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TÖRMÄLÄ, T.: Structure and dynamics of reserved field ecosystem
in central Finland 3

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Structure and dynamics of reserved field ecosystem in central Finland

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This study deals with the plant community, decomposition activity, soil fauna and field-layer fauna of reserved fields in central Finland, with special attention to primary production, herbivory, succession, trophic structure and management of reserved fields. In addition, when five methods were evaluated experimentally, suction sampling was the most reliable for sampling most field-layer arthropods.

After abandonment, reserved fields were colonized by weeds typical of open cultivations. The plant community gradually became meadow-like; and after ten years of secondary succession, the proportion of big forbs (*Filipendula*, *Geum*) increased rapidly in the relatively moist main study field. Generally, the species of early successional stages were more r-selected than were those of later successional stages.

Dicotyledonous *Achillea ptarmica* decomposed faster than did graminid species. Decomposition rate was determined mainly by moisture. About one-third of the plant litter produced annually decomposed during the snow period.

The biomass of consumers, especially that of herbivores, increased with successional age of the field. Leafhoppers were the most important aboveground herbivores. By biomass, earthworms were most important decomposer animals.

The impact of herbivores on primary productivity was assessed. They obviously increased the rate of nutrient circulation and biomass turnover.

The net aerial primary production was increased by mowing in early July. Ploughing (in late May) had no effect on the net primary production, but it created a weed dominated community.

The ecosystem of a successional reserved field is compared to its initial state (cropland) and to stable climax grasslands (American prairies).

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1. Introduction

Grasslands cover 23 % of the land surface of the globe and provide man with the major part of his food supply (Coupland 1979a). Owing to their great economic importance and relatively simple structure, grasslands are the most intensively studied terrestrial ecosystems. Grassland is a broad concept that includes a wide spectrum of habitats (meadows, pastures, old-fields, croplands, prairies, tropical grasslands etc.). They all, however, share a common feature: the dominant vegetative component is comprised of herbaceous species. Consequently, there is a single major vegetation layer.

Coupland (1979a) divides grasslands into six categories on the basis of climate, successional status and land-use. Prairies and other temperate natural grasslands (1) are usually controlled and maintained by climatic conditions or, to a lesser extent, by edaphic factors and they are under variable grazing pressure by ungulates. They are stable climax ecosystems, in contrast to semi-natural grasslands (e.g. pastures (2) and meadows (3)), which occur in the regions of forest climate and are maintained in early successional stages by grazing, mowing and other means induced mainly by man. They are dominated by perennial graminoids mostly native to the region. If the controlling factors are eliminated, semi-natural grasslands develop through successional old-fields and eventually become climax forests typical of the climate and soil of the region. Tropical grasslands (4) are segregated from temperate grasslands. Coupland (1979a) recognises two types of arable grasslands, namely, those seeded to perennial forages (5) and those planted to annual crops (6). When cultivated fields (e.g. croplands) are abandoned, their succession is basically similar to that in semi-natural grasslands.

The number of abandoned fields (reserved or old-fields) increased rapidly in Finland with the Field Reservation Act of 1969. The Law of Restrictions in Land-Use was established to relieve over-production problems in agriculture. By the end of 1974 8 % of the cultivated land was reserved and thus subject to secondary succession. Reserved fields can be regarded as semi-natural meadows (3) in Coupland's (1979a) system. Cessation of cultivation has drastic effects

on functioning of the ecosystem. Principal primary producers, numbers of weed and pests, nutrient status etc. are no longer controlled by man; the composition and development of the communities are now determined by natural ecological processes.

One of the main objectives of the International Biological Programme (IBP) was to investigate the structure and function of the grassland ecosystem. The IBP study of the grassland biome included about 55 different sites in 20 countries around the world. The most comprehensive studies were made in the United States and Canada. Some of the data accumulated in 1969-1975 have been gathered into handbooks (Heal & Perkins 1978, Innis 1978, Coupland 1979a, French 1979, Breymeyer & Van Dyne 1980). Successional old-fields received considerable interest before the IBP especially in the United States (e.g., Golley 1960, Odum 1960, Wiegert & Evans 1964, Golley & Gentry 1965, Nicholson & Monk 1974, Bazzaz 1975, Wiegert & McGinnins 1975).

Studies of the ecology of reserved fields were initiated in 1973 in the Department of Biology, University of Jyväskylä. The use and management (Hokkanen 1979), as well as the early succession of floral and faunal communities have been discussed in detail elsewhere (Hokkanen & Raatikainen 1977a, b).

The aim of this study was to document the main characteristics of successional reserved field ecosystem in central Finland. Special attention has been paid to primary producers, herbivores, succession, and ecosystem structure. The effects of two kinds of treatment (mowing and ploughing) were also assessed. To allow comparisons the approach and methods have been similar to those in the IBP studies.

Data published in the following reports have been used in this synthesis:

- I Törmälä, T. & Raatikainen, M. 1976: Primary production and seasonal dynamics of the flora and fauna of the field stratum in a reserved field in Middle Finland. - *J. Scient. Agric. Soc. Finland* 48: 363-385.
- II Törmälä, T. 1977: Effects of mowing and ploughing on the primary production and flora and fauna of a reserved field in central Finland. - *Acta Agric. Scand.* 27: 253-264.

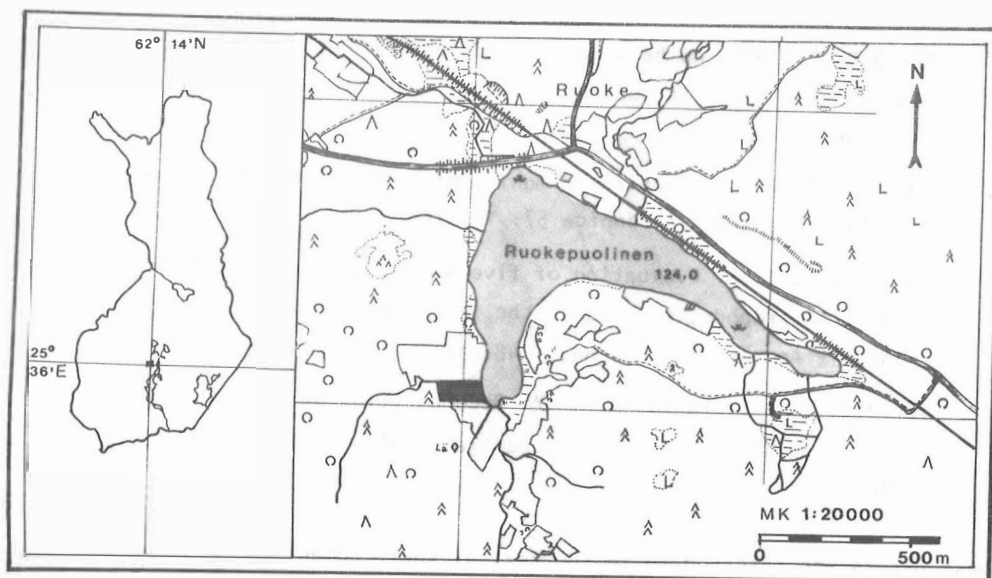
- III Törmälä, T. 1979: Numbers and biomass of soil invertebrates in a reserved field in central Finland. - J. Scient. Agric. Soc. Finland 51: 172-187.
- IV Törmälä, T. 1980: The bird community of reserved fields in central Finland. - Ornis Fennica 57: 161-166.
- V Törmälä, T. 1982: Evaluation of five sampling methods of field layer arthropods, especially the leafhopper community, in grassland. - Ann. Entomol. Fennici 48: 1-16.
- VI Törmälä, T. & Eloranta, A. 1982: Decomposition of dead plant material in an abandoned field in central Finland. - Ann. Bot. Fennici 19:

These papers are referred to in the text by their Roman numerals. In addition, unpublished data have been used.

2. Study areas

The main study field (Ruoke) is situated in the rural commune of Jyväskylä (62°14' N, 25°36' E). The six hectare field with open ditches is limited by a lake and mature *Myrtillus*-type spruce forest (Fig. 1). The field had been established about 1920 but has lain uncultivated and unmanaged since 1969. The soil is fine sand; pH of the soil (0-9 cm) was 5.66 (S.D. = 0.11) in 1981. Vegetation, invertebrates and small mammals were sampled (I, III, V, VI) from six adjacent strips (0.6 ha), in which oat had been the last cultivated crop (1968). The strips slope towards the lake ca. 3.6 m per 100 m.

The management experiment (II) was made in Konttila in Muurame (62°10' N, 25°33' E). The experimental plots were situated on two adjoining strips limited on two sides by mature *Myrtillus*-type forest. The contract on field reservation had been signed in 1972. The open-ditch strips had sandy soil and last been sown in barley. On both strips two sets of three 10 x 10 m plots were established. From each block one plot was ploughed in early summer, one was mown in the beginning of July, and one was left unmanaged.



△ = 1, △ = 2, ○ = 3

Fig. 1. Location of the main study field (Ruoke). The study area is blackened. 1 = spruce, 2 = pine, and 3 = broad-leaved trees dominated forest. Ruokepuolinen is a lake.

Censuses of the bird communities were made (IV) in the whole clearing of Ruoke and Konttila as well as in 20 other reserved farms (see Hokkanen & Raatikainen 1977a, b) in Jyväskylä, Jyväskylä rural commune, Petäjavesi, and Uurainen.

3. Material and methods

3.1. Vegetation

Aboveground vegetation (aerial vegetation, shoots) was sampled using the harvest method (Milner & Hughes 1968). Vegetation was clipped at ground level from 0.25 m^2 areas delimited by a metal circle. Detached plant litter was included in the samples. Belowground parts of the vegetation were sampled to a depth of 20 cm using corers with an area of 100 or 150 cm^2 . In meadows the roots of some plants may penetrate deeper than 20 cm, but probably more than 90 % of the biomass was obtained (cf. Linkola & Tiirikka 1936, Golley 1960, Wiegert & Evans 1964). The sampling programme is given in Table 1.

Table 1. Sampling programme.

Subject	Site	Year	Methods	No. of sampling dates	Sample size/ date
Vegetation	Ruoke	1973-74	harvest	9	20
-"-	-"-	1978	-"-	1	20
-"-	-"-	1979	-"-	1	10
-"-	-"-	1980	-"-	1	8
-"-	-"-	1981	-"-	1	10
Decomposition	Ruoke	1978-79	4 methods	10	10 (5 for specific litter)
Field layer arthropods	Ruoke	1973	suction	8	20
-"-	-"-	1978	-"-	2	7,10
-"-	-"-	1980	-"-	2	10
Method experiment for arthropods	Ruoke	1978	5 methods	2	10
Soil arthropods	Ruoke	1976	5 methods	4	10
Birds	20 fields	1974	study area	1	20
-"-	Ruoke, Konttila + 17 others	1979	-"-	1	19
-"-	Ruoke + 16 others	1980	-"-	1	17
-"-	Ruoke	1981	nest searching	1	1
Small mammals	Ruoke	1973	live trapping	6	100 traps
Management experiment	Konttila	1975			
- vegetation			harvest	5	3x8
- arthropods			suction	5	3x16

The green parts of plants were sorted according to the species or, in a few cases, to generic level (*Agrostis*, *Carex*). Belowground parts of the vegetation were separated from soil using a water jet and a set of sieves. No attempt was made to distinguish between live and dead roots or rhizomes. The crowns and roots were not separated (see, e.g., Sims & Coupland 1979). All results are expressed in dry weights (including ash) or energy contents per square meter.

There are numerous ways of computing an estimate of the net aerial primary production from harvest data. Peak biomass of green plants is the most conventional one, but it ignores the fact that different species reach their maximum biomass asynchronously. In unmanaged reserved fields summation of green peak biomasses of individual species was used. This method has also been criticized recently: in some cases it may overestimate (Wiegert & McGinnis 1975) or underestimate the actual primary production (Sims & Coupland 1979). However, it is considered to be one of the best methods for determining net production of shoots (Singh et al. 1975, Sims & Coupland 1979).

The following procedures were developed on managed plots (II) for estimating the net aerial primary production:

Ploughed plots:

- (1) $P = B_1 + B_5$, where B_1 is the green biomass in early summer before the ploughing; B_5 is the final biomass in mid September. The procedure was justified because virtually no withering was observed in the gradually recovering vegetation before the last sampling date.

Mown plots:

- (2) $P = B_2 + B_5 - B_3$, where B_2 is the total green biomass before cutting; B_3 is the same immediately after cutting (stubble); and B_5 is the final biomass in the autumn. Because some species withered before the last sampling date, the following modification was considered to be more reliable:

- (3) $P = B_2 + \sum b_{i\max_{4,5}} - B_3$, where $b_{i\max_{4,5}}$ is the larger biomass of the i^{th} species on the fourth and fifth sampling dates.

