Grasslands, systems analysis and man

EDITED BY

A. I. BREYMEYER

Associate Professor of Ecology,
Institute of Geography,
Polish Academy of Sciences

AND

G. M. VAN DYNE

Professor of Biology,
College of Forestry and Natural Resources,
Colorado State University

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7. Decomposer subsystem

COORDINATORS D. C. COLEMAN & A. SASSON

Contributors A. I. Breymeyer, D. C. Coleman, M. C. Dash, Y. Dommergues, H. W. Hunt, E. A. Paul, R. Schaefer, B. Ülehlová & R. I. Zlotin

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Introduction

It is our intention in this chapter to examine all major decomposition and soil heterotrophic processes in grasslands worldwide, in both tropical and temperate regions. We shall explore, in turn, such key processes as soil respiration and carbon turnover, organic matter decomposition, and turnover, and then discuss the use of simulation and other models in further understanding the principles behind the processes of decomposition kinetics in grasslands.

Our approach is principally twofold: (1) to examine the key processes of dissimilation of organic matter, noting the commonality of these processes worldwide, and (2) to make a comparison of the relative importance of these processes and the organisms responsible for them within the various habitats. Thus, the dry steppe regions have a decomposition pattern much different from the savannah regions of central and western Africa. In this regard, key abiotic factors, such as soil water and temperature, play an important role and account for a great part of the variability. We wish to emphasize the marked event-oriented responses of soil organisms to ambient climatic conditions and to stress the difficulty of understanding, through monthly or seasonal averages, the processes performed by fast-growing organisms.

By the late 1960s, it was understood that from 88 to 99% of the annual net primary production entered the soil subsystems of a terrestrial ecosystem without going through the grazers (Wiegert, Coleman & Odum, 1970). In fact, numerous studies undertaken within the IBP, and covered later in this chapter, indicate that indeed grazing by large mammal herbivores in many grassland regions does not materially alter the high percentage which goes into the decomposition and mineralization pathways of energy flow. There are some exceptions, such as the African savannas; we shall explore the reasons for this.

The close interconnections between decomposition and mineral cycling are many and complex. Pertinent data on decomposition are given, and then a decomposition sub-model is presented, illustrating the importance of these processes at the subsystem and total-system levels. The interactions between our carbon-oriented chapter and the nutrient cycling chapter of Clark *et al.* (Chapter 8, this volume) should be kept in mind.

Our concern in this chapter is to characterize, in a global fashion, decomposition processes in the approximately 25 to 30% of the earth's land area (9% of the total area) which are considered as grassland and semi-arid and arid shrubland (Reiners, 1973). Because of constraints on length we shall discuss many processes in general and emphasize some site or area data perhaps unduly. This is inevitable, reflecting biases of editors and participants who have generously given of their time and data for what has been an arduous and frustrating task.

We have considerable incentive to emphasize this portion of global heterotrophic activity. Evolutionarily, the organisms doing the majority of the work (soil microflora) had been around for billions of years before the origin of a land flora (Devonian period), and are still responsible for the assimilation of > 90–95% of the total net primary production in terrestrial ecosystems (Wiegert *et al.*, 1970).

For global and interbiome comparisons of carbon inputs and fluxes, it is imperative to have much more information on temperate and tropical savannas and dry, grazed grasslands (Reiners, 1973). We submit that virtually all terrestrial ecosystems, but particularly grasslands, are only now receiving the total-system study which they require if adequate understanding of production biology is our intent. Thus, partitioning of primary production below ground in many grasslands exceeds 75% (Coleman, Andrews, Ellis & Singh, 1976), and the amount assimilated by cattle may be only 3 to 5% of the total net primary production.

For the purpose of this chapter, we have used not only first-hand publications, covering work mostly occurring during or sponsored by IBP, but also pre-IBP books and review articles, such as those of Clark & Paul (1970), Dommergues & Mangenot (1970), Phillipson (1970), and Sasson (1972). This chapter is as cosmopolitan as any in the volume, and, we feel, reflects the true spirit underlying the International Biological Programme effort. Several of our contributors made major compilations of not only their own, but literally dozens of other workers' efforts in various parts of the world. The contributions of Úlehlová, Zlotin, Schaefer and Dommergues are especially noteworthy in this regard. Dr Zlotin provided also a complete English review of literature printed in Russian. All of the other contributors furnished considerable amounts of materials and advice as well. The able assistance of Professor Sasson in translations of papers otherwise inaccessible to me was invaluable.

David C. Coleman

Main microbial groups and activities

The microbial population in temperate grasslands

Increased attention has been paid recently to energy flow in ecosystems, with calories (or joules) being a common denominator of their diverse structural units (Odum, 1971). Theoretical yields of bacterial cells in a given system are about 0.118 g of bacterial dry matter formed under aerobic or anaerobic conditions per 1 kcal removed from the nutrient medium (Payne, 1970). The biomass of bacterial cells that could potentially be formed from the annual production of the above- and belowground biomass in some grassland ecosystems are given in Table 7.1. The total production, e.g. of the uncut plant

Table 7.1. *Calorific values of substrates and bacterial biomass in various grasslands*

Site	Plant community	Net primary production			Potential bacterial biomass ($g \cdot m^{-2}$)	Potential calorific value ($kcal \cdot m^{-2}$)
		Above ground ($kcal \cdot m^{-2}$)	Below ground ($kcal \cdot m^{-2}$)	Total ($kcal \cdot m^{-2}$)		
Ojców, Poland	*Arrhenatheretum*	1250–1360	1320–1760	3120	368	1840
Ispina, Poland	*Arrhenatheretum*	1520	1260–1680	3192	375	1875
Lanžhot, Czechoslovakia	*Serratulo–Festucetum commutatae*	1062–1912	1560–2080	3992	468	2340
Lanžhot, Czechoslovakia	*Gratiola officinalis–Carex praecox-suzae*	4847	1152–1536	4383	518	2590
Lanžhot, Czechoslovakia	*Glycerietum maximae*	4037	2592–3442	7479	873	4365
Pawnee Site, USA	*Bouteloua gracilis* shortgrass prairie	496	3290	3786	447	2235 (700)[a]

See text for details. Ranges in aboveground and belowground values reflect error estimates and variability in climate.
[a] Calculated.

community of *Glycerietum maximae*, amounts to 1009 g of aboveground and to 765 g of belowground dry matter $\cdot m^{-2} \cdot yr^{-1}$, corresponding to 4037 and 3442 kcal, respectively. The total of 7479 $kcal \cdot m^{-2} \cdot yr^{-1}$ would theoretically yield about 870 $g \cdot m^{-2} \cdot yr^{-1}$ of dry microbial biomass. In contrast, the maximum dry weight of bacterial biomass in the upper 25 cm of soil of the same plant community is about 30 $g \cdot m^{-2}$, calculated from microbial plate counts (Úlehlová, 1973). Taking into account the short generation times of the bacterial and fungal share of the biomass, it is obvious that the decomposition of dead plant matter may be restricted to rather short periods of favourable conditions of temperature and humidity. For example, if one assumes that all organic matter produced per year is subjected to microbial action, then 2235 $kcal \cdot m^{-2}$ of microbes would be produced per year. However, a more reasonable estimate for the shortgrass prairie is 700 $kcal \cdot m^{-2} \cdot yr^{-1}$, or 9.7 generations per year for an average microbial population of 65 $g \cdot m^{-2}$ at 30 cm depth (Sparrow & Doxtader, 1973). In contrast, the mixed-grass prairie microbial biomass was higher (*c.* 200 $g \cdot m^{-2}$: Clark & Paul, 1970), with an estimated turnover rate of $< 0.001\ h^{-1}$ (Shields, Paul, Lowe & Parkinson, 1973), or about 1800 $kcal \cdot m^{-2}$ in new microbial tissue alone. The turnover rate of microbial biomass on a yearly average is much lower than that attained during the short periods of microbial outbursts. A more meaningful estimate of microbial activity is obtained from total respiration measurements or mineralization rates (see Chapter 8, this volume), and it is our intent to focus on these major processes.

The microbial population in tropical grasslands

Little information is available for various tropical grasslands. Our sole entry in this chapter concerns microbial studies in a *Borassus* palm savanna, the 'Lamto' savanna on the Ivory Coast. For edaphic, physiographic and meteorological information, the reader is referred to Lamotte (1975).

Total microbial counts

Soil samples (0–10 cm) were taken at Lamto toward the end of the dry season (February and March) and of the humid season (October to November) in the unburnt as well as in the burnt savanna. They were compared by plate counts (suspension–dilution method and growth on synthetic media). It was found that fire reduced the fungal and bacterial populations, but actinomycetes increased, resulting in a higher total microbial density in the burnt savanna soil (Pochon & Bacvarov, 1973; see Table 7.2).

The dynamics of the evolution of the various microbial groups under the influence of fire are not yet known. Although the total microflora has an apparent uniformity, there is an extreme heterogeneity of fungal species in the diverse sampling sites of every habitat as well as between the unburnt and

Table 7.2. *Microbial numbers per g dry wt soil in burnt and unburnt savanna, Lamto, Ivory Coast, March 1970*

	Fungi	Bacteria	Actinomycetes	Total
Unburnt savanna	103000	945200	1901800	2950000
Burnt savanna	30600	758400	2598600	3387000

After Pochon & Bacvarov (1973).

burnt savanna soils. More than 60 species of fungi have been isolated (Rambelli, 1971; Rambelli & Bartoli, 1972; Rambelli, Puppi, Bartoli & Albonetti, 1973), some of them very uncommon (*Periconia*, *Chaetoceratostoma*, *Anguli-maya*, *Gonytrichum*). No precise relationship with soil or vegetation types has been shown; on the other hand microbial densities were relatively uniform in soil samples taken toward the end of both the dry and humid seasons.

Counts of functional groups of microbes

Physiological groups of microflora have been enumerated, but results should be interpreted with caution. Thus Pochon & Bacvarov (1973) noted that the effects of delay in sample analysis and mode of sample storage are more marked than those caused by the various local pedological, microclimatic and botanical conditions.

Table 7.3 shows mean numbers of different microbial groups for two sites on two dates. A marked variability is evident. Total microflora count in October, for example, ranged from 8×10^6 to 90×10^6 for the *Hyparrhenia* savanna and *Loudetia* savanna. In addition, these differences were not consistent with the samples' organic carbon, which varied considerably between samples. Anaerobic flora is present throughout the year, mainly in the *Loudetia* sites where drainage is poor and waterlogging heavy, as indicated by the high number of anaerobic nitrogen-fixers in October.

The variations between the samples collected in October and in May probably originated, for the *Hyparrhenia* site, from a marked increase in actinomycetes and, for the *Loudetia* site, from a marked decrease in fungi and bacteria during the dry season. The latter site seems to be characterized by a very fast and frequent shift between aerobic and anaerobic phases. In contrast to these sandy soils, the more clayey ones of the *Hyparrhenia* sites on the plateau are predominately aerobic, and the water content remains near an optimal level for a longer duration.

The wide variation in total microflora counts (unburnt savanna, dry season, for example, 3×10^6 to 3×10^7) means that sites cannot thus be characterized in an absolute way, but only compared among themselves by the amplitude and direction of the seasonal numerical variations.

Table 7.3. *Functional microbial groups in two habitats*, Borassus *palm savanna*

	Total flora	Anaerobic N-fixers	Anaerobic cellulolytic	Aerobic cellulolytic	Nitrifiers
October 1969					
Hyparrhenia savanna	8	7	1.3	5.2	1.5
Loudetia savanna	90	23	4.5	7.0	3.2
May 1970					
Hyparrhenia savanna	30	7	0.8	12.4	2.3
Loudetia savanna	20	4	2.0	16.4	4.7

After Pochon & Bacvarov (1973).
Values for total flora are $\times 10^{-6}$ g^{-1} soil, all others $\times 10^{-3}$ g^{-1} soil.

