the indirect consequences to plant growth may be important, particularly when disease or nematode pressure is reducing crop yields. The role of earthworms as vectors of plant diseases, parasites, and pests depends on the type of organism and species ingested, the amount of soil and inoculum ingested, the extent of beneficial or antagonistic intestinal secretions, the number of organisms digested in the earthworm gut, the amount of organisms deposited in casts, the infectivity of surviving organisms deposited in casts, the feeding and casting behavior of the earthworms (dependent on the earthworm species and ecological category), and the mobility and behavior of the earthworm.

Potential Role of Earthworms in the Reduction of Plant Disease and Pest Problems

Several reports of beneficial results to plants of earthworm-induced reductions of plant pathogens are known. For instance, work in the Soil Ecology Laboratory at The Ohio State University has shown that vermicomposts can suppress plant diseases such as *Pythium* and *Rhizoctonia* (Chaoui et al. 2002, 2003) in the greenhouse and *Verticillium* in the field. When cabbages were grown in the presence of the earthworm *Pheretima hilgendorfi*, Nakamura et al. (1995) observed lower incidence of club-root disease (*Plasmodiophora brassicae*) damage in the seedlings. They attributed this decrease to the physical, chemical, and biological changes in the soil environment because of earthworm activity, reinforced by possible consumption of the pathogens by the earthworms (Nakamura 1996).

In Australia, several complementary studies (Stephens et al. 1994a,b,c,e,f,g; Stephens and Davoren 1997) reported that the earthworms *Aporrectodea rosea* and *Aporrectodea trapezoides* could increase yields of wheat, ryegrass, and subterranean clover under greenhouse and field conditions by decreasing the incidence of *Rhizoctonia solani* (bare patch disease). Furthermore, wheat yields were also increased by these earthworms through a reduction in incidence of *Gauemannomyces graminis* var. *tritici* (take-all disease); *A. trapezoides* appeared to be more effective in disease suppression, probably because of higher feeding and casting levels compared with *A. rosea*.

Although the exact mechanisms by which earthworms influence root diseases (including take-all) remain unknown, Clapperton et al. (2001) suggested that they are most probably mediated through changes in the soil microbial community, possibly via stimulation of biocontrol agents, antagonists, or microbial competition with the pathogens. Various other indirect mechanisms have also been proposed, such as acceleration of residue decomposition, burial of infected litter, increased soil porosity, and greater availability of plant nutrients in earthworm-worked soils. For instance, in various fruit-tree orchards, the burial of 12 fungal pathogens overwintering in the surface leaf litter (including *Venturia inaequalis*, the causal agent of apple scab) by the anecic earthworm species *L. terrestris* (Raw 1962) reduced their survival and ability to disperse, colonize, and infect the apple trees the following spring (Hirst and Stedman 1962; Niklas and Kennel 1981; Laing et al. 1986; Kennel 1990).

Decreases in plant parasitic nematode populations by earthworm activity have also been documented for various (tropical and temperate) earthworm and nematode species combinations (Dash et al. 1980; Roessner 1981, 1986; Senapati 1992; Boyer 1998). For instance, Boyer (1998) observed a reduction of *Pratylenchus zeae* populations in small pots (200 g soil) sown with rice and containing the earthworm species *P. corethrurus*. However, the effects of the earthworms on plant shoot and root growth was negative. Conversely, Boyer et al. (1999) observed significantly greater maize productivity and decreased *Pratylenchus vulnus* populations on maize roots when maize was undersown with the legume birdsfoot trefoil, and earthworms (*Amynthas corticis*) were introduced into the field. Yeates (1980, 1981) also reported greater plant productivity and lower populations of nematodes, including some plant parasitic species in pastures inoculated with lumbricid earthworms in New Zealand. Reduction of plant parasitic nematode populations in the field have also been observed after application of vermicomposts (Arancon et al. 2002, 2004a,b).