None of these or other conventional procedures account for losses due to leaching of organic compounds or herbivory. Thus the estimates refer to apparent net production aboveground.

The difference between maximum and minimum biomass was used as an estimate for production of underground parts of vegetation (Coupland 1979b). This as well as the summing of significant positive increments (Lauenroth 1979) leads to an underestimate because, e.g., within-season mortality is ignored (Singh et al. 1980).

3.2. Decomposition

Disappearance of dead plant material was studied in Ruoke using four methods (VI):

- 1) Litterbag method. Four kinds of litter (*Agrostis capillaris*, *Deschampsia cespitosa*, *Achillea ptarmica*, and unsorted litter) were enclosed into 15 x 25 cm (mesh size 1.25 mm) white nylon bags. The first set of bags filled with a weighed amount of the previous year's litter was placed among undisturbed litter on the ground after the snow had melted. A second set of bags with newly withered plant material was introduced in autumn. The bags were collected for weighing at intervals of 11-31 days during the snow-free period and also the next spring.
- 2) Harvest method. Mass data for plant litter obtained by using the harvest method were used when applying (as, e.g., Abouguendia & Whitman 1979) the paired plot method of Wiegert & Evans (1964). The mean values from two consecutive sampling occasions were used as values for paired plots. The method was applicable only for periods when negligible amounts of litter were formed.
- 3) Cellulose sheet method. The seasonal pattern of decomposition activity was investigated using 25 mm x 60 mm sulphite cellulose sheets (pH 4.8, ash content 0.5 %); they were placed on the ground among the litter, collected on the next sampling date, and replaced by new ones.

- 4) Litter heap method. A weighed amount of litter collected from the study field was placed on plots where biomass samples had been harvested. They were loosely tied to the ground with a twig. On the next sampling dates the heaps were collected, and new ones were put at the sites.

Disappearance rates for all methods were calculated using the formula (Wiegert & Evans 1964):

$$(4) \quad r = \frac{\ln (W_0/W_1)}{t_1 - t_0}, \text{ where } r \text{ is disappearance rate (g/g } \times \text{ day),}$$

W_0 is weight of the sample at sampling date 0, W_1 is weight of the sample at sampling date 1, $t_1 - t_0$ the time interval (in days) between sampling dates.

In general the disappearance rates obtained by different methods correlated positively. An exception, however, was the litter heap method; in the form tested, it was considered unreliable during the snowfree period. If litter is very unevenly distributed, the applied paired plot method is not reliable for detecting small changes in litter biomass, unless an extremely large sample is used.

3.3. Experiment on sampling methods for field-layer arthropods (V)

3.3.1. Introduction and methods

Even though grasslands are relatively simple terrestrial ecosystems structurally, the sampling of field-layer arthropods is often complicated. A large variety of invertebrates with highly different ecological features inhabit the vegetation and litter layers. In addition, owing to gradually decomposing plant material there are seldom distinct borders between vegetation, litter, and soil layers. Many arthropods, according to their life stage or season shift their microhabitats between the herb layer and the soil.

Five methods - suction, sweep net, pitfall, large dry funnel and photoeclector - were selected for comparison and evaluation. On 1 July and 28 July 1978 ten samples were taken from Ruoke by each method. In addition to the standard 3 minute sample from a 0.25 m^2 area, four

successive 1.5-minute suction samples were taken from the same enclosure. Two consecutive 1.5-minute samples were pooled for calculating a total estimate of the population using removal catch procedure (Southwood 1978). These corrected suction estimates were considered to be absolute figures and other methods were compared to them.

3.3.2. Results

With all methods the time required to take the set of ten samples was relatively short (less than 4 hours). Handling time for the samples (picking animals from the samples and counting them according to broad taxonomic units) was much more important in determining the relative costs of the methods. One standard 3-minute suction sample took an average of 3.5 hours to handle. Pitfall, dry funnel, and photoeclector samples were less laborious, because they were relatively free of trash.

The selectivity of the methods was assessed on the basis of dominance (%). With sweep net Diptera, Heteroptera and winged Hymenoptera were overrepresented. Araneae and Staphylinidae were underrepresented in sweep net samples. The pitfall method was efficient for Araneae, Auchenorrhyncha and Diptera. The flies in the pitfall samples were mainly Calliphoridae attracted by the carrions of small mammals in the traps.

Most mobile arthropods in the field and bottom layers escaped when the dry funnel samples were taken. To avoid this bias, an improved sampling device was developed later (Törmälä, in prep.). In dry funnel samples mainly litter- and soil-dwelling spiders were represented in great numbers. Aphids were the most dominant group in the dry funnel samples, presumably owing to hatching in the laboratory. Photoeclector favoured clearly Diptera, and the method was inefficient for other groups.

Three of the methods, namely suction, dry funnel and photoeclector gave direct estimates of densities, while the others gave only relative indices of abundance. Suction gave the best estimates of density for most groups. Dry funnel, however, was more efficient, for Araneae and Staphylinidae than suction was. Because of obvious hatching in the laboratory, the high densities of aphids obtained by dry funnel method must be considered with caution.

The efficiency of suction varied depending on the arthropod group. For Auchenorrhyncha and Diptera the first 3-minutes suction give fairly accurate estimates (Table 2).

Table 2. Correction factors (V) for the most abundant taxa in suction samples. When the original figures are multiplied by these factors absolute densities (removal catch procedure) are obtained.

Suction time min	July 1			July 28		
	3	6	9	3	6	9
Araneae	2.30	1.57	1.23	9.52	4.90	3.48
Heteroptera	1.25	1.03	1.02	2.14	1.43	1.18
Heteroptera nymphs	1.33	1.10	1.00	1.95	1.34	1.13
<i>Aphrodes bifasciatus</i> (L.)	1.44	1.13	1.02	2.70	1.80	1.43
<i>Arthaldeus pascuellus</i> (Fn.)	-	-	-	1.79	1.29	1.09
<i>Diplocolenus abdominalis</i> (F.)	1.05	1.01	1.00	1.14	1.03	1.00
<i>Paluda flaveola</i> (Bh.)	1.16	1.03	1.00	1.11	1.03	1.00
<i>P. preysleri</i> (H.-S.)	-	-	-	1.20	1.06	1.00
<i>Streptanus marginatus</i> (Kb.)	-	-	-	1.15	1.05	1.00
<i>S. sordidus</i> (Zett.)	-	-	-	2.35	1.43	1.23
Auchenorrhyncha total	1.11	1.02	1.00	1.39	1.12	1.01
A. nymphs	1.38	1.08	1.02	1.69	1.20	1.07
Aphidina	1.91	1.43	1.11	2.75	1.75	1.36
Diptera	1.04	1.00	1.00	1.18	1.04	1.00
Formicidae	2.02	1.33	1.15	5.32	2.67	2.22
Hymenoptera, others	1.61	1.40	1.00	1.91	1.33	1.12

The most prevalent arthropod group, Auchenorrhyncha, was studied at the species level. All methods proved to be selective to some extent. Clearly, the least unbiased dominance was obtained by suction (Fig. 2). In spite of having the greatest number of total species and specimens, many species (*Aphrodes bifasciatus*, *Muellerianella brevipennis*, *Streptanus marginatus*, *S. sordidus*) were caught very poorly using sweep net. Both sweep net and pitfall methods favoured *Diplocolenus abdominalis*. Even within a genus (*Paluda flaveola* and *P. preysleri*) there were distinct differences in the selectivity of the methods.

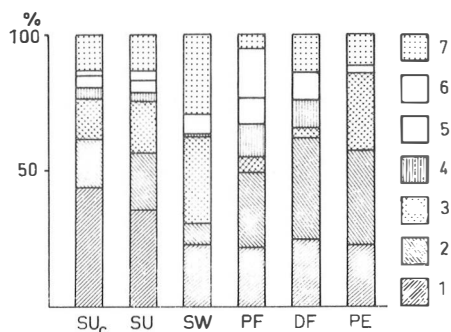


Fig. 2. Dominance (%) of the most common leafhopper species in samples taken by (3 minute) suction (SU), sweep net (SW), pitfall (PF), dry funnel (DF), and photoelector (PE) methods on 28 July 1978 in Ruoke (IV). SU is based on corrected densities obtained by removal catch procedure. 1 = *Arthaldeus pascuellus*, 2 = *Paluda preysleri*, 3 = *P. flaveola*, 4 = *Streptanus sordidus*, 5 = *S. marginatus*, 6 = *Diplocolenus abdominalis*, and 7 = others.

Efficiency of suction varied according to species, but generally it was acceptable with only 3-minute suction time.

The parameters describing the community structure had different values, depending on the method. The errors in, e.g., diversity values, were caused mainly by biased proportions of the dominant species.

In population studies data for unbiased sex ratio and age structure are essential. Sweep net and pitfall (with dry funnel and photoelector the data were too small for analyses) generally gave too high ratios (statistically significant) of adults to nymphs and males to females, making their value, even as index tools, highly questionable.

3.3.3. Conclusions

From these results, strong arguments can be made for using the suction method, even if density data are not of primary interest. As index methods sweep net and pitfall seem to be feasible only in very specific conditions (similar habitats, same time of the season, etc.). The outcomes of attempts to turn sweep net and pitfall catches to densities using conversion factors are doubtful because season, habitat, species,

sex and age as well as parasitism (Heikinheimo & Raatikainen 1962) greatly affect the magnitude of conversion factors.

Because even suction is not an absolute method (at least with short suction times), its efficiency should be checked using, e.g., removal catch procedures.

If the focus of the study is, e.g., on the whole beetle community of a grassland, the suction data should be complemented by dry funnel sampling because many beetles (e.g., Staphylinidae) owing to their partly terricolous habits, are inefficiently sampled by suction.

3.4. Invertebrates

Using standard procedures soil invertebrates (III) were sampled and extracted from Ruoke in 1976 (Table 3).

Table 3. Sample areas, extraction methods and source for description of equipments used for soil invertebrates studied.

Group	Sample area cm ²	Extraction method	
Nematoda	9.51	filtration	Huhta and Koskenniemi (1975)
Enchytraeidae	24.2	wet funnel	O'Connor (1962)
Lumbricidae	625	large wet funnel	Huhta & Koskenniemi (1975)
Acari, Collembola	9.51	infrared high gradient	Huhta & Koskenniemi (1975)
Araneae, Coleoptera, Dipterous and Coleopterous larvae	625	large dry funnel	Huhta (1972)

For earthworms and macroarthropods the sampling depth was 8 cm. Microarthropods, nematodes and enchytraeids were usually sampled from 0-3 and 6-9 cm. For analysis of vertical distribution, samples to a depth of 15 cm were taken in July.

The animals were measured: weights were obtained from length-weight equations; and dry/wet weight proportions were taken from the literature. Taxa of the soil invertebrates were assigned to trophic levels on the bases of data in the literature. Larval Coleoptera and Diptera were identified to family and adult Coleoptera to species.

Field-layer arthropods were sampled using Burkard suction apparatus. In Ruoke the sample area of 0.25 m^2 was delimited using a metal cylinder. Suction time was 3 minutes. In the management experiment in Konttila the sample area was 0.1 m^2 , and suction time was 2 minutes.

Field-layer arthropods were divided into functional categories (herbivores, carnivores, sapro-/microbivores) and weighed. To make up for losses during preservation in alcohol, legs detached during sampling etc, 30 % was added to the weights. Specific weights were determined for adult leafhoppers (own weighing and data from the literature).

3.5. Birds

The birds were censused using study area method (IV). Using extensive observation and nest searching the efficiency of the method was tested in two fields, the method was found to be reliable. The accuracy was assumed to be owing to the relatively open view, mainly single vegetational layer, and relatively low densities of birds.

The weights of birds were taken from the literature (v. Haartman et al. 1963-72), and dry weight was assumed to 30 % of fresh weight (e.g. Kendeigh & Pinowski 1973).

3.6. Small mammals

Density of small mammals was studied using live trapping (Ugglan Special traps). The vole population in Ruoke, however, was so low in 1973 that no reliable estimates could be made using catch-mark-recatch procedure (I). As shrews usually died in traps, the small mammal densities obtained were crude estimates based on total catches. The weights were taken from field data and from the literature (Siivonen 1975). Dry weight was assumed to 30 % of live weight (French 1979).

4. Results

4.1. Primary production

In Ruoke the primary productivity was studied most thoroughly in 1973 (I). The peak standing crop of vegetation was 328 ± 18.7 (S.E.) g/m^2 on July 21. By summing the peak biomasses for individual species the annual primary production aboveground was estimated to be 405 g/m^2 , 1.2 times the maximum green standing crop.

In 1973 the proportion of monocotyledons was 59.8 % of the primary production. The figures for dicotyledons, horsetails and mosses were 38.4 %, 0.8%, and 1.3%, respectively.

