BELOW-GROUND HERBIVORY IN NATURAL COMMUNITIES: A REVIEW EMPHASIZING FOSSORIAL ANIMALS

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ABSTRACT

Roots, bulbs, corms, and other below-ground organs are almost universally present in communities containing vascular plants. A large and taxonomically diverse group of herbivores uses these below-ground plant parts as its sole or primary source of food. Important within this group are plant-parasitic nematodes and several fossorial taxa that affect plants through their soil-disturbing activities as well as by consuming plant tissues. The fossorial taxa are probably best exemplified by fossorial rodents, which are distributed on all continents except Australia. All other fossorial herbivores are insects. The impact of below-ground herbivory on individual plant fitness will depend upon the extent to which, and under what circumstances, the consumption of plant tissue disrupts one or more of the six functions of below-ground plant parts. Below-ground herbivory is probably more often chronic than acute. Indirect evidence suggests that plants have responded evolutionarily to herbivory by enhancing the functional capacities of below-ground organs, thus developing a degree of tolerance, and by producing compounds that serve as feeding deterrents. Many plant species respond to the removal of root tissues by increasing the growth rate of the remaining roots and initiating new roots. Soil movement and mixing by fossorial rodents influence the environment of other below-ground herbivores as well as that of plants and plant propagules. The relationships among the various groups of below-ground herbivores, and between below-ground herbivores and plants, are at best poorly known, yet they appear to have major roles in determining the structure and regulating the functioning of natural communities.

INTRODUCTION

AN IMMENSE literature has developed concerning the topic of plant/herbivore interactions, prompting at least one attempt at a general synthesis (Crawley, 1983). Nevertheless, an attempt to find even qualitative statements concerning the impacts of below-ground herbivory on natural plant populations suggests that this particular sub-discipline has been relatively ignored by ecologists. Widely used textbooks seldom devote more than a paragraph or two to below-ground herbivory, thereby suggesting it is either unimportant or insufficiently different from above-ground herbivory to warrant individual attention (cf. Allee et al., 1949; Ashby, 1969; Odum, 1971; Krebs, 1985). Monographs on root systems seldom mention the topic (e.g., Russell, 1977). Crawley (1983) distills the information on root feeding and plant fecundity to a single page.

The paucity of research on below-ground herbivory in natural systems probably stems from the long-term, labor-intensive research commitment required for most studies. Research during and since the International Biological Program, however, has shown that such continued neglect may seriously hinder our ability to elucidate phenomena at both community and ecosystem levels. Data from diverse ecosystems indicate that more than 50 per cent of net primary production is commonly allocated to below-ground plant parts (Coleman, 1976; Fogel, 1985), and values for particular plant species approach 90 per cent.

Below-ground tissues, developed in some form in nearly all terrestrial vascular species (Bold, 1973:478), are a resource to which consumers from diverse taxa have become committed through evolution.

This review examines the agricultural, botanical, and zoological literature in order to address three sets of questions. First, what are the consequences of the removal of below-ground plant parts on plant fitness? Does removal of root tissue always lead to a reduction in plant fitness? Are nutrients or assimilates stored in excess of future needs? Might at least some green plants indeed be "pathological" over-producers of carbohydrates (Harper, 1977:656), the excesses of which are channeled into below-ground organs? Second, what generalizations can be made regarding the magnitude and variability of below-ground herbivory in natural communities? How does the amount of biomass removed by below-ground herbivores compare to that taken by above-ground consumers? Finally, what are the implications of below-ground herbivory with respect to community and ecosystem structure and functioning? Do below-ground herbivores limit the distribution or abundance of particular species? Are some communities or ecosystems shaped by below-ground herbivory to a greater extent than others?

Ideally, this review would consider all of the potentially competing organisms that remove living below-ground tissue from plants—i.e., the ecological guild (*sensu* MacMahon et al., 1981) centered about below-ground plant parts. In dealing with the primary literature, however, I have emphasized fossorial herbivores—animals whose physical activities in acquiring both food and shelter below ground contribute to the formation or modification of the soil. Information on the nonfossorial root-feeding nematodes is largely abstracted from existing comprehensive reviews (Wallace, 1973; Norton, 1978; MacDonald, 1979; Gommers, 1981; Nicholas, 1984; and Nickle, 1984). I ignore those soil organisms, such as the lumbricids (earthworms), that may have a major impact on soil formation but are primarily saprotrophic (see Swift, Heal, and Anderson, 1979), as well as fungi, plants, and microorganisms that parasitize plants (see Dinoor and Eshed, 1984).

THE RESOURCE
Below-Ground Plant Structures

Below-ground plant parts, which include both roots and stems, are diverse in function and form. Basic functions are (1) mineral and water absorption and conduction; (2) mechanical support for the aerial portion of the plant; (3) synthesis of products necessary for normal growth and development of the shoot; (4) storage of metabolites and photosynthates; (5) physical protection of dormant meristematic tissue; and (6) vegetative propagation (Steeves and Sussex, 1972; Torrey, 1976; Salisbury and Ross, 1978). Structures not primarily associated with nutrient uptake or mechanical support (modified stems: rhizomes, tubers, corms, bulbs, and caudex) are hypothesized to be adaptations to unfavorable (either dry or cold) abiotic conditions during some part of the year (Raunkiaer, 1934) or to above-ground herbivory (Whigham, 1984) or other catastrophic events (Bloom, Chapin, and Mooney, 1985).

In most dicotyledons, the primary root develops from the radicle and remains functional for the life of the plant. In monocotyledons, the radicle and associated pairs of embryonic roots may have no permanent function and often disappear as they are replaced by roots originating from the bases of the shoots (cladogenous roots, also termed crown, nodal, or adventitious roots—e.g., Jordan, McCrary, and Miller, 1979). In either taxon, new roots may arise from dormant primordia, located on shoots as well as on roots, when the existing root system is placed under stress. Adventitious roots [by definition, roots arising from the shoot (Cannon, 1949) but most often from stems, stolons, rhizomes, bulbs and corms] may appear and disappear rapidly in response to variations in environmental conditions.

Distribution of Species Featuring Below-Ground Storage Organs

Although most flowering plants, including some annuals (Chiariello and Roughgarden, 1984), probably use roots or below-ground stems for storing assimilated material, prominent storage organs are most commonly found among species in highly seasonal environments and outside the tropics. Runkiaer (1934:428) reported that geophytes, which usually have

well-developed subterranean storage organs, made up 3 per cent of the flora on several tropical Caribbean islands, compared to 13 per cent on arctic Spitzbergen Island. Richards (1964:9) produced values of 0 per cent for a British Guianan rain forest, and 23 per cent for a deciduous woodland in Germany. Whitaker (1975:64) estimated that 6 per cent of the earth's vascular plants are geophytes. Tropical plants featuring below-ground storage tissues have become major food sources — e.g., yams (*Dioscorea* sp.) and sweet potatoes (*Ipomoea batatas*), which are both vines featuring tuberous roots, and the starchy-rooted shrub, cassava (*Manihot* sp.), from which tapioca is produced. Root and tuber crops comprise more than half of the food production in tropical and semitropical countries, compared to 25 to 35 per cent for more temperate areas (Yamaguchi, 1983).

Nutritional Value of Below-Ground Plant Tissues

The nutritional value of below-ground plant tissues can differ markedly from those of above-ground tissues. The root system is the major site of mineral acquisition, and assimilated materials may be concentrated for storage in below-ground structures. The average concentrations of soluble carbohydrates and minerals in below-ground tissues of temperate zone herbs may be higher, lower, or equal to those in above-ground tissues at the point of peak above-ground biomass, depending upon species (Peterson and Rolfe, 1982). Individual plants typically show shifts in nutrient concentrations as development proceeds. Abrahamson and Caswell (1982) showed that, although biomass and energy content of plant parts were significantly positively correlated at flowering, biomass and elemental mineral concentrations were not, nor were intrapopulation trends in patterns of mineral allocation reflected in patterns of biomass allocation. Thus, estimating nutrient intake of below-ground herbivores requires species-specific and population-specific information on nutritional quality as well as on digestibility of below-ground plant parts.

The mineral concentrations in below-ground plant parts may make them a highly preferred food. For example, below-ground plant parts typically have higher concentrations of sodium than do above-ground tissues, probably because of the sequestering of sodium

ions absorbed by roots (Gauch, 1972:191). Although most plants do not require sodium, all animals do, and a seasonal attraction to sources of sodium has been observed in several species of mammalian herbivores. The requirement for dietary sodium is exacerbated by unavoidable and excessive elimination of the ion resulting from consumption of foliage high in potassium (Weeks and Kirkpatrick, 1978). These authors found ratios of K:Na exceeding 300 for most above-ground foods and diets in spring, with Na values commonly less than 100 ppm. In contrast, *Trillium* rhizomes contain on average 210 ppm Na, and show a much more favorable K:Na ratio of 49.