Earthworm-induced decreases in nematode populations may be caused by direct ingestion and digestion of nematodes (Dash et al. 1980; Boyer 1998; Dominguez et al. 2003) or the release of fluids (enzymes, etc.), which affect the fertility, viability, and germination of cysts present in earthworm-worked soils and casts (Ellenby 1945; Roessner 1981; Boyer 1998), or they may be caused indirectly through modifications by earthworms of soil structure, water regimes, and nutrient cycling processes (Yeates 1981). Edwards and Fletcher (1988) and Manku (1980) have also suggested that earthworms may spread nematode-trapping fungi and nematode cyst pathogens of major importance in controlling nematode populations. Nematodes that pass unharmed through the earthworm gut or are able to take advantage of or adapt to earthworm-induced changes in soil properties and processes may be dispersed by earthworms. In the case of plant parasitic species, this could lead to potential problems, but for entomopathogenic nematodes commonly used in insect pest biocontrol, this may be beneficial (Shapiro et al. 1993).

Several studies have demonstrated the potential effects of earthworms in reducing plant-pest incidence and damage. Boyer et al. (1999) reported fewer maize plants infested with the stalk borer *Sesamia calamistis* when the earthworm *A. corticis* was inoculated into field soils. The percentages of fertile maize plants infested by the borer were 75% without earthworms and 55% in soils with earthworms, although the total aboveground biomass of the two treatments did not differ significantly. In another study, *L. terrestris* was shown to reduce the numbers of leaf miners (*Phyllonorycta blancardella*) and leaf suckers (*Psylla piri*) overwintering in leaf litter of fruit-tree orchards by promoting leaf burial and decomposition (Laing et al. 1986; Kennel 1990), thus reducing their potential to damage the orchard trees. However, leaf-litter burial also reduces populations of the natural biocontrol agents (brachonid wasps) of these insects (Laing et al. 1986).

Potential Role of Earthworms in Increasing Plant Disease or Pest Problems

Several species of plant pathogenic fungi have been found in earthworm casts (Hutchinson and Kamel 1956; Hoffmann and Purdy 1964; Thornton 1970; Melouk and Horner 1976; Toyota and Kimura 1994), and plant parasitic nematodes may survive passage through the earthworm gut (Ellenby 1945; Russom et al. 1993). However, there are relatively few data available on the potential negative effects that earthworm-induced microbial dispersal may have on incidence of plant diseases (of fungal or bacterial origin) or nematode damage.

Increased dispersal of a plant pathogenic fungus, *Syntrichium endobioticum,* the causal agent of wart disease of potato, by *L. terrestris* and various other (probably lumbricid) earthworms was reported by Hampson and Coombs (1989), resulting in increased infection of several potato plants. Similarly, Melouk and Horner (1976) reported infection of mint seedlings by verticillium wilt (*Verticillium dahliae*) when the plants were grown with earthworm casts that contained viable spores of these pathogens.

Dispersal of plant parasitic nematodes by earthworms was reported by Ellenby (1945) and Russom et al. (1993), but the potential of this for increased damage to plant roots was not evaluated. Casts of the Nigerian earthworm species *Agrotoreutus nyongii* had larger and more diverse populations of parasitic nematodes than did the surrounding soil (Russom et al. 1993). Casts of *Aporrectodea longa* contained nematode cysts with greater fertility, viability, and germination potential than those in surrounding soil (Ellenby 1945). Ilieva-Makulec and Makulec (2002) reported an increase in plant parasitic nematode populations in soil cores inoculated with *Lumbricus rubellus* after 60 and 90 days, but no negative effects on growth of grass roots were observed.

The interactions between earthworms and plant insect pests still remain poorly explored. Kirk (1981) reported large numbers of the northern maize rootworm (*Diabrotica*: Coleoptera) eggs in earthworm burrows and suggested that this may contribute to the spottiness of rootworm distribution and damage often observed in maize fields. More recently, Wurst and Jones (2003) and Scheu et al. (1999) showed effects of lumbricid earthworms (*Aporrectodea* sp.) on increased numbers of leaf sap sucking aphids (*Myzus persicae*) and their offspring.