Schaefer (1978) comments on humification and microbial activities in several tropical soil types at Lamto, and the reader is referred to his paper for pertinent details of these processes.

Roles of saprophagic fauna

Temperate grasslands

The role of invertebrate saprophages in grassland functioning varies widely. Several scientists have synthesized many aspects of these functional roles (Ghilarov, 1960*a*; Müller, 1965; Tischler, 1965; Phillipson, 1970). We use a somewhat modified version of Wiegert & Owen's (1971) definition of saprophagy: namely, saprophagic fauna are considered to feed on living and dead micro-organisms and/or decaying organic detritus. Striganova (1971) characterizes activities of invertebrate saprophages as follows:

(1) In the process of feeding the animals comminute small pieces of plant tissue, creating an enormous surface area and rendering them accessible to active microbiological, physical and chemical influences.

(2) By means of their own enzymes and those from symbiotic micro-organisms, the animals split some organic substances and promote their further mineralization. Additionally, they assist in the synthesis of new organic substances and the humification of plant remains.

(3) In the process of horizontal and vertical shifts within the litter and soil, the animals redistribute organic and mineral substances inside the soil profile and promote the creation of a particular soil structure favourable to active aerobic processes of transformation of organic matter (see also Kühnelt, 1957).

Undoubtedly all forms of invertebrate saprophage activity are displayed in close interaction with soil microbial complexes. The symbiotic relations of saprophages and micro-organisms have been the subject of many special studies (see Kozlovskaya & Zaguralskaya, 1966; Stebayev, 1968; Kozlovskaya, 1970; Breymeyer, Jakubczyk & Olechowicz, 1975).

Table 7.4. *Functional characteristics of various soil invertebrate saprophagic groups*

Animal group	Mechanical destruction of litter	Mineralization (destruction of cellulose)	Primary humification
Collembola	**	—	—
Oribatei	***	—	—
Diplopoda	***	***	—
Oniscoidea	***	***	—
Mollusca	***	***	—
Enchytraeidae	**	***	—
Diptera (larvae)	***	*	*
Lumbricidae	*	—	***

From Striganova (1971).
*, Participation of one or two species.
**, Participation of several species.
***, Participation of a majority or all of the species.

In the feeding process many saprophages inoculate organic materials passing through them with bacteria and fungi. Thus, it is difficult to differentiate saprophagic and microphagic feeding modes (Ghilarov, 1965). There are three size categories of invertebrate saprophages. These are: macrofauna (lumbricids, enchytraeids, millipedes, gastropods and some insect larvae); mesofauna (Acarina, Collembola, Protura and others); and microfauna (protozoans, rotifers, tardigrades and nematodes). Functional trophic classifications of these main systematic groups of soil invertebrates are presented in Table 7.4.

The Lumbricidae carry out mechanical destruction of plant litter and partial humification of plant remains. Mineralization of litter is low where the cellulolytic microflora is scarce. Dipteran larvae destroy litter fall and stimulate microbial processes and thus mineralization and humification. Enchytraeidae, molluscs, oniscoid sowbugs and diplopods both comminute and mineralize plant tissues. Oribatei and Collembola take part only in the mechanical destruction of leaf fall; many species are typical mycetophages (but see the extensive review by Luxton, 1972). Nematodes use only the contents of cells without destroying their walls (see Nielsen, 1961). The relative proportions of the three size groups of soil invertebrates change as a function of aridity. In meadow grasslands in either tundra, forest or forest-steppe zones, the macrofauna dominates the saprophagous complex, comprising ⩾ 90% of the total saprophagic fauna biomass (Table 7.5). With increasing aridity, the dominance of the macrofauna decreases and the fraction of the biomass in the mesofauna and microfauna increases. In dry steppe ecosystems, the macrofauna comprises 35% and the mesofauna and microfauna about

Table 7.5. *Biomass of invertebrate saprophages in natural grasslands of various geographic regions in the USSR* (mean values g live weight · m⁻²)

Animal group	Taiga				Forest-steppe		Steppe		Semidesert		Tien Shan Mountains			
	Tundra[a]	Middle		South	Meadow steppe	Steppe meadow	Typical	Dry			Moist meadow	Steppe meadow	Dry steppe	Semi-desert
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Lumbricidae	60.00	27–34	111.2	26.9	82.90	26.50	18.44	4.02	—	—	49.80	19.00	0.10	—
Enchytraeidae	25.69	—	—	—	4.04	5.60	1.20	—	1.20	0.10	1.20	0.10	—	—
Nematoda	7.70	—	—	—	5.55	4.15	1.49	3.76	0.74	1.20	1.30	0.56	0.18	0.19
Collembola	2.22	—	—	—	0.41	0.62	2.03	1.34	0.11	0.09	0.32	0.38	0.16	0.01
Acarina	0.10	—	—	—	0.56	0.44	1.00	0.37	0.04	0.01	0.23	0.09	0.05	0.03
Diplopoda	—	—	—	—	2.72	7.86	0.38	0.06	—	—	—	—	—	—
Others	4.00	—	—	—	0.86	1.10	0.64	1.76	0.01	0.01	0.29	0.28	0.08	0.06
Total					97.04	46.27	25.18	11.31	2.1	1.41	53.14	20.41	0.57	0.29

Data of R. I. Zlotin.
1, meadow, Taimyr (Chernov, 1973); 2, bottomland meadow, Arkhangelsk region (Matveeva, 1966); 3, bottomland meadow, Moscow region (Matveeva, 1969); 4, meadow in valley, Moscow region (Matveeva, 1969); 5 and 6, Kursk region (Zlotin, 1969); 7 and 8, the Ukraine (Zlotin, 1969); 9 and 10, the western Kazakhstan (Zlotin, 1969); 11–14, Tien Shan Mountains, 3200–3700 m above sea level (Zlotin, 1975).
[a] Maximal values.

Table 7.6. *Energy flow through populations of soil invertebrate saprophages measured as active metabolism in kcal·m⁻²·yr⁻¹*

Animal group	Forest-steppe 5	Forest-steppe 6	Steppe 7	Tien Shan Mountains: Moist meadow 11	Steppe meadow 12	Dry steppe 13	Semi-desert 14
Lumbricidae	230	75	28	68	40	0.4	—
Enchytraeidae	30	50	8	10	2	—	—
Nematoda	180	120	220	22	16	6	—
Collembola	15	18	40	7	13	5	0.3
Acarina	11	7	21	3	3	2	2
Others	9	10	5	2	3	1	2
Total	475	280	322	112	77	14	12

Data of R. I. Zlotin.
For explanation of numbered ecosystems, see Table 7.5.

30% each of the total biomass. In semideserts a saprophagous macrofauna is almost totally absent and about 90% of all the saprophage biomass is due to the free-living nematodes. It should be noted that Protozoa are not included in these calculations; they represent from 0.2 to 0.3 g dry wt·m⁻² in North American steppes (Elliott & Coleman, 1977) and 1 to 2 g dry wt·m⁻² in mesic agro-ecosystems (Stout & Heal, 1967).

These changes in soil zoomass structure are the result of the different environmental requirements of the three groups (Ghilarov, 1965). The macrofauna requires the highest humidity and thus is abundant only in those soils having capillary-free soil water. Meso- and microfauna require less free water as they inhabit pores and natural pockets that remain constantly saturated with water, even in drier soils. The total biomass of invertebrate saprophages in grasslands ranges from < 1 to 100 g live wt·m⁻². The largest biomass is found in meadow-steppe in the forest-steppe zone (100 g·m⁻²) and decreases to 1 g·m⁻² in semideserts. Arid high-mountain grasslands (dry steppe and semidesert) have the lowest biomass level of all (approximately 0.3 to 0.6 g·m⁻²: Table 7.5).

More importantly for our estimates of ecosystem function, the energy flow through various faunal groups has been calculated (Table 7.6; see Phillipson (1970) and Zlotin (1975) for methods of calculating energy flow in these groups). The total energy flow decreased markedly with increasing aridity. Note that Lumbricidae and Enchytraeidae are very active in the most mesic sites, whereas nematodes are equally active in wet and mesic areas and continue into the drier steppes. In all cases the amount of energy flowing through the fauna (as respiration plus production) is only 10% or less of the total; as a further example, in North American shortgrass prairies the total flow

through the fauna is only *c.* 0.6% (Coleman *et al.*, 1976). This contrasts with the more faunal-dominated energy flow in tropical wet and savanna grasslands (see below).

Tropical grasslands

In the Lamto Project (Ivory Coast) the saprophagic soil meso- and macrofauna were divided into two main groups:

(1) *Consumers of more or less decomposed dead plants and animals (i.e. saprophages)*

The main consumers of undecomposed litter are the fungi-growing termites. With only a moderate mean biomass (0.49 g dry wt·m⁻²), they use not less than 1200 g·m⁻²·yr⁻¹ of dry litter. With their symbiotic fungi and bacteria they contribute to the mineralization of organic matter (Lamotte, Barbault, Gillon & Lavelle, 1974).

The rest of the saprophages (only 10% of the earthworm biomass, the Collembola, the pauropods, the diplopods, 52% of the Acari, part of the ant population (Levieux, 1971) and some Coleoptera larvae make up a chain of organic matter degradation. This chain of events includes digestion, excretion and elimination and reingestion over time, which augments the continuous microbial activity.

(2) *Earth-eating organisms (i.e. geophages)*

These organisms ingest soil particles and assimilate the debris and the more or less humified organic matter, as well as the edaphic microflora. In terms of biomass (28 g dry wt·m⁻², emptied digestive tube), the geophages predominate among the soil fauna; they are nevertheless little diversified and include essentially the enchytraeids, the earthworms, and the 'humivorous' termites.

During their period of activity – that is when soil water is > 10–20% by volume – earthworms ingest daily 5 to 30 times their own weight of soil, according to the species and the size of the individuals. The weight of dry soil recycled every year by these oligochaetes is thus estimated as 100 kg·m⁻² (Lavelle, 1973). Yet, because of the soil's deficiency in organic matter and because of their poor assimilating capacity, their mineralizing activity amounts only to 80 to 100 g·m⁻²·yr⁻¹ of detrital input.

When compared with temperate grassland populations, the savanna mesofauna of Lamto contains less enchytraeids, Collembola and Acari. In contrast, the Symphyla, Protura, Diplura and scale insects are relatively abundant. But it is the termites which characterize the tropical environment at Lamto. They are relatively less abundant than in other African ecosystems (Wood, 1976), but very much diversified (more than 50 species). The same is

true of the ants, of which there are more than 150 species exerting an influence at all trophic levels.

The consumers of living plants and saprophages, among which the fungi-growing termites play a prominent role, are characterized by the fact that they collect most of their food on the soil surface. They therefore have little effect on roots, even though these represent, after degradation by the microflora, a very important available source of food. We anticipate, however, that phytophagous nematodes may also be important, if their activity and numbers are similar to those in temperate grasslands (Smolik, 1974; Coleman *et al.*, 1976).