Nitrogen is an important nutrient for both plants and animals; the nitrogen content of leaves has been suggested to represent a trade-off between photosynthetic capacity and attractiveness to above-ground herbivores (Mooney and Gulmon, 1982). Leaf nitrogen is primarily invested in photosynthetic machinery (Chapin, Bloom, Field, and Waring, 1987), suggesting that below-ground plant tissue should be relatively low in nitrogen, except when storage is involved. In the latter case, values may be relatively high. Stuebe and Andersen (1985) found the mass-specific nitrogen content of below-ground storage organs to vary from 3.3 to 17.6 mg N/g of ash-free dry matter (DM) for six species of dormant montane herbs, although the energy content varied by only 15 per cent. The average N content (9.4 mg N/g DM) was higher than any values tabulated for other plant parts by Mattson (1980; calculated by assuming 10% ash).

Storage of assimilate in below-ground tissue can result in large food packages featuring high mass-specific energy content. Nevertheless, energy content of below-ground tissues may or may not be greater than that of above-ground tissues, even when below-ground storage organs are involved. It is well established that total carbohydrate reserves in below-ground tissues can show rapid temporal change (Mooney and Billings, 1960). The translocation of carbohydrate out of below-ground tissue would concomitantly reduce the mass-specific energy content of that tissue and reduce its digestibility to a herbivore because the proportion of largely indigestible cell-wall constituents increases.

In summary, below-ground plant tissues may represent a more variable resource, in terms of nutritional value, than above-ground tissues. Whether below-ground herbivores must cope with a diet of lower average nutritional value than that of above-ground relatives remains unclear.

BELOW-GROUND HERBIVORES

Taxonomy and Classification of Below-Ground Herbivores

Below-ground herbivores are found in three phyla (Table 1). Differences among taxa in size and mode of locomotion through the soil lead to important differences in their relationships to plants. Herbivorous nematodes are very small (mean biomass values of 0.1 to 7.5 ng; Norton 1978: Table 4.4) and their movement is between and around soil particles in soil water. Larger below-ground herbivores must burrow, and include "excavators" — animals that redistribute soil from in front of them to behind them — and "tunnelers" — animals that force their way through the soil by pushing soil particles aside (Kevan, 1962; Kuhnelt, 1955). Excavators may use limbs (e.g., mole-crickets), mouth parts (e.g., scarabaeid beetle larvae — Kevan, 1962:90) or both (e.g., geomyid rodents) for burrowing. Tunnelers may be soft-bodied forms that move by means of peristaltic motion (e.g., tipulid fly larvae) or rigid forms (e.g., elaterid beetle larvae) that use hard body surfaces to push aside the soil. I will use the term "fossorial herbivore" throughout this paper to refer to animals, either vertebrate or invertebrate, that burrow through soil in order to access below-ground plant parts for food.

Distribution and Abundance of Below-Ground Herbivores

Vertebrates

Fossorial herbivorous vertebrates are distributed over much of the earth's temperate zones. Representatives have evolved independently within at least seven families in the Rodentia (Table 2). The lack of a representative in Australia is puzzling, especially in light of the fact that fossorial insectivores (Notoryctidae), ecological equivalents to the Holarctic moles, have evolved there (Eisenberg, 1981). Some North American moles (Insectivora: Talpidae) include below-ground plant parts in their diet (e.g., Whitaker and Schmeltz, 1974).

TABLE 1
Taxa within which species have adopted below-ground herbivory as their primary feeding mode

Nematode taxonomy follows Nicholas (1984).

Phylum	Class	Order
Nematoda	Secernentea	Dorylaimida
		Tylenchida
Arthropoda	Insecta	Coleoptera
		Diptera
		Homoptera
		Lepidoptera
		Neuroptera
		Heteroptera
		Orthoptera
Chordata	Mammalia	Rodentia

The body mass of adult vertebrate below-ground herbivores ranges from 35 to 1500 g.

The evolution of below-ground herbivory in the North American Geomyidae (Table 2) has been linked to a climate shift toward warm and xeric conditions within their ancestral range (Russell, 1968:556). An increasingly more arid climate has also been postulated to be responsible for the evolution of below-ground storage organs in plants (Raunkiaer, 1934). The distributions of other vertebrate fossorial herbivores are also coincident with arid and semi-arid areas (Table 2) or with alpine areas, which also tend to be rich in plant species that have large subterranean stem or root storage systems (Billings, 1974). Populations of many of these herbivores appear to be patchily distributed in space (Nevo, 1979; Davies and Jarvis, 1986). The causal relationships linking local and regional distributional patterns to climate, soil, and vegetation are only now coming under the scrutiny of ecologists (McNab, 1979; Andersen, 1982; Contreras, 1986).

Digging is energetically expensive (Vleck, 1979) and tunneling costs will usually preclude a positive energy balance for burrowers in habitats where palatable below-ground plant parts are uncommon. Areas of closed-canopy forest, whether deciduous or coniferous, temperate or tropical, are probably incapable of supporting fossorial vertebrates because of the consistently small amount of digestible plant material available (Andersen and MacMahon, 1981).

The evolution of an energy-efficient, caste-

TABLE 2

Taxonomic, geographic, and ecological distributions of fossorial herbivorous vertebrates

All animals meeting classification criteria are rodents

Family	Genera	No. Species	Geographic Distribution	Ecological Distribution	Food Items Cached Yes	No	Unknown
Spalacidae*	*Spalax*	3	E. Europe and E. Mediterranean, Asia Minor, S. Russia[1]	Forest-steppe, steppe, and semidesert[19]	x[15]		
Cricetidae	*Myospalax**	5	Central Russia through N. China, Mongolia and E. Siberia[2]	Steppe and semidesert[19]			
	Arvicola	3	Palearctic	Grasslands and cultivated fields[18]	x[18]		
	Ptymys	11	Holarctic	Diverse	x[16]		
	Prometheomys*	1	Caucasus Mountains[13]	Alpine and subalpine meadows; open spaces in forests[2]			x
	Hyperacrius*	2	Northern Pakistan and Kashmir	Meadows and forests; alpine tundra[2,8]			x
	Ellobius*	2	E. Asia Minor, S. Russia, Iran east to Mongolia[2]	Generally drier areas, steppe, semidesert, and desert[14,19]	x[19]		
Octodontidae	*Spalacopus**	2	Coastal Chile, inland hills to 3000 m; S. Chile[2]	Semi-arid areas[9]			x
Ctenomyidae*	*Ctenomys*[a]	?50	Altiplano of S. Peru to Tierra del Fuego[2]	Drier areas[3]	x[4]		
Bathyergidae*	*Georychus*	1	S. Africa through the Cape Province[2]	Loose sandy soils[2]	x[17]		
	Cryptomys	?50	Africa south of the Sahara[5]	Woodland and savanna, second growth montane forest; areas with moderate rainfall[5]	x[6,7]		
	Heliophobius	3	Congo, Kenya, E. Africa south to South Africa[5]	Open plains or woodlands; can withstand long dry season[5]	x[2,6]		
	Bathyergus	1	Eastern coast of South Africa[2]	Mediterranean-type climate	x[2]	x[6]	
	Heterocephalus	1	E. Ethiopia, Somaliland, Kenya[5]	Semidesert[5]		x[6]	
Rhizomyidae	*Tachyoryctes**	2	East Africa: Ethiopia to Malawi, Cameroon Highlands[2]	Open grassland; upland (moist) savanna[5]	x[6]		
	Rhizomys[a]	3	S. E. Asia, southern China[2]	Dense bamboo thickets[2]	x[2]		
Geomyidae*[10,11]	*Geomys*	7	Coastal plain of Georgia, Alabama & Florida; Great Plains	Semi-arid to moist areas with suitable soil	x		
	Thomomys	?7	Most of western U.S.; northwest Mexico	Semi-arid grasslands to alpine meadows	x		
	Pappogeomys[b]	14	Central Mexican Plateau; north to S. E. Colorado	Steppe, thicket and scrub desert			x
	Orthogeomys[b]	11	Southern Mexico, Middle America to Colombian border	Openings in (?) evergreen to deciduous forest ["seasonal formation series"]; tropical rain forest[12]			x
	Zygogeomys	2	Southwestern Mexico	Openings in (?) montane forest			x

Notes:

Starred (*) families or genera are entirely fossorial.

[a] These genera include fossorial species indicated to "commonly" utilize above-ground as well as below-ground plant parts: for *Ctenomys*, see Reig (1970); for *Rhizomys*, see Ognev (1928).

[b] Taxonomy of Russell, 1968: *Orthogeomys* includes *Heterogeomys* and *Macrogeomys* of Hall and Kelson (1959); *Pappogeomys* includes *Cratogeomys* of Hall and Kelson (1959).

[c] Jarvis and Sale (1971) found *Tachyoryctes* to store food, whereas *Heterocephalus* and *Heliophobius* did not. These workers noted *Heliophobius* did store food in other parts of its range, as Walker (1975) reports. They also imply, citing Shortridge (1934), that *Bathyergus* does not store food, perhaps as a result of its ankylosed lower jaw. Jarvis and Sale (1971) suggest storing food may be impossible where the diet is largely made up of large tubers, as it is for *Heterocephalus* in the area they examined.