3. Earthworms and Plant Growth-Regulating and Growth-Influencing Substances

The first suggestion that earthworms might produce plant growth regulators (PGRs) was by Gavrilov (1963). This was supported by the first report of the presence of PGR substances in the tissues of *Aporrectodea caliginosa, L. rubellus,* and *Eisenia fetida* by Nielson (1965), who extracted indole substances from earthworms and reported increases in the growth of peas because of them. He also extracted a substance that stimulated plant growth from *A. longa, L. terrestris,* and *Dendrobaena rubidus,* but his experiments did not exclude the possibility that the PGR substances he obtained came from microorganisms living in the earthworm guts and tissues.

The presence of PGR substances in the tissues of *A. caliginosa, L. rubellus,* and *E. fetida* was confirmed by Nielson (1965), who isolated indole substances from whole earthworm tissues. This was confirmed for *A. rosea* and *A. caliginosa* by Nardi et al. (1988). More recently, El Harti et al. (2001a,b) isolated indole acetic acid (IAA)-like substances from gross extracts of tissues and feces of *L. terrestris*. These substances stimulated rhizogenesis and enhanced root growth of *Phaseolus vulgaris* (common beans) in a manner very similar to that of IAA.

Graff and Makeschin (1980) tested the effects of substances produced by *L. terrestris, A. caliginosa,* and *E. fetida* on the dry matter production of ryegrass. They added liquid eluates from pots containing earthworms to pots containing no earthworms and concluded that PGI substances were released into the soil by all three species, but the authors did not speculate further on the nature of these substances.

Earthworms may liberate PGRs or PGIs themselves (Atlavinyte and Daciulyte 1969; El Harti et al. 2001a,b), or their production may be mediated by interactions with microorganisms in the drilosphere in a process that is not fully understood.

It is clear that microorganisms are capable of producing PGR and PGI substances such as hormones, auxins, gibberellins, cytokinins, ethylene, and abscisic acid (Arshad and Frankenberger 1993; Frankenberger and Arshad 1995). Many microorganisms commonly found in the rhizosphere can produce PGR substances.

Krishnamoorthy and Vajranabhaiah (1986) showed, in field experiments involving large earthworm populations, that seven species of earthworms could promote the production of cytokinins and auxins in soils. They also demonstrated significant positive correlations ($r = 0.97$) between earthworm populations and the levels of cytokinins and auxins present in ten different field soils and concluded that earthworm activity was linked strongly with PGR production. They reported that auxins and cytokinins produced through earthworm activity could persist in soils for up to 10 weeks although degraded in a few days if exposed to sunlight. For a more in-depth discussion of the role of earthworms in producing PGR substances through promoting populations and activity of microorganisms, see Chapter 18 this volume.

4. Root Abrasion and Ingestion of Living Plant Parts by Earthworms

Because earthworms burrow and cast near or within the rhizosphere, the soil disturbance and abrasion may affect plant roots negatively, particularly the small, fine roots or the root tips, which have not yet produced a protective cortex and are more susceptible to physical disturbance. This abrasion may also break up the mycorrhizal hyphal network (mechanism 1), decreasing root colonization and the many potential benefits of these fungi to plants.

Several authors have reported damage by earthworms to rice crops in Southeast Asia (Stephenson 1930; Otanes and Sison 1947; Chen and Liu 1963; Inoue and Kondo 1962, cited in Lee 1985; Pradhan 1986; Barrion and Litsinger 1996), which may be caused by root abrasion if the earthworm population is large, although other factors such as excessive casting on the rice tillers, soil loosening, water drainage, and increased water turbidity have been proposed as the main factors responsible for the damage (Kale et al. 1989; Stevens and Warren 2000).