Activities of the soil fauna, particularly the soil oligochaetes, of tropical wet grasslands in India were studied by Thambi & Dash (1973), Dash, Patra & Thambi (1974), and Dash & Patra (1977). Oligochaete numbers reached a maximum of 7800 m^{-2} during the rainy season (September–October), while the minimum density of around 560 m^{-2} was recorded during the summer drought months of May and June. There was a significant correlation between the percentage of soil water and oligochaete numbers, and between soil temperature and oligochaete numbers. The monthly average oligochaete biomass was 8 g dry wt·m^{-2} with an annual secondary production of 35 g·m^{-2}. The energy input into the grassland site from net primary production was 7680 kcal·m^{-2}·yr^{-1}. Energy utilization by the oligochaetes was chiefly through population metabolism, growth and reproduction. Oxygen consumption, about 60 l·m^{-2}·yr^{-1}, amounted to an energy equivalence of 288 kcal·m^{-2}·yr^{-1}. The energy value of mucus production (142 g dry wt mucus·m^{-2}·yr^{-1}) was 568 kcal·m^{-2}·yr^{-1}. Oligochaete tissue production was 35 g dry wt·m^{-2}·yr^{-1}, or 162 kcal·m^{-2}·yr^{-1}. All these energy values add up to 1018 kcal·m^{-2}·yr^{-1}, which is about 13.2% of the total energy input into the study site. About 15% of the total energy assimilated by earthworms is stored in their tissue, of which 95% is subsequently used in metabolism.

The belowground invertebrate biomass in different tropical grasslands in Panama amounts to 6.3 g dry wt·m^{-2}, and this represents 78–98% of the total invertebrate biomass of the grasslands (Breymeyer, 1974). The average biomass and secondary production of oligochaetes in savannah-type grasslands in the Ivory Coast was 6.5 g·m^{-2}·yr^{-1} and 46 g·m^{-2}·yr^{-1}, respectively (Lamotte, 1975). The biomass turnover of the population was about seven times the average biomass.

Oligochaetes dominate the invertebrate biomass in tropical grasslands, and the annual population biomass turnover (five to seven times the average biomass) indicates that they are of importance in these ecosystems. It is evident from the data of the three sites studied that the total invertebrate biomass varies greatly between sites, and that perhaps the total primary production determines the total belowground invertebrate biomass.

Wormcast production and the amount of nitrogen returned to soil by the

activity of oligochaetes were studied in the Indian site (Patra & Dash, 1977). Some 77 tonnes dry wt·ha^{-1}·yr^{-1} of wormcast were produced. There were seasonal variations in rates and amounts, with lows in the summer (May and June), and maxima during the latter part of the rainy season (September and October). This huge cast production shows the rate of soil turnover and the magnitude of the processing activity of plant material through the earthworm gut.

The nitrogen returned to the soil through earthworm mucus, dead tissue and wormcasts amounts to about 72 kg·ha^{-1}·yr^{-1} – more than the requirement of crop plants. However, the amounts actually available to plants are not known. If one assumes no significant loss of nitrogen to the atmosphere, then the nitrogen returned to soil by earthworm activity and the inferred amount available to plants seems large.

Loss rate of organic matter from litter

Wiegert–Evans paired plots

The extent and rate of aboveground litter decomposition can be estimated by the method proposed by Wiegert & Evans (1964), or by various modifications of it (Łomnicki, Bandola & Jankowska, 1968; Titlianova, 1973). Table 7.7 sums up the results obtained by the Wiegert–Evans method in several IBP projects on temperate zone meadows (Jankowska, 1971; Ketner, 1973; Titlianova, 1973). The Wiegert–Evans method uses 'paired plots'. Dead material is removed from one plot of a given area and weighed at time t_0; then the dead material is removed from a paired plot of the same area some time later, at time t_1. Thus the instantaneous rate of disappearance of dead material from this plot can be calculated as:

$$r = \frac{\ln (W_0/W_1)}{t_1 - t_0},$$

where r is disappearance rate in g·g^{-1}·d^{-1}, $t_1 - t_0$ is the time in days, W_0 is the dry weight removed from the initial plot, and W_1 is the dry weight removed from the second plot. The amount of material decomposed per year often exceeds the maximum standing crop of the plant community. Thus, considerable amounts of plant material, such as dead leaves or litter of the moss layer, can enter the decomposition chain during the vegetative period after having contributed only temporarily to the standing crop. The seasonal patterns of decomposition often reflect the inputs of organic matter and in this sense are in some cases typical of the plant community. However, they mostly reflect changing environmental conditions (weather, floods, etc.).

Table 7.7. *Amount and rate of litter decomposition in grasslands (using the Wiegert–Evans (1964) method)*

Plant community	Country	Year	Litter decomposition ($g \cdot m^{-2} \cdot yr^{-1}$)	Rate of decomposition ($mg \cdot g^{-1} \cdot d^{-1}$) Min–Max	Average
Serratulo-Festucetum avennutatae dry meadow *Gratiola officinalis*	Czechoslovakia	1972	166.4[a]	3.4–9.3	6.4
Carex praecox-suzae moist meadow	Czechoslovakia	1972	375.8[a]	6.2–16.1	10.5
Junco-Caricetum extensae	Netherlands	1968	335	0–40	18
		1969	205	2–40	14
Plantagini limonietum	Netherlands	1968	235	6–20	14
		1969	310	0–16	9
Arrhenatheretum elatioris association, unmown	Poland	1965	742.9	1–16	9
		1966	776.9	1–14	9
		1967	560.0	1–14	10
Arrhenatheretum elatioris association, mown	Poland	1966	248.5	1–14	9
Tnalictro-Salvietum association	Poland	1965	498	0.8–8	5
		1966	517.6	1–13	5
Meadow-steppe	USSR (Karachi)	1968	140		
		1969	393		
		1971	90		
		1972	309		
Solonetz steppe	USSR (Karachi)	1969	156		
Calamagrostis meadow	USSR (Karachi)	1968	323		
		1969	376		
		1970	257		
		1971	303		
		1972	381		
Puccinellia meadow	USSR (Karachi)	1968	42		
		1969	292		
Grass fen	USSR (Karachi)	1968	169		
		1969	473		

[a] In $g \cdot m^{-2} \cdot 240\ d^{-1}$.

Litter mesh bags

Another method for assessing decomposition is that of the 'litter mesh bag', described by Witkamp & van der Drift (1961). The data obtained by the 'litter mesh bag' method on a *Junco-Caricetum extensae* association in Holland (Ketner, 1973) can be used for a simple comparison of litter input and decomposition rate. If the decomposition of litter continued for a month at the average rate actually measured, i.e. 14 $mg \cdot g^{-1} \cdot d^{-1}$, then 113.4 g, or 42%

of the 270 g (2-year average) of litter originally available, would be decomposed, and 53.5 g of bacterial biomass (see p. 613) would be formed. Thus more than one-third of the annual litter input can be decomposed during a single outburst of microbial activity. Similar conclusions can be drawn from the data for 1970.

None of the methods is error-free. Thus, for instance, the packing of material in the bag as well as the efficiency of its contact with the soil may vary considerably. There is also a nonlinearity between time of exposure and the litter decomposed. Estimates of decomposition using the litter mesh bag are usually lower than those obtained by the Wiegert–Evans method.

The litter mesh bag method was used in studies on the decomposability of different plant materials. In the Leningrad region, Miroshnishchenko, Pavlova & Ponyatovskaya (1972) found that in most grassland species the leaves are the part most easily decomposed, followed by the rootlets, roots and stems. The decomposition of *Alchemilla monticola* material was the fastest and that of *Alopecurus pratensis* the slowest. Ten-Chak-Mun & Fedorova (1972) showed that the decay of roots is the fastest in the tallgrass species of Sachalin, with the exception of *Fagopyrum sachalinum*. Differences between materials originating from different plant species were also observed.

Zlotin (1971, 1974) and Zlotin & Khodashova (1974) tried to differentiate various types of decomposition by using bags with different mesh sizes and by chemically excluding microbial activity with an organic microbistatic compound (toluene). They found that 24% of the litter was decomposed by abiotic processes alone, principally photochemical oxidation, 28% (an additional 4%) when micro-organisms were present, and 34% (an additional 6%) when the participation of saprophagic macrofauna was possible. Thus, about 70% of the total litter decomposition was the result of abiotic factors (principally ultraviolet and blue light at wavelengths < 500 nm, as determined by selective filters), and only about 30% was due to the saprophagous microbes and animals. While these data are intriguing, inferences about contributions of abiotic factors to decomposition should be viewed with caution because of the difficulty of maintaining complete sterility of litter treated with an organic microbistatic compound (toluene).

An experiment to test the roles of abiotic and biotic factors in decomposition was recently carried out on the northeastern Colorado prairie (Pawnee Site) (Vossbrinck, Coleman & Woolley, 1978). Samples of blue grama grass litter were placed in 1 mm or 53 μm nylon mesh bags. The large mesh allowed meso- and microfauna to enter, the small mesh allowed only microfloral activity, and the narrow mesh with saturated mercuric chloride and copper sulphate additions (for microbistasis) had abiotic activity only. Bags were retrieved over a 9-month period. By the end of 9 months only 8% dry weight had been lost from 'abiotic' bags, 15% from bags with microflora alone and 18% from bags with flora and fauna.

As the Kursk Station (USSR) site of Zlotin is at a lower elevation, with higher precipitation, and thicker litter layer than the Pawnee (all factors tending to favour biological activity), the contrast in experimental results is striking and as yet unexplained.

Cellulose materials

More defined materials, such as cellulose, have been used as substrates in mesh bags instead of litter. Soviet workers have used cotton and linen material, while in Europe and North America an analytical grade of filter paper or cotton-wool is usually preferred. Most data on microbial activities in grassland ecosystems have been obtained with several modifications of the mesh bag method (Petrova, 1963; Yershov, 1966, 1972; Hundt & Unger, 1968; Tesarová & Úlehlová, 1968; Řehořková, Kopčanová & Řehořek, 1968; Naplekova, 1972; Zaguralskaya, Yegorova & Smantser, 1972; Zlotin & Chukanova, 1973). Hundt & Unger (1968) studied the rate of cellulose decomposition in 44 types of grassland ecosystems in East Germany. The microbial activity was generally very low in wetland plant communities such as *Caricetum fuscae* and *Cladietum marioci*, somewhat higher in *Scirpetum silvatici* and *Caricetum gracilis*, and very high in *Glycerietum maximae* and *Phalaridecum arundinaceae*. High rates of cellulose decomposition were measured in wet meadows (*Alopecuretum*), i.e. 23 to 55 mg·d^{-1}, with low rates in *Molinietum caeruleae*. In moist meadows the decomposition was usually good (*Trisetetum*, *Arrhenatheretum*). It was low in dry plant communities growing on sand (*Corynephoretum*), while in dry communities on loess or loamy soil (*Brachypodietum*, *Stipetum*) it was relatively high. Very low cellulose decomposition rates were observed in the alpine grassland biomes in the western part of the High Tatra Mountains (Rusek, Úlehlová & Unar, 1975).

The vertical gradients of cellulose decomposition in grassland soils were studied by Zlotin & Chukanova (1973). The highest rates of cellulose losses were generally found in the upper soil layer, i.e. 0 to 10 cm (Table 7.8), but the zone of maximum cellulose decomposition may shift from the upper soil layer in the spring to the lower parts of the soil profile in summer and fall under the influence of changing moisture and, probably, temperature conditions.

In the USA, a series of litter bag decomposition studies were carried out on nine IBP Grassland Biome Sites. Burials of bags containing Whatman filter paper spanned the years 1969–73, with most data generated in 1971–2. Nearly 900 bags were buried to ensure adequate replication at each retrieval time (retrievals were designed to be after about 20% loss, in increments, across the growing season).

With few exceptions, mean decomposition rates followed climatic and production figures (Table 7.9), with Pawnee Site having the lowest and Osage Site the highest, the two values being significantly different (Tukey's Q test) at the

Table 7.8. *Intensity of cellulose decomposition in meadow-steppe in a watershed; expressed as losses in % dry weight per month (Kursk station)*

Location	Season			Mean monthly loss in year
	Spring–summer	Summer–fall	Fall–winter–spring	
Surface				
Litter	2.2	2.0	0.2	1.3
Soil	4.4	4.4	1.3	2.7
In soil				
0–10 cm	21.1	8.5	4.1	8.7
10–20 cm	11.7	13.0	1.3	6.2
20–30 cm	8.2	10.0	1.0	4.6
0–30 cm	13.7	10.5	2.1	6.5

5% level. Osage, the one mesic site, differed significantly from all others at the 10% level.