Sources: [1] Ranck (1968); [2] Walker (1975); [3] Weir (1974); [4] Pearson (1959); [5] Kingdon (1974); [6] see Note c; [7] Genelly (1965); [8] Roberts (1977); [9] Reig (1970); [10] Hall and Kelson (1959); [11] Russell (1969); [12] Hall and Dalquest (1963); [13] Ognev (1926); [14] Bashanov and Belosludov (1941); [15] Nevo (1979) citing his own earlier work; [16] Soriguer and Amat (1980) for *P. duodecimcostatus*; [17] Du Toit, Jarvis, and Louw (1985); [18] Nowak and Paradiso (1983) for fossorial *A. terrestris* in central Europe; [19] Formozov (1966).

based foraging system in colonies of *Heterocephalus glaber* (Table 2) has been linked to their occupancy of habitats characterized by low average primary productivity, but in which scattered tubers, some of which can exceed 30 kg, can be found (Jarvis, 1978). Several workers have suggested that fossorial vertebrates universally realize a reduction in metabolic costs relative to coexisting surface-dwelling animals (e.g., Pearson, 1959); comparative studies of ecological production efficiencies would be insightful. It is noteworthy that numerous nonfossorial vertebrate herbivores make use of below-ground plant parts for food in areas that are unsuitable for fossorial forms.

The only fossorial vertebrate herbivores

residing in the moist tropics may be among the Geomyidae of Middle America (cf. Nevo, 1979: Fig. 2). Most tropical geomyids are found in grassland or scrub habitats, but at least one species, *Heterogeomys hispidus*, although usually found in either natural or artificial clearings, apparently also occupies areas "beneath trees in the forest and jungle" (Hall and Dalquest, 1963).

Invertebrates

Nematodes that feed on higher plants ("plant-parasitic" nematodes) have perhaps received more attention than any other taxonomic group of below-ground herbivore. This attention is a direct response to their economic importance: the annual reduction in crop yield attributed to nematodes has been estimated to average 10 per cent worldwide (Dowler and Van Gundy, 1984). Plant-parasitic nematodes can be found in soils from the arctic to the tropics, virtually wherever vascular plants exist (see Procter, 1984). Most are contained within two orders (Table 1). According to Procter (1984), the highest nematode species richness, as well as densities and biomass may be reached in temperate areas, particularly grasslands. He suggests that tropical forests support among the lowest nematode densities of any habitats. Relatively few studies, however, have been conducted in either high latitudes or uncultivated tropical environments.

Plant-parasitic nematode populations are clumped in space (Boag and Topham, 1984), in part because active dispersal is limited to a few decimeters. Individuals tend to be associated with the thin (0.3 to 3 mm diameter) "feeder" roots responsible for absorbing water and nutrients, and thus are usually concentrated in the upper few decimeters of the soil profile. Densities within uncultivated habitats can reach 1×10^6 individuals m^{-2} (Overgaard-Nielson, 1949; Ferris and Ferris, 1974), with seasonal peaks of more than 7000 individuals per gram of root tissue reported for some plant species (Ingham and Detling, 1984). Reay and Wallace (1981), working in Australia, found both numbers of taxa and numbers of individuals to be positively associated with precipitation. They suggested that the distribution and abundance of vegetation, also correlated with precipitation, largely determined the character of nematode assemblages. Ferris and

Ferris (1974), summarizing their work in temperate hardwood forests (Johnson 1972, Johnson, Ferris, and Ferris, 1973, 1974), suggested that a variety of edaphic factors have important roles in determining local plant-parasitic nematode diversity. They noted populations of these taxa were less sensitive to site disturbance (plant community changes) than other trophic forms. Boag (1985a) showed that bulk density of the soil can influence population density. Reay and Wallace (1981) found some species of plant-parasitic nematodes to be well adapted for long-term survival (3 years at 10°C) in the absence of a host plant. Boag (1985b) provides data consistent with the hypothesis that intraspecific competition for food regulates populations of at least some species.

Insects that rely on below-ground plant parts for food are found on all continents, save Antarctica (e.g., see Allsopp, 1980). Most attention has focused on species within four orders (Table 1): the beetles (Coleoptera), butterflies and moths (Lepidoptera), flies (Diptera) and cicadas (Homoptera). In most cases, only immature stages of these insects feed on below-ground plant parts. Typically the last instar or adult emerges from the soil and the adult then either does not feed or, if herbivorous, relies on above-ground plant tissues. Other insects that have adopted below-ground herbivory as the primary feeding strategy (Kevan, 1962; Wallwork, 1976) include the lacewings within the Neuroptera (Ithonidae: *Ithone fusca*), burrower bugs within the Heteroptera (Cydnidae: *Scaptocoris talpa*), and mole crickets within the Orthoptera (Gryllidae: *Gryllotalpa gryllotalpa*, *Scapteriscus vicinus*). The life history of many of these species is only poorly known. For example, it remains unclear whether the extensive damage to Bahiagrass (*Paspalum notatum*) generally attributed to mole cricket (*Scapteriscus* spp.) feeding activity is in any way due to the presence of the crickets (Walker, Little, and Dong, 1982).

Local distributions of fossorial insects, just as those of other below-ground herbivores, are typically patchy. Soil texture, moisture, and temperature affect both the regional and local abundance through their influence on oviposition sites, the number of eggs laid, larval feeding sites, or larval mortality rates (Fox, 1973; Marrone and Stinner, 1984). A tight coupling between variable abiotic environmen-

tal conditions on the one hand and survivorship and reproductive performance on the other could account for the periodic irruptions noted for some species (e.g., Hartman and Hynes, 1977). Intraspecific competition for food can act to regulate population density (Ridsdill Smith and Roberts, 1976), but its role in natural populations at moderate densities is unknown. The role of natural predators and parasitoids in determining the distribution and abundance of insect below-ground herbivores also remains unclear (see Fox, 1961). Some species show irruptions only outside their native ranges (Nickle and Castner, 1984), within which potential density-regulating predators have been identified (Hull, 1973; Irwin and Lyneborg, 1981).

Drought can have a significant impact on invertebrate below-ground herbivores, although some species of nematodes have stages resistant to desiccation (Demeure and Freckman, 1981). Larval development of some (perhaps most) beetle and dipteran species requires air that is saturated, or very nearly saturated, with water vapor (Jones, 1951; Pritchard, 1983). Temporary flooding of soils does not reduce, and may actually increase, survivorship in some species of invertebrate below-ground herbivores (Fox, 1959; see also Pritchard, 1983). Trapped O_2 would be available even in flooded soil, allowing small invertebrates to respire aerobically, for at least short periods. Brown (1983) reported that a substantial proportion of root-knot nematode eggs were still viable in an agricultural field after submergence for one year, and were considered to be eliminated only after submergence for nearly two years.

In summary, the distributions of vertebrate and invertebrate below-ground herbivores indicate that below-ground herbivory occurs at some level in all communities of terrestrial vascular plants. Plant communities of temperate zones are unique in that they may harbor representatives of all three phyla of below-ground herbivores; densities of individuals may also reach highest values there. Abiotic factors may strongly influence densities of invertebrate species; stochastic events that affect soil properties and microclimate may have a large role to play in determining the numbers and kinds of below-ground herbivores present at a site. All forms of below-ground herbivores

share the characteristic that populations tend to be clumped in space. Thus the impact of these consumers will show spatial variability at both local and broader levels.

THE EFFECTS OF BELOW-GROUND HERBIVORY ON INDIVIDUAL PLANTS

Allocation of Photosynthate to Below-Ground Tissues

There are major differences in patterns of energy and materials allocation to below-ground plant parts among plants having different life histories (i.e., monocarpic vs. polycarpic) or faced with different abiotic environments (e.g., length of growing season) (Monk, 1966; Chapin, Johnson, and McKendrick, 1980; see also Bazzaz, Chiariello, Coley, and Pitelka, 1987). Caldwell (1979) points out that the need for perennial plants to maintain access to water and nutrients may demand that root production be a major component of total plant growth, but that selective pressures operating to maximize or optimize the efficient use of energy will ensure that excessive growth of the "heterotrophic" root system is minimal. The apparent excesses in stored material (see below, p. 268 ff.) and in the capacity of the root system to supply water and nutrients to the shoot (Seinhorst and Kozlowska, 1979) need to be reevaluated in the light of all factors that influence fitness, including the activities of below-ground herbivores.

The effect of the loss of part or all of the root system on plant fitness will depend upon the plant's ability to do without or substitute for the functions lost, or to restore those functions to normalcy (Fig. 1). A capacity to form adventitious roots is nearly universal among plant species. A plant may have a very high probability of surviving even total root removal if physical support for the aerial portion is available, and physiological and environmental conditions promote the rapid establishment of new roots. Whether below-ground herbivores can chemically promote root development is unknown (but see McNaughton, 1985).