Some authors have proposed that earthworms (mainly lumbricid species) can feed on living plant roots (Stephenson 1930; Carpenter 1985; Baylis et al. 1986; Sackville-Hamilton and Cherret 1991; Cortez and Bouché 1992; Gunn and Cherrett 1993; Hameed et al. 1993), although only in a few instances was this associated with decreased plant productivity. This phenomenon does not seem to be widespread because studies on the crop, gizzard, or gut contents of over 30 earthworm species revealed that roots form a very minor component of the ingested materials in most species (see Brown et al. 1999). The extent of root feeding by earthworms, the identification of the species involved, the conditions encouraging this to happen, and its possible damage to plant productivity still need further evaluation.

Other negative effects, probably mostly caused by anecic earthworm species, involve the burial of living plant leaves (Darwin 1881; Zicsi 1954) or damage to germinating seedlings (Walton 1928; Olson 1929; Trifonov 1957; Patel and Patel 1959; Lee 1985; Shumway and Koide 1994). For instance, Darwin (1881) noted that the end of a *Triticum repens* leaf, still attached to the plant, had been pulled into the burrow of an anecic earthworm species and had dried and turned dark brown; although the rest of the leaf remained fresh and green. He attributed this to the fluids secreted by the earthworm mouth, which rapidly stained the plant tissues, causing cortical cell discoloration and disintegration. Edwards and Bohlen (1996) reported that *L. terrestris* destroyed a large part of a lettuce crop when soil containing large numbers of the earthworms was taken into a greenhouse.

Summarizing the available results on earthworms as pests of crops, Lee (1985) and Edwards and Bohlen (1996) stated that, although earthworms occasionally damage healthy plants, more commonly they attack very tender or moribund plants already damaged by some other mechanism, and that there is no reason to regard earthworms as serious pests of plants. However, there are clearly some instances when earthworms can damage plants either directly or indirectly (Edwards and Bohlen, 1996; Brown et al. 1999). Care should be taken to prevent these situations from occurring whenever possible.

5. Interactions of Earthworms with Seeds

From the moment a seed germinates, it comes into contact with the soil, a physicochemical environment and a wide range of soil organisms, all of which may have variable degrees of influence on its growth and success as a plant. Moreover, even before a seed germinates, some of these factors may already be influencing its fate. For example, some earthworm species (e.g., *L. terrestris*) appear to show a preference for ingesting the seeds of certain plant species, depending on their size, shape, texture, and taste (Piearce et al. 1994; Shumway and Koide 1994). Observations made more than a century ago by Hensen (1877) and Darwin (1881) demonstrated the potential importance of surface-feeding anecic and endogeic earthworms in ingesting, transporting, and distributing seeds in the soil. Moreover, seed germination may be slower or more rapid in egested earthworm castings than in surrounding soils (McRill 1974; Atlavinyté and Zimkuviene 1985; Piearce et al. 1994). For example, Grant (1983) and Decaëns et al. (2001) observed lower germination rates and slower germination of the seeds of several weed species in earthworm casts. Furthermore, many seeds are damaged by passage through the earthworm gut, often affecting their germination success or vigor (Grant 1983).

In view of the selective consumption and the digestive processes of earthworms, the preferential germination of different seed species in earthworm-linked structures, the dispersal of seeds through the soil, and the physical-chemical effects of earthworms on the soil environment, it has been suggested that earthworms may influence plant recruitment and the composition of plant communities considerably (Piearce et al. 1994; Willems and Huijsmans 1994). Some authors have suggested that earthworms seem to favor the proportion, and often biomass, of clover in pastures (Stebler et al. 1904; Bates 1933; Hopp and Slater 1948; Nielson 1953; Satchell 1955; Thompson et al. 1994; Nuutinen et al. 1998). Positive associations of earthworm casts with the frequency and distribution of the weeds *Plantago* spp., *Trifolium,* and *Ranunculus* were also observed in meadows in the U.K. (Bates 1933; Piearce et al. 1994).