Because of extensive variations in dry matter losses, both within and between retrieval dates, differences must be very large to be detected in the analysis of variance. Thus only the desert grassland (Jornada) showed a significant ($P < 0.10$) effect of burial date, with all retrievals from 22 January averaging 0.13 g·month^{-1} while those after 26 June averaged 0.31 g·month^{-1}. Jornada's growing season does not begin until late July.

Several sites showed significant differences in weight losses on various retrieval dates. Cellulose buried on 19 July 1972 at Pawnee Site, showed high losses (0.14 g·g^{-1}·month^{-1}) by 9 September, reflecting the effects of the mid-summer rains, while retrievals after 21 November showed monthly losses of half that size. Osage, in contrast, showed significant differences between mid-May and mid-June retrievals following mid-April burial, but these, like the more mesic Cottonwood Site had relatively large loss rates of 0.04 to 0.05 g·g^{-1}·month^{-1}.

Field experiments using cellulose strips at the Canadian Matador Station (Saskatchewan) and associated sites were of two types (Biederbeck *et al.*, 1974). The first type, termed 'single placement', was designed so that all cellulose strips were placed in the soil at the beginning of the experiment and replicates were removed at subsequent sampling dates. This type of experiment should effectively evaluate cumulative cellulose decomposition by a population of micro-organisms allowed to establish over the period of the experiment. The second type of experiment, termed 'replacement', was set up so that cellulose strips were left in the soil for 3- or 4-week periods only, at consecutive intervals during the season. This type of experiment should evaluate the initial attack of micro-organisms on new cellulose being introduced to the soil at different times during the season. Particularly in grassland, and

Table 7.9. *Abiotic, primary production and soil respiration information on North American and Eurasian grassland studies (all production values in g C·m^{-2}·yr^{-1})*[a]

Country, Site Reference	Vegetation type[a]	Temperature (°C)			Precipitation (mm)		Annual net primary production	CO_2-C output (g·m^{-2}·d^{-1})		
		January mean	July mean	Annual mean	Annual total	Growing total		Minimum	Maximum	Annual
USA, Tucker Kucera & Kirkham (1971)	Tallgrass	1	25	13	900	594	452	0.10	2.84	452
USA, Osage May & Risser (1973)	Tallgrass	3	27	15	1000	600	398	0.5	4.15	593
USA, Cottonwood V. Lengkeek (personal communication)	Mid-grass	−7	24	9	385	280	344	0.25	3.5	215
Canada, Matador Redmann (1978)	Mid-grass	−13	20	4	388	251	242	0	4.3	120 (18 May–30 Sept.)
USA, Pawnee D. C. Coleman (unpublished data)	Shortgrass	−4	23	10	300	240	197	0.25	2.34 (1972) 3.43 (1973)	227
USA, ALE Wildung *et al.* (1975)	Bunchgrass	−2	24	13	158	34	150[b]	0.18	1.21	165
USA, Jornada E. E. Staffeldt (personal communication)	Desert grass	4	26	16	277	125	252	1.0	5.0	NA
USA, San Joaquin J. Pigg (personal communication)	Annual	6	27	15	486	454	375	0.85	3.25	NA
USA, Bridger T. Weaver (personal communication)	High mountain	−8	15	1	960	125	136			NA
USA, South Carolina Coleman (1973)	Old field				1010	700	420	0.30	2.28	409
USSR, Kursk Zlotin (1974)	Forest-steppe zone meadow-steppe	−8	19	5	512	332	568			572+
USSR, Tien Shan Zlotin (1975)	Dry steppe	−20	8	−4	230	180	71			
Poland, Kazuń meadow Kubicka (1973)	*Arrhenatheretum*	−5.7	19.5	7.5	600		301	0.80	1.83	
Poland, Strzeleckie meadow Breymeyer (1971), Breymeyer & Kajak (1976), Kubicka (1973)	*Stellario-Deschampsietum*	−5.7	19.5	7.5	600		279	0.87	1.20	
Czechoslovakia, Lanzhôt Tesarová & Gloser (1972)	*Gratiola-Carex*	−1.5	20	9.5	585	365	538	1.93	3.90	441+ 150 days

[a] Tallgrass is dominated by *Andropogon gerardi* and *A. scoparius*; mid-grass by *Agropyron smithii* (Cottonwood), and *Koeleria cristata* and *Stipa* sp. (Matador); shortgrass by *Bouteloua gracilis* and *Artemisia frigida*; bunchgrass by *Agropyron spicatum*; desert grass by *Bouteloua eriopoda*; annual by *Bromus mollis*; high mountain by *Festuca idahoensis*; old field by *Andropogon virginicus* and *A. ternarius*; meadow-steppe by *Bromus riparius* and *Stipa pennata*; dry steppe by *Festuca kryloviana* and *Ptilagrostis subsessiliflora*.

[b] Total root C = 240 g.

to some extent in cultivated land, both types of cellulose decomposition are proceeding continually. New leaves, stems and roots, constantly being added to the decomposer cycle, are undergoing initial attack; decomposition of material previously attacked also continues, so that the cumulative phase of decomposition is constantly in progress.

Cumulative percentages of decomposition of the cellulose strips in natural grassland (single placement experiment) are shown in Fig. 7.1. Less than 35% of the cellulose had been decomposed during the 15-week period in the untreated area, and the rate of decomposition was similar at both the 5 and 25 cm depths. The rate of decomposition was higher in the irrigated, fertilized and irrigated + fertilized plots. The highest rates of decomposition were recorded in the area receiving irrigation only, where close to 70% of the cellulose had disappeared after 15 weeks. It is postulated that the increased plant growth on the irrigated + fertilized plots resulted in increased transpiration and dried the top soil layer, but left residual moisture at 25 cm. As a result, decomposition was limited to some extent by lack of water at 5 cm, but not at 25 cm. With irrigation alone, the drying effect of added plant growth was not as great; consequently, the rate of decomposition at the two depths was similar.

The second type of experiment (replacement) was designed so that the cellulose strips were left in the soil for 3 or 4 weeks and then replaced with new strips. This type of experiment measured the rate of initial attack on new material at intervals throughout the season. In the natural grassland treatments the rates of decomposition were low in May and early June when soil water was adequate but temperatures were too low for maximum microbial activity. The maximum rates occurred in late June and July when soil water levels were still high and temperatures were high enough to produce conditions that were probably close to the optimum for the populations of microorganisms. In August and September the rates of decomposition declined sharply again to reach minimum values in September (Table 7.10). This decline in microbial activity was apparently correlated with the drying out of the soil in mid-summer. To facilitate comparison with the single placement experiment, percentages of decomposition for the 3- or 4-week intervals were also expressed on a cumulative basis over the season. When this was done, it was found that the cumulative curves for percentages of decomposition for the two types of experiments were quite similar, but that the final cumulative percentages were greater for the replacement experiment.

In the experiments described above the weight loss of cellulose was expressed as a percentage of the initial weight before placement on an ash-free basis. This method of calculation underestimates the amount of decomposition, however, because frequently the undecomposed cellulose is impregnated with fungal hyphae and bacteria that cannot be removed by washing. A method for correcting the percentage of decomposition was developed by using the

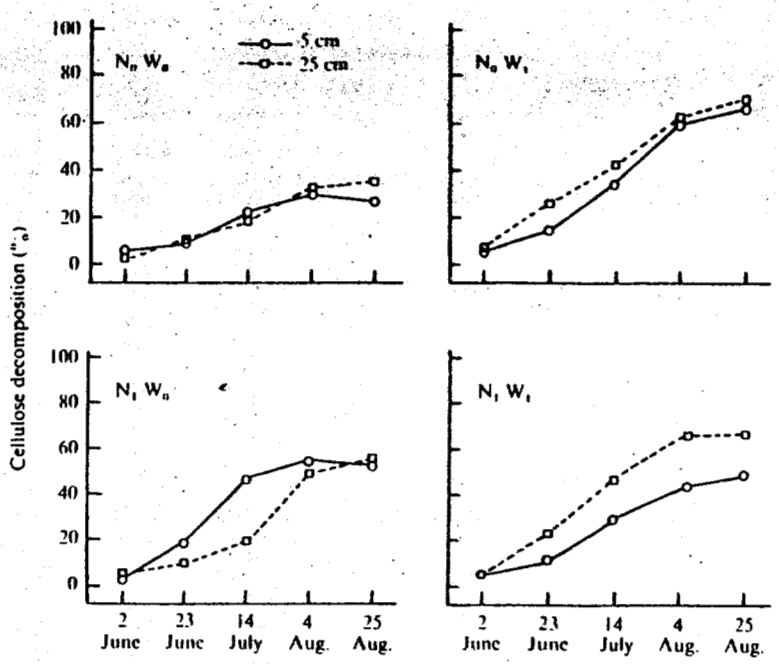

Fig. 7.1. Cumulative percentages of decomposition of cellulose strips in Matador natural grassland. All strips were put in place on 12 May 1971. N_0W_0, untreated; N_0W_1; irrigated; N_1W_0, fertilized; N_1W_1, fertilized and irrigated. (After Biederbeck *et al.*, 1974.)

phosphorus content of the recovered cellulose strips as an indicator of the amount of microbial biomass present. The phosphorus content was measured after the trace amount initially present in the cellulose itself was estimated, so it was possible to calculate (by addition) that portion of the phosphorus that originated from microbial biomass (Biederbeck *et al.*, 1974).

The same technique was also employed to estimate microbial yield coefficients (i.e. milligrams microbial biomass produced divided by milligrams substrate consumed in terms of carbon). Yield coefficients estimated from the replacement experiments averaged 0.40 for the 5 cm depth and 0.38 for the 25 cm depth (assuming a 2:1 ratio of fungal to bacterial biomass).

The loss rate of cellulose filter paper in tropical conditions was measured in the Panamanian savannah (Breymeyer, 1978). The decomposition rate was found to be relatively low in the top horizon (0 to 10 cm) of the soil (Table 7.11), being 3.76 $mg \cdot d^{-1}$ for the seed reservation and 2.62 $mg \cdot d^{-1}$ for the pasture. This corresponded to 7.84 $mg \cdot g\ cellulose^{-1} \cdot d^{-1}$ for the reservation and 5.73 $mg \cdot g\ cellulose^{-1} \cdot d^{-1}$ for the pasture.

Interesting results were also obtained in Panama in an experiment on the decomposition of standing plant material. Filter paper hung among the grasses, particularly that which was close to the ground, was decomposed at

Table 7.10. *Comparison of mean percentages of cellulose strip decomposition per week (strips replaced at 3- or 4-week intervals) in Matador natural grassland, 1971*

Depths (cm)	Treatment	Sampling dates: 2 June	30 June	28 July	25 Aug.	24 Sept.	Means
0–10	Untreated	1.50	1.44	3.37	0.82	1.46	1.72
	Irrigated	1.15	6.99	5.67	2.10	0.42	3.27
	Fertilized	1.37	6.48	5.02	3.21	0.61	3.34
	Irrigated + fertilized	1.89	4.30	5.01	3.84	1.65	3.34
	Means	1.48	4.80	4.77	2.49	1.03	2.91
20–30	Untreated	0.83	0.93	3.97	3.33	1.26	2.06
	Irrigated	0.79	8.62	9.57	4.28	1.08	4.87
	Fertilized	1.48	4.36	4.31	0.84	0.42	2.28
	Irrigated + fertilized	2.03	4.92	5.80	5.00	1.87	3.92
	Means	1.28	4.71	5.91	3.37	1.16	3.28

After Biederbeck *et al.* (1974).