The effect of below-ground herbivory will also be a function of the phenological stage of the plant at the time of damage (Fig. 1). Perennials that rely on underground food stores for survival or reproduction during the next year may begin allocating photosynthate to below-ground organs prior to current-year flowering
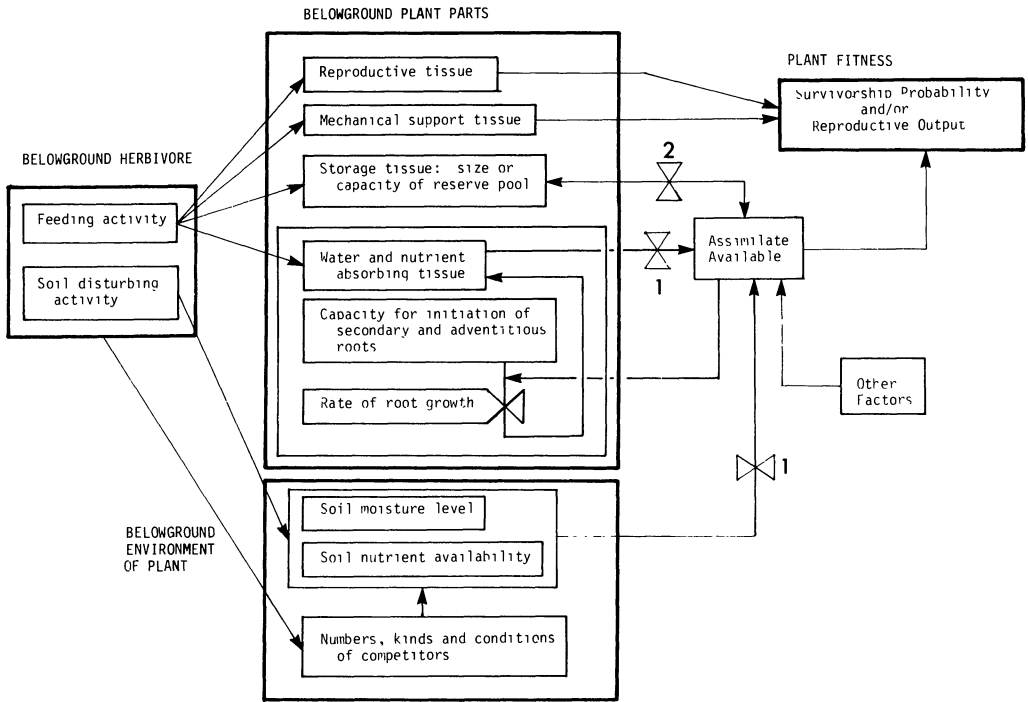
FIG 1.   THE PATHWAYS THROUGH WHICH BELOWGROUND HERBIVORES CAN AFFECT PLANT FITNESS
     Fossorial herbivores effect changes through feeding and soil-disturbing activities; nonfossorial below-
ground herbivores effect changes by way of their feeding activities. Numbered "valves" refer to (1) the
rate of water and nutrient uptake by the plant; and (2) the rate of plant matter input to or output from
below-ground storage. "Other factors" affecting the available assimate would include the quantity of
photosynthesizing tissue. The rate of root growth can be influenced by both herbivore feeding activities
and the availability of assimilate.

(Mooney and Billings, 1960). The loss of stored
material late in the growing season would se-
verely reduce the probability that new reserves
sufficient to meet requirements could be se-
questered prior to dormancy.

Inferences from Studies Involving Root-Pruning

Experimental studies investigating the ef-
fects of partial root removal are relatively few
in number yet difficult to synthesize because
of the variety of methods used and nature of
the data presented. Most of the studies have
addressed the processes of plant growth or hor-
ticultural techniques, with no reference to or-
ganisms that consume plant tissues. Few geo-
phytes have been studied.

Many plant species, both fibrous and tap-
rooted, show compensatory increases in
growth of root tissue and a reduction in shoot

growth following mechanical root pruning.
Humphries (1958) removed up to one-half of
the adventitious roots of 23-day-old barley
plants and found no significant change in the
amount of root growth (absolute growth:
grams of new tissue added) compared to con-
trol plants after a further 11 days of growth in
nutrient solution. The growth rate of roots rel-
ative to root biomass present after pruning [ex-
pressed as log (initial dry mass/final dry mass)]
thus increased in proportion to the amount of
tissue removed, and "compensated" for the
reduction in root biomass. This would consti-
tute exact compensation in the terminology of
Belsky (1986:872). The level of root nutrition
appeared to have little effect on root growth
after pruning, and experiments using youn-
ger barley plants and rye plants produced simi-
lar results. Root trimming had a marked ef-

fect on shoot growth, however: the greater the amount of root biomass removed, the lower the absolute shoot growth rate, and the nature of the root nutrient solution played a role in determining the ultimate impact. At trimming levels greater than 50 per cent, even absolute root growth declined.

Excision of up to 40 per cent of the lateral roots of 39-day-old tomato plants, a tap-rooted species, had no effect on root mass increase over the subsequent two weeks. Removal of all lateral roots reduced root growth to 54 per cent of that of the controls—undercompensation, in Belsky's terminology. Removal of 25 per cent of the lateral roots did not affect shoot growth, whereas larger removals led to sharp reductions of both stem and leaf biomass increases, especially of the latter.

Lovett Doust (1980) removed the lower 50 per cent of the root stock that had formed on one-year-old, potted *Smyrnium olusatrum*, a "biennial," and compared the treated plants to controls the following year. Root pruning had little effect on the total biomass of plants that flowered (as relatively small individuals) in their second year, although it reduced the biomass of nonflowering individuals by about 30 per cent. Lovett Doust (1980) interpreted the lack of an effect on flowering individuals as evidence for "luxury growth and storage," a trait that would be selectively advantageous if it either reduced the impact of below-ground herbivory or deprived competing plants of resources.

Detling, Winn, Procter-Gregg, and Painter (1980) found that the net photosynthesis rate declined and both biomass and tillering capacity of the grass *Bouteloua gracilis* were reduced following root pruning. These authors pruned the roots of 45-day-old, hydroponically grown plants at 5 cm below the crown base. An average of 37 per cent of root biomass, and 9 per cent of total plant biomass was removed; nearly all primary root apices were removed. During the subsequent 21 days, significant differences appeared in both total biomass and the number of above-ground shoots (tillers), whereas no difference could be detected in rates of root growth (g/day). This indicates that exact compensation in growth of root tissue took place, just as observed by Humphries (1958). Net photosynthesis rate (P_n), monitored from pruning to Day 10, was initially re-

duced in the treated plants, but returned to control levels by Day 8. Such a reduction in P_n after removal of tissues that act as photosynthate sinks, such as roots or storage organs, has been established in other studies (Neales and Incole, 1968). The proportion of photosynthate translocated to roots was initially reduced by approximately 50 per cent in the pruned plants, but steadily increased and surpassed controls (30% vs. 20%) by Day 21. The total biomass of controls was 25 per cent greater than pruned plants by Day 21. Thus, removal of 9 per cent of the plants' biomass led to almost a 20 per cent reduction in their total net primary production, and whereas root growth was exactly compensated, plant growth as a whole was undercompensated. The authors suggested that the increase in root biomass of pruned plants was due to the formation of new adventitious roots, whereas the larger biomass of control plants was due to their greater number of shoots.

The stimulation of new root growth, one aspect of compensatory root growth, appears to be a general consequence of root pruning (Sutton, 1967). Hermann (1977) reviewed root growth in trees and noted a series of studies supporting the concept that "injury" results in the rapid formation of new lateral "replacement" roots, or the reactivation of growth in small dormant roots.

Some plant species appear to be able to maintain both normal shoot and root growth (i.e., exhibit exact compensation, on a whole-plant basis) when root losses are held at low to moderate amounts. Jordon, McCrary, and Miller (1979) found that the presence of six nodal roots was sufficient for normal shoot growth in a hydroponically grown grain, *Sorghum bicolor*, even though an average of 21 were present on control plants. The total root biomass of treated plants was equal to controls, presumably because of increases in branching and size of the remaining roots. Kolek (1974:362) suggested that many cereals possess much greater root biomass than is required for normal growth.

In his review of research on the mechanisms regulating root and shoot growth, Troughton (1974) noted that in some studies partial root pruning decreased absolute growth rates of both root and shoot systems (total plant growth thus was undercompensated), but that the

growth rate of the shoot showed the greatest reduction. In other studies, root pruning led to temporary increases in shoot growth, but overcompensation on a whole-plant basis was not indicated to have occurred. The differences in the results observed in these studies may be due to either genetic factors or environmental factors (e.g., temperature, nutrient status) or to both. Troughton (1974) emphasized that plants must adapt to a variety of stressors in their natural environments, although below-ground herbivory was not specifically mentioned.

In summary, root-pruning studies suggest that the loss of a modest portion of the root system may have no discernable impact on the subsequent functioning of a plant. As effects become apparent at higher pruning levels, they are initially expressed most strongly in the above-ground portion of the plant. This suggests that species capable of exact compensation on a whole-plant basis have no need for (or ability to evolve) a defense against low levels of below-ground herbivory, or that the response is a result of natural selection having operated to adjust current allocation patterns to the predictable occurrence of such herbivory in the past. It is important to note, however, that few root-pruning studies have actually measured effects on plant fitness, either in terms of differential seed production or in terms of the capacity of control plants to vegetatively out-compete the pruned plants. Further, in those studies using laboratory-grown plants, especially hydroponic methods, the outcome of experimental root pruning may have little relevance to natural herbivory. As Detling et al. (1980) recognized, "death or reduced growth also may result from water stress or reduced nutrient uptake if a high proportion of the roots are severed, especially if functional roots are restricted to the upper layers of soil" (p. 776).