The effect of earthworms on the soil weed seed bank, particularly the influence of anecic species that preferentially ingest seeds, should not be underrated. Decäens et al. (2001) estimated that 1 to 13% of the total germinatable soil seed bank of a native savanna and two pastures were deposited in the surface casts of the anecic earthworm species *Martiodrilus carimaguensis* from the Colombian Eastern Plains. However, if there is preferential ingestion of weed seeds and differential growth of weed seedlings in earthworm casts or earthworm-worked soils (Piearce et al. 1994), this may eventually increase the level of weed infestations of crop fields or grasslands, potentially increasing competition of weeds with the crops or desired plants (Edwards and Bohlen 1996; Stinner et al. 1997).

6. Changes in Soil Structure Caused by Earthworms

The activities of earthworms in the physical "engineering" of soils can modify a wide range of chemical and biological properties and processes influenced by soil structure (see Chapters 10 and 11 this volume). Earthworm pedoturbation of soils can change soil structure by affecting aggregation (mostly by casting) and porosity to water and air (by burrowing and casting), thereby affecting soil physical functions important in root growth and penetration, such as aeration, gaseous exchange, water infiltration. and water-holding capacity (Figure 2.5). Earthworm burrowing creates mostly macropores (pores larger than 30 μm), and casting affects mainly the meso- and microporosity in

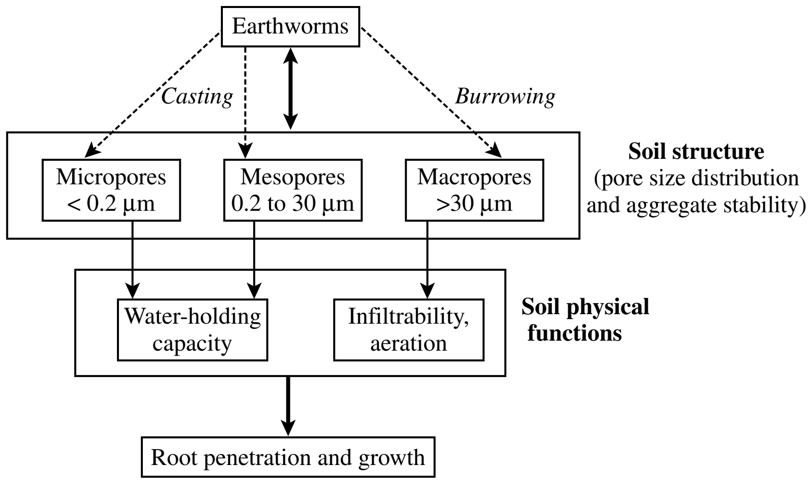

FIGURE 2.5 Diagrammatic representation of ways by which earthworms can affect plant growth via physical changes in the soil environment by burrowing and casting. (Expanded from Syers and Springett, 1983.)

soils (pores smaller than 30 μm) and the stability of soil aggregates. However, earthworm species differ greatly in their ability to modify soil structure, depending on their ecological strategies and behavior. Plants also differ tremendously in their nutrient and water requirements and rooting strategies. The minimum pore size for effective penetration of the roots of most crop species is approximately 200 μm (Wiersum 1957), so many roots become concentrated in macropores, although some root hairs may penetrate mesopores 5 to 20 μm wide (Hofer 1996).

Earthworm Casts

Earthworms produce basically four types of casts (Lee 1985; Lavelle 1988; Edwards and Bohlen 1996):

1. Globular, consisting of coalescent round or flattened units, generally produced by the larger earthworm species (anecic and endogeic species).
2. Pastelike slurries, mainly produced by endogeic or anecic species and excreted as single masses of soil without a distinct shape, but that take on irregular shapes once dried.
3. Tall vertical heaps or columns of variable shapes, usually deposited on the soil surface where they are most visible by endogeic or anecic species. These are usually created by the sequential deposition of globular casts and, when in tower form, often have a hole in the middle (Darwin 1881; Edwards and Bohlen 1996).
4. Granular, typically in the form of pellets, produced mainly by smaller earthworm species (epigeic, small endogeic, and some anecic species) and distributed on or beneath the soil surface.