Table 7.11. *The rate of cellulose decomposition in the soil of Panamanian grasslands*

Time of exposure	Seed reservation (mean loss) $mg \cdot d^{-1}$	Seed reservation (mean loss) $mg \cdot g^{-1} \cdot d^{-1}$	Pasture (mean loss) $mg \cdot d^{-1}$	Pasture (mean loss) $mg \cdot g^{-1} \cdot d^{-1}$
17–24 August 1971	2.92	5.91	3.70	8.05
17–28 August 1971	5.98	12.44	2.53	5.23
17 August–2 September 1971	4.50	9.18	2.39	4.97
17 August–7 September 1971	1.64	3.85	1.87	3.85
Mean	3.76	7.84	2.62	5.73

After Breymeyer (1978).
The experiment was carried out over a period of 21 days in the rainy season. Cellulose was buried in the top 0–10 cm of soil. Each value is the mean of 5 samples.

a relatively high rate. More than 50% of the grass was decomposed above the ground. Such a high decomposition rate of standing vegetation results primarily from favourable conditions of temperature and humidity. This is in marked contrast to dry steppeland conditions in North America and Eurasia, where probably much less decomposes as 'standing dead'.

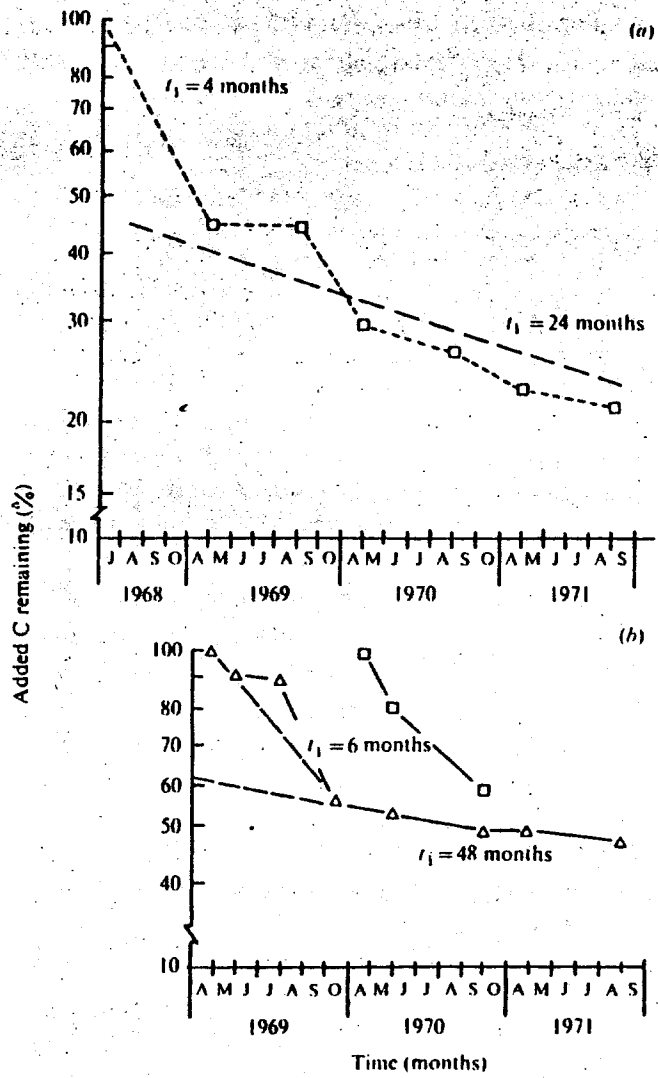

Fig. 7.2. (*a*) Decomposition of ^{14}C-labelled wheat straw on a cultivated field. (*b*) Degradation of native vegetation on the surface of natural untreated grassland soil at Matador, Saskatchewan, Canada. Time shown does not include freeze periods. For explanations see text. (After Biederbeck *et al.*, 1974.)

^{14}C-labelled straw

Further experiments using labelled wheat straw and labelled shoots of natural grasses were carried out to measure the rate of decomposition of plant residues. In these experiments the distribution of ^{14}C throughout various fractions of soil organic matter was determined at intervals as decomposition progressed (Biederbeck *et al.*, 1974).

The decomposition curves for straw added to field soil and grass shoot material added to the surface of natural grassland soil depart from a simple exponential pattern (Fig. 7.2). The losses were biphasic: first a rapid initial loss of easily degradable plant components, followed by a much slower release of more resistant components.

The ^{14}C-labelled straw added in 1968 degraded rapidly in 1968, but remained unchanged during the summer of 1969. Further degradation in 1970 and 1971 continued at a slower rate, particularly during the summer periods. Straw added in the spring of 1971 decomposed more slowly in plots sown to wheat than in similar fallow plots.

Very little loss of the ^{14}C added in natural grass occurred during spring and early summer of 1969 when rainfall was low. However, rapid decomposition in autumn resulted in a half-life of 6 months for ^{14}C added during the first season. Subsequently, the rate of loss was slower with a half-life of approximately 48 months of growing season or almost 8 years under natural field conditions. Decomposition of grass added in May 1970 followed a pattern similar to that observed in 1969.

The labelled carbon was found initially to occur largely in the recognizable plant material. As the label disappeared from this fraction, there was a corresponding increase in label in the organic material of $> 0.2\ \mu m$, and after 2 years about 50% of the residual labelled carbon was found here.

Carbon dioxide evolution as an indicator of decomposition

Carbon dioxide production is another internal measure of soil biological activity, including microbes, fauna and roots (Macfadyen, 1970). A number of methods of measurement using outflow (dynamic) or diffusion (static) techniques have been employed, and their strengths and weaknesses reviewed (Haber, 1958; Domsch, 1962; Dommergues, 1968; Ino & Monsi, 1969; Schlesinger, 1977). Field data show carbon dioxide production to be an important carbon output from terrestrial ecosystems.

It is our intention to examine critically the carbon dioxide flux from a wide variety of grasslands (20 or more), over a wide gradient of temperature and moisture regimes. In the temperate and tropical localities we have examples ranging from mesic to xeric conditions. Temperature regimes remain more similar in tropical than in temperate localities, however.

In the following pages we present data on net primary production (NPP), precipitation, mean air/soil temperatures and soil carbon dioxide evolution. Where possible, a comparison is made between yearlong NPP and carbon dioxide evolution. In many cases there is information only for a few months during the year. We further compare and correlate daily carbon dioxide outputs with soil water and temperature regimes to determine the proportion of total variability accounted for by these abiotic factors.

Contributions of roots and litter to 'soil respiration'

Total soil respiration represents the activity of several biotic groupings. Even before IBP studies it was generally assumed that the soil fauna contributes < 10% of the total carbon dioxide output (Macfadyen, 1970). There is considerable disagreement, however, over the amount of carbon dioxide which is due to root respiration – in effect a 'maintenance cost' for plant nutrition and storage tissue below ground. Thus Jagnow (1958) estimated a range of 9 to 90% for roots in various plant communities; Wiant (1967) calculated root respiration in a spruce forest as 50% of the total respiration; and Mina (1960) estimated that the roots of several broad-leafed and coniferous trees accounted for 33 to 36% of the total. Recent estimates of root respiration activity in grasslands worldwide include 8–17% for *Andropogon* old fields (Coleman, 1973), 19% for mixed-grass prairie (Warembourg & Paul, 1977), 40% for tallgrass prairie (Kucera & Kirkham, 1971), and 15–51% (mean 32 ± 6%) for meadow and steppe in Europe (Zlotin, 1974). Interestingly, these values compare closely with Lundegårdh's (1924) estimate of about 30% for root respiration in a North European mesic grassland.

There is no room in this review for further exposition and commentary on the differing techniques used by various workers. However, as there is a general convergence of several findings at values of 20–30%, we will use this figure and take the remaining 70–80% as being due to heterotrophic activity in grassland soils worldwide. As will be seen, this should enable us to estimate carbon input–output for a variety of habitats, comparing season- or yearlong decomposition activities.

Tropical savanna soil respiration

The experiments on the Lamto tree savanna soils were done using the technique of Lundegårdh (1924), with Hilger's (1963) modifications: carbon dioxide was absorbed *in situ* under a jar (after Schaefer, 1979).

Experiments were performed *in situ* in some savanna sites characterized by the dominance of either *Loudetia simplex* or Andropogonae grasses. Respiration of bare soil in the savanna was compared with that of soil covered by vegetation (Table 7.12). Cumulative evolution (over 20 days) as well as circadian rhythms of respiration and temperature (Figs. 7.3 and 7.4) were measured.

The differences observed from one year to another reflect not only different water contents in the soil at the time of the experiments, but also reflect the previous rainfall regime. There was significant respiratory activity at just above the permanent wilting point, e.g. in February when the soil humidity under *Loudetia* was near 0.5% (dry soil) or 7% of the field capacity. Evolution of carbon dioxide from ferruginous tropical soil under a cover of

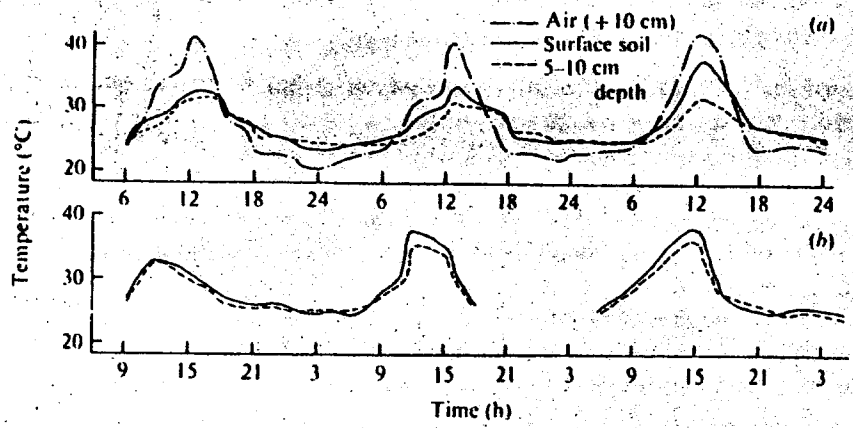

Fig. 7.3. Circadian rhythm of temperature: (*a*) *Loudetia* savanna, 9–12 October 1969, and (*b*) *Hyparrhenia* savanna, 20–23 October 1969. Station of tropical ecology, Lamto, Ivory Coast. (After Schaefer, 1979.)

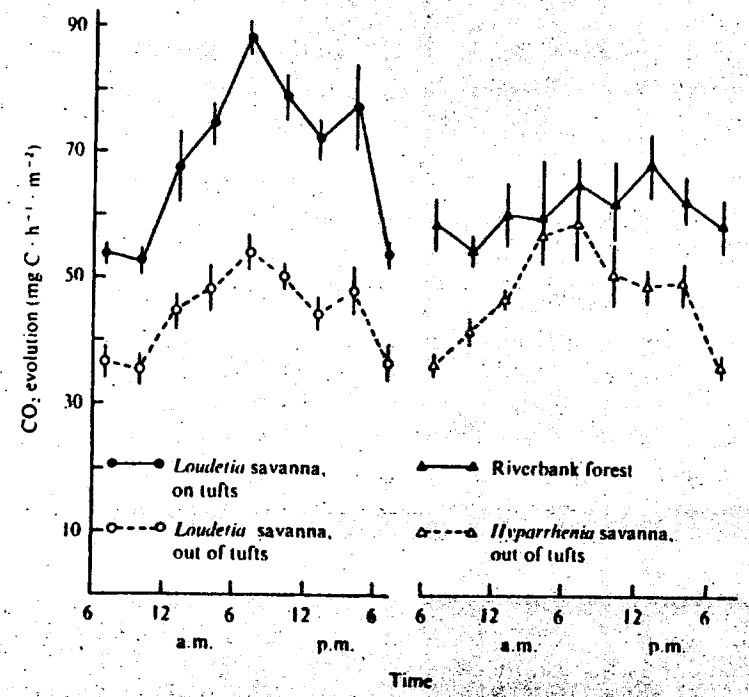

Fig. 7.4. Circadian rhythm of carbon dioxide evolution, October 1969. Type days, with standard error of the mean. Savanna and riverbank forest soils. Station of tropical ecology, Lamto, Ivory Coast. (After Schaefer, 1979.)