Experimental Studies Examining Below-Ground Herbivory

A large number of greenhouse and laboratory experiments have examined the relationship between nematode population dynamics, the nature and magnitude of the plant injury they cause, and plant fitness. Most species of root-feeding nematodes are capable of completing their life cycles on a large variety of plants (Dao, 1970, in Procter, 1984), although some appear limited to a single genus (Stone, 1979). A species may be associated with particular sites on the root, such as meristem, zone of elongation or region of maturation, and particular cells within a site may be attacked (Wallace 1973:94).

Feeding mode and nematode size determine, in part, the extent of plant injury (Atkinson, 1985). Some species of root-feeding nematodes function as ectoparasites, others as endoparasites. Southwood (1985:8) repeats the comment of Stone (1979) that most plant-parasitic nematodes browse externally on root systems, but neither author provides a compilation of data or cites the work upon which the generalization is based. Many tylenchid species attack individual cells sequentially, moving as necessary between attacks. The ectoparasitic nematodes that feed on root hairs and epidermal tissue are probably less damaging to plant tissue, on an individual basis, than the endoparasitic forms, whose movement into and within below-ground plant tissues results in mechanical damage to plant cells (Wallace, 1973:134). Some endoparasitic nematode species become sedentary, at least temporarily, once a cell suitable for feeding is reached. Enzymes capable of predigesting both cell contents and the cell wall are injected into the food cell by means of a hollow stylet, through which nutrients are also extracted. Further mechanical damage may ensue when mature males travel to locate mates.

Plants respond to nematode disturbance in a variety of ways that presumably are adaptations either to compensate for the damage or to inhibit the nematode (Wallace, 1973:69). In some species, damaged cells release compounds that are toxic to both the nematode and the plant, and that result in the cell's own death. The toxin and necrosis are suggested to be a mechanism both to control the extent of damage and to preclude establishment of secondary pathogens. The adaptive significance is less clear in cases where the plant response includes the formation of a syncytium, which then serves as a food source for the nematode (Gommers, 1981).

The effect of nematode herbivory on individual plant fitness is manifested through root destruction or the formation of metabolic sinks (e.g., gall tissue or syncytial cells). The

level of fitness reduction will thus depend upon both the species and the number of nematodes involved. Root injury may lead to reduced translocation, inadequate nutrient absorption, abnormal production of growth regulators or other effects that could in turn lead to relatively low growth rates, smaller ultimate size or reduced quality and quantity of seed output (Fig. 1). Small numbers of nematodes may have little if any negative impact on fitness, and can actually enhance it under some circumstances, presumably through overcompensatory production of absorbing (= feeder) roots (Rebois and Johnson, 1973; Wallace, 1973:30). Such results suggest that the resource allocation patterns of unparasitized plants may be suboptimal.

Because they can disrupt the plant's functional integrity, the detrimental effect of large numbers of nematodes can be disproportionate to the amount of biomass consumed. Ingham and Detling (1986) calculated that nematode consumption accounted for only 1 per cent of the total reduction in net primary production of the grass *Bouteloua curtipendula* grown in pots with and without the herbivore.

The complexity of the relationship between herbivore abundance, herbivore feeding pattern, and plant fitness in the plant-nematode system is mirrored in the plant-insect system. Ridsdill Smith (1977) calculated that the consumption associated with various densities of the larvae of *Sericethis nigrolineata* (Coleoptera: Scarabaeidae) accounted for only 5 to 14 per cent of the reduction in standing crop of ryegrass roots at the end of a 16-week experiment. He attributed most of the reduction in root yield to the fact that feeding was concentrated on the youngest tissues, a condition that prevented root growth (Fig. 1). Ridsdill Smith found a negative correlation between root yield and larval density, but a regression of yield on the number of larvae was not significant when the control value (no larvae) was deleted—i.e., the largest reduction in yield occurred between control plants and those with a single larva. One explanation for such a yield curve is the simultaneous feeding of several larvae on a single host root, with the larva located most proximally on the root branch largely determining the effect on the plant. Ridsdill Smith discounted this hypothesis because no evidence

of wasteful feeding—e.g., severed roots—was apparent.

Ridsdill Smith's (1977) negative correlation between root yield and larval density over all levels differs from the result that would be predicted on the basis of Humphries' (1958) root-pruning study, where maintenance of normal growth rates at lower clipping levels prevented root biomass reduction from exceeding the amount mechanically "consumed." This discrepancy may be a consequence of differences in the nature of tissue removal. In pruning studies, tissue is removed once or at least relatively infrequently, and subsequent root growth is possible. Foraging larvae may constitute a continuous tissue removal system that can prevent growth by eliminating incipient roots. Thus, root-pruning studies may have more applicability to the consequences of below-ground herbivory by vertebrates, where tissue damage may be a one-time or infrequent affair. Whether fossorial vertebrates continuously graze roots growing into established tunnels has not been established.

Ridsdill Smith (1977) found that below-ground herbivory by beetle larvae had no influence on foliage production despite the loss of root biomass, again counter to Humphries' (1958) results. When above-ground foliage was also regularly removed, however, a negative correlation between green foliage yield and larval numbers was apparent. Presumably, the loss of photosynthetic tissue reduced the assimilate available for supporting compensatory root growth, and the impaired ability to restore water and nutrient uptake levels led to a decline in above-ground production (Fig. 1). Ridsdill Smith did not compare root biomass of defoliated and nondefoliated plants at equal larval densities. If the suggested causal mechanism is the one actually operating, defoliated plants should show smaller root masses at all levels of below-ground herbivory. In fact, this was found to be the case in similar studies involving nematode herbivory (Stanton, 1983; Ingham and Detling, 1986).

No research detailing the effect of below-ground herbivory by a vertebrate on a particular plant species has been published, although O. J. Reichman at Kansas State University has initiated such a study, involving *Geomys bursarius* and an exotic annual, *Berteroa incana*. Because

of their size and excavating abilities, vertebrates are capable of removing most of a plant's below-ground biomass. No quantitative description of foraging damage is available, however, for any plant species. A small, palatable geophyte may have its entire storage organ excavated and eaten or cached (Table 2). The effect of vertebrates on fibrous-rooted plants without storage organs is unclear. It appears that some roots intercepted during burrowing are attacked merely to create an unimpeded passageway, while large, palatable roots or storage organs may be left partially exposed in the tunnel as a form of in situ storage (Andersen, unpub.; Jarvis, 1978). The effects of herbivory by these relatively large and mobile consumers are technically difficult to separate from effects resulting from modification of the soil's physical, chemical, or biological properties. Outdoor enclosures (Andersen, in press; O. J. Reichman, unpub.) show promise as a tool for elucidating these relationships.

Corms, bulbs, tubers and other below-ground plant parts capable of acting as propagules are cached by most fossorial herbivorous rodents (Table 2), and some caches are subsequently abandoned, allowing the propagules to develop (Cook, 1939; Galil, 1967). Propagules of some cached species can send up shoots from depths exceeding 40 cm (Galil, 1967; Davies and Jarvis, 1986). Lovegrove and Jarvis (1986, cited in Davies and Jarvis, 1986) document dispersal of geophytes by fossorial rodents in South Africa, and suggest that the plants and rodents have coevolved traits that facilitate the relationship.

In summary, knowledge gained from root-pruning studies is of limited value for gaining insights into relationships between individual plants and their below-ground herbivores. Both the form and temporal pattern of tissue loss to herbivores have been shown to be important determinants of the effect on plant fitness, and pruning may adequately mimic only the acute form of herbivory associated with vertebrates. The presence of a threshold level of below-ground herbivory, above which deleterious effects become magnified, has been suggested in both pruning and invertebrate herbivory studies, but remains to be evaluated as a general phenomenon. There appears to be no evidence for overcompensation (on a whole-plant basis) for damage incurred by a fossorial herbivore, although it has been suggested for nematode-damaged plants. The role of below-ground herbivory in plant population processes is undoubtedly as complex as is that of above-ground herbivory (see Belsky, 1986; McNaughton, 1986). Very limited evidence suggests that some plants and their below-ground herbivores may have coevolved toward a mutualistic relationship.

Feeding Deterrents in Below-Ground Structures and Tissues

Circumstantial evidence that below-ground herbivory negatively affects plant fitness is provided by the fact that below-ground tissues frequently contain metabolites that can act as feeding deterrents (McKey, 1979). The compounds may be produced endogenously or translocated from above-ground plant parts, and levels may be greater or less than those found in above-ground plant parts (Frohne and Pfander, 1983). The storage organ of carrot (Daucus carota) contains carotatoxin, and potato tubers contain the alkaloid solanine (Orgell, Vaidya, and Hamilton, 1959). One of the most potent mitogens is found in the large taproot of pokeweed, Phytolacca americana (Shortman, Byrd, Cerottini, and Brunner, 1973, in McKey, 1979). Nicotine is synthesized in the roots of tobacco, Nicotiana sp. (Dawson, 1942). Alkaloids are present in the roots of the annual Lupinus luteus until seed maturation, and furanocoumarins are found in the fleshy taproot of wild parsnip, Pastinaca sativa (Simsova and Blazek, 1967, in Berenbaum, 1981). Peach tree (Prunus persica) roots contain a cyanogenic glucoside (see MacDonald, 1979). Many species of tropical yams, Dioscorea spp., contain sapogenins and alkaloids in the enlarged storage structure (Onwueme, 1978:89) and the cassava (Mahihot tuber) contains a cyanogenic glucoside (Onwueme, 1978:109). The roots of raspberry and many other plant species contain a nematicide (Taylor and Murant, 1966; Gommers, 1981). The effectiveness of these compounds in limiting below-ground herbivory is totally unknown in most cases.