Casts from different earthworm species can have very different effects on soil structure. The first three types of casts tend to be larger, heavier, and more compact and are usually produced by "compacting" earthworm species; the granular casts are normally smaller, lighter, and looser and break down more easily, and are mostly produced by "decompacting" earthworm species (Blanchart et al. 1997, 1999). Often, the casts of compacting species are consumed by decompacting species, a process that breaks up the larger aggregates into smaller ones, helping regulate overall soil aggregation (Blanchart et al. 1997; Decäens and Rossi 2001) and liberate nutrients that were protected in the casts for plant roots (see Figure 2.6).

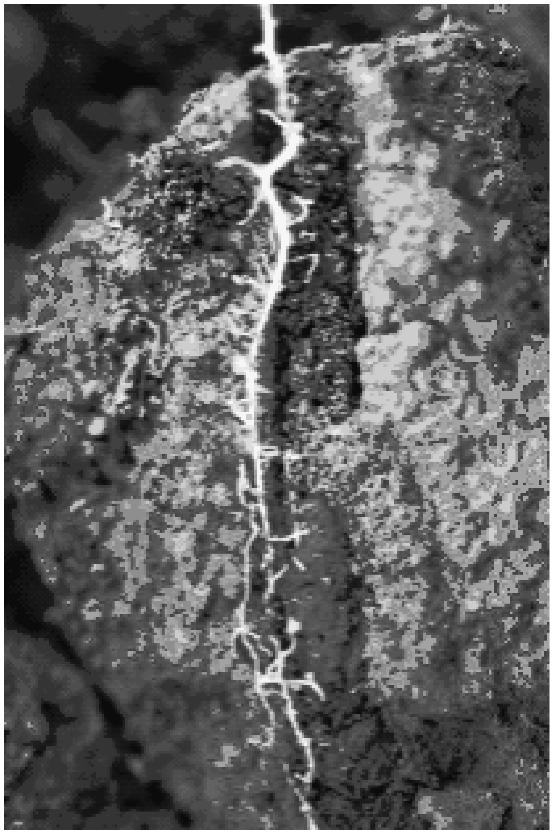

FIGURE 2.6 Pasture root growth into burrows and casting of earthworms from native savannas and pastures planted on highly weathered soils of the Colombian Eastern Plains. Note the two different types of structures: globular "compact" castings created by *M. carimaguensis* and their breakdown by smaller polyhumic endogeic "decompacting" earthworm species and mesofauna. (Photo P. Lavelle.)

The inner porosity of earthworm casts is also very variable depending on the earthworm species producing them, particularly the earthworm's anterior and posterior internal morphology and musculature (Lapied and Rossi 2000). A predominance of mesopores (10 to 20 μm) was reported in the casts of *M. anomala* (Blanchart et al. 1999), whereas pores in the casts of the compacting species *P. corethrurus* were all smaller than 1 μm (Chauvel et al. 1997). Thus, casts are much more important for retaining plant-available water (fresh casts of many species have water contents above 70%) (Blanchart et al. 1999) and nutrients, whereas earthworm burrows are more important for water by-pass flow, infiltration rates, gaseous exchanges, and root penetration and elongation. Subsequently, several authors (Doube et al. 1997; Stockdill 1966; van Rhee 1969) reported increased water use efficiency by crops in soils inoculated with earthworms in both pot and field experiments.

Earthworm casts, once they have undergone a stabilization process still not well understood (Edwards and Shipitalo 1998), become water-stable aggregates, although their stability is very dependent on the soil type, earthworm species, and earthworm feeding habits (Blanchart et al. 1999). Often, an important part (5% or more) of the surface (A) horizon of soils passes annually through earthworm intestines, particularly in tropical regions that are dominated by endogeic species (Lavelle 1988). Under some circumstances, most of the topsoil may be composed of earthworm castings of different ages, sometimes remaining long after the earthworms have disappeared (Buntley and Papendick 1960; Graff 1971b; Pop and Postolache 1987; Lavelle 1988). Thus, because interaggregate spaces are important in soil macroporosity, the physical arrangements of casts, particularly the larger casts containing mostly water-stable macroaggregates (>2 mm diameter), can also have an important effect on the total number of macropores in soils (see Chapter 10 this volume). Furthermore, casting on the soil surface may open new pores in the soil and can even break surface crusts, thereby helping germinating seedlings reach the soil surface (Kladivko et al. 1986).