Table 7.12. *Soil respiration, in situ, in three habitats of the Lamto Site, Ivory Coast*

Habitat	Date	Soil respiration		Water content	
		mg C·d⁻¹·m⁻²	g C·yr⁻¹·m⁻²	% dry soil	% field capacity
Loudetia (Hydromorphic sandy soil)	Oct. 1969[a] (bare soil)	1108	404	10	100
	Oct. 1969 (soil + vegetation)	1723	629	10	100
	Oct. 1973	601	216	10	100
	Oct. 1973 (vertisol)	1831	659	20	100
	Nov. 1970	2100	767	7	100
	Dec. 1970	1999	558	6.8	97
	Jan. 1971 (before bushfire)	1530	558	2.5	36
	Feb. 1971 (after bushfire)	1110	405	0.5	7
Andropogonae (ferruginous tropical soil)	Oct. 1969	1192	435	10	100
	Oct. 1973	1966	708	10	100
Riverbank forest	Oct. 1969	1485	542	15	100

After Schaefer (1979).
[a] Absorbent used: 1969, sodium hydroxide; 1970–1, limed sodium hydroxide (= sodium hydroxide × 3); 1973, barium hydroxide.

Hyparrhenia and the vertisol under *Loudetia* were similar (Fig. 7.4). Determinations were made with bare soil (between the tufts of the grasses), soil covered with vegetation, and soil cleared of the roots.

Activity at the level of the tufts (Fig. 7.4) reflected the rhythm of the plant's physiological activity: directly from root respiration and indirectly from microbial respiration due, in part, to the energy from root exudates. The bare soil still reflected this rhythm; here a remote rhizosphere effect added to the thermal stimulation. The bare soil of the *Hyparrhenia* site had a little more activity than that of *Loudetia* vegetation, under which the thermal effect was less marked.

Temperate grassland soil respiration

A wide variety of temperate grassland sites was sampled for soil respiration, ranging from moist mesic meadow tallgrass to arid shortgrass–bunchgrass steppe and desert and annual grassland. To facilitate comparison of organic

matter carbon inputs and carbon dioxide carbon outputs, these data are presented (Table 7.9) along with pertinent air temperatures and precipitation information.

A general pattern of decreasing production and decomposition with decreasing rainfall holds across all the sites. Other data on Central European and Russian studies are incorporated in Table 7.9, or commented on below.

Tesarová & Gloser (1972) estimated by alkali absorption that the soil carbon dioxide production in a *Gratiola officinalis/Carex praecox-suzae* plant community was 7–14 $g \cdot m^{-2} \cdot d^{-1}$ during the vegetative period and an average of 10.8 $g \cdot m^{-2} \cdot d^{-1}$. Kubicka (1973) measured the carbon dioxide production in Kazunskie and Strzeleckie meadows, Poland (*Arrhenatheretum* and *Stellario-Deschampsietum* communities, respectively), using the method of Walter (1951) and Haber (1958), and found that during the vegetative period it varied from 2.9 to 6.7 $g \cdot m^{-2} \cdot d^{-1}$ for *Arrhenatheretum* and from 3.2 to 4.4 $g \cdot m^{-2} \cdot d^{-1}$ for *Stellario-Deschampsietum*. This technique was non-quantitative, however, as the surface:volume ratio of absorbent in the jar was too low to absorb all the carbon dioxide (Domsch, 1962). Ten-Chak-Mun & Fedorova (1972) studied the carbon dioxide produotion of soils under natural conditions in Sachalin by the method of Makarov (1957). The ranges encountered during the vegetative period corresponded to 4.3 to 7.3 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ in the communities of tallgrasses and to 1 to 5 g $CO_2 \cdot m^{-2} \cdot d^{-1}$ in the shortgrasses. The maximum production occurred in mid-summer, coinciding with the period of the most intensive plant growth.

For simulation and regression model studies, the effects of soil water and temperature were investigated further.

Abiotic factors affecting soil respiration

This study was undertaken to determine the feasibility of regressing carbon dioxide evolution on soil temperature and water. R. K. Steinhorst & D. C. Coleman (unpublished data) used a general-purpose multiple regression model of the form:

$$y\,(CO_2 \text{ evolution}) = a + b_1 \ln x_1 + b_2 \ln x_2,$$

where x_1 and x_2 are soil temperature and soil water, respectively, and a, b_1 and b_2 are parameters. The combined fit was usually good for all of the western North American sites. The coefficient of determination, multiple R^2, usually exceeded 0.60 (Table 7.13). The logarithm of temperature was entered first (underlined values) for Osage (tallgrass) and ALE (Pacific northwest bunchgrass) but with markedly different effects. For Osage, a mesic site, there was little effect of adding water in the equation, whereas the ALE (arid site) equation showed a strong multiplicative effect (addition of two log values) of temperature and water. This effect is discussed in detail by Wildung *et al.*

Table 7.13. *Abiotic factors affecting soil respiration in North American sites*

Site	Year	Treatment[a]	*N*	ln water	ln temperature
Osage (tallgrass)	1971	G	30	0.67[b]	0.54
		U	30	0.75	0.71
	1972	G			
		U	20	0.49	0.49
Cottonwood	1972	U	11	0.24	0.24
Matador (mid-grass)	1970	U	8	0.37	0.40
	1971	U	8	0.23	0.38
ALE (bunchgrass)	1971	G	20	0.72	0.17
		U	20	0.76	0.15
	1972	G+U	116	0.60	0.21
Pawnee (shortgrass)[c]	1971	U	80	0.64	0.71
	1972	U	80	0.82	0.82
	1972	G	80	0.78	0.79
	1973	U, D	20	0.31	0.55
	1973	U, E	12	0.80	0.80

[a] Treatments: G, grazed; U, ungrazed; D, control area; E, irrigated only. For further explanation see text.

[b] The underlined R^2 values are for a single independent variable – the first entered. Multiple R^2, with both ln water and ln temperature included in the equation, are not underlined.

(1975) who note that this 'hydrothermal' effect, recorded by earlier European workers, is well described by the statistical relationship given above.

Other drier sites, including Cottonwood, Matador & Pawnee (Table 7.9), shifted to a water response foremost (Table 7.13). The shift in response in the Pawnee irrigated treatment is of interest. Total net primary production increased 228 % to 449 g $C \cdot m^{-2} \cdot yr^{-1}$, effectively shifting from the water response of dryland to a 'wetland' response of a tallgrass prairie.

As a preliminary step in determining whether a balance exists between annual litter and root decomposition and carbon dioxide output during an annual cycle of biological turnover, the data of Kokovina (1972) were used (Table 7.14). The total respiration for the 8 months of the warm season (2100 g $CO_2 \cdot m^{-2}$) corresponds to 7350 kcal, assuming approximately 3.5 kcal per g CO_2 (Zlotin, 1975). In comparison, studies in the US/IBP Grassland Biome have shown an average respiratory quotient (RQ = moles CO_2 evolved/moles CO_2 consumed) of 0.7 for shortgrass prairie soil cores (Klein, 1977). Thus 0.7 mol $CO_2 \cdot$ mol O_2^{-1} (oxycalorific equivalent = 4.8 kcal $\cdot l^{-1}$) gives a value of 15.7 l CO_2 = 107.5 kcal. This calculates to 1 g CO_2 = 3.49 kcal, an interesting convergence in international usage. From this quantity saprophagic organisms get about 4900 kcal and roots 2450 kcal, or 30%. After independent estimations of the annual input of organic remains, there is a balance in the ecosystem of about 1100 $g \cdot m^{-2}$ (Afanasieva, 1966; Drozdov & Zlotin, 1974), from which roots get about 64% and

Table 7.14. *Summed flow of carbon dioxide from soil (typical chernozem meadow-steppe watershed, Kursk) measured over 1964–70 by Kokovina (1972).*

	Months								
CO_2 outputs	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Sum[a]
mg $CO_2 \cdot m^{-2} \cdot h^{-1}$	200.0	466.0	550.0	610.0	530.0	305.0	120.0	90.0	2100
g $C \cdot m^{-2} \cdot d^{-1}$	1.32	3.08	3.63	4.03	3.50	2.01	0.79	0.59	572

[a] Sum: $g \cdot m^{-2}$ across April–Nov. period. (Unpublished data of R. I. Zlotin.)

aboveground biomass 36%. Assuming 1 g of plant litter corresponds to 4.5 kcal and annual input comprises 4950 kcal $\cdot m^{-2}$, the calculation shows very close conformity (within 50 kcal or 1%) of the annual carbon dioxide flux with the annual input of litter. Interestingly the Kursk meadow steppe respiration of 2100 g CO_2 = 572 g C was quite high (excluding output during the four colder months). This productivity was higher than for either tall-grass prairie site in North America (Table 7.9).

The amount of carbon dioxide efflux was higher than the organic carbon input in the range of 40 to 60%. It is probable that in soils with higher amounts of carbonates (steppes, semideserts and other semi-arid grasslands) a considerable amount of carbon dioxide is formed as a result of physico-chemical decomposition of salts such as calcium carbonate, magnesium carbonate and others (Zlotin, 1975). This abiotic carbon dioxide flux must be subtracted during calculation of the carbon dioxide from biological turnover. It is also necessary to account for a quantity of root exudates and exfoliates which may be considerable (Coleman, 1976), and the production of biomass of algae (Shtina, 1968) and autotrophic micro-organisms. Accounting for the possible variance in errors in the construction of a balance between annual carbon dioxide flux and yearly input of organic matter thus becomes a real problem.

Calculations of the balance of carbon dioxide output and litter and root decomposition were carried out for the high-mountain dry steppe and semi-desert of Tien Shan (Zlotin, 1975). The value of current carbon dioxide from the soil for a year comprised 70 to 90% of the annual input of plant litter (above and below ground).

Ecosystems with large contents of calcium carbonate in the soil (Kursk) had a large release of carbon dioxide observed not only from the humus horizon, especially the upper 0 to 30 cm, but also from carbonate horizons to a depth of 200 cm (Fig. 7.5; Zlotin, 1975). Microbial numbers at that depth are extremely small (Bondarenko-Zozulina, 1955), and invertebrates are also very scarce (Ghilarov, 1960*b*; Zlotin, 1969), and as any roots were removed

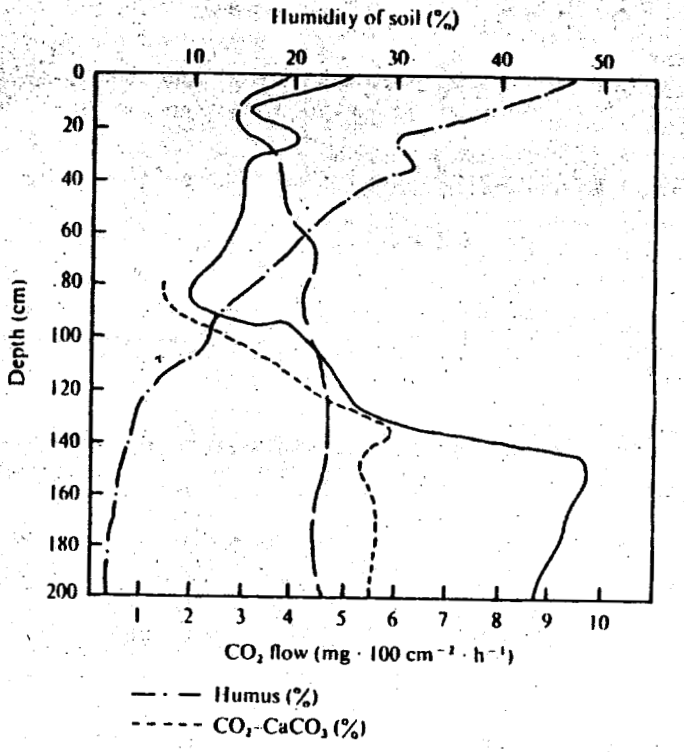

Fig. 7.5. Carbonate contents; carbon dioxide flow, humus content and soil humidity in a typical chernozem meadow-steppe watershed (Kursk). (After Zlotin, 1975.)

from the soil in these experiments a sizeable carbon dioxide flux from deep soil horizons may be explained only by physicochemical processes of disintegration of carbonates. Thus the abiotic portion of the carbon dioxide flux from a whole soil profile may reach 60% in carbonate chernozems and in typical chernozems about 30%.