The maximum biomass of the belowground vegetation was $827 \pm 146 \text{ g/m}^2$ on 4 September 1973, and the difference between maximum and minimum belowground biomass was 343 g/m^2 , which was used as an estimate of belowground net primary production.

The apparent net primary production (disregarding herbivory, leaching and withering) amounted to $750 \text{ g/m}^2 \times \text{year}$ in Ruoke. This corresponds to ca. 13 200 kJ (1 g dry plant material 17.6 kJ, Cummins & Wuychek 1971). The amount of photosynthetically active radiation (45 % of the total) during the study period (April 29 - September 26) was about 1 140 000 kJ/m^2 . Thus the efficiency of energy capture was about 1.16 %. On an annual basis the efficiency drops to 0.8 %.

Over 90 % of the aboveground production took place by the end of July, while almost 90 % of the increase in underground biomass was thereafter, indicating marked translocation of material from aboveground to belowground parts of plants during late summer.

The management experiment (II) in Konttila made it possible to assess the effect of two kinds of treatment on the primary production. The production in mown (cutting on July 5) plots was highest ($328 \text{ g/m}^2 \times \text{year}$), while the production of natural and ploughed (May 29) plots was identical (273 and $274 \text{ g/m}^2 \times \text{year}$). The composition of primary producers was affected by the treatments (Table 4). Ploughing increased the contribution of dicotyledons and decreased that of monocotyledons. The effect of mowing was the reverse, but not as great.

Table 4. Participation of the most important (over 5 % at least in one treatment) taxa in the primary production in natural (control), mown and ploughed plots in Konttila in 1975 (II).

Taxon	Production					
	Natural		Mown		Ploughed	
	g/m ²	%	g/m ²	%	g/m ²	%
<i>Achillea ptarmica</i> L.	44.1	15.8	42.6	13.0	43.3	15.8
<i>Agrostis</i> spp.	114.3	41.8	161.2	49.2	51.3	18.7
<i>Deschampsia cespitosa</i> (L.)	18.3	6.7	16.5	5.0	8.5	3.1
<i>Festuca rubra</i> L. Beauv.	13.4	4.9	23.8	7.4	18.8	6.9
<i>Galeopsis bifida</i> Boenn.	-	-	-	-	92.7	33.8
<i>Phleum pratense</i> L.	17.8	6.5	24.0	7.3	7.9	2.9
<i>Poa pratensis</i> L. s. lat.	14.4	5.3	23.8	7.3	12.1	4.4
<i>Ranunculus repens</i> L.	14.2	5.2	8.4	2.6	2.1	0.8
<i>Spergula arvensis</i> L.	-	-	-	-	20.6	7.5
Monocotyledons	189.2	69.2	250.8	76.6	88.6	32.4
Dicotyledons	82.7	30.3	76.6	23.4	185.4	67.6
Number of taxa	38		34		31	
Total	273.3	100.0	327.5	100.0	274.1	100.0

The timing of aboveground production in natural plots resembled that observed in Ruoke. In ploughed plots the daily production rates increased constantly towards autumn in spite of reduced daily radiation energy. Consequently, the efficiencies of energy capture based on the aboveground subsystem were highest in the autumn. In mown plots the rate of primary production was fairly low during the first month after cutting. Thereafter it accelerated almost to the same level as in the ploughed plots.

4.2. Seasonal dynamics of the plant taxa

The amount of green biomass in Ruoke remained relatively stable from early July to early September 1973. The combined biomass of grasses especially showed only minor variations during that period (I). The biomass of roots kept increasing until early September. Many dicoty-

ledons (*Achillea millefolium* L., *Trifolium repens* L., *Ranunculus acris*, *R. repens*) had a rapid increase in green biomass followed by fast withering immediately after they reached maximum biomass. None of these species was abundant. Most of the abundant grasses (*Agrostis capillaris*, *Poa pratensis*, *Deschampsia cespitosa*) had long maxima with obvious bimodality, owing to a midsummer depression. *Achillea ptarmica*, the most abundant species, and e.g. *Phleum pratense* had parabolic shaped curves for biomass.

Most monocotyledons recovered after mowing, and their autumn biomass exceeded or at least almost equaled that prior to cutting (II). Ploughing was much more detrimental to monocotyledons than mowing was, and their biomass increased very sluggishly towards autumn.

Ploughing caused the annual dicotyledonous seeds to germinate and the green biomass of, e.g., *Galeopsis bifida* and *Spergula arvensis* increased steadily at least to mid-September. Perennial *Ranunculus* species did not recover from ploughing during the first season. *Ranunculus* species also recovered from cutting more sluggishly than did *Achillea* species.

4.3. Plant community and its succession

In Ruoke the structure of the plant community was investigated most intensively in 1973 (I). Grasses (7 taxa) contributed 51 % to the net shoot production, while forbs (41 taxa) contributed only 37 %. The total number of vascular plant species sampled was 60. The number of species was highest (54) on July 21. In spring and autumn the number of species in the 20 sample sets varied between 30 and 40. The Shannon diversity ($H' = - \sum (\ln p_i \times p_i)$) of the herbaceous plant community was highest in the end of July (Fig. 3). Seasonal fluctuation of the evenness component ($J' = \frac{H'}{H_{\max}}$) of diversity was similar to that of the diversity index, but the maximum was reached already in mid June.

There was no superdominant in any phase of the season. The maximal contribution by a single species was 26.2 % (*Deschampsia cespitosa* on May 21). The number of species constituting 5 % or more of the herbaceous community varied from 5 to 8 ($\bar{X} = 6.6$) during the vegetative season. On the other hand many species, especially dicotyledons, were very scarce.

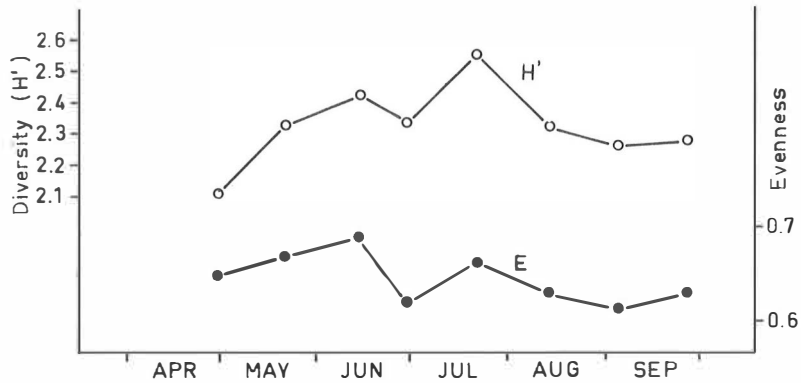


Fig. 3. Seasonal variation in vascular plant diversity (H' , Shannon index) and its evenness component (E) in Ruoke in 1973 (I).

There was a clear seasonal pattern in the composition of the plant community in Ruoke. In early spring and late autumn the proportion of dicotyledons was only 10-20 % of the total aboveground live biomass. During summer months (June-August), however, they contributed 30-35 % to the total live biomass.

The effects of the treatments (ploughing and mowing) on the plant community were profound (II). Ploughing created a community dominated by annual weeds. Two dominant species (*Galeopsis bifida* and *Spergula arvensis*) as well as the less abundant *Erysimum cheiranthoides* L., *Gnaphalium uliginosum* L., *Polygonum aviculare* L., and *P. lapathifolium* L. were found only in ploughed plots. The monocotyledons grew mainly in furrows between the ridges.

Mowing naturally caused a decrease in the biomass of all species. At the end of the season, however, mown plots closely resembled the control plots (Fig. 4). Quantitative application of Sørensen's (1948) index, which equals to Odum's (1950) index was used as a measure of similarity. The proportion of monocotyledons was somewhat higher in mown plots than in control plots.

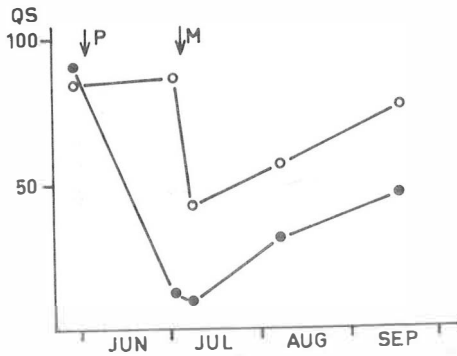


Fig. 4. Effect of mowing and ploughing on the vegetation on Konttila in 1975 (11). The similarities with control plots are calculated using Odum's (1950) index (QS = quotient of similarity). P = time of ploughing, M = time of mowing.

The composition of the plant community in Ruoke changed drastically from 1973 to 1981 (Table 5). By 1973 (5th year) the secondary succession had proceeded 4 years and by 1981 (13th year) 12 years. The standing crop of green herbaceous biomass remained relatively stable (C.V. = 0.10) throughout the study period. Dicotyledonous *Achillea ptarmica*, *Ranunculus acris*, and *R. repens* decreased markedly. The decrease in *Phleum pratense* took place earlier than that of other grasses (*Agrostis capillaris*, *Festuca rubra*, *Poa pratensis*). The steep decrease in *Deschampsia* from 1980 to 1981 may be partly owing to sampling error because the species was unevenly distributed; but undoubtedly the species was declining. The biomass of *Geranium sylvaticum* and *Filipendula ulmaria* has increased since 1973. Especially on the upper part (adjacent to the forest), they form wide patches of almost pure monospecies stands. *Chamaenerion angustifolium* was never observed on the strips before 1981, when it ranked fourth in abundance and grew on many strips. *Angelica sylvestris* L. became more abundant. The trend was, however, difficult to document by harvest sampling because of the extremely clumped biomass distribution of the species.

Table 5. Percentage composition for species constituting 5 % or more of the plant community for at least one year. *Salix* spp. excluded. Samples taken in late June or in early July.

	1973	1978	1979	1980	1981
<i>Achillea ptarmica</i>	13.1	12.2	12.2	5.1	3.2
<i>Agrostis capillaris</i> L.	18.5	22.2	24.7	18.6	8.4
<i>Chamaenerion angustifolium</i>	-	-	-	-	6.3
<i>Deschampsia cespitosa</i>	8.9	12.9	20.3	17.6	1.8
<i>Festuca rubra</i>	6.8	10.1	11.2	5.7	2.3
<i>Filipendula ulmaria</i> (L.) Maxim.	1.6	9.0	0.6	13.9	22.7
<i>Geranium sylvaticum</i> L.	0.1	4.4	7.5	13.8	25.5
<i>Phleum pratense</i>	8.3	-	1.7	1.3	1.2
<i>Poa pratensis</i>	19.5	9.7	8.8	2.0	3.8
<i>Ranunculus acris</i> L.	7.2	4.6	1.1	1.1	3.4
Monocotyledons	66.7	61.2	69.8	48.8	20.6
Dicotyledons	31.5	38.3	29.4	49.1	78.0
Green biomass g/m ²	286.6	221.5	268.6	211.9	254.0
Litter g/m ²	186.7	364.8	258.8	296.0	235.0
Roots g/m ²	599.0	1419.0	1732.0	?	1060.0

From 1979 to 1981 the proportions of monocotyledons and dicotyledons changed rapidly. The increase in dicotyledons was accompanied by a change in the species composition.

Samples were taken only from the strips. The bushes at the ditches were cut in 1973, and had grown 2-4 m high by 1981 in spite of herbivory by elk, *Alces alces* L. On the strips *Salix phylicifolia* L. occurred sparsely already in 1973 but was not abundant even by 1981.

4.4. Decomposition (VI)

Since the chemical composition and quality of plant material changes as decomposition progresses, cellulose sheets can be used as an index tool. In Ruoke the most rapid decomposition rates were measured in late summer. Rain index (the product of number of rainy days and natural logarithm of rainfall in mm), which accounted for both amount

and distribution of precipitation explained 57 % of the seasonal component of variation in decomposition activity, while temperature seemed to have no detectable effect during the snow-free period.

Of the plant materials tested *Achillea ptarmica* disappeared most rapidly and *Deschampsia cespitosa* disappeared most slowly from the litter bags. During one year's incubation (May-May) the proportion of the previous year's litter that had disappeared ranged from 33 % to 43 %. The current year's litter disappeared much faster. In late autumn after 30 days 7 % (*Deschampsia*) to 20 % (unsorted) had disappeared.

Decomposition under snow cover was rapid, from 4 October 1978 to 8 May 1979 the decrease in weight of the current year's litter ranged from 18 % (*Deschampsia*) to 36 % (*Achillea*). The decomposition of cellulose sheets was faster during the snow period than during the dry early summer.

The paired-plot method could best be applied to winter decomposition. Disappearance of litter during snow cover was 151 g/m^2 in 1973-74 and 137 g/m^2 in 1978-79 or 1.9 and 1.4 mg/g x.d, respectively. This indicates that about one third of the annual aerial net primary production is decomposed during the winter.