Compacted soils may also benefit from the activity of decompacting earthworm species (Blanchart et al. 1997, 1999), the incorporation of OM (aggregating agent) by anecic species, and the burrowing strength and stable aggregate formation by endogeic species (Zund et al. 1997; Larink and Schrader 2000). For example, the introduction of various endogeic and deeper-burrowing anecic species of lumbricid earthworms into New Zealand pastures aided the rates of decomposition of accumulated thatch and physical incorporation of lime, fertilizers, and pesticides into the soil, reducing physical, chemical, and biological limitations to root growth and pasture productivity (Stockdill 1982; Springett 1985). However, excessively loose soils or soils with greater proportions of sand that are prone to water stress, may actually benefit from the aggregating action of compacting earthworms.

Not all the effects of earthworms on soil structure help plants to grow better. First, the deposition of fresh earthworm casts on the soil surface and the burial of protective surface litter by anecic earthworm species can expose soil particles to splash erosion (Darwin 1881; Sharpley and Syers 1976; Sharpley et al. 1979; van Hoof 1983; Binet and Le Bayon 1999), promoting their downhill soil movement if the area is sloping. In particular situations and over long time periods, this could reduce the topsoil layer upslope considerably and increase its downslope, as well as change its texture (Nooren et al. 1995) and suitability for plants.

In addition, when soils are prone to compaction and a single earthworm species of the compacting type dominates the community, reaching large populations, biomass, and activity levels, the ultimate effect of the earthworms on plant growth may be negative. Hence, Puttarudriah and Shivashankara-Sastry (1961), Blackemore (1994), Barros et al. (1996, 1998), Chauvel et al. (1999) and Ester and Rozen (2002) all observed increased soil compaction and "clodding" caused by earthworm (*P. corethrurus* and various other species) activities and related the lower soil porosity and water infiltration rates that occurred with decreased plant (radish, carrot, bean, pasture, sorghum, and potato) productivity. Excessive casting on the soil surface and base of plants by lumbricid earthworms in England caused difficulties in harvesting cereals and hay (Stephenson 1957; Edwards and Bohlen 1996), and large amounts of casts on the soil surface of grazed pastures led to "poaching" from cattle trampling, decreasing grass growth in the Netherlands (Hoogerkamp 1984) and New Zealand (Lee 1959).

Earthworm Burrows

Macropores usually represent only a very small part of the total soil porosity (particularly in clayey soils), yet they are very important in hydraulic conductivity and water infiltration rates when connected with the soil surface and in increasing aeration (Kretzschmar 1998, see Chapter 11, this volume). The positive effects of earthworms on water infiltration may help decrease runoff rates (Roth and Joschko 1991), thereby allowing more water to enter the soil and reducing overall erosion (Hopp 1946, 1973; Sharpley et al. 1979), as well as increasing the potential for water storage in the soil. Thus, the effect of earthworms on soil porosity and infiltration, as well as on organic matter breakdown, has been associated consistently with increased yields in New Zealand pastures (Stockdill 1959, 1982) and reclaimed Dutch polders (e.g., van de Westeringh 1972; Hoogerkamp 1984) and with greater hay and bean yields in large container experiments (Hopp and Slater 1948, 1949), although the interactions with incorporated or surface OM (another aggregating agent) are also likely to be implicated (Cogle et al. 1994) in some responses observed by these authors.