Soil enzymes

It is well known (Skujins, 1967) that many biological transformations occurring in soil are catalysed by enzymes found outside living soil organisms. These enzymes are often named free enzymes (Kiss, Dragan-Bularda & Radulescu, 1972), soil enzymes (Kuprevich & Shcherbakova, 1966), or sometimes extracellular enzymes (Dickinson & Pugh, 1974).

Modern investigations of soil enzymes are presently oriented toward the study of fundamental problems such as their origin and localization (e.g. Burns, Pukite & McLaren, 1972*a*; Ladd & Paul, 1973) or stabilization by inorganic and organic colloids (e.g. Burns, El Sayed & McLaren, 1972*b*), or

towards discovering new enzymes (e.g. Tabatabai & Bremner, 1970; Kiss & Dragan-Bularda, 1972). However, numerous systematic investigations were concerned with the variations in activity of various enzymes in different types of ecosystem. Most of this systematic work is related to cultivated soils, but there is a small body of work on grasslands. Here we will present only a critical review, illustrated by examples, and examine the three following points: methodology, influence of environmental factors, and the role of soil enzymes in decomposition processes.

Methodology

Comparison of results found in the literature is hampered by four difficulties.

(1) Lack of precision regarding the sampling site. If the sampling depth is indicated, it is often not defined whether rhizosphere or nonrhizosphere soil is being considered. Such information is important because of the rhizosphere effect on the activity of soil enzymes (Koslov, 1964; Voets & Dedeken, 1966). As this imprecision is common, one concludes that the published analyses have been done on soil samples made up of variable proportions of rhizosphere and nonrhizosphere soils, the rhizosphere soil being evidently more important in the case of grassland than in the case of weedless cultures.

(2) Storage of samples. The content of enzymes varies during the course of transportation and drying. It is clearly desirable that the analysis be run as soon as possible after the sampling, so as to correspond exactly to the content *in situ*. Unfortunately, this precaution has not always been taken by most authors.

(3) Methods of titration. These methods vary to a great extent, particularly as far as the techniques of sterilization are concerned (Skujins, 1967).

(4) Expression of results. These vary markedly, and results are often expressed differently for the same enzyme activity. Conversions from one unit into another may cause problems if certain methodological indications are lacking.

In the examples given here, the following units have been adopted:

(*a*) Saccharase (invertase) activity is expressed in μmol reducing sugars (glucose)·g soil^{-1}·24 h^{-1}.
(*b*) Amylase activity is given in μmol reducing sugars (glucose)·g soil^{-1}·96 h^{-1}.
(*c*) Urease activity is expressed in mg NH_3-N·g soil^{-1}·3 h^{-1}.
(*d*) Asparaginase activity is given in mg NH_3-N·g soil^{-1}·21 h^{-1}.
(*e*) Phosphatase activity is expressed in mg phosphate·g soil^{-1}·3 h^{-1} (method of Hoffmann, 1967).

In conjunction with examples of enzyme activity, we have chosen to present some data on dehydrogenase activity. In this context it should be

stressed that the measure of dehydrogenase activity, as it is generally used, is not a measure of enzymatic activity but a measure of overall soil biological activity, just as is the evolution of carbon dioxide or the absorption of oxygen. The dehydrogenase activity has been expressed here in μmol of TPF (formazan) formed by the reduction of TTC (triphenyl tetrazolium chloride)·g soil^{-1}·24 h^{-1}.

Enzyme content in soils of grasslands and environmental factors acting at this level

Table 7.15 shows, for some grasslands, the activity of some enzymes usually tested, e.g. dehydrogenase (AD), invertase (SAC), amylase (AMY), urease (URE), asparaginase (ASP) and phosphatase (PHO). From this table, as from more detailed studies (e.g. Kuprevich & Shcherbakova, 1971; Pancholy & Rice, 1973), it is clear that three groups of factors govern enzyme activity in grassland soils: vegetation, climate and edaphic factors.

In the tropical environment the enzyme activity of grassland soils is consistently lower than that of forest soils. Thus, at Lamto, Ivory Coast, the invertase, amylase, urease, asparaginase and phosphatase activities of grassland (savanna) were respectively 23.0, 26.3, 0.05, 0.24 and 0.19, as against 31.8, 44.0, 0.14, 0.57 and 1.00 in forest soils (Bauzon *et al.*, 1977). In a temperate environment the situation seems, in general, to be reversed since the soils of grassland biomes are characterized by much higher enzyme activities than are those of forest biomes. This fact has been emphasized in particular by Pancholy & Rice (1973) in the framework of a comparative study between soils corresponding to three types of plant associations which recolonize formerly cultivated fields (old-field succession) in Oklahoma and Kansas.

Viewed in the framework of a given biome, it is much more difficult to show *in situ* the particular effect of each plant species on the enzyme activity of soils. Thus Ross & Roberts (1970) could not detect this specific influence when they compared grasslands showing variable proportions of grasses and legumes (essentially clover). The difficulties encountered when studying the effect of the plant species *in situ* are possibly a consequence of the interaction of numerous environmental factors.

Edaphic factors exert an influence chiefly through enzyme-protecting substances contained in the soil. That is why a positive correlation could be detected between enzyme activity (especially that of invertase) and soil organic carbon content (e.g. Ross & Roberts, 1970). The low clay content (5 to 6%) of the grassland soils at Lamto partly explains their low enzyme activity (Bauzon *et al.*, 1977). Other soil characteristics seem to be involved equally when they play the role of limiting factors. Thus low exchangeable potassium in Lamto soils caused a very low level of asparaginase activity (Bauzon *et al.*, 1977).

Table 7.15. *Biological characteristics of soils, including enzyme activities (nos. 3–8), from grassland ecosystems in tropical and temperate regions*

Country	Type of soil	Biome ecosystem	1 pH	2 C/N	3 AD	4 SAC	5 AMY	6 URE	7 ASP	8 PHO	References
Ivory Coast (Lamto)	Ferruginous - tropical soil on sandy colluvium	Grassland with *Hyparrhenia* sp. and *Loudetia* sp.	6.4	15.9	0.28	23.0	26.3	0.05	0.24	0.19	Bauzon *et al.* (1977)
Central African Republic	Slightly ferrallitic soil	Grass savanna	5.8 6.1	—	—	—	—	—	1.14 0.45	— —	Mouraret (1965)
Tunisia	Sierozem	Artificial	7.9	11.6	0.13	317.0	—	—	—	—	Bauzon *et al.* (1968)
Southern France (Montpellier)	Mediterranean red soil	Grassland with *Brachypodium ramosum*	8.8	10.5	—	214.6	63.4	0.46	—	—	J. Cortez (personal communication)
New Zealand	S_4 Wakiwi	Mixed grassland with grasses (70–87 %) and legumes (10–20 %)	6.0	11.7	3.17	184.3	4.7	—	—	—	Ross & Roberts (1970)
	C_4 – 2 Ngaumu		5.7	14.3	2.74	155.5	31.2	—	—	—	
	C_4 – 2 Pirinoa		6.0	10.4	2.30	169.9	47.2	—	—	—	
	C_8 – 4 Levin		6.0	11.1	2.59	128.1	31.2	—	—	—	
	N_4 Mangawheau		5.4	10.5	2.16	126.7	35.7	—	—	—	
Australia (New England)	Krasnosem	Grassland with grasses and legumes	5.2	—	—	—	—	0.31	—	—	McGarity & Myers (1967)
	Chocolate		5.7	—	—	—	—	0.22	—	—	
	Yellow podzolic		5.5	—	—	—	—	0.08	—	—	
	Gley podzolic		5.3	—	—	—	—	0.07	—	—	
	Red-brown earth		6.0	—	—	—	—	0.16	—	—	

AD, dehydrogenase; SAC, invertase; AMY, amylase; URE, urease; ASP, asparaginase; PHO, phosphatase.
In order to make the comparisons easier between data from different sources, the original units have been converted into units as defined in the text. In the case of the slightly ferrallitic soil of the Central African Republic and in the case of the Mediterranean red soil, the two extreme values of the variables are given and not the mean as in all other cases.

The influence of climate may be approached at two levels. At the level of the seasons, in a given ecosystem variations in enzyme activity can appear. But the amplitude of these variations is smaller than that caused by variations bound to climatic zonation. The theory of zonality (Mishustin, 1964) of bacterial or fungal micropopulations seems to be applicable in the case of enzymes (Table 7.15), where a striking difference between tropical biomes and temperate biomes may be seen. The enzyme activity of tropical soils is in general very low. The principal determining factor is temperature, as suggested by the *in vitro* study of Cortez, Lossaint & Billes (1972) and the comparison carried out *in situ* by Ross & Roberts (1970). The latter authors have compared enzymic activities in a sequence of five New Zealand soils (Wakiwi, Ngaumu, Pirinoa, Levin and Mangawheau) located in ecological conditions identical except for their mean annual temperatures, which were respectively 9.7, 11.4, 12.5, 12.9 and 13.4 °C. The invertase activity decreases from 184.3 to 126.7 and their dehydrogenase activity fell from 3.17 to 2.16 on going from the coldest to the warmest soils. These results indicate that the higher the temperature, the more active is the degradation of soil enzymes (in the range of temperatures remaining compatible with the activity of soil micro-organisms). Under these conditions the question arises whether enzymatic processes are less active in tropical environments than in temperate ones. It is possible but not certain that the low enzyme activity of tropical soils may be compensated for by the fact that the more favourable temperature conditions allow these enzymes to be active for longer periods during the year.

The existence of significant negative correlations between annual rainfall and the invertase activity in New Zealand soils suggests likewise the possibility that rain may also be an influencing factor (Ross & Roberts, 1970).

Role of soil enzymes in decomposition processes

What are the relative roles of living micro-organisms (acting through their own enzymes) and of soil enzymes in decomposition processes? This question is important because of its implications when interpreting results concerning soil enzyme activity. Indeed, one may be aware of instances in which living micro-organisms (e.g. cellulolytic fungi) play a major role in a decomposition process (cellulolysis) whereas the free enzymes (free cellulases) are not active enough to intervene. In such cases no conclusions can readily be drawn from the enzyme analysis.

Thus far, this problem has only been approached by experimenting with soils incubated in the laboratory (Durand, 1965; Paulson & Kurtz, 1969). Using multiple regression analysis, the latter were able to show that, in the model system investigated, 79 to 89 % of the variations in hydrolysis of urea could be attributed to free soil enzymes adsorbed on clays. To our knowledge, no study of this type has been conducted on grassland soils.

The contribution of root versus microbial enzymes to the total soil enzyme 'pool' remains problematic. Thus Kuprevich & Shcherbakova (1966) assert that root-elaborated enzymes are indeed much more prevalent, while other authors are less certain.