The development of monophagy by some invertebrate below-ground herbivores, both among insects and nematodes, probably reflects biochemical adaptation circumventing the "toxic" compounds produced by the plant. For example, corn root worms (Diabrotica spp.,

Coleoptera: Chrysomelidae) are a serious agricultural pest in the north central United States (Shaw, Paullos, and Luckmann, 1978). Corn, a monocotyledon, appears to be the only host for practical purposes; larvae show reduced survivorship on other grass species, and apparently cannot tolerate dicotyledon species (Branson and Ortman, 1970).

THE FORM AND MAGNITUDE OF BELOW-GROUND HERBIVORY

Patterns in Plant Use

Whether vertebrate fossorial herbivores concentrate their herbivory on particular plant species is unclear. Results from many studies indicate that these rodents are generalist foragers, but tend to concentrate on geophytes or other plants with relatively large below-ground concentrations of digestible material when they are abundant (see Nevo, 1979, for citations). Most diet analyses, however, have relied on the identification of plant fragments in stomach contents or feces, a method yet to be critically evaluated for use with below-ground tissues. Andersen and MacMahon (1981) suggested that *Thomomys talpoides* should show relatively catholic tastes, at least with regard to below-ground plant parts, because of the high metabolic costs incurred in obtaining food by excavation. In fact, below-ground parts of only 4 of 26 species these workers offered in cafeteria tests were refused. Food items found in caches may represent excavated plant parts set aside in order to enable consumption of items of greater nutritional value (Stuebe and Andersen, 1985).

Vertebrate fossorial herbivores appear to concentrate their foraging in particular areas. Reichman and Smith (1985) documented a correlation between *Geomys bursarius* tunnel locations and habitat patch productivity, but their study was not designed to provide evidence of active selection. Tilman (1983) found the highest levels of soil disturbance by *Geomys bursarius* (assumed to reflect local foraging activity) in plots where fertilization had favored the growth of perennial grass species over annuals. It is unclear whether the pocket gophers were responding to differences in plant species composition, plant nutrient content, or both. The magnitude of the herbivory involved was not examined. Davies and Jarvis (1986), on the basis of an analysis of burrowing ener-

getics, inferred that *Georychus capensis* must differentially exploit geophyte-rich patches within its habitat.

Many invertebrate below-ground herbivores specialize on particular plant species. Even within a particular population of plants, however, the greatest amount of herbivory may fall on those individuals already stressed by above-ground herbivory or some other factor (Ingham and Detling, 1984; Norton, 1965). Ingham and Detling (1984) found plant-parasitic nematode numbers higher on roots of *Andropogon scoparius* from an area heavily grazed by prairie dogs (*Cynomys ludovicianus*) than from a nearby ungrazed area.

Consumption rates for individual invertebrate fossorial herbivores will depend upon abiotic conditions, the species and age of the herbivore, and the plant involved. Ridsdill Smith, Porter, and Furnival (1975) used gravimetric methods to examine feeding rates and growth of third-instar *Sericesthis nigrolineata* (Coleoptera: Scarabaeidae) which were fed carrot at various ambient temperatures. Consumption increased curvilinearly with increasing temperature between 4° and 30°C, whereas larval growth rate was maximum at 17.5°C and the efficiency of biomass conversion (mass gained/mass eaten) was greatest (11%) at 14°C. These workers also provided evidence corroborating that of Hurpin (1960), which showed feeding rates to be dependent on age: highest rates occur between molts, and minimum rates occur just prior to molting.

Food plant preferences may evolve in response to differences in acquisition costs or the nutritional value of the below-ground plant parts. King, Mercer, and Meekings (1981a) fed black-beetle larvae (*Heteronychus arator*) roots from three pasture plant species and calculated consumption indices [mass of fresh root eaten per unit mass of larva (wet) per week] of 0.75, 0.55, and 0.18 for two grasses and a clover, respectively. Because biomass conversion efficiencies were comparable on all three foods, ranging from 18 to 24 per cent, larval growth and development rates differed greatly. Conversion efficiencies of *H. arator* were substantially higher than the value reported by Ridsdill Smith (1975) for *Sericesthis* at the same experimental temperature (20°C). King, Mercer, and Meekings (1981b) demonstrated through the use of glass bead markers that

black-beetle larvae ingest grass roots at a faster rate than they do clover roots. The authors did not speculate as to whether the cause of the differential ingestion rates was a chemical or mechanical difference in the roots tested.

The methods by which below-ground herbivores locate food plants remain largely unknown. In a laboratory study, Jones and Coaker (1979) provide data suggesting that carrot-fly larvae actively move to roots of host plants by following chemical gradients in soil air or soil water. They documented detection at a distance of 7.5 cm from the source, but how meaningful this is to field situations is unknown. Carbon dioxide, which is produced by respiring root tissue, has been implicated in attracting both nematodes (Nicholas, 1984:77) and beetle larvae (Strnad, Bergman, and Fulton, 1986) to roots. Many arthropods undoubtedly rely on above-ground travels by adults or larvae to locate suitable food plants. Vertebrate fossorial herbivores appear to search their habitat systematically as they construct tunnel systems (Andersen, unpub.). The ability of these rodents to visit the surface easily means that visual cues may also play an important role.

If the dispersion pattern of a plant's below-ground tissues within the soil matrix determines the probability of discovery of those tissues by a fossorial herbivore, then differential below-ground herbivory is likely to have contributed as a selective agent to the morphology of roots and storage organs observed today. The shape of the root system is in part under genetic control, in part a consequence of physical and nutrient conditions of the soil (see Clarkson and Hanson, 1980), and in part a consequence of the intensity of above-ground defoliation (e.g., Schuster, 1964; Harradine and Whalley, 1981). The structure of below-ground plant parts should be evaluated in the light of both their vulnerability to below-ground herbivores and their functional utility.

Below-Ground Herbivory by Insects in Natural Communities

The few studies documenting the impact of below-ground herbivory by insects in natural plant communities have primarily involved irruptions of commercially important species. The larvae of June and May beetles (*Phyllophaga* spp., Coleoptera: Scarabaeidae), often called "white grubs" in the United States, can reach significant densities in both grassland and eastern deciduous forests. Ueckert (1979) reported densities of *Phyllophaga crinita* averaging 46 individuals m^{-2} in patches of shortgrass prairie. Perennial grass cover on these sites was reduced by 88 per cent and below-ground biomass was reduced by 43 per cent relative to control areas. Perennial forbs did not appear to be affected. *P. crinata* is apparently cyclic and Ueckert (1979) estimated that populations on the high density sites fell to 4.3 and then 0.0 individuals m^{-2} during the two subsequent years. Fowler and Wilson (1974) were able to document that root feeding by May beetle larvae caused 25 per cent mortality in red pine (*Pinus resinosa*) seedlings during the five years following planting. Most deaths occurred during the first and second years after planting. Use of an insecticide reduced *Phyllophaga*-caused deaths by 83 per cent compared to controls, and resulted in surviving seedlings showing increased vigor. All nonlarval growth-reducing agents were considered to have been unaffected by the insecticide.

The larvae of *Tipula* sp. (Diptera: Tipulidae), known as leatherjackets in Europe, significantly affect plant productivity in local areas. White and French (1968) showed that pasture yields in Great Britain were significantly reduced (18% and 34% in two consecutive years), with clover affected to a greater extent than the grasses. The densities of larvae were greater than 400 individuals m^{-2}. Hartman and Hynes (1977) reported densities of *T. simplex* reaching 3000 larvae m^{-2} in California grassland during a population irruption. Vegetation was severely damaged over several hundred hectares.

Periodical cicadas (Homoptera: *Magicicada* W. T. Davis), both the 13-year and the 17-year forms, are examples of a rare type of fossorial herbivore, xylem feeders (White and Strehl, 1978). Root xylem sap is a dilute solution containing amino acids, the apparent energy source for the cicadas. Use of this sap may circumvent the need to deal with toxic compounds that may be present in phloem sap, and may also explain the slow growth rates of these animals. The first through third instars construct short burrows, whereas the last two instars (4th and 5th) maintain smaller "mud cells" (White and Lloyd, 1975). Little quantitative work has been undertaken, but the sub-

stantial burrows constructed by nymphs in order to reach the soil surface may affect plant root distribution for some time (White, Lloyd, and Zar, 1979). Burrows are typically concentrated in the upper 30 cm of the soil.

Cicadas may be a major contributor to below-ground herbivory as a result of their high densities. Dybas and Davis (1962) estimated a density of 260 nymphs m^{-2} following the emergence of a population of 17-year periodical cicadas in a flood plain (*Ulmus-Celtis*) forest in Illinois. An upland *Quercus-Carya* forest in the same locality supported an average of 23 emerging nymphs m^{-2}. Differences in the species involved resulted in estimates of standing crop biomass (live nymphs) of between 1900 to 3700 kg ha^{-1} on the floodplain and 230 to 430 kg ha^{-1} in the upland forest. The authors indicated that the former estimate was at that time the "highest mean biomass per unit of habitat recorded for a terrestrial animal under natural conditions" (p. 443). They calculated the net average annual production for the floodplain and upland sites (mass of live nymphs) to be 110 to 215 kg ha^{-1} and 13 to 25 kg ha^{-1}, respectively. Hamilton (1961) estimated that root systems of individual trees within an apple orchard harbored 21,000 to 73,000 nymphs.