The litter turnover ratio k (litter fall = apparent aerial net primary production/annual mean standing crop of aboveground plant litter) was 1.34 in 1973-74 and 0.86 in 1978-79, indicating relatively slow turnover. The litter turnover ratio does not account for stages beyond the point at which detritus is no longer recognisable as plant litter. $3/k$ is used as an estimate of the time taken for 95 % of the standing crop of litter to disappear (Swift et al. 1979). In Ruoke the $3/k$ values were 2.2 years for 1973-74 and 3.5 years for 1978-79.

4.5. Soil invertebrates (III)

The community of soil- and litter-dwelling invertebrates was limited on a taxonomic basis. All worms, Araneae, Acari, Collembola, Coleopterous and Dipterous larvae, as well as adult Coleoptera known to inhabit soil or litter (Staphylinidae, Carabidae etc.) were included, while other groups (Homoptera, Heteroptera etc.) occurring in the samples were excluded. Protozoa, Tardigrada and Rotatoria were not

included.

In numbers *Dendrobaena octaedra* (Sav.) was the most abundant (180-300/m²) of the four lumbricid species. The other species (*Allolobophora caliginosa* (Sav.), *Lumbricus rubellus* Hoffm., and *Octolasion lacteum* (Örley)) were much fewer in numbers; but their combined contribution to the biomass was relatively high (22-70 %) during the summer. By biomass, Lumbricidae was clearly the most dominant group (Fig. 5), e.g., 73 % in July when their total biomass exceeded 7 g dwt/m². In numbers Nematoda was by far the most abundant group (almost 99 %).

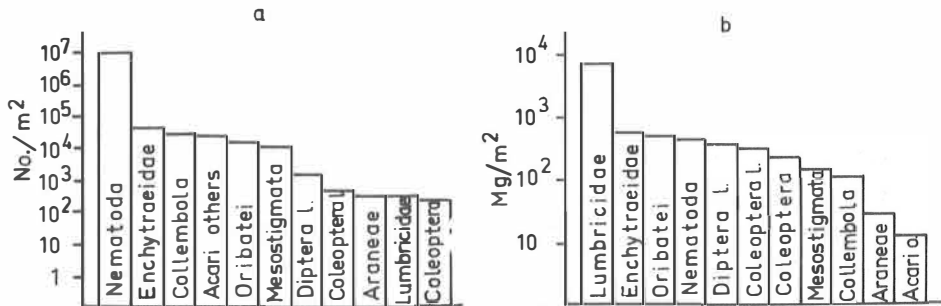


Fig. 5. Numbers (a) and biomass (b) of the soil invertebrates in Ruoke on 19 July 1976 (III). Note the logarithmic y-axis.

Mites, springtails, nematodes, and enchytraeids were most abundant in the topmost layer (0-3 cm) sampled, e.g., 99 % of the biomass of Oribatei was in the uppermost three centimetres in July. The biomass of enchytraeids (65 %), springtails (84 %), and mesostigmatid mites (96 %) was also strongly concentrated in the topsoil. Other Acari (mainly Prostigmata) and nematodes had a more even vertical distribution (58 % and 50 %, respectively). In all the above-mentioned groups the mean weight of individuals decreased with sampling depth. The vertical distribution of other groups was not investigated.

In terms of biomass, 90.7 % of the soil and litter fauna belonged to sapro-/microbivores. The proportions of predators and herbivores were 6.7 % and 2.6 %, respectively.

4.6. Field-layer invertebrates

4.6.1. Leafhopper community

In Finland all leafhopper species have only one annual generation, but the time of peak densities of adults varies.

Aphrodes bifasciatus, *Diplocolenus abdominalis*, *Doliotettix pallens* (Zett.), *Javesella foreipata* (Bh.), and *Stiroma bicarinata* (H.-S.) had their maxima in June or early July in 1973 (I). These species hibernate at the egg or nymphal stage. The most abundant species (*Agallia brachyptera*, *Arthaldeus pascuellus*, *Elymana sulphurella*, *Streptanus sordidus*) had their maxima in late July. Many other species that hibernate in the egg stage were also most abundant in late July or early August. *Delphacodes venosus* (Gm.) had its maximum in late summer. The other species that hibernates as an adult, namely *Balclutha punctata* (Thb.) was not abundant. The time when adults emerge, however, was not stable. For example, in the warm summer of 1980 *Arthaldeus pascuellus* already occurred in the adult stage on June 30.

Results of the treatment (mowing and ploughing) experiment (II) agreed with the above classification. *Diplocolenus abdominalis*, however, had a second maximum in mown plots in early August, probably owing to migration from areas with less fresh plant material.

Parameters of community structure also showed clear seasonal patterns. The number of species was highest in late July or early August (Fig. 6). After most species had become adults in late July, the diversity index based on adults decreased gradually, but not as steeply as the number of species per sample. The evenness component of diversity increased towards autumn.

Mowing and ploughing had drastic effects on the leafhopper community (II). Mowing temporarily decreased both densities and number of species. In late summer the leafhopper community in mown plots closely resembled that in the control plots (QS = 78-81). In ploughed plots both density and species richness (no. of species) were below the control throughout the season (Fig. 7). The late summer dominant, *Delphacodes venosus*, was almost absent from ploughed plots.

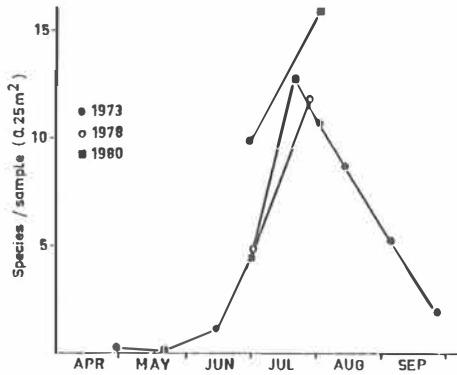


Fig. 6. Mean numbers of leafhopper species per 0.25 m² suction sample in Ruoke.

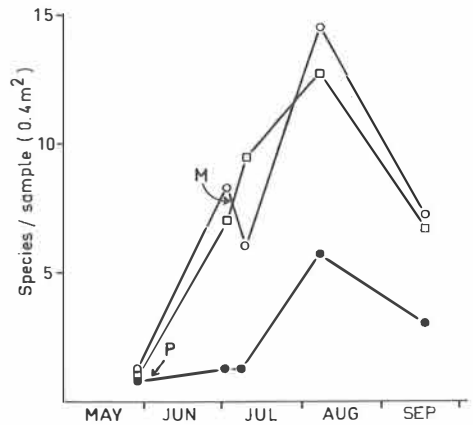


Fig. 7. Mean number of leafhopper species in four 0.1 m² samples in the treatment experiment in Konttila in 1975 (II). Dots = ploughed, circles = mown and squares = control. M and P indicate the times of mowing and ploughing, respectively.

The leafhopper community in Ruoke (Table 6) changed with the plant succession. From 1973 to 1980 the total density increased more than twofold. The species composition also changed markedly. The changes in the abundance of all species given in Table 6 were highly significant (χ^2 -test, or analysis of variance, when appropriate). The appearance or increase of many species (*Eupteryx signatipennis* (Bh.), *Idiocerus elegans* Fl., *I. confusus* Fl., *Neophilaenus lineatus*, *Philaenus spumarius*, *Sagatus punctifrons*, *Sorhoanus assimilis*) was not balanced by the decrease in *Agallia brachyptera*, *Aphrodes bicinctus* (Schrk.), *A. flavostriatus*, *Deltocephalus pulicaris* (Fn.) and *Streptanus sordidus*.

The between year (or successional) differences in the number of species in the leafhopper community on corresponding sampling dates were clear ($F = 28.31^{***}$ d.f. = 2,26) in early summer as well as in later sampling dates ($F = 8.02^{**}$ d.f. = 2,23). In both early and later summer samples the species richness was highest in 1980, but because the values for 1973 and 1978 were almost identical

(Fig. 6) the material did not reveal any directional change in species richness as it had for densities.

Table 6. Densities of the most common leafhopper species in Ruoke in late July or early August. Figures are corrected according to results of the efficiency experiment (V). Category classes for moisture (Kontkanen 1950, Raatikainen & Vasarainen 1976) are: 1) stenotopic species of wet biotopes, 2) eurytopic species of more or less moist biotopes, 3) stenotopic species of fresh biotopes, 4) eurytopic species of dryish biotopes 5) stenotopic species of dry biotopes.

Species	No./m ²			Moisture category
	1973	1978	1980	
<i>Agallia brachyptera</i> (Bh.)	54.7	1.2	1.2	4
<i>Aphrodes flavostriatus</i> (Don.)	31.7	-	-	-
<i>Arthaldeus pascuellus</i>	130.7	415.9	273.5	2
<i>Diplocolenus abdominalis</i>	14.3	21.0	254.0	4
<i>Elymana sulphurella</i> (Zett.)	67.8	11.4	86.9	4
<i>Muellerianella brevipennis</i> (Bh.)	23.9	34.7	186.7	3
<i>Neophilaenus lineatus</i> (L.)	-	-	21.3	2
<i>Paluda flaveola</i>	6.7	140.6	115.4	3
<i>P. preysleri</i>	9.6	166.7	44.6	4
<i>Philaenus spumarius</i> (L.)	2.9	1.2	149.2	2
<i>Sagatus punctifrons</i> (Fh.)	-	0.6	24.8	-
<i>Sorhoanus assimilis</i> (Fn.)	-	1.7	54.1	-
<i>Streptanus marginatus</i>	-	34.1	8.3	3
<i>S. sordidus</i>	127.5	45.1	11.3	3
Total	517.3	947.3	1327.3	

4.6.2. Main arthropod groups

Field-layer arthropods other than Auchenorrhyncha were usually dealt with as broad taxonomic units.

In Ruoke in 1973 Hymenoptera, Diptera, Aphidina, and Psyllina had their seasonal maxima already in late June (1). Heteroptera and Auchenorrhyncha were most abundant in late July, and Araneae and Coleoptera (mainly Staphylinidae) in the beginning of August.

Seasonal dynamics in the control plots of the treatment experiment were basically the same.

The abundance (initial figures were corrected by factors in Table 2) of field layer arthropods in 1973, 1978, and 1980 for Ruoke are given in Table 7. Araneae, Formicidae, and Coleoptera were not included because of the low efficiency of the suction method for these groups.

Table 7. Densities (No./m²) of some main arthropod taxa in Ruoke in early- and midsummer 1973, 1978 and 1980 obtained by the suction method. The figures are corrected according to the efficiency of the suction (V). Significance levels (p) for one-way analyses of variance are given. N.S. = not significant.

Group	June 30 1973	July 1 1978	June 30 1980	p	July 21 1973	July 28 1978	August 2 1980	p
Diptera	33.9	16.0	15.0	.05	7.1	78.7	261.5	.001
Heteroptera adults	7.0	45.0	46.5	.001	126.1	142.9	425.4	.001
Heteroptera nymphs	18.6	84.4	13.8	.001	23.7	17.2	267.5	.001
Auchenorrhyncha adults	54.0	212.2	330.8	.001	455.7	909.6	1 306.6	.05
Auchenorrhyncha nymphs	299.5	912.3	13.8	.001	142.4	232.0	17.6	.001
Psyllina	9.6	7.4	0.8	.05	-	2.0	-	N.S.
Aphidina	47.0	20.8	51.2	N.S.	5.5	258.3	861.3	.001
Hymenoptera (Formicidae excluded)	70.2	14.6	32.8	.01	59.4	72.5	175.7	.001
Total	539.8	1 312.7	504.7	-	819.9	1 713.2	3 315.6	-

The increase was most consistent in Auchenorrhyncha but other herbivorous insects (Heteroptera, Aphidina) were also more abundant in later years. In general, the densities are much higher than these in young reserved fields studied by Hokkanen & Raatikainen (1977b). Only a few larval Auchenorrhyncha, however, were obtained in 1980. The exceptionally warm summer probably caused leafhoppers to develop faster to the adult stage. The biomass of field layer arthropods (July-August) increased from 0.7 g/m² in 1973 to 2.4 g/m² in 1980.

Ploughing decreased the densities of the main epigeal arthropod groups. Only beetles (mainly Staphylinids) did not decrease significantly.

The effects of mowing were less pronounced than those of ploughing. Compared to control plots there was a slight temporary decrease in Aphidina, Heteroptera and Auchenorrhyncha, but differences in average densities for the whole season were small.

4.7. Birds (IV)

Size of the cleared area and successional stage of the reserved field were important in determining occurrence of individual species and composition of whole avian community in reserved fields. *Alauda arvensis* L. was found on young reserved fields in large cleared areas. When the vegetation had become meadow-like with plenty of litter on the ground, *Alauda* disappeared. *Saxicola rubetra*, *Motacilla flava* and *Emberiza citrinella* had a wide range of habitats, but were most frequent in fields with scattered bushes. *Phylloscopus trochilus*, *Carpodacus erythrinus*, *Sylvia borin*, and *Aerocephalus schoenobaenus* appeared at the field when at least part of it had relatively closed shrubby vegetation.

The densities were generally low (the mean in material accumulated until 1980 was 77.2 pairs/km²). Number of species per field ($\bar{X} = 2.3$) was also generally low. This was partly owing to the small areas of the fields (0.3-6.0 ha) on which the census was made.

Changes in the bird community on Ruoke were studied intensively in 1979-81 when the height and cover of bushes increased rapidly. The density and diversity of the bird community rose especially from 1980 to 1981 (Table 8). During the last study year many shrub and forest species appeared on the field or became more abundant. The density was 30 pairs/10 ha in 1981, which is much higher than the density in young open reserved fields.

The food resources of the field were also used by swallows, thrushes, and crows, which did not breed in the field.

4.8. Small mammals (I)

The small mammal populations in Ruoke were low early in the summer of 1973. *Microtus agrestis* L. was very scarce throughout the summer. *Sorex araneus* L. was the most abundant small mammal in the field; in late August its density was about 40 individuals per hectare. Predatory *Mustela vison* Bangs was also trapped in the field. The total density of small mammals (8 species) in late August was roughly estimated to be 60 animals per hectare.

Table 8. Composition of the bird community in the 6-ha clearing of Ruoke, based on extensive observation and nest searching.

Species	No. of pairs		
	1979	1980	1981
<i>Gallinago gallinago</i> (L.)	1	-	2
<i>Tringa hypoleucos</i> L.	-	-	1
<i>Saxicola rubetra</i> (L.)	2	2	1
<i>Turdus iliacus</i> L.	-	-	1
<i>Acrocephalus schoenobaenus</i> (L.)	1	1	1
<i>Sylvia borin</i> (Bodd.)	-	-	1
<i>Sylvia communis</i> Lath.	-	1	1
<i>Phylloscopus trochilus</i> (L.)	-	-	3
<i>Prunella modularis</i> (L.)	-	1	1
<i>Motacilla flava</i> L.	-	1	1
<i>Carpodacus erythrinus</i> (Pall.)	1	1	3
<i>Emberiza schoeniclus</i> L.	2	2	2
No. of species	5	7	12
Total no. of pairs	7	9	18

5. Discussion

5.1. Succession on the vegetation

Hokkanen & Raatikainen (1977a) described the pathways of vegetational development on reserved fields in central Finland both in dry and moist conditions until the 6th year of secondary succession. In the relatively moist main study field (Ruoke) the succession was followed from the 5th to the 13th year. By combining these two sets of data, it was possible to outline a general pattern of succession (Fig. 8) in moist conditions.

After cereal crops, the vegetation was dominated by weedy dicotyledonous species typical of open cultivations. The most abundant species during the colonization phase are *Galeopsis* spp., *Achillea millefolium*, *Tripleurospermum inodorum* Schultz Bip., and *Sonchus arvensis* L.

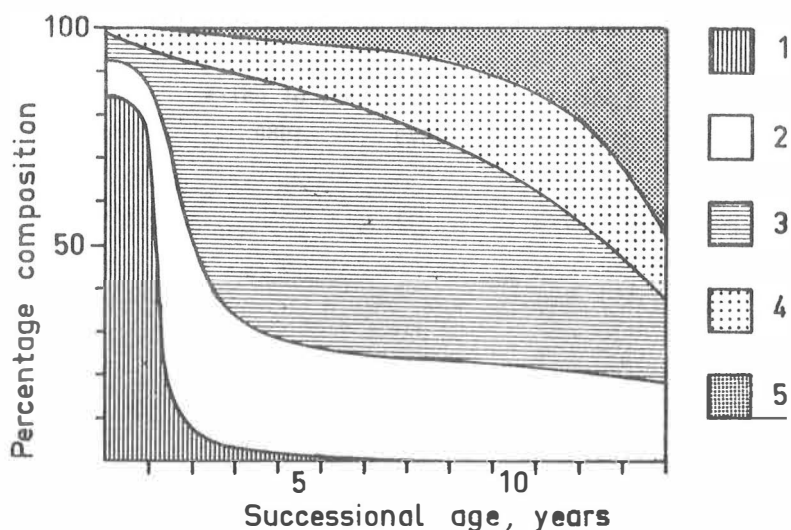


Fig. 8. Model of secondary succession in fresh reserved fields. 1 = annual and biennial weeds, 2 = small perennial forbs (*Achillea* spp., *Ranunculus* spp. etc.) 3 = graminoids, 4 = *Deschampsia cespitosa* and 5 = big perennial forbs (*Filipendula*, *Geranium*).

In one or two years monocotyledonous graminoids, *Agrostis capillaris*, *Poa pratensis*, *Festuca rubra*, *Phleum pratense*, and dicotyledonous *Achillea ptarmica* and *Ranunculus* species totally replace the weed dominated community. This kind of community prevailed in Ruoke until about the 10th year of secondary succession. Gradually, however, the proportion of tussock-forming *Deschampsia cespitosa* increased, while graminoids that do not form tussocks (*Festuca*, *Phleum*, *Agrostis*, *Poa*) decreased. In later phases of succession the large dicotyledons *Filipendula ulmaria* and *Geranium sylvaticum* become a dominant group forming almost pure, patchily expanding stands between the grassy areas. Increase of these big forbs was accompanied by a decrease in *Deschampsia*. The next phase in this line of succession is probably an almost pure *Filipendula* stand, which, in fact, is common in central Finland on old reserved fields with moist soils (K. Pracht, personal communication). The field will become bushy and eventually forest succession will begin.

Owing to more extensive management vegetation on the open ditches is at a more advanced successional stage already during cultivation. In Ruoke small spruces (climax species) grow already in mid-1970s in ditches.

The rate of succession is very rapid during the first 2-3 years, whereafter the changes are much slower. Especially in drier fields which are invaded very sluggishly by bushes, the field layer vegetation is very stable for a long time.

The observed line of succession (Fig. 8) can be related to origin of seeds and other propagules, life history (annual-perennial), r - K (Pianka 1970) and C , S and R (Grime 1977) strategies of the plant species.

Seeds of weedy species that colonize reserved fields after abandonment are present in high numbers in the agricultural soils (Paatela & Erviö 1971, Raatikainen & Raatikainen 1972). These seeds can germinate in the bare soil, and the seedlings can grow relatively free from competition. When the field is in agricultural use, such plants are usually kept at low population densities by herbicides and other management practices. The seeds of most grasses are also present in the soil. The dicotyledonous seeds of later successional stages (*Filipendula*, *Geum*, *Angelica*) come mainly from surrounding habitats. The colonization of reserved fields by bushes is mainly vegetative, starting from the edges or open ditches.

The change in the proportion of various life history strategies can be outlined on the basis of data in Hokkanen & Raatikainen (1977a) and data from Ruoke. During the first year, an average of 40 % of the species and 50 % (85 % in a *Galeopsis* dominated field) of the biomass was contributed by annual and biennial plants. During the course of succession, they disappeared almost totally, e.g., in 1981 in Ruoke only *Galeopsis* sp. and *Cirsium palustre* were sampled and their biomass was merely 0.8 % of the total. Most of the annuals and biennials that occur in early stages can be regarded as fugitive species (Platt & Weiss 1977). They can exist in ruderal, disturbed places in absence of competition and also in open cultivations (Raatikainen & Raatikainen 1979). In grass leys they are rapidly pushed out by perennials (data in Raatikainen & Raatikainen 1975).

Grime (1977) found evidence that supported the division of plants into three groups based on their primary strategies. Each group is associated with evolution of a distinct type of strategy. As a generalized summary, the competitive (C) strategy prevails in productive, relatively undisturbed vegetation; the stress-tolerant (S) strategy is associated with stressing (arid, shaded, cold) conditions; and the ruderal (R) strategy is characteristic of severely disturbed but potentially productive habitats. Between the three extremes there are species adapted to intermediate intensities of competition, stress and disturbance.

At the beginning of the sere the plant community in reserved fields are dominated by typically ruderal species (*Galeopsis*, *Spergula*, etc.), which benefit from disturbance of the habitat (e.g., ploughing). These species can be considered highly opportunistic (e.g., Connell & Slatyer 1977). *Achillea* and *Ranunculus* species are obvious intermediates between the ruderal- and competitive-strategists. Graminids, especially *Deschampsia*, are competitive species which outcompete ruderal-species and weaker competitors. The tussocks of *Deschampsia* are stable and can expand during many years. In a removal experiment in an old-field Pinder (1975) showed that the suppression of many forbs by perennial graminoids is owing to interspecific competition.

Filipendula and *Geum* occurred sparsely in the field already in 1973 but became abundant in 1979-81. Consequently, their slow establishment in the lower parts of the field can not be attributed totally to the late dispersal. The relatively slow establishment of *Filipendula* and *Geum* stands does not suggest superior competitive abilities, especially in unshaded patches. The rapid phase of their increase coincided with the fast growth of shrubby plants. The upper part of the field was shaded on the forest from south and west. The bushes on the ditches made the strips like corridors causing additional shading. Probably *Filipendula* and *Geum* are more stress selected in relation to shading than the earlier dominants. In addition, *Filipendula* has a well developed root system, which is capable to efficient nutrient competition. *Filipendula* shoots are high, and a dense stand shades efficiently other species resulting in monospecies patches.

In the traditional r-K -selection continuum R-strategists are typically r-selected and S-strategists are on the other end of the continuum (Grime 1977). Many of the attributes of r-selective species (Pianka 1970), such as fast development, short life span, and high number of offspring fit to pioneer species in reserved fields (see also Newell & Tramer 1978). The weed community also was fairly productive. As the biomass of the weed community, as shown by the ploughing experiment in Konttila (II), increases until mid-September, the sampling date of Hokkanen & Raatikainen (1977a) was too early resulting in an underestimate of the maximum standing crop. Many species occurring at later successional stages (e.g. *Deschampsia*, *Filipendula*) are perennial, adapted to competition, relative large for herbaceous plants, slower to develop, and thus typically K-selected. This observation fits to the general ecological theory that in the course of succession r-selected species are gradually replaced by K-selected species (Odum 1969). This generalization, however, has been questioned (e.g. Connell & Slatyer 1977). The early colonizers probably also have much broader precompetitive niches than do species occurring later in the successional continuum (Pickett & Bazzaz 1978).

During the treatment experiment (II), succession in Konttila was in the graminoid dominated phase. These plants recovered very rapidly from cutting, and thus there were only minor one-season disturbances in the community. If the vegetation is mown at intervals of 1-2 years, the composition of the graminoid dominated community will probably remain very stable. Mere cutting of bushes is sufficient to delay the succession.

The disturbance caused by ploughing was more profound than that caused by mowing. In ploughed plots, however, the succession was more rapid than normally occurs after open cultivation, because many graminoids started fast regrowth from the furrows. In the beginning of August the proportion of graminoids was about 19 % in Konttila: but in first year reserved fields abandoned after open cultivation, it averaged 9 % (Hokkanen & Raatikainen 1977a).

There are controversial data and opinions about the relationship of progressive succession, and diversity of vegetation in grasslands (see, e.g., Horn 1974, Nicholson & Monk 1974, Bazzaz 1975, Mellinger &

McNaughton 1975, Whittaker 1975, Hokkanen & Raatikainen 1977a, Denslow 1980). Generally, diversity seems to increase with advancing succession. There is, however, often decrease when the climax is approached (e.g., Horn 1974, Whittaker 1975). For example, abandoned fields in American forest climate regions follow this pattern (Nicholson & Monk 1974). For community index (combined percentage for the two most abundant species) the opposite trend holds true. In central Finland, **diversity** (Shannon function) tended to increase at least during the first six years of succession (Hokkanen & Raatikainen 1977a). The mean number of species increased from 18.3 (1st year fields) to 23.8 (6th year fields), but the trend was neither linear nor statistically significant. In Ruoke the diversity index, dominance index, and number of dominant herbaceous plants were variable from 5th to 13th years of secondary succession (Fig. 9). The changes were minor and nondirectional, in spite of the great turnover in species composition.

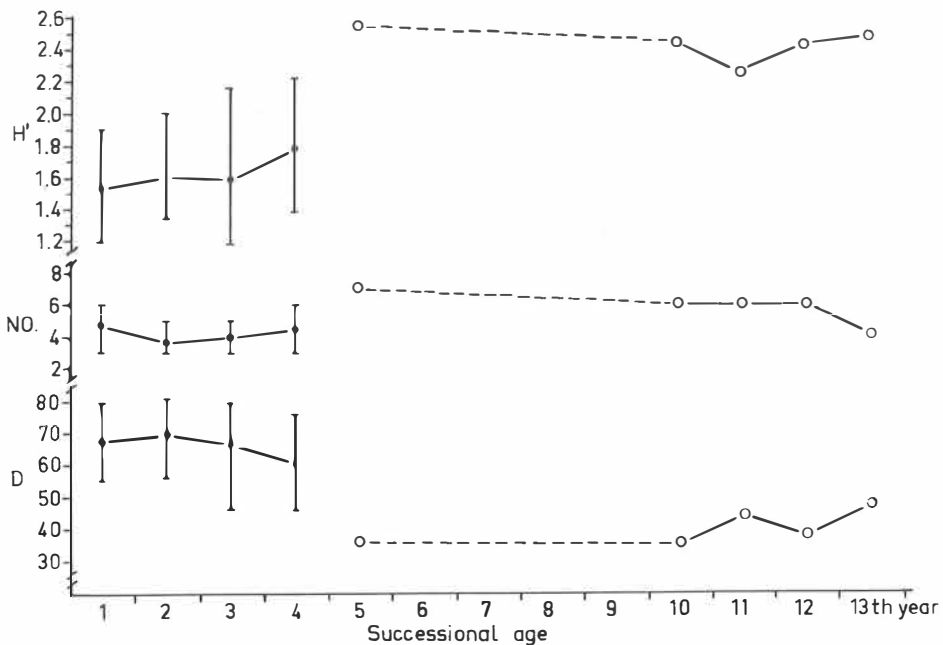


Fig. 9. Structure of the plant community in the succession after open cultivations. H' = Shannon diversity index, No. = number of dominant species (>5% of the biomass), and D = index of dominance (joint dominance of the two most abundant species). Dots = mean + range from data of Hokkanen & Raatikainen (1977a), circles = data from Ruoke.

Generally, the vegetation in Ruoke seemed to be more diverse than the fields studied by Hokkanen & Raatikainen (1977a). The index of diversity in Ruoke was especially high compared to their fields. One explanation for this is the greater than average spatial heterogeneity in moisture, light and soil conditions that enabled several abundant species to coexist in Ruoke.

5.2. Animal communities

The leafhopper community in Ruoke was both abundant and rich in species. A total of 53 species was found from the samples taken in the 5th (I), 10th (V) and 12th years of secondary succession. This is about 18 % of the species known in Finland, but such number of species is not exceptional for European grasslands (Whittaker 1969, Morris 1971, Waloff & Salomon 1973, Müller 1978). The figure, however, is high compared to American natural grasslands (e.g., Blocker & Reed 1976) or cultivated fields (Raatikainen 1971).

The number of species tended to increase with the successional age of the field. This can partly be explained by the increase of species living on shrubs or trees (*Sagatus punctifrons*, *Idiocerus elegans*, *I. confusus*, *Macropsis infuscata* (J.Sb.)). *Macrosteles septemnotatus* and *Eupteryx signatipennis* live on *Filipendula*; and their appearance can be linked to an increase in the number of host plants. Most of the species in Ruoke were polyphagous (Linnavuori 1969a, b, Raatikainen & Vasarainen 1975), and changes in their abundance can not easily be explained by changes in the species composition of the host plants. The great abundance of *Philaenus spumarius* in 1980, however, can be related to the increased biomass of dicotyledonous host plants (Halkka et al. 1967).

One year after abandonment the leafhopper density averaged only $6.9/m^2$ in mid-July (Hokkanen & Raatikainen 1977b). In Ruoke the density of the leafhopper community increased from 520 in 1973 (5th year) to $1305/m^2$ in 1980 (12th year) during the high summer aspect. These figures, in contrast to those in the literature, are corrected for sampling efficiency. Densities, especially that in 1980, are very high compared to other European grasslands (Andrzejewska 1979a, Waloff 1980). In uncultivated

American grasslands leafhopper densities tend to be markedly lower than in European meadows (Blocker & Reed 1976, Andrzejewska 1979a).

Recently Waloff (1979) has proposed that some mechanisms, which leafhoppers have for reducing interspecific competition in grasslands. Segregation in time is one of the suggested mechanisms. In Ruoke all species had one annual generation, and three partly overlapping groups of species were distinguished on the basis of seasonal occurrence. However, during the relatively short summer, curves for seasonal occurrence of the most common species were very similar. In addition, the seasonal pattern was not stable; e.g., in 1980 *Diplocolenus abdominalis*, normally an early summer species, was clearly more abundant in late summer. Many late summer species also occurred in the adult stage already on June 30. The variable timing of seasonal occurrence is usually connected with weather factors (Kontkanen 1950, Müller 1978). Thus the segregation in time seems to be fairly inefficient.

Andrzejewska (1965) noticed that the leafhopper species divide the meadow habitat vertically among themselves (see also Schaefer 1973). The same has been observed for cercopid larvae (Halkka et al. 1977). In Ruoke, great differences between the species were also observed in their vertical distribution (V). Based on pitfall catches compared to actual densities, mobility of these species was very variable. The importance of differences in short distance dispersal for division of resources has, however, not been assessed (see Waloff 1979).

Occurrence of competition in communities of meadow leafhoppers is poorly documented; and for example Schaefer (1973) concluded that competition was of minor importance in a coastal meadow. Thus it is possible that predation, parasitism, and abiotic factors are more important than competition in limiting the sizes of populations, and that, at normal densities, populations are not limited by such factors as food resources.

Probably the most important factor contributing to great number of species and abundance in Ruoke was the diversity of the vegetation (high number of relatively abundant host plants). Tussocks and the well-developed litter layer offered shelter and various microhabitats (cf. Denno 1977, Usher 1978).

The patchy variation in moisture conditions and consequently in vegetation, was also reflected in the species composition in Ruoke. Kontkanen (1950 pp. 41, 81) divided field-layer leafhoppers in Northern Karelia into five categories on the basis of habitat moisture. Raatikainen & Vasarainen (1975) revised and complemented the classification. In Ruoke the most abundant species belonged to species of moist, fresh and dryish habitats (Table 6).

The leafhopper community responded vigorously to the treatments (mowing and ploughing). After mowing, the species diversity and abundance first decreased but later increased to a higher level than the control (II). In a similar experiment by Morris & Lakhani (1979) the number of species and abundance of the Hemiptera community persisted, however, below the control throughout the season. The fresh regrowth of graminoid plants probably attracted leafhoppers to the mown plots in my experiment.

The Shannon diversity index for the leafhopper communities in Konttila gave results which are difficult to interpret ecologically (II). The diversity index had the highest value in ploughed plots in autumn. In ploughed plots, however, the community had the fewest species and specimens. Parallel data are given by Wakefield & Barret (1979): a herbicide treatment that significantly decreased the biomasses of plants resulted in higher values for the diversity index. In both cases the treatment strongly affected the dominants and in the "residual community" evenness was (incidentally?) higher than in the control. It is, however, highly questionable, whether these communities can be considered ecologically richer and more diversified than the controls. These results bring into question the validity of this kind of index in situations, where the abundances (or densities) in the compared communities are very different (see also McNaughton 1977, Purvis & Curry 1980). The Shannon index, as well as many others, accounts only for relative abundance of the species but not for the total density or absolute abundance of the community.

Bird communities in reserved fields were relatively poor (IV), probably mainly owing to the simple habitat structure of the fields. The 6 ha clearing of Ruoke, however, had 12 species in 1981. The

forest-field and shore-field ecotones as well as shrubs with variable density and height provide explanation for the species diversity.

The nests of *Phylloscopus trochilus*, *Prunella modularis*, and *Sylvia borin* were located relatively close to the edge of the forest, and their feeding areas included parts of the forest habitats, and mapping of nests and feeding ranges in 1979-81 revealed a possible mechanism of the colonization of the successional fields by forest species. When the bushes are still low and scattered these birds nest in the forest and may occasionally use the abundant food resources of abandoned fields. Gradually, with increasing scrubby vegetation a greater proportion of their feeding territory is in the field. When already nesting in the field, these species may still use the forest for feeding (*Phylloscopus* or e.g. for singing (*Prunella*)). *Carpodacus erythrinus* bred far from the edges already in relatively open fields, but its large home ranges also included parts of the forest.

5.3. Ecosystem synthesis

5.3.1. Trophic relationships

When constructing a model of trophic structure, the most convenient units are biomass or energy content (e.g., Breymer 1978, 1980, French 1979).

Building of the trophic pyramids required the determination of the trophic position of each taxon. For many groups (e.g. aphids, spiders) this was easy, but for others, such as nematodes the proportion of different feeding categories had to be estimated on the basis of available literature. Herbivory was defined as consumption of living plant material only. The energy contents of various organisms were taken from Scott et al. (1979).

The pyramids constructed for Ruoke (Fig. 10) are combinations of two seasons. The aboveground subsystem represents the year 1980 and belowground 1976, because the soil animals were only studied in 1976 and the most accurate biomass determinations for aboveground fauna are from 1980. The biomass or energy content of microbes was not estimated. The pyramid based on energy content is less steep than that for biomass, because the consumers generally have higher energy content than the plants.

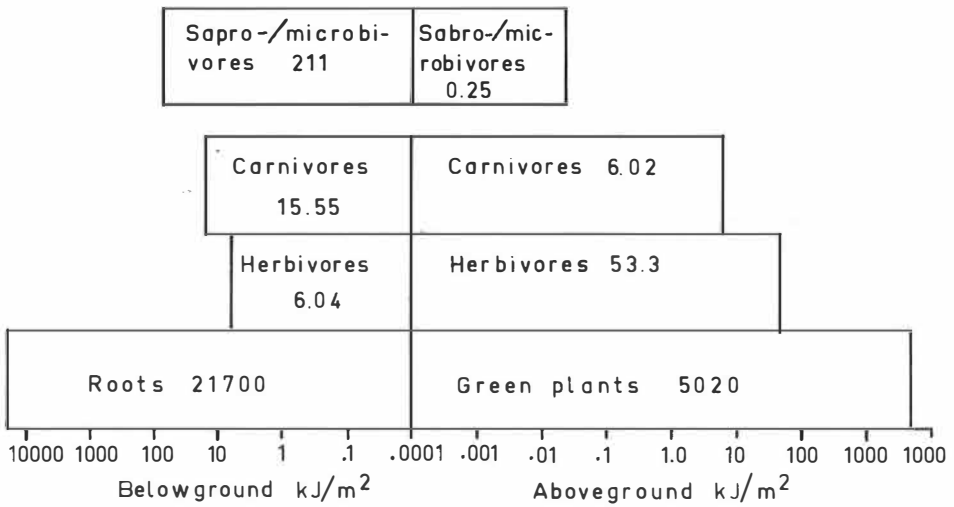
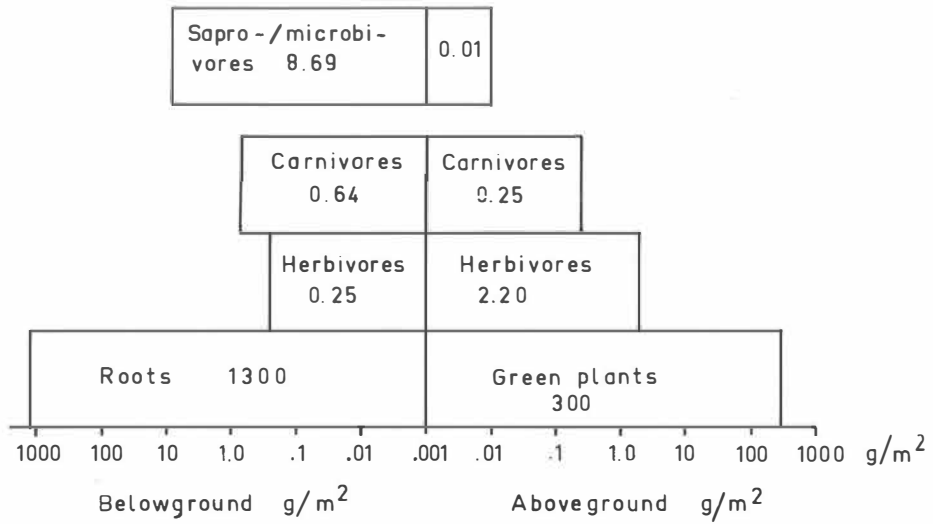


Fig. 10. Biomass and energy pyramids for Ruoke (late July-early August). The belowground data are from 1976 and aboveground from 1980 (8th and 12th year of secondary succession).

Andrzejewska (1979a) has gathered the available information about the biomass of herbivores in grasslands. Among 33 grasslands the value in Ruoke ranks second after a Russian steppe meadow. Consequently, the ratio of producer biomass to consumer biomass is among the lowest observed in grasslands (Brey Meyer 1980, French et al. 1979). The aboveground predator biomass in later successional stages was higher in Ruoke than in any of the 14 grasslands listed by Kajak (1980). Decomposer animals were clearly concentrated in soil and litter.

Several factors, such as lack of disturbance, shelter given by litter, diversity and productivity of the vegetation, and absence of long dry periods obviously contribute to the diversity and abundance of invertebrates in Ruoke (see, e.g., Coupland 1979a, Brey Meyer & Van Dyne 1980).

In American grasslands the shape of trophic pyramids had a high degree of temporal stability both between and within the seasons (French et al. 1979). In order to detect between-year (successional) changes in the trophic pyramids in reserved fields I constructed pyramids for Ruoke after the 5th, 10th and 12th year of succession in Ruoke (Fig. 11).

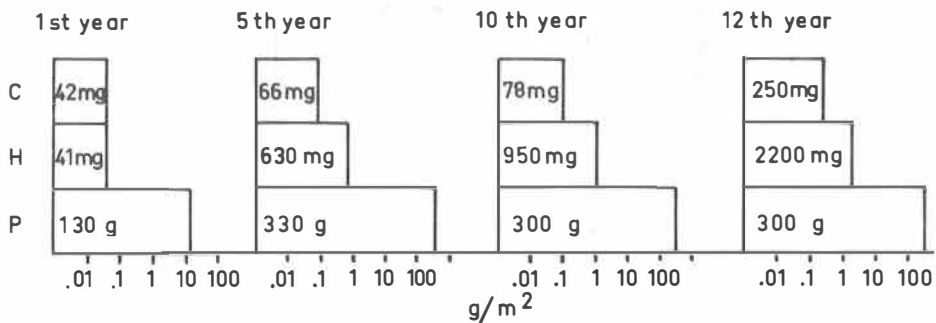


Fig. 11. Successional changes in the aboveground trophic pyramids of reserved field. The data for the 1st year field is from the material of Hokkanen and Raatikainen (1977 a, b), others are from Ruoke. Based on samples taken in late July - early August.

P= primary producers, H= herbivores, and C= carnivores.

The pyramid for 1st year field is a mean based on the material of Hokkanen & Raatikainen (1977a, b). Correction factors for suction efficiency were not applied for 1st-year fields, because the method can be considered quantitative in sparse vegetation in the absence of litter. During the course of succession, the maximum biomass of primary producers stabilized relatively rapidly after a peak during the 3th year (see also Golley & Gentry 1965, Hokkanen & Raatikainen 1977a).

In 1st-year fields leafhoppers were very scarce, and the total biomass for herbivores was also low. The carnivore: herbivore ratio was high owing to predaceous carabid beetles which were relatively common in structurally open young fields. The biomass of aboveground herbivores increased about 54 times during the first 12 years of secondary succession. The increase in the biomass of predators was only sixfold during the same period. The predators in grasslands, however, are concentrated mainly in the litter layer (Kajak et al. 1971) and are consequently not obtained efficiently in aboveground samples. Obviously, they efficiently link the aboveground and belowground consumer (grazing) food webs. By 1976 (8th year) the predatory biomass in soil and litter was 640 mg. Thus in later successional stages the total predatory biomass in the ecosystem may be as high as about 1 g/m^2 . In contrast to American climax grasslands the trophic relations and absolute values were subject to directional between-season changes in the seral communities of the abandoned field, especially at the consumer levels.

In central Finland (62°N) the organisms are subject to great seasonal variation in amount of daily solar radiation and, consequently, in temperature. This naturally causes a distinct seasonal pattern in the structure and function of the ecosystem. Not all the biomass or energy flow rates, however, fluctuated synchronously. The driving force in the ecosystem is the input of solar radiation (Fig. 12), which was maximum in June and July. The maxima of the main components of the vegetation came in the following sequence: green biomass, belowground biomass and detritus aboveground (litter and standing dead). After mid-June only a small portion of the primary production was allocated to the increase of aboveground biomass.

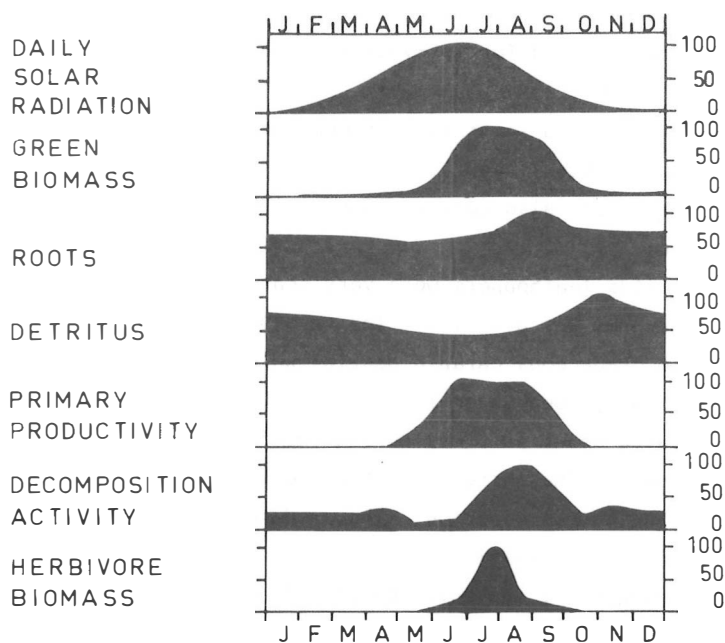


Fig. 12. Generalized model of the seasonal pattern for some ecosystem variables in a reserved field ecosystem. Maximum for each variable has a value of 100.

Most of it is transferred to the belowground parts of the vegetation. In Ruoke in midsummer there was no increase in plant biomass (1, Fig. 3), but even then as supposed in Fig. 12 the rate of primary production must have been relatively high because the consumption of herbivores is maximum then.

In contrast to primary productivity and field-layer herbivory, decomposition of aboveground litter is not confined to summer; marked activity is maintained during the snow period (cf. Abouguendia & Whitman 1979), and is at least partially biotic (cf. Bleak 1970, Vossbrinck et al. 1979).

The possible variation within the growing season in the shape of trophic pyramid can be studied using, e.g., the 1980 data. The producer biomass in June 30 and August 2 can be assumed to be equal.

The aboveground herbivore biomasses for those dates were 313 mg and 2200 mg and predator biomasses 30.0 and 247 mg, respectively. Thus the data indicate that field-layer consumers, especially predators, reach their maximal biomass considerably later than the producers do, confirming the observation based on densities in Ruoke in 1973

5.3.2. Herbivory and primary production

Consumption by leafhoppers was calculated using the data of Wiegert (1964) for *Philaenus spumarius* (see also Andrzejewska & Wójcik 1971). The total annual consumption by leafhoppers in Ruoke 1980 was estimated to be 550 kJ/m^2 . This figure also concurs with consumption data in Prestidge (1982) applied to populations in Ruoke. Total aboveground herbivory consumption was estimated to 750 kJ/m^2 using data from Andrzejewska & Gyllenberg (1980). This is high figure for ungrazed and unsown grassland. The sap-sucking insects consumed about 90 % of the total consumption in the aboveground subsystem. Consumption of belowground invertebrates is even more difficult to assess than that of aboveground invertebrates. The biomass of belowground herbivores was relatively small, compared to, for example, values in Spikbole, Sweden (Persson & Lohm 1977). Herbivorous Coleoptera larvae were very scarce in Ruoke compared to Spikbole. The feeding habits of many soil invertebrates are poorly known and some animals classified as sapro-/microbivores may as well feed on roots or rhizomes (Persson & Lohm 1977). Thus the annual consumption of belowground herbivores (200 kJ/m^2) is more guess than accurate estimate. It is large compared to the estimated biomass of belowground herbivores because, as stated above, only strict herbivores were included in the biomass value. In addition the soil animals were probably more active during the cold season owing to higher temperatures in soil than in air. Thus in 1980 the total herbivore consumption was estimated to be about $950 \text{ kJ/m}^2 \times \text{year}$ or 7 % of the primary production. For above-ground subsystem the figure is 10.5 %. In Polish meadows the losses in aboveground grass biomass, mainly by arthropod herbivores, were estimated to be from 5.4 % to 9.0 % (Breymer 1978).

It would, however, be greatly misleading to state that the decline (or "damage" to plants; Andrzejewska & Gyllenberg (1980)) in primary production would be that 7 % (or 10.5 % for shoots) in Ruoke. To demonstrate the complexity of the question, I will discuss the effects of herbivores in the better-studied aboveground subsystem. Leaf-hoppers, bugs, and aphids feed on plant sap, which has a very low concentration of organic compounds and consequently low energy content per unit wet weight (Andrzejewska & Gyllenberg 1980). Thus the sap-feeders have to suck huge quantities of sap to fulfill their energy demands. In 1980 sucking insects in Ruoke consumed about 660 kJ/m^2 or 16-53 litres of sap per square meter (Andrzejewska & Gyllenberg 1980). This is 3-9 % of the annual precipitation, and thus during draughts the sucking insects may affect the water balance of plants if water evaporates rapidly (cf. Weaver & Hibbs 1952).

The organic matter in sap is almost exclusively (98 %) composed of amino acids and their amides (Wiegert 1964). According to Wiegert (1964), the total depression of plant production is about five times the amount of amino acids removed, since protein content in vegetation is about 20 %. This would mean that the sap-feeding insects in Ruoke cause a depression of about 3300 kJ/m^2 (175 g/m^2), or about 43 % of the apparent (herbivory not included) net aerial primary production. If consumption by other herbivores is added, the total effect would be about 4000 kJ/m^2 (200 g/m^2). The effect of wastage (food removed but not used) by herbivores is hard to assess.

Would the harvestable aboveground yield have been about 600 g/m^2 instead of 400 g/m^2 in the absence of herbivores in Ruoke? Often the consumption (and wastage) by herbivores is assumed to be direct loss in harvestable yield or primary production. The fundamental role of herbivores, however, is difficult to assess (see, e.g. Andrzejewska 1979a, b, Andrzejewska & Gyllenberg 1980). One must distinguish between the effects of herbivory on the harvestable yield and primary production. For example grazing may decrease standing crop but increase the primary production. Although the consumption of herbivores is high in Ruoke, their maximal standing crop was about 2.2 g. Consequently, the amount of nutrient immobilized in the consumer biomass at any one instant is negligible compared to other nutrient storages in the ecosystem.

By late June the plants have probably used bulk of the free nutrients. The sucking herbivores remove amino acids and sugars from the plants; and the honey-dew of sap feeders, as well other excreta and remains of arthropods, are high quality substances for decomposer. These substances are rapidly mineralized and provide the plants with mineral nutrients. Thus the herbivores obviously accelerate the cycling of nutrients and shorten the turnover of nutrients and biomass. This leads into a marked increase in the total amount of organic material produced. This concurs with Owen's & Wiegert's (1976) theory that in some cases plants benefit from herbivores eating them (see also Owen 1980).

The rapid release of nutrients from consumed plant material could partially explain how the reserved field could maintain about the same level of maximum biomass (=increase of primary productivity), in spite of greatly increased consumption in later stages of the succession (Table 5).

5.3.3. Matter and energy balance

In principle the reserved fields have closed nutrient cycling without external subsidies. Hokkanen & Raatikainen (1977a) noticed a decrease in aboveground standing crop after three years of succession, probably owing to accumulation of nutrients into the dead plant material. The same was observed by Odum (1960) in South Carolina old fields. Organic matter accumulates in reserved fields during the first years of succession owing to relatively long turnover (2-4 years) of aboveground litter (VI) and increase in perennial root biomass (Hokkanen & Raatikainen 1977a). Positive energy and matter balance is typical of early successional communities (e.g., Odum 1969, Whittaker 1978). After a few years a relatively stable situation is achieved in the aboveground subsystem (e.g., Table 5). The biomass of belowground parts of plants increase during at least the first six years of secondary succession (Hokkanen & Raatikainen 1977a) but thereafter the changes seem to be nondirectional (Table 5). During the first years after abandonment the roots/shoots ratio increases consequently. In later successional stages the change in the plant composition from graminoids to forbs which are more rapidly decomposed (VI),

can speed the rate of mineralization and the amount of available nutrients.

5.3.4. Comparison with croplands

In this study, construction of a whole ecosystem model (Perkins 1978, Scott et al. 1979, Hutchinson & King 1980, Innis et al. 1980) with energy flow values between functional units was not attempted, because many of the flows were not measured directly and a model built on data from the literature and derived from different conditions would not allow any accurate estimates. Moreover, the biomasses and activity of soil microflora were not estimated at all. Of the numerous IBP ecosystem studies, only a few have dealt with as many components of the ecosystem as the present work. Although the abandoned field ecosystem (Spikbole) in Sweden was investigated in detail, it is not suitable for comparison; owing to randomized sampling dates, there were no data between June 15 and September 13 (Persson & Lohm 1977). Therefore, it was decided that the successional old-field (Ruoke) would be compared with croplands (pre-succession stage) and prairies (climax grasslands).

The initial stage of succession in a reserved field was often crop field. Several changes and trends can be observed when the ecosystem is no longer controlled by man. The vegetation becomes more diversified, with several dominant species instead of the former almost pure monoculture. The apparent net aerial primary production drops from at least 650 g/m^2 (Halinen 1979) to $300\text{-}400 \text{ g/m} \times \text{year}$. The one-season production of underground parts of vegetation is markedly higher after abandonment (ca. 200 g vs. 350 or more per m^2). The maximum standing crops of aboveground vegetation in Ruoke (1973) and a near by rye field (Halinen 1979) were 330 g/m^2 and 615 g/m^2 . The belowground peak biomasses were 830 g/m^2 and 856 g/m^2 , respectively. The peak belowground biomass increased later to more than 1000 g/m^2 in reserved fields.

During the growing season the biomass of litter is negligible in rye fields compared to old fields.

The number of consumers increased rapidly in abandoned fields, and already at the very beginning was larger than in a rye field in Poland (Ryszkowski 1979). Unless controlled by pesticides,

however, there may be mass occurrence of pests in rye fields but even then the biomass usually remains below that in older abandoned fields.

Decomposer animals were more abundant in Ruoke than in rye fields. Ryszkowski (1979) gives an estimate of 2.3 g d.w. for soil animals excluding Protozoa. The corresponding value in Ruoke was about four times as great. Thus compared to a rye field an old field harbours a much higher biomass of animal consumers in spite of its smaller biomass of producers. (In the Polish study fields insecticides were applied against the Colorado beetle).

In addition to differences in biomasses, there are fundamental differences in ecosystem function. In abandoned fields the input of organic matter into the soil is about equal to net primary production. Part of the net primary production is lost in the respiration of the consumers of grazing food chains. In rye field a substantial amount of the aboveground primary production is harvested by man. The low input and constant mechanical and chemical disturbance obviously limit the populations of Lumbricids and other soil animals in rye fields. In spite of this at least in Polish conditions, the decomposition of organic matter is rapid in croplands (Gołębiewska & Ryszkowski 1979).

The cropland ecosystem loses great amounts of vital nutrients with the harvested crop each year; these must be replaced by mineral fertilizers. In reserved fields nutrients are recycled through the activities of decomposing organisms. At an early stage of succession apparently a balance is not achieved, because the amount of litter and soil organic matter increases. As discussed earlier, the heavy consumption of herbivores in later successional stages may actually increase the primary productivity (not the standing crop!) due to fastened nutrient cycling.

5.3.5. Comparison with prairies

A European successional abandoned field (Ruoke) was compared to two American natural climax grasslands (Table 9). The values of primary producers at all three sites were relatively similar, but the primary production seems to be subject to greater between-year variation in prairies than in Ruoke (see also Table 5), presumably

owing to great variation in amount and seasonal distribution of precipitation in prairies that are mainly limited by moisture (Sims & Singh 1978a, b).

Table 9. Comparison of ungrazed shortgrass prairie (Pawnee, Colorado), ungrazed tallgrass prairie (Osage, Oklahoma), and abandoned successional field (Ruoke, Finland) ecosystems. Data for American ecosystems is derived from French (1979) and Coupland (1979a). Data for Ruoke is a combination of 1976 (belowground subsystem) and 1980 (aboveground subsystem) data. The standing crop data for the prairies refer to July 1972 data. For prairies ranges (1970-72) for primary producers are given, too.

	Pawnee	Osage	Ruoke
Latitude	40°49'	36°57'	62°10'
Precipitation (mean) mm	311	930	620
Temperature (mean) °C	7.7	15.1	2.8
Live vegetation (g/m ²)	111	203	300
Dead standing crop + litter (g/m ²)	189	811	290
Aboveground net primary production (herbivory not included) g/m ² (1970-72)	138 (138-218)	290 (290-416)	ca. 400 ¹
Belowground net primary production (herbivory not included) g/m ² (1970-72)	607 (411-687)	592 (431-602)	ca. 350 ¹
Total net primary production (g/m ²) (1970-72)	745 (571-904)	882 (847-933)	750
Efficiency of energy capture (%) (growing period)	.98 (0.64-0.80)	.70 (0.70-0.77)	1.16
Aboveground invertebrates (g/m ²)	0.03	0.25	2.44
Belowground arthropods (g/m ²)	0.83	0.33	2.40
Nematoda	0.43	0.40	0.42
Annelida	-	-	7.56
Total consumers (g/m ²)	1.34	1.05	12.82
Microbes (g/m ²)	67	635	not estimated

1) estimated from 1973 data

Allocation of products of photosynthesis to underground parts was greater in the prairie ecosystem. This is a response to low water table and to grazing in evolutionary time (Coupland 1979a). The total apparent primary production was of the same magnitude at all three sites. Efficiency of energy capture was highest in Ruoke.

During the relatively short growing period, producers at high latitudes receive large amounts of solar energy, and if, as in Ruoke, the moisture is not seriously limiting, the plants are also very efficient.

The amount of aboveground invertebrates (mainly herbivores) was greatest in Ruoke. In Pawnee in July 1972 the value was only about one per cent of the highest value in Ruoke. In Pawnee the maximal aboveground invertebrate biomass during the three study years was only 0.1 g. In prairies the consumption by belowground sap-feeding insects (Pseudococcidae, Margarodidae) was very high ($192 \text{ kJ/m}^2 \times \text{year}$ in Pawnee and $600 \text{ kJ/m}^2 \times \text{year}$ in Osage), while the aboveground consumption was very small. In Ruoke the situation was the reverse. For example, the role of leafhoppers was very small in the prairies. In the Osage site their highest biomass during three seasons was only 13.5 mg/m^2 compared to 1630 mg/m^2 in Ruoke. The total biomass of consumers (including sapro-/microbivores) in Ruoke was 9-12 times greater than in the two prairies. An important factor that contributed to the greater consumer biomass in Ruoke is abundance of annelids. Belowground arthropods also were less abundant in prairies than in Ruoke, but their proportional contribution to soil animal biomass was higher in prairies. In the prairies litter is decomposed to a greater extent by mere soil micro-organisms. In Ruoke the ratio of aboveground to belowground consumers was 1:3.9 (Fig. 10), while the belowground proportion was generally higher in prairies. In general, a much greater proportion of the biological activities is confined to soil subsystem in prairies than in reserved fields.

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Selostus

Pellonvarauslaki ja sitä täydentävät asetukset säädettiin vuosina 1969 ja 1970 maatalouden ylituotanto-ongelmien lievittämiseksi. Vuonna 1974 oli 8 % viljelysalastamme paketissa. Jyväskylän yliopiston biologian laitoksella aloitettiin pakettipeltojen ekologian, käytön, hoidon ja merkityksen selvittäminen v. 1973.

Tämä osatutkimus keskittyy lähinnä pakettipeltoekosysteemin rakenteen ja toiminnan tarkasteluun. Erityisesti on huomiota kiinnitetty kasvillisuuden tuotokseen, karikkeen hajoamiseen, kasvi- ja eläinyhteisöjen sukkessioon, sekä kasvien ja kasvinsyöjien vuorovaikutukseen. Tutkimuksessa on myös vertailtu kenttäkerroksen eläinten näytteenottomenetelmiä sekä pakettipelton hoitotapoja.

Päätutkimusalueena oli Jyväskylän maalaiskunnassa sijaitseva pelto (Ruoke), joka oli paketoitu kauran jälkeen vuonna 1969. Ensimmäiset näytteet pellolta otettiin v. 1973 ja viimeiset v. 1981.

Kasvillisuuden biomassa pysyi melko tasaisena (220-285 g/m² kuivapainona) koko tutkimuskauden kesä-heinäkuun vaihteessa otettujen näytteiden perusteella. Tämä on hieman vähemmän kuin heinänurmien keskimääräinen sato. Maanalaisten kasvinosien biomassa kasvoi selvästi paketoimisen jälkeen.

Kasvillisuuden koostumuksessa tapahtui huomattavia muutoksia. Avo-
viljelyksen jälkeen pellon valtaavat viljapeltojen rikkakasvit (pilkkeet, peltovalvatti, saunakukka jne.). Parin vuoden kuluessa pelto heinittyy (timotei, nurmiröllli, punanata). Myös leinikit ja kärsämöt esiintyvät sukkession alkuvuosina melko runsaina. Kosteahkolla Ruokkeen pakettipellolla mätästävällä nurmilauha syrjäytti vähitellen muita heinäkasveja ja kaksisirkkaisia lajeja. Noin kymmenen vuoden kehityksen jälkeen lähinnä ojissa ja niiden pientareilla kasvava pensaikko oli kasvanut 2-4 metriä korkeaksi. Tällöin alkoi varjoisista paikoista levittäytyä nopeasti saroille mesiangervoa ja metsäkurjenpolvea.

Sukkession alkuvaiheessa kasvillisuuden tuotos ja hajoaminen eivät olleet tasapainossa, vaan kuollutta orgaanista ainetta kasaantui ekosysteemiin. Hajotustoimintaa tutkittiin Ruokkeella v. 1978. Ojakärsä-mö hajosi kärkepusseissa selvästi nopeammin kuin nurmilauha ja nurmiröllli. Selluloosaliuskojen hajoamisaktiiviteettiin vaikutti kosteus huomattavasti enemmän kuin lämpötila. Maanpäällisen karikkeen hajoaminen oli varsin nopeata myös talviaikana. Lukumäärältään runsaimpia hajottajaeläimiä olivat sukkulamadot, änkyrimadot, hyppyhäntäiset ja punkit. Biomassaltaan olivat lierot selvästi merkittävin ryhmä.

Kenttäkerroksen selkärangattomista otettiin näytteet kenttäimurimenetelmällä, joka todettiin varsin luotettavaksi kokeessa, jossa vertailtiin kenttäimurin, kenttähaavin, kuoppapyydyksen, isosuppilomentelmän ja valopyydyksen valikoivuutta ja kvantitatiivisuutta. Sukkession edetessä kenttäkerroksen eläinten, erityisesti kaskaiden, tiheys kasvoi jatkuvasti. Havaitut tiheydet ja biomassat olivat hyvin suuria muihin lauhkean vyöhykkeen ruohostoekosysteemeihin verrattuna.

Pakettipellon lintuyhteisöä tutkittiin näytealamenetelmällä noin 20 pakettipellolla vuosina 1974, 1979 ja 1980. Linnusto oli niukkaa sekä laji- että yksilömäärältään etenkin sukcession alkuvaiheessa. Pakettipeltojen tyyppilaji oli pensastasku. Sukkession alkuvaiheessa kiuru oli tavallinen, ja peltojen pensoituessa niille ilmestyi punavarpunen, pajulintu, lehtokerttu ja muita pensastojen ja metsien lajeja.

Pakettipellon ravintopyramidissa perustuottajien (kasvit) maanpäällinen biomassa pysyi melko tasaisena koko tutkitun sukcessionjakson (1-13. vuosi) ajan. Kasvinsyöjien ja petojen biomassa kasvoi sen sijaan jatkuvasti. Vuonna 1980 (12. vuosi) Ruokkeen maanpäällisten kasvinsyöjien biomassa oli kuivapainona peräti 2.2 g/m^2 . Kasvinsyöjien kulutus oli tällöin varsin suuri, mutta niiden eritteistä vapautuvat ravinteet kuitenkin nopeasti kasvien käytettäväksi. Ilmeisesti tämän vuoksi kasvinsyöjien voimakas kulutus ei alentanut kasvillisuuden kesäisiä biomassoja.

Pakettipellossa on sitä edeltävään ekosysteemiin (esim. ruispelto) verrattuna huomattavasti suljetumpi ravinteiden kierto ja energian virtaus. Maanpäällisten kasvinosien tuotos on viljapellolla suurempi. Maanalaisten kasvinosien kohdalla tilanne on päinvastainen. Karikkeen määrä on viljapelloissa hyvin vähäinen pakettipeltoihin verrattuna. Samoin sekä elävää että kuollutta kasvimassaa kuluttavien eläinten lajisto ja runsaus kasvavat pellon hylkäämisen jälkeen.

Pohjoisamerikkalaisilla, ilmaston ylläpitämällä preerioilla kasvillisuuden biomassa ja tuotos on samaa luokkaa kuin keskisuomalaisella pakettipellolla. Kenttäkerroksen selkärangattomien määrä ja merkitys on kuivuuden usein vaivaamilla preerioilla pieni pakettipeltoon verrattuna. Suhteellisesti hyvin suuri osa biologisesta aktiivisuudesta keskittyy preerialla maaperään.

Kyntöä ei voida suositella pakettipellon hoitotavaksi, koska sen seurauksena rikkakasvit lisääntyvät voimakkaasti ja vähäkasvinen maaperä on altis eroosiolle etenkin rinnemailla. Säännöllinen niitto pitää pakettipellon nurmea muistuttavassa tilassa ja estää pensoittumisen, jolloin pelto on tarvittaessa helppo ottaa uudelleen viljelykseen.

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