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ANT POPULATIONS, THEIR REGULATION AND EFFECT ON SOIL IN MEADOWS*

ABSTRACT: The role of ants in meadow habitats is analysed with reference to their contribution to the trophic structure, amount of organic matter used, and changes in soil processes. The role of ants is determined by their social organization and associated high metabolic costs, as well as by their population dynamics, which is mainly controlled by intrapopulation factors. A hypothesis on the mechanisms of number regulation in ant populations is presented. The effect of ant colonies and environmental factors on soil processes in ant nests is analysed.

KEY WORDS: Meadows, pastures, ants, trophic structure, population, number regulation, soil processes in ant nests.

Contents

1. INTRODUCTION

The role of ants in an ecosystem can be analysed from the standpoint of their contribution to the total energy flow and matter cycling, interactions with other organisms, and changes they cause in soil.

The role of ants as utilizers of organic matter is largely determined by their high ecological tolerance, due to which they can reach high densities, and also by their population dynamics which, as a result of social organization, depends more on intrapopulation than on environmental factors. Social life requires some additional energy losses for transport and communication. Hence energy requirements in ant populations can sometimes exceed those of some vertebrates.

Ants interact directly and indirectly with various animals, plants and microflora. These interactions range from predation and competition to cooperation and comensalism. They have an effect on changes in the population size of these organisms, their distribution, as well as physiology and, in consequence, on their effect on the environment. These results in many adaptations difficult to a quantitative estimation on the scale of an ecosystem.

Changes caused by ants in the soil habitat are related to the construction of earth nests. These nests enable ants to control microhabitat and to maintain a social homeostasis. As a result of nest building, soil particles are transferred, physico-chemical properties of soil are modified and, consequently, soil microflora and also vascular plants are affected.

These aspects of the role of ants were studied under the International Biological Programme, which was concerned with the productivity and main pathways of energy flow in ecosystems, and also within the framework of the Polish national problem, mostly dealing with the effect of intensive mineral fertilization on the structure and productivity of meadow ecosystems.

The present paper is based on the study carried out under these programmes at the Institute of Ecology, PAS, in 1964–1974. Some results concerned with ants have already been published (Pętal 1967, 1968, 1972, 1974, 1976, 1977a, 1977b, Czerwiński, Jakubczyk and Pętal 1969, 1971, Pętal, Jakubczyk and Wójcik 1970, Kajak, Breymeyer and Pętal 1971, Pętal et al. 1971, 1977, Jakubczyk, Czerwiński and Pętal 1972, Kajak et al. 1972, Jakubczyk et al. 1975).

The objectives of the present paper are (a) an analysis of the role of ants as utilizers of organic matter in meadow habitats, (b) an analysis of regulatory processes responsible for their population size, and (c) an analysis of the effect of ants on changes in soil processes.

2. METHODS

Population size of ants, composition and amount of food carried by ants to the nest, and the density of potential prey available for ants were estimated. Also soil properties of ant nests and the surrounding habitat were analysed. They included the composition and abundance of soil microflora and some physico-chemical soil properties.

The number of individuals in ant populations was estimated on the basis of the density of nests and the number of individuals per nest. A series of 3—5 nests was sampled every week from May to September inclusive. Production of an average ant colony was calculated as the sum of differences in the number and biomass of the young generation in various periods of the season. The amount of food carried into the nest was estimated on the basis of the daily and seasonal dynamics of foragers. Also a quantitative and qualitative analysis of the food carried by ants was done (P ę t a l and P i s a r s k i 1966, P ę t a l 1972).

The density of prey available was measured by means of permanent and temporary biocenometers (O l e c h o w i c z 1970) and by the method of sampling by hand the areas delimited with metal frames.

Soil for microbiological and chemical analyses was taken from ant nests and at a distance of 20 cm from them. Each sample was replicated 5—6 times. For microbiological analyses 1 g of soil was taken each time and for chemical analysis 100 g of soil. The abundance of ammonifying bacteria, fungi, and Actinomycetes was determined by the plate method and using standard culture media.

The pH of soil was estimated by the electrometric method, the content of exchangeable cations by the Pallman method, and the content of carbon by the Tjurin method (C z e r w i ń s k i, J a k u b c z y k and P ę t a l 1969, 1971, J a k u b c z y k et al. 1975).