Earthworm burrows can serve as preferential pathways for root elongation (Ehlers 1975; Edwards and Lofty 1980; Kirkham 1981; Ehlers et al. 1983; Wang et al. 1986; Kladivko and Timmenga 1990; Hirth et al. 1997; Jiménez 1999), especially in compacted zones found typically in deeper soil layers. In open, abandoned earthworm burrows, the greater aeration and the small amounts of nutrients associated with the earthworm burrow walls can benefit root growth (Graff 1971a), and cast-filled earthworm burrows usually have large quantities of plant-available nutrients stored in the casts (mechanism 7). The distribution of roots in soil is often related closely to the zones of earthworm activity (Edwards and Lofty 1978, 1980), and root densities can be increased significantly by earthworm activities. In newly reclaimed polders inoculated with earthworms and planted with fruit trees in the Netherlands, van Rhee (1977) reported significantly greater root densities in the earthworm-inoculated sites but no effects on fruit production. Conversely, in a pot experiment in Mexico that compared pots inoculated with earthworms those with no earthworms, Brown (1999) observed significantly greater root densities, as well as more root and shoot biomass, but no increase in productivity of beans in the presence of *Polypheretima elongata*. The earthworm burrows were commonly filled with roots, and the root distribution throughout these pots showed a much more even (homogeneous) distribution, a factor considered to confer greater plant resistance to environmental stresses (Smucker 1993).

The proportion of roots found in deep earthworm burrows (e.g., in the B horizons) compared with those in the soil matrix can be very high (Kirkham 1981; Logsdon and Linden 1992), and these roots may be important in maintaining plant water dynamics. However, estimates of the proportion of roots in earthworm burrows may be exaggerated because roots in earthworm burrows are more easily observed, whereas the rest of the root system may be concealed in the soil matrix (Logsdon and Linden 1992; Kretzschmar 1998). A three-dimensional estimation of interactions between roots and earthworm burrows is still not available (Kretzschmar 1998), and considerable efforts need to be made to understand these interactions and the mechanisms that control them (Tisdall and McKenzie 1995).

Thus, it is a combination of the composition (ecological category, species) of the earthworm community present at a given location, the placement of their casts (surface, belowground, deep in soil, near roots, etc.), the quantities of casts deposited and their age, and the amount, type, depth, and openness of the earthworm burrows produced, the interaction of microorganisms with earthworm structures, the physicochemical soil environment, and land management that determine the ultimate effects of earthworms on soil structure and the rooting environment.

7. Changes in Nutrient Spatiotemporal Availability Caused by Earthworms

The availability of many essential plant nutrients has been shown to increase in structures produced by various earthworm species, especially in their casts (e.g., Mulongoy and Bedoret 1989; Barois et al. 1999) and burrow walls. This greater nutrient availability is mainly a result of the selective feeding of earthworms on regions of the soil rich in organic matter, clay, and nutrients (Barois et al. 1999; Cortez and Hameed 2001), gut-associated processes, and cast-associated processes (Figure 2.7), together with some earthworm burrow-associated processes (especially with anecic earthworm species; Devliegher and Verstraete 1997; Brussaard 1999). Such processes include the grinding action of the gizzard, the priming of microbial activity in the gut, and the greater populations and activity of microorganisms in the earthworm casts and burrows (Figure 2.7), that induce chemical changes in earthworm-worked soil (e.g., Lee 1985; Edwards and Bohlen 1996).

These nutrient enrichment processes (Devliegher and Verstraete 1995; Brussaard 1999) differ greatly according to the earthworm species involved, their ecological categories, and the feeding habits, particularly the amounts of plant litter they ingest. The type and placement of the earthworm casts are also important, affecting the spatiotemporal availability of the nutrients they contain (Figure 2.7). Surface earthworm casts dry out much more quickly, harden, and, if compact, are likely to limit root penetration, thereby reducing the ability of plant roots to obtain the nutrients stored inside the casts (nutrient protection) until they are broken down (Figure 2.6 and Figure 2.7). Belowground earthworm casts remain fresh and moist for much longer periods of time and, if they are of the decompact types (with more meso- and macropores and macroaggregates), allow roots to penetrate more easily (Figure 2.6) and profit from the greater nutrient contents available to plants.