Conclusions

Our present knowledge about the free soil enzymes of grassland ecosystems is essentially limited to comparisons between these and forest ecosystems and to the role of various environmental factors (plants, climate and soils) on the soil enzyme activity. This knowledge is obviously insufficient. In order to improve on it, it is necessary (1) to develop laboratory investigations on the origin of soil enzymes and on their fundamental mechanisms, mainly the processes by which they are protected, and (2) to develop a reliable field methodology with regard to sampling and analytical methods, which should further be strictly standardized.

Conceptual and simulation models

It should be apparent by now that the impressive array of taxa involved in saprophagic heterotrophy are, in terms of their functional role in grassland ecosystems, as yet inadequately understood. Microflora are too often enumerated by plate counts, and direct counts in the literature are seldom informative on the total numbers or biomass which are active (Parkinson, Gray & Williams, 1971). Certain soil fauna have been studied in considerable detail, particularly the mesofauna (Harding & Stuttard, 1974), while the functional roles of important macroarthropods, such as termites, and microfauna, such as Protozoa, are just beginning to be elucidated.

At the current level of our understanding it is necessary to view overall processes, looking for general effects of driving variables, such as available soil water, temperature regimes and the quality of organic substrates. An important conceptualizing and integrating tool is the simulation model. One subsection of the total-system ELM grassland model (Hunt, 1977) is concerned with decomposition and it is briefly presented below.

The model (Fig. 7.6) has a series of state variables (boxes) and flows (arrows between boxes). The computer calculates flows and changes in state variables on a 1-day time step.

The three principal types of substrates in the model are humic material, faeces and dead plant and animal remains. The plant and animal tissues are further divided into labile (rapidly decomposing) and resistant (slowly decomposing) fractions. The initial nitrogen content of a given substrate predicts the proportion of rapidly decomposing material within it. Decomposition rates for each type of substrate are then predicted from temperature,

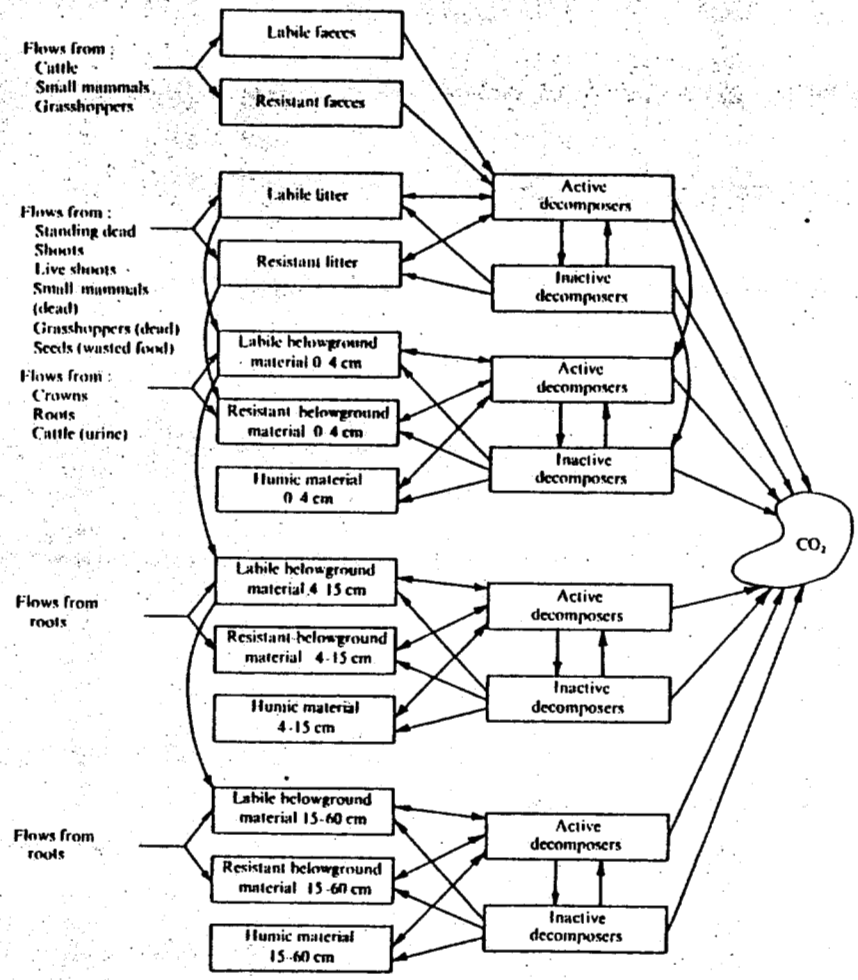

Fig. 7.6. Compartment diagram for the decomposition submodel of ELM. (After Hunt, 1977.)

water tension and inorganic nitrogen concentration (Hunt, 1977). To facilitate manageable yet meaningful population dynamics, all microbes are pooled, irrespective of taxonomic category, and only the active decomposer fraction assimilates substrate. Certain fractions of the microbes die from freezing and drying or from starvation (Fig. 7.7). The model suggests considerable recycling of material, with almost half the substrate decomposed consisting of dead microbes.

For a comparison of the model's predicted carbon and energy flow with a data-based analysis of saprophagic energy flow, we compared a 1972 model-

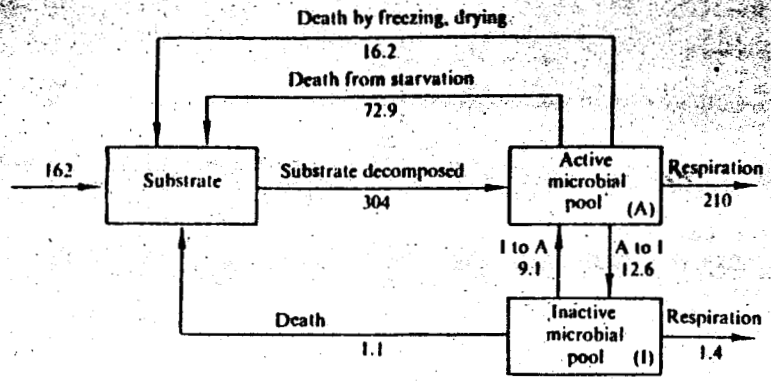

Fig. 7.7. Simulated carbon budget for decomposers on the ungrazed treatment (Pawnee Site, Colorado) in 1972. Numbers on the arrows are g C·m^{-2}·yr^{-1}. (After Hunt, 1977.)

run with the energy flow in a lightly grazed pasture in 1972 (Coleman *et al.*, 1976). Total carbon inputs in the field were determined from 'peak–trough' calculations of shoot and root biomasses. Total carbon dioxide output was based on measurements of carbon dioxide evolution taken in warm and cool months, and extrapolated by an optimization routine described in Coleman *et al.* (1976) (Table 7.16).

During the 1972 model-run (ungrazed treatment only), 162 g C of new plant and animal material were put into the system, with 304 g C total substrate decomposed, reflecting up to 60% microbial assimilation efficiency (Payne, 1970) and repeated feeding of later microbial populations on earlier ones. Fig. 7.8 shows the correspondence between observed and predicted carbon dioxide output from the soil. The predicted values are highly correlated ($P < 0.01$) with the data. The predicted output of carbon as respiration, 775 g CO_2, is equivalent to 2706 kcal when converted to oxygen uptake (respiratory quotient = 0.7). Data-based estimates of saprophagic carbon dioxide output on the ungrazed treatment totalled 2318 kcal·m^{-2}·yr^{-1}, which when compared with the predicted output show a discrepancy of 14%. This is a moderate disparity for the assumptions involved in calculating yearlong carbon dioxide output from the data could easily be out by 15 to 20%.

The model, in its interaction with other parts of the total-system model, is serving to emphasize areas where more work is needed. For example, with abundant evidence that root production and turnover events are more marked and complex than previously thought (Coleman, 1976), we have considerable incentive to develop new intertrophic approaches to the study of ecosystem dynamics. Thus microbial turnover and elemental uptake, particularly in the rhizosphere regions discussed by Dommergues (p. 640), are virtually unknown in a field context. The belated recognition of the important role of mycorrhizas in ecosystems, and certainly grasslands and shrublands, is

Table 7.16. *Energy flow in a lightly grazed pasture, Pawnee Site, 1972* (1 steer per 10.8 ha)

Energetic parameters	kcal·m^{-2}		% of NPP	
Gross primary production	5230			
Net primary production	3452			
Above ground	517		15.0	
Below ground (crowns and roots)	2935		85.0	
Heterotrophic production (P) and respiration (R)	P	R	P	R
Above ground	6.0	29.6	0.2	0.8
Herbivores (total)	5.8	27.8		
Cattle	3.2	22.2		
Carnivores	0.2	1.8		
Below ground	720.9	2347.5	21.0	68.0
Herbivores (total)	16.4	25.9		
Carnivores	1.1	3.6		
Saprophages (total)	703.4	2318.0	20.5	67.1
Microbial saprophages	700.0	2302.0		
Saprophagic nematodes	2.8	14.5	0.08	0.4
Other saprophagic grazers (excluding Protozoa)	0.6	1.6	0.02	0.05
Net heterotrophic production or respiration	727.0	2377.7	21.1	68.9

From Coleman *et al.* (1976).
All values in kcal·m^{-2} per time period. For primary production this was 154 days; for poikilotherms and cattle 180 days; for saprophagic production and respiration and all other homoiotherms 366 days.

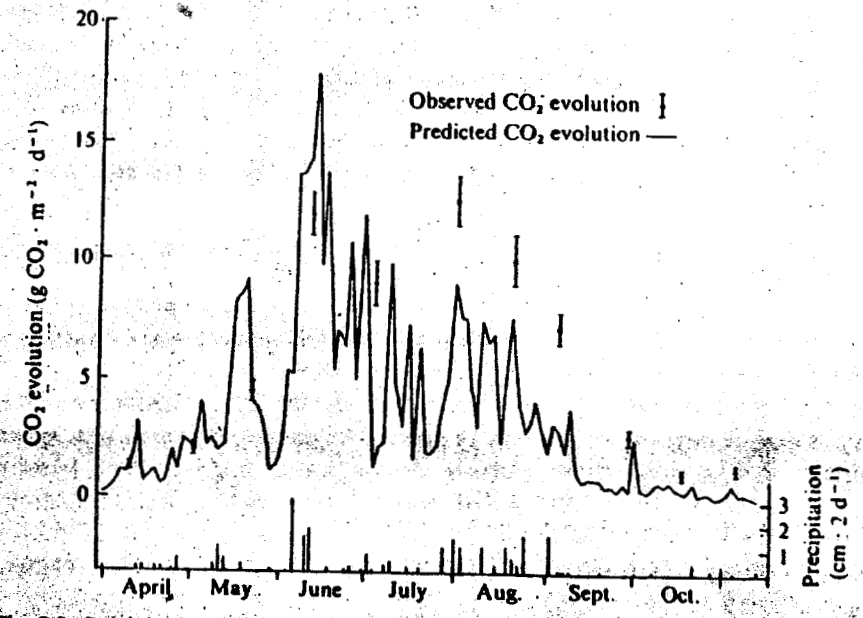

Fig. 7.8. Precipitation and carbon dioxide evolution at Pawnee Site in 1972. Bars indicate 95% confidence limits. (After Hunt, 1977.)

important, and should lead to new interdisciplinary plant function–decomposition and elemental cycling in ecosystems (Sanders, Mosse & Tinker, 1975). Indeed, it may have been mandatory for the mycorrhizal habit to develop in Siluro-Devonian times to enable a land flora to become successfully established (Pirozynski & Malloch, 1975).

Thus our major need for future work in grasslands, indeed in all biomes, is a more unified viewpoint of ecosystem operation, including an appreciation of the importance of decomposition and other heterotrophic processes in system maintenance and function.

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