A linear multiple correlation test was used to analyse the data. The relative importance of each independent variable was calculated from the formula quoted by G u i l f o r d (1960):

$$R^2 = \beta_1 r_1 y + \beta_2 r_2 y + \ldots + \beta_n r_n y$$

where: R^2 is the percentage of the explained variability, r is the covariant correlation coefficient for each pair of variables, β — beta weight, i.e., the standardized regression coefficient for each pair of variables.

Each term of the formula concerns only one independent variable and shows its effect on the total variance of the dependent variable y as expected by R^2. Expressing R^2 in per cent, it can be assumed that the independent variable x_1 at a constant value of the part common to the other independent variables $(x_2, x_3, \ldots, x_n)$ influences in $a\%$ the dependent variable y, and that x_2 at a constant value of the part common to the other independent variables influences it in $b\%$, etc.

The coefficient of the multiple correlation not only expresses the correlation between the dependent and independent variables but also characterizes the intercorrelation of independent variables. If two independent variables are correlated with each other, then one of them can have a negative weight of regression, though its correlation with the dependent variable is positive. It follows from this that the effect of the independent variable calculated from the formula can have a negative sign, though the coefficient

of partial correlation is positive. Such variables have a negative (damping) effect on the variance of the dependent variable y explained by R^2.

The significance of the multiple correlation for different numbers of independent variables was verified by the test F. This test was also used to verify the coefficients of partial correlation for pairs of analogical equations.

3. CHARACTERISTICS OF THE STUDY AREA

3.1. INTRODUCTION

The study was carried out in meadow habitats near Warsaw in the Vistula valley and in mountain pastures located in the Pieniny mountain range. These habitats differ in the type of soil, plant cover, and the type of management. Consequently, there were differences in the trophic structure of consumers, and ant populations were diversified.

3.2. SOIL AND VEGETATION

Soil and vegetation of the study areas have the following characteristics:

1. Unmanaged meadow, a nature reserve surrounded by the Kampinos Forest. It supports the Stellario-Deschampsietum Freitag 1957 association on poor, black muck-like soils;

2—4. Three mown meadows of the Arrhenatheretum medioeuropaeum association (Br.--Bl. 1919) Oberd. 1951 growing on alluvial brown soils (2), black soils (3), alluvial gley soils (4), and

5. Mountain pastures of the Lolio-Cynosuretum cristati association RTX 1937, developed on pseudogley brown soils.

The mown meadows were either unmanaged (habitats 1, 2a, 4a) or managed; in the latter mineral fertilizers were applied at differing rates: habitat 2b — 680 kg NPK $\cdot$ ha^{-1}, habitats 3 and 4b — 200 kg NPK $\cdot$ ha^{-1}. In the pastures organic fertilizers were supplied at a rate of 3600 kg of sheep manure $\cdot$ ha^{-1} in habitat 5a, and 9000 kg of sheep manure $\cdot$ ha^{-1} in habitat 5b.

These meadows and pastures are arranged along the gradient of an increasing soil fertility and an increasing index of organic matter decomposition. An increase in the primary production along this gradient is accompanied by a simplification of the trophic structure.

3.3. TROPHIC STRUCTURE

The primary production of aboveground plant parts ranged from 243.8 to 969.3 g d. wt $\cdot$ m^{-2} in different habitats (Table I). The trophic level of saprophages was

Table I. Trophic structure of meadow habitats and the contribution of ants to the biomass of consumers (in g d. wt $\cdot$ m^{-2})
Phytophages: Orthoptera, Homoptera, Nematoda; larvae: Lepidoptera, Diptera, and Coleoptera; predators: Aranea, Formicidae, Diptera, Staphylinidae, Chilopoda, Nematoda; larvae: Carabidae; Saprophages: Lumbricidae, Enchytraeidae, Acarina, Collembola, Nematoda, Coleoptera; larvae: Diptera. Data after three sets of papers: (1) Productivity investigation of two types of meadows in the Vistula Valley (Ekol. pol. 19: 93—262, 1971), (2) Analysis of sheep pasture ecosystem in the Pieniny mountains (the Carpathians) (Ekol. pol. 22: 475—732, 1974), (3) The effect of intensive fertilization on the structure and productivity of meadow ecosystems (Pol. ecol. Stud. 2 (4): 332 pp., 1976). Data collected in different years: for habitat 1 in 1967—1968, 2 — in 1973—1974, 3 — 1967, 5 — in 1970—1971. For explanation of symbols see Section 3.2.

Elements compared	Stellario-Descham-psietum (reserve)	Arrhenatheretum medio-europaeum (mown meadows)			Lolio-Cynosuretum cristati (pastures)	
		2			5	
	1			3		
		a	b		a	b
Aboveground primary production (g d. wt $\cdot$ m^{-2} $\cdot$ year^{-1})	476.0	243.8	969.3	588	554.2	957.2
Phytophages	0.28	2.36	1.81	0.32	0.28	0.92
Predators	0.59	0.57	0.19	0.30	0.15	0.14
Saprophages	6.30	27.66	22.08	13.00	4.93	20.90
Total biomass of consumers	7.17	30.58	24.08	13.62	5.35	21.96
Formicidae	0.22	0.24	0.03	0.19	0.05	0.02
Ant biomass in per cent of predator biomass	36.6	42.7	16.4	64.5	35.8	16.3
Ant biomass in per cent of total consumer biomass	3.0	0.8	0.1	1.5	1.0	0.1

most abundant. Its biomass ranged from more than 80% to more than 90% of the total biomass of invertebrate consumers. The biomass of phytophages accounted for 2—8%, and that of predators for 1—8% of the consumer biomass. The average biomass of ants varied from 0.02 to 0.24 g d. wt $\cdot$ m^{-2}. It accounted for 0.1—3.0% of the total invertebrate biomass and for 16.4—64.5% of the predator biomass.

The application of high doses of mineral fertilizers (680 kg NPK $\cdot$ ha^{-1} in habitat 2b) and organic fertilizers (9000 kg of sheep manure $\cdot$ ha^{-1} in habitat 5b) was followed by a substantial increase in the primary production and by a differentiation in the structure of consumers. As a result, the biocenosis used rapidly the nutrients added, that

is, organic and mineral fertilizers. A side-effect was a disturbance in the balance of eco-system functioning.

After the application of the two fertilizer types, primarily the structure of plant and animal communities was simplified and proportions in the trophic structure of consumers were modified.

The response of ants to fertilizers was more pronounced than that of other predators. The reason was the destruction of ant nests by these treatments and the following rapid development of the vegetation, which produced unfavourable conditions for the regulation of microclimate in nests.

4. ANT POPULATIONS

The number of ant species ranged from 1 to 14 in different grasslands under study (Table II). The density of their colonies varied from 0.08 to 0.30 per m². Both the

Table II. Species composition of ants and the density of ant nests (number of nests $\cdot$ m^{-2}) in various meadow types
+ — very sparse nests. For explanation of symbols see Section 3.2.

Species	Stellario-Deschampsietum (reserve) 1	Arrhenatheretum medioeuropaeum (mown meadows)					Lolio-Cynosuretum cristati (pastures)	
		2 a	2 b	3	4 a	4 b	5 a	5 b
Myrmica laevinodis Nyl.	0.03	0.01		0.03	0.12	0.16	0.01	<0.01
M. ruginodis Nyl.	0.01	<0.01		0.08	0.04	0.08	+	
M. sulcinodis Nyl.							0.01	<0.01
M. lemanica ssp. *jacobsoni* Kutter	0.01							
M. rugulosa Nyl.							0.04	0.02
M. scabrinodis Nyl.	0.09	<0.01			0.10		<0.01	0.01
M. sabuleti Mein.							+	<0.01
Tetramorium caespitum L.							+	
Lasius niger L.	0.01	0.11	0.08	0.03	0.04		0.07	0.01
L. flavus F.	0.02			0.04			0.03	0.03
L. affinis Schenek							0.03	0.01
Formica pressilabris Nyl.							+	+
F. fusca L.							+	
F. rufibarbis F.	+						+	+
F. cunicularia Latr.							+	+
Number of species	7	4	1	4	4	2	14	11
Total density of nests $\cdot$ m^{-2}	0.17	0.12	0.08	0.18	0.30	0.24	0.19	0.10

number of species and the density of nests in the unmanaged or little managed meadows and pastures were higher than in the managed ones. The species of the genus *Myrmica* and *Lasius niger* were most common. They occurred in almost all habitats, either the former or the latter being dominant.

The species of the genus *Myrmica* and *Lasius niger* differ in their biology and effects on the habitat (P ę t a l 1967, 1971b, J a k u b c z y k et al. 1975). *Myrmica* spp. produce young generation throughout the growing season, with a maximum in July. These ants are mostly polyphagous predators feeding on small invertebrates. Their nests are small, 12—13 cm in diameter, 3—7 cm high and 10—20 cm deep. In the period from May to September they move from one nest to another two or three times. In summer, larger colonies divide into smaller ones so that the difference between the spring-autumn density and the summer density can reach 50%. Over long-term cycles the density of colonies is largely stable.

The young generation of *L. niger* develops in the first half of the growing season and mainly in this period the workers of this species hunt for small invertebrates. They feed also on seeds, nectar, and honeydew of aphids. Their nests, usually 20—30 cm in diameter, 6—20 cm high, and by 20 cm deep, are inhabitat by the same society by many years.

Table III. Colony size and $P : \bar{B}$ of dominant ant species in various meadow habitats
A — *Myrmica* spp., B — *L. niger*. For explanation of the other symbols see Section 3.2.

Elements compared	Stellario--Descham-psietum (reserve)	Arrhenatheretum medioeuropaeum (mown meadows)					Lolio-Cynosuretum cristati (pastures)	
	1	2		3	4		5	
		a	b		a	b	a	b
Mean number A	888.9	2225.0	—	1059.7	643.5	1109.6	280.5	309.5
of ants B	7200.0	1009.3	1088.0	2414.5	—	—	394.0	232.2
per colony								
$P : \bar{B}$ A	0.48	0.15	—	0.67	0.38	0.44	0 62	0.82
B	—	0.67	0.68	0.29	—	—	0.65	0.58

The colonies of the species of *Myrmica* contained from 280 to 2225 individuals, and the colonies of *L. niger* were made up of 232—7200 inhabitants (Table III). The biomass turnover of a colony was largely diversified. It ranged between 0.15 and 0.82 for *Myrmica* spp. and from 0.29 to 0.68 for *L. niger*. The highest values of this index were noted in the periods of the highest nest density.

The response of dominant ant species to the application of fertilizers primarily consited in a decrease in the density of nests, at relatively small changes in the num-

ber of individuals per colony and even a little increased production and biomass turnover $(P : \bar{B})$.

5. NUMBER DYNAMICS AND FACTORS LIMITING THE GROWTH OF ANT POPULATIONS

5.1. INTRODUCTION

Changes in habitat conditions are not directly reflected in the number dynamics of ants. Their effect is modified by social phenomena. Here such components are involved as living in nests, where microclimatic conditions can be regulated to some extent, social behaviour including communication among individuals and transfer of pheromones controlling reproduction and the differentiation of castes, as well as labour division among groups of different age classes.

5.2. DENSITY OF NESTS

In habitats not subjected to violent changes, the density of ant nests is relatively stable. It is limited by the structure of plant cover and by the number of suitable sites for nests. These factors have also an effect on the colony size and on the body size of ants (Brian 1956). A kind of the population maturation can be observed, which lies in an increase in the proportion of old, large colonies, combined with a decrease in the proportion of young, small colonies, the level of the density of colonies being only little changed.

According to Scherba (1963) young colonies disappear mostly as a result of intra-specific competition. He studied a population of *Formica opaciventris* Emery which maintained a density of 0.04 nests per m^2 over a three-year period. During this time the rate of the establishment of new colonies was 5—13% and the rate of disappearance was 8—9%, mostly new colonies being involved in the latter case.

Similarly, no significant changes were observed in the density of *Myrmica lemanica* ssp. *jacobsoni* nests for eight years in a relatively homogeneous habitat of the reserve, Stellario-Deschampsietum meadow. Instead, seasonal changes in the density were observed. In spring (May) there were 36—43 nests per 250 m^2. In the first half of the growing season the colonies split into smaller ones and, as a result, in summer (July) the number of nests increased to 37—62 (Table IV). In autumn, i.e., when the colonies joined, the number of nests dropped to the spring level.

The spatial distribution of nests was more variable than their density. This distribution was calculated by means of the index of dispersion V (see Table IV). It ranged from 0.52 to 1.33 in spring and from 0.54 to 1.66 in summer. Therefore, it was possible to

Table IV. Density and spatial distribution of *Myrmica lemanica* ssp. *jacobsoni* nests in the reserve meadow in May and July of 1964–1971

Elements compared	1964		1965		1966		1967		1968		1969		1970		1971	
	May	July	May	July	May	July	May	July	May	July	May	July	May	July	May	July
Number of nests per 250 m^2	43	60	45	62	47	52	45	62	43	39	38	37	36	44	38	46
Dispersion index V^*	1.33	1.66	0.79	1.22	0.90	1.21	0.75	0.54	0.52	0.64	0.62	0.39	0.70	0.61	0.60	0.73

$^*V = \dfrac{S^2}{\bar{x}}$, where V is the index of dispersion, S^2 is the variance, $\bar{x}$ is the average number of nests per 12.5 m^2.

find that the spatial distribution of nests varied from uniform $(V < 1)$ to clumped $(V > 1)$. The changes in the spatial distribution of nests were related to the colony size. The correlation between the dispersion index of nests and the number of their inhabitants was high $(r = 0.86, P = 0.01)$. This relationship follows the equation

$$y = 1.14 + 0.0003 \ x$$

where: y is the index V, and x is the number of ants per colony.

The clumped distribution of nests when the colonies were large resulted from their division and probably protected ants from overcrowding. On the other hand, the transition from the clumped to the uniform distribution of nests, observed in the periods of food deficiency in the habitat (P ę t a l 1968, 1977b), was an effect of the competition among colonies. As a result all colonies had more equal chance to meet their food requirements.

It is a general rule that the density of nests is less variable than the number of individuals. The density of nests in *Myrmica ruginodis*, *Formica fusca*, and *Lasius flavus* populations living in heathland of northern England increased about two times over five years, while the number of individuals showed several times higher fluctuations and not synchronized with changes in the density of nests (P i c k l e s 1940). Similarly, the *M. laevinodis* population inhabiting an unmanaged meadow in Poland (habitat 1) maintained a density of 0.15–0.18 nests per m^2 over eight years, while the number of individuals ranged from 900 to 3200 over this period (P ę t a l 1977a).

Due to their colonial structure, ant populations can reach a high stability if the environment is not subjected to drastic changes. At minimum changes in the number of nests, it enables ants to adjust the number of individuals to actual environmental conditions. Moreover, little variable density of the colonies enables ants to maintain a high position in competitive interactions within a biocenosis.

5.3. COLONY SIZE

The number of ants in a colony largely depends on the type of habitat, on its climate, available food resources, and suitable sites for nest construction. It also depends on the age of a colony, old colonies being larger than young. In many-year cycles, ant colonies show changes in numbers which depend not only on environmental but also on intrapopulation factors (B r i a n 1965, P ę t a l 1977a, 1977b).

To find which of the population and environmental factors are mostly responsible for the colony size and production of ants, a multiple regression analysis was done for *Myrmica* spp. and *L. niger*, these being dominants in eight variants of the meadow habitats under study. The average number of individuals in a colony (a), total biomass production over the growing season (b), the number of workers produced (c), and the number of sexuals produced (d) were analysed as variables dependent on the following independent variables: (1) the number of old workers in a colony, (2) the

number of foragers expressed as the average number of workers leaving the nest in five-minute periods over the season, (3) the density of nests per m^2, (4) the density of prey available (in the number of individuals per m^2), and (5) mean seasonal temperature at the ground surface (in $^{\circ}$C). Numerical values of these variables are given in Table V.

Table V. Values of different ecological variables for dominant ant species in various meadows (see Section 3.2) in 1964—1974

Variables	Myrmica spp.		Lasius niger	
	mean	range	mean	range
Number of ants per colony	1003.30 ± 169.57	140–3157	1181.5 ± 162.88	76.2–24.14
Total number of young	396.17 ± 83.96	22–1759	634.15 ± 88.49	33 –1340
Number of young ♀♀ and ♂♂	61.15 ± 11.59	4–187	29.22 ± 7.60	0 –126.5
Production (mg d. wt · colony^{-1})	453.84 ± 87.11	23.7–1648.8	512.22 ± 70.04	16.3–1027
Number of old workers per colony	546.01 ± 93.26	52–1824	547.30 ± 98.61	43.2–1691
Number of foragers (ind. · 5 min.$^{-1}$ · nest^{-1})	22.89 ± 3.28	6.7–85.2	20.56 ± 1.49	10–30.3
Density of nests per m^2	0.11 ± 0.01	0.01–0.28	0.08 ± 0.01	0.01–0.15
Food available (No. of ind.· · m^{-2})	201.17 – 65.19	40–1606	–	–
Mean seasonal habitat temperature ($^{\circ}$C)	16.74 – 0.20	14.3–18.42	14.45 – 0.38	12.48–18.14

The coefficients of multiple correlation characterizing the strength of the relationship between the size and production of ant colonies, on the one hand, and population and environmental factors, on the other, ranged from 0.63 to 0.93 and were statistically significant at confidence levels of 0.01 and 0.05. They explained from 39.7 to 86.5% of the variability in the size production of ant colonies (Table VI).

The effects of the independent variables on the size and production of colonies are presented as the percentage variability explained by the coefficients of multiple correlation raised to the second power. Hence it was possible to determine interrelations between the variables and to find whether they increase or lower the part of variability explained by the other variables. The results of this analysis show that old workers had the highest effect on the colony size (81.13% for Myrmica and 88.22% for L. niger). The number of foragers and the density of nests determined the colony size of Myrmica spp. in 4.79 and 4.81%, respectively, and in a much lower percentage the colony size of L. niger. The effect of temperature, instead, was negative. This could be due to the fact that more ants left the nest in search of food during warmer periods and as a result their mortality from predation was increased.

Table VI. Percentage contribution of population and environmental factors to changes in the size and production of ant colonies, explained by the multiple correlation coefficients

Independent variables	Dependent variables							
	Myrmica spp.				Lasius niger			
	number of individuals per colony	production			number of individuals per colony	production		
		biomass	number of workers	number of sexuals		biomass	number of workers	number of sexual
Number of old workers	81.13	30.63	43.66	9.90	88.22	39.12	37.19	2.72
Number of foragers	4.79	15.64	9.46	1.04	−0.13	0.03	−0.03	16.19
Density of nests	4.81	2.19	10.96	−1.83	1.02	3.89	1.89	10.79
Food available	−0.03	0.55	−0.38	4.74	−	−	−	−
Ambient temperature	−3.78	3.49	−7.00	32.23	−6.75	−0.15	1.19	18.18
R^2 = per cent of explained variability	86.92	52.50	56.70	46.08	82.36	42.89	40.24	47.88
$1 - R^2$ = per cent of unexplained variability	13.08	47.50	43.30	53.92	17.64	57.11	59.76	53.12

The number of old workers has also the most pronounced effect on the colony production. Old workers determined the total biomass production in 30.63% for Myrmica spp. colonies and in 39.12% for L. niger colonies. They also mostly controlled the production of young workers (43.66% in Myrmica spp. and 37.19% in L. niger), while their effect on the production of sexuals was smaller. The latter variable was most influenced by ambient temperature (32.23% for Myrmica spp. and 18.18% for L. niger). In turn, the effect of temperature on the production of workers was small (1.19% for L. niger) or even large but negative (−7% for Myrmica spp.).

Also the density of nests and the number of foragers had a differentiating effect on the production of castes. Having a positive effect on the total biomass production, these factors determined 20.42% of the production of workers in Myrmica spp. and decreased the production of sexuals in 0.79%, while for L. niger they influenced the production of sexuals in 26.98% and only slightly (1.86%) the production of workers.

These differences in the effect of these factors on caste production between Myrmica spp. and L. niger can result from differences in the ecology of these species. The increase in the number of young workers related to these factors in Myrmica spp. populations, thus also the increase in the colony size, probably depends on the formation of the aggregations of colonies, which remain in contact with each other. This

does not occur in *L. niger* populations. In this species the increase in the density of nests and in the frequency of contacts among them through foragers is rather accompanied by a tendency to dispersion of the population due to an increased production of sexuals.

A low relationship between biomass production in a colony and the available food supply can be an effect of the adequate abundance of food in the habitat, as well as of the plasticity of foraging through changes in the diet spectrum and in the number of foragers.

5.4. REGULATORY MECHANISMS OF THE COLONY SIZE

The size of ant colonies is mostly regulated by intrapopulation factors. The earlier studies (B r i a n 1957, 1965, P ę t a l 1967, 1977a, 1977b) show that these factors primarily include reproduction, that is the production of castes (workers and sexuals) and the mortality of workers of older generations. These factors are density dependent.

Young colonies follow the exponential curve of growth, the increase in the number of individuals being proportional to the number of workers. When a colony reaches maturity, i.e., when it can produce sexuals, its size approaches an asymptote or even drops. According to B r i a n (1965), the limiting factor is the production of sexuals. They leave the nest in the same season, thus they do not contribute to an increase in the colony size. The production of the two castes is proportional to the number of workers from older generations. Therefore, it is enough that the production of sexuals is favourized and the production of workers has to decrease, this in turn having an effect on the colony size and production in next years.

The factors promoting the development of sexuals can include age structure of workers in a colony and also habitat conditions. The eight-year cycle in the dynamics of the *Myrmica lemanica* ssp. *jacobsoni* population inhabiting an unmanaged meadow can be used here as an example. The production of biomass in this population is proportional to the biomass of old workers in colonies (Fig. 1). The number of old workers depends not only on their production in earlier seasons but also on their mortality, which in turn depends on the number of foragers, i.e., workers providing the colony with food. Foragers are more subject to the mortality from predation than the workers remaining in the nest. Hence the elimination of old workers is in direct proportion to the number of foragers (Fig. 2). A high elimination rate of older workers can disturbe the age-related division of labour in the colony. Young, one--year old workers usually remain in the nest and take care for offspring, queen, and other workers, while older workers build the nest and provide food (O t t o 1958, W e i r 1958a, 1958b). An increase in the proportion of young workers in the nest may be followed by increasing care for larvae, particularly large ones, which will develop into sexuals. Their behaviour attracts more attention of workers than the behaviour of small larvae. Hence the elimination of older workers can be followed by an increase in the proportion of sexuals in the next-year production (Fig. 3).
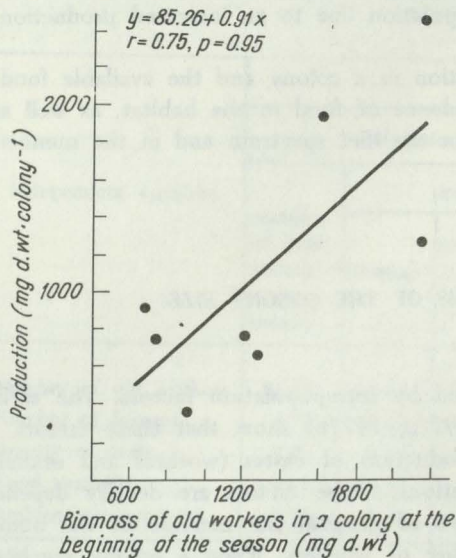
Fig. 1. Relationship between total biomass production and the biomass of old workers in the colonies of *Myrmica lemanica* ssp. *jacobsoni* in the reserve meadow in springs of 1964–1971
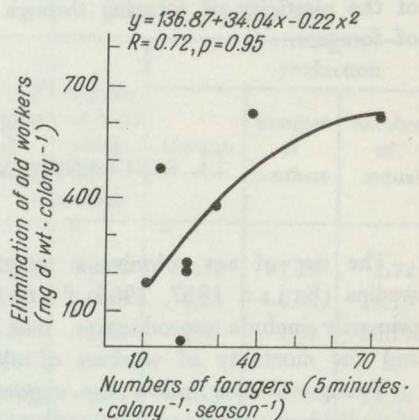

Fig. 2. Relationship between the elimination rate of old workers and the number of foraging individuals of *Myrmica lemanica* ssp. *jacobsoni* in the reserve meadow in 1964–1971
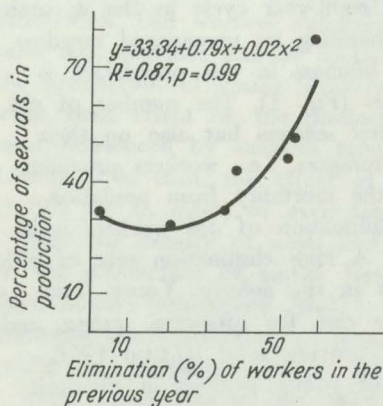

Fig. 3. Relationship between the contribution of sexuals to the production of a colony and the elimination rate of *Myrmica lemanica* ssp. *jacobsoni* workers in the preceding season in the reserve meadow in 1964–1971

A shift in the production toward the increased proportion of sexuals can also be an effect of food deficiency and adverse weather conditions in spring and early summer (P ę t a l 1967, 1977a, 1977b). In this situation the production of workers, mostly occurring in early summer, is reduced, while the production of sexuals is neither limited nor largely shifted in time and it falls within the driest and warmest period (P ę t a l 1977b). This can also be due to the fact that workers care more for large larvae of sexuals, as noted above.

Therefore, the increase in the colony size is determined by the production of workers, this depending on the number of workers from older generations. But also the number of young workers determines the number of old workers, since at the end of the growing

season there is a strong, directly proportional relationship between the biomass of
young and old workers (Fig 4).

$$y = 492.60 + 1.43x$$
$$r = 0.97, p = 0.99$$

Biomass of young workers in a colony (mg d.wt) — vertical axis: 100, 400, 700, 1100, 1400

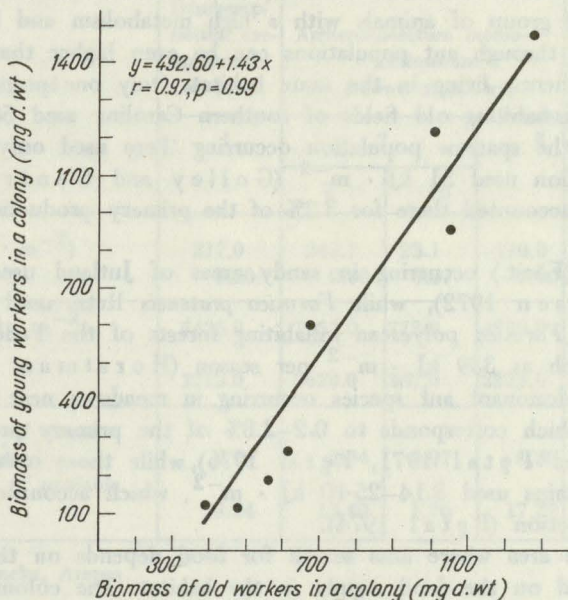Biomass of old workers in a colony (mg d.wt) — horizontal axis: 300, 700, 1100

Fig 4. Relationship between the biomass of young workers and the biomass of old workers at the
end of the growing season in *Myrmica lemanica* ssp. *jacobsoni* in the reserve meadow in 1964—1971

6. ANTS AS CONSUMERS

6.1. ENERGY REQUIREMENTS

Ants need much energy, which is related not only to their individual metabolism but
also to the maintaining of social homeostasis, i.e., to energy expenditure for informa-
tion and transport, as well as for securing a suitable microclimate in the nest.

The earlier studies show that there are large differences in bioenergetics between
ants and other invertebrates (G o l l e y and G e n t r y 1964, A y r e 1966, D l u s s-
k i j and K u p i a n s k a y a 1972, P ę t a l 1972, R o g e r s 1972, B r i a n 1973, N i e l-
s e n and J e n s e n 1975, H o r n-M r o z o w s k a 1976, R e i c h l e 1977, and S t r a d-
l i n g 1977).

Ants as polyphages, mostly predatory, take food rich in energy. But their index
of production expressed as the efficiency of ecological growth, i.e., as the ratio of

net production to food intake ($NP : I\%$) is low in relation to the food intake and assimilation. It varies between 2 and 50%. The respiration coefficient ($R : NP$), instead, is much higher in ants than in other invertebrates, and it ranges from 2 to 60. These values are close to those in homoiotherms (M c N e i l and L a w t o n 1970). Thus ants belong to the group of animals with a high metabolism and low production.

Flow of energy through ant populations can be even higher than through the populations of homoiotherms living in the same habitat. Only one population of *Pogonomyrmex badius* Latr. inhabiting old fields of southern Carolina used 58—75 kJ · m^{-2} per season, while the sparrow population occurring there used only 17 kJ · m^{-2}, and the mouse population used 31 kJ · m^{-2} (G o l l e y and G e n t r y 1964). The consumption by ants accounted there for 3.2% of the primary production (W i e g e r t and E v a n s 1967).

Lasius alienus (Först.) occurring in sandy areas of Jutland used 272 kJ · m^{-2} per season (N i e l s e n 1972), while *Formica pratensis* Retz. used 11.1 kJ · m^{-2} (J e n s e n 1978). *Formica polyctena* inhabiting forests of the Federal Republic of Germany used as much as 339 kJ · m^{-2} per season (H o r s t m a n 1974).

Populations of dominant ant species occurring in meadows near Warsaw used 24—280 kJ · m^{-2}, which corresponds to 0.2—2.8% of the primary production (K a j a k, B r e y m e y e r and P ę t a l 1971, P ę t a l 1976), while those occurring in pastures of the Pieniny mountains used 3.14—25·10 kJ · m^{-2}, which accounted for 0.01—0.11 of the primary production (P ę t a l 1974).

The size of the area where ants search for food depends on the colony size of a given species and on the food supply in the habitat. The colonies of ants living in meadows of the Warsaw region consisted of 2000—5000 individuals and they searched an area of 5—10 m^2. As the density of their nests was 0.1—0.2 · m^{-2}, they searched for food throughout their habitat area.

6.2. UTILIZATION OF ORGANIC MATTER BY ANTS IN MEADOW HABITATS

The dominant ant species in the study meadows and pastures reached a biomass of 