The cicada density data of Dybas and Davis (1962) may be very unusual for natural forest stands. Ausmus, Ferris, Reichle, and Williams (1978) estimated the density of periodical cicadas to be 6.3 individuals m^{-2} in a mesic, 45-year-old hardwood forest in Tennessee. They suggested, without substantive support, that densities of 3 to 7 individuals m^{-2} were typical. Karban (1984) reported densities of 1 to 26 individuals m^{-2} within 50 to 225 m^2 areas in a New York hardwood forest. An extensive sampling program involving 1600 one-square-meter quadrats within a 16 ha portion of Arkansas forest produced an estimate of 7 individuals m^{-2} during the 1985 emergence (K. G. Smith, unpub.). Ausmus et al. (1978) estimated an annual average standing crop biomass of 0.5 g m^{-2} and a "root consumption" of nearly 200 KJ m^{-2} yr^{-1}, or approximately one per cent of the biomass of roots with a diameter of less than 0.5 cm (Table 3). The proportion of the net primary production going to the cicadas was not indicated. These authors point out sev-

TABLE 3
Estimates of annual consumption of plant biomass by below-ground herbivores in various ecosystems

Relative values are presented as proportions of net below-ground primary production (BPP) or net total primary production (NPP)

Organism	Site	Consumption		Source
		Absolute	Relative	
Nematodes	Ungrazed mixed-grass prairie	57 g m^{-2}	—	Smolik, 1974, in Ingham and Detling, 1984
	Grazed mixed-grass prairie	39 g m^{-2}	—	Smolik, 1974, in Ingham and Detling, 1984
	Grazed mixed-grass prairie	36 g m^{-2}	6–13% BPP	Ingham and Detling, 1984
	Ungrazed prairie	30 g m^{-2}		Ingham and Detling, 1984
	Short-grass prairie	35 g m^{-2}	7–26% BPP	Scott, French, and Lettham, 1979
	Short-grass prairie	—	20–30% NPP	Stanton et al., 1981
	Coniferous forest[a]	38 KJ m^{-2}	—	Sohlenius, 1979
Periodical cicada	Hardwood forest	192 KJ m^{-2}	—	Ausmus et al., 1978
Pocket gopher	Montane meadow	38–79 KJ m^{-2}	10–30% BPP	Andersen and MacMahon 1981

[a] Includes fungal feeders.

eral assumptions that, because of the paucity of natural-history information, must be made in order to calculate consumption.

An interesting result of the study of Ausmus et al. (1978) was the conclusion, based on consumption estimates, that root-feeding ("phloem-feeding") nematodes removed seven times as much energy from the primary producer level as did the xylem-feeding cicadas. It is unclear if the assimilation efficiencies used to calculate consumption from invertebrate biomass and respiration data were realistic. Both phloem and xylem feeders may have to consume large amounts of sap in order to ensure appropriate intake levels of nutrients found in low concentration. Root-feeding aphids, also phloem feeders, can have a substantial impact on above-ground primary production, based on the 45 per cent increase in NPP from plots treated with carbofuran, as reported by Vogel and Kindler (1980).

Below-Ground Herbivory by Nematodes in Natural Communities

The impact of root-feeding nematodes on productivity of natural plant communities may be large. Smolik and Lewis (1982) found the biomass of plant-feeding nematodes (0.54 g/m²) to be greater than that of either birds or plant-feeding arthropods at a mixed prairie site in South Dakota. The nematode biomass probably was also greater than that of small mammals, and was probably exceeded only by that of the dominant consumers, cattle. Scott, French, and Lettham (1979) suggested, however, that nematodes consume three times as much vegetation as cattle in mixed prairie, a consequence of their great abundance and relatively high mass-specific metabolic rate. Sohlenius (1980) tabulated abundances, biomass, and estimates of total metabolism for total nematode faunas from a variety of ecosystems; he stressed, however, that values were based on data sets of varying quality. An updated version of his data is presented in Nicholas (1984:166). Nematodes are especially difficult organisms to deal with at the population level, even among the generally difficult below-ground herbivores.

Ingham and Detling (1984) found root-feeding nematode densities to be higher on areas heavily grazed by an above-ground herbivore than on adjacent, lightly grazed areas,

a pattern corroborated by laboratory studies (Stanton, 1983). Ingham and Detling estimated that nematodes consumed 13 per cent of the net annual root production in the upper 10 cm on the heavily grazed site, compared to 6 per cent on the lightly grazed site (Table 3). Within both study areas, densities were highest within the rhizosphere of particular plant species, and consumption was presumed to be, as well. Nematicide treatments resulted in growth increases ranging from 28 to 59 per cent in a mixed prairie ecosystem (Smolik, 1977). Such "consumer-removal" studies, however, should be viewed cautiously. Although they are enlightening in respect to the potential effect of herbivory, the unavoidable removal of fungivorous and predatory nematodes may result in misleading values. In dry areas especially, myceliophagous nematodes that damage mycorrhizae may be killed, and a plant response to increases in mycorrhizal symbionts observed (Ruehle, 1972). Nevertheless, it seems reasonable to expect that root-feeding nematodes play a role in the distribution and abundance of some plant species similar to that documented for plant pathogens (see review by Dinoor and Eshed, 1984).

Below-Ground Herbivory by Vertebrates in Natural Communities

The only attempt to assess the magnitude of below-ground herbivory by a vertebrate fossorial herbivore appears to be the field study by Andersen and MacMahon (1981). By modelling the energy requirements of a population of *Thomomys talpoides*, and estimating the below-ground plant biomass available to them, these authors calculated that up to 30 per cent of the annual primary production allocated to below-ground plant parts may be consumed by the rodents (Table 3). The authors did not evaluate the ratio of energy production to consumption for individual plant species.

In summary, although data on herbivory by either invertebrate or vertebrate below-ground herbivores are meager in depth and extremely variable in breadth, studies indicate that the amount of below-ground herbivory can vary dramatically between communities as well as among plant species within a community and that the magnitude will vary temporally at all spatial scales. Local values may be high, certainly comparable to those reported for above-

ground herbivores (Crawley, 1983:15). A long-lived plant may develop a large load of invertebrate herbivores over its lifetime, because of the growth of populations present in the soil at germination and because of colonization by immigrating species. Data are insufficient to discern whether patterns in the magnitude of combined below-ground herbivory by all taxa differ between grasses, forbs, and woody plants.

EFFECTS ON COMMUNITY STRUCTURE AND FUNCTIONING

The effect that a particular species of below-ground herbivore has on the structure of a plant community is the net result of all of its influences on the dynamics of particular plant species. Some interactions could have positive value to the plant—e.g., dissemination of propagules (see above, p. 272), innoculation with mycorrhizal symbionts (Maser, Trappe, and Nussbaum, 1978; Allen, MacMahon, and Andersen, 1984), or increases in numbers of feeder roots or growth hormone production (Wallace, 1973:33). None of these interactions has been examined in detail in any community.

A problem confronting researchers attempting to explain empirical observations of plant community dynamics is the complexity of interactions within the soil/below-ground herbivore/plant system. The confounding effects of variable resource levels, competition, and above-ground herbivory may lead to effects that are unpredictable from studies based on only a single factor or a few factors. In a series of papers, Radcliffe (1971a,b,c,d) presents the results of experiments that illustrate how a below-ground herbivore ["grass grubs," *Costelytra zealandica* (Melolonthinae: Scarabaeidae)], soil-nutrient levels, and soil-moisture levels can interact to determine the outcome of competition among three species of pasture plants. Examination of the effects of the larvae on each plant species in monoculture showed varying degrees of damage, as measured by depression of root and shoot biomass. The experiments suggested that compensatory root growth can mask the effects of the grubs on shoots, but that there is a critical point in the level of root damage, which is dependent upon the plant species involved, its age, and the soil conditions (fertility and moisture status), above which shoot damage accelerates.

Stress that is due to low soil moisture or low fertility can greatly enhance the susceptibility of plants to grub damage.

In mixed-species trials, patterns of plant damage at a given grub density changed, presumably as a result of the grubs exhibiting food preferences. Thus, although grubs reduced root and shoot yields of white clover by 93 per cent and 76 per cent, respectively, when tested in a monoculture, tests in pots that also contained ryegrass showed no significant reduction in shoot yield of clover, and root yield presumably was also close to control levels (Radcliffe, 1971c). Yields of ryegrass, in contrast, were significantly depressed in both monoculture and the two-species mix. Radcliffe (1971d) suggested that root morphology and growth patterns were factors producing differences in susceptibility to grubs. Although she commented on Soper's (1959) work indicating variability in the degree of tissue lignification among the species tested, no mention of a role for chemical feeding deterrents was made. Radcliffe's work underscores the need for attention to the simultaneous operation of numerous factors in assessing how below-ground herbivores may affect natural communities. Furthermore, impacts may be insignificant under most (i.e., "normal") environmental conditions, but strong and long-lasting effects may be produced when "uncommon," albeit natural, sets of conditions prevail (see Wiens, 1977).

Indirect interactions between fossorial herbivores and plants can also influence community structure (Fig. 1). Hole (1981) provides a detailed, qualitative assessment of the effects of fossorial herbivores (as well as other animals) on soil and thus, indirectly, on vegetation. The lack of experimental studies on this topic is glaring. An important indirect effect of below-ground herbivores on plants is the predisposing of plants to attack by pathogenic fungi. Relationships involving both insect larvae (e.g., Latin and Reed, 1985) and nematodes have been studied, the latter leading some workers to suggest that indirect effects are of greater significance than direct effects (MacDonald, 1979).

A relatively large number of studies have addressed the indirect impact of fossorial vertebrates on plant communities. These effects accrue from the creation of large spaces within

the soil matrix, the mixing of soil horizons, the creation of exposed soil surfaces, and the burying of plants. All of these factors originate from burrowing activities (excavation and transport of soil) rather than herbivory per se, and thus can have either positive or negative influences on any given plant population.

Tunnel construction by fossorial vertebrates is often accompanied by the creation of soil mounds, which modify local physical and biotic conditions (Grant, French, and Folse, 1980; Grant and McBrayer, 1981; Andersen and MacMahon, 1985). These disturbances tend to promote the maintenance of annuals in plant communities (Laycock, 1958; McDonough, 1974; Tilman, 1983; Hobbs and Mooney, 1985; Williams et al., 1986). The rate of mound production is related to food resource levels (Andersen, in press). Nutrient redistribution through soil mixing activities is considered an important role of the fossorial *Spalax micropthalmus* in Asian steppe ecology (Zlotin and Khodashova, 1980). On a different scale, other indirect effects of fossorial vertebrate herbivores are the large (up to 14 m diameter), convex soil lenses found in widespread areas throughout the globe, resulting from generations of fossorial herbivores concentrating their activities in specific areas (see Cox and Roig, 1986).

Overall effects (herbivory plus other direct effects, and also indirect effects) of geomyid rodents on rangeland have been examined in numerous studies (Ellison and Aldous, 1952; Foster and Stubbendieck, 1980; Laycock and Richardson, 1975; Julander, Low, and Morris, 1959, 1969; Moore and Reid, 1951; Turner, 1973; Williams and Cameron, 1986). Many of these studies, however, are based on a "remove-the-herbivore" design, and suffer from a lack of adequate controls. In effect, comparisons are often made between effects of "low" and "normal" numbers of individuals (Moore and Reid, 1951; Laycock and Richardson, 1975; Julander, Low, and Morris, 1969; Williams and Cameron, 1986). Although the total consumption of plant biomass is undoubtedly reduced in such studies, the effects from below-ground soil disturbances existing at the start of the experiments and those created as a result of incomplete control of the geomyids are unclear. Unoccupied tunnels may themselves affect plant community dynamics. Tunnel systems may be rapidly repaired by colonizing individuals. In some cases, control methods (poison) undoubtedly affected populations of other herbivores present (Julander, Low, and Morris, 1969), making interpretation of results difficult. Another problem resides in the heterogeneity of the vegetation within and between the areas that are compared and the failure to ensure that biotic factors other than geomyid numbers are equivalent across treatments (Foster and Stubbendieck, 1980). Although these studies do provide insights into which components or attributes of the community might be strongly influenced by geomyids, the results can be misleading in terms of how and to what degree these fossorial herbivores influence the communities in which they reside. Studies in which geomyids are introduced into established communities are more likely to demonstrate conclusively their overall effect.

Invertebrate and vertebrate below-ground herbivores may affect ecosystem energy flow and nutrient cycling more strongly than above-ground folivores. Consumption of root tissue by beetle larvae accounted for less than 15 per cent of the total reduction in root biomass in the pot experiments of Ridsdill Smith (1977). Similarly, Ingham and Detling (1986) calculated that consumption (5.7 mg of tissue) accounted for only 1 per cent of the total reduction in net primary production of the grass *Bouteloua curtipendula* (398 mg) grown in pots with nematodes, whereas tissue removed during simulated grazing accounted for nearly 100 per cent of the reduction in NPP (see also McNaughton, 1983). Thus, a relatively small amount of matter going to support populations of below-ground herbivores may be associated with a large reduction in total energy flow through the community. This effect on productivity may be very large when the biomass of below-ground herbivores is also large and distributed throughout the plant community (see above, p. 274 ff; p. 276).

Below-ground herbivory, because of its magnitude (Table 3) and nature, may have a substantial role in ecosystem nutrient dynamics. Below-ground herbivores are in close physical proximity to decomposer organisms, and operate in an environment often favorable for decomposition. Because of this, nutrient turnover in a plant/below-ground herbivore system

should be more rapid than that in a plant/ above-ground herbivore system.

Given the large amount of soil mixing attributable to vertebrate fossorial herbivores (Andersen, in press) and the strong relationship between the population dynamics of invertebrate below-ground herbivores and the physical properties of soil, a linkage between these two groups of herbivores seems likely. Short-distance dispersal of plant-feeding nematodes (in soil or via feces: see Martin, 1969) is one potential relationship. The increases in inorganic and organic compounds noted in below-ground plant tissues parasitized by nematodes (Wang, Hodges, and Bergeson, 1975; see also MacDonald, 1979) may alter their nutritional value or palatability to fossorial rodents. Insect larvae encountered by a foraging fossorial rodent may constitute a food source of high nutritional quality, yet soil conditions brought about by the rodent's burrowing may enhance survivorship of those larvae not contacted. The relationships between and among these three major groups of below-ground herbivores constitute a rich area for exploration.

CONCLUSIONS

The below-ground parts of plants constitute an abundant and diverse set of resources for herbivores, just as do above-ground plant parts. The unique characteristics of the below-ground resource, the animals involved, and the soil environment, however, suggest that simple extrapolation of the effects of above-ground to below-ground herbivory may be seriously misleading. Data on below-ground herbivory in natural communities are meager, and thus generalizations are speculative and can best be considered a framework for hypotheses to guide future research efforts.

Below-ground herbivores appear to be distributed more patchily in space, and they may have abundances more variable in time than above-ground herbivores. The probability of attack and the form, magnitude, and impact of damage to a plant may be influenced by the specific site history and by stochastic events that influence herbivore movement and dispersal more strongly in cases of below-ground than in above-ground herbivory. The feeding ecology of many of the most prominent below-ground herbivores remains only poorly understood, but theory suggests that the high cost of locomotion for vertebrate forms should preclude their specializing in any but highly productive habitats. The production of physiologically active chemical deterrents seems to be the primary mechanism employed by plants to reduce below-ground herbivory, although changes in the levels of the fiber content of cell walls may operate as a structural deterrent against vertebrates and some insects. The necessity to continuously maintain a root system during all but the seed stage largely precludes perennial plants escaping herbivory.

Many plant species respond to the removal of root tissue by increasing the growth rate of the remaining roots and by initiating new roots. Shoot growth rate may simultaneously decrease, with the magnitude of the reduction determined by the degree of root loss. Most studies involving the removal of below-ground plant parts have considered only root removal; the effects of the removal of storage tissue on plant fitness is virtually unknown. Laboratory studies suggest that many plant species produce below-ground tissue in excess of requirements. An excess in functional capacity may be valuable for its availability in an environment where below-ground herbivory is chronic but of unpredictable magnitude. No studies have been undertaken to address any aspect of this issue in natural communities.

The few community-level studies available indicate that below-ground herbivores consume substantial proportions of the net primary production in natural communities. Furthermore, consumption and ecosystem-level effects may be highly disproportionate. Below-ground herbivores may have a major role in determining the level of energy flow through the community. Most studies have tended to focus on particular taxa; additional work is needed to describe the impact of the entire herbivore assemblage and to elucidate patterns among communities and ecosystems. Distributional data suggest temperate-zone communities may be especially influenced by below-ground herbivores, but how that influence might be partitioned between dicotyledons and monocotyledons, or between herbaceous plants and woody plants remains unknown.

The roles of vertebrate below-ground herbivores in determining plant community com-

position have been superficially examined in a few, typically highly disturbed communities, but with contradictory results. Work in undisturbed environments is needed to clarify their importance. The recent surge in studies of nematode herbivory in natural communities is promising, although grasslands seem to be the only biome receiving attention. The indirect effects of below-ground herbivory on the composition and dynamics of plant communities by means of nutrient cycling and soil modification may be great, especially in temperate areas harboring both vertebrate and invertebrate below-ground herbivores. Also in need of elucidation are the indirect interactions among members of the below-ground herbivore assemblage, and between above-ground and below-ground herbivores that can influence the susceptibility and resistance of plants to herbivore attack. Crawley (1983:343), after examining the results of experiments in which broad-spectrum insecticides were used to remove insect herbivores, concluded that vertebrate herbivores have more impact than invertebrates on plant secondary succession and plant community structure. The large increases in productivity noted when similar kinds of experiments were performed to quantify the impact of below-ground herbivores suggest, however, this conclusion may be erroneous, or at least premature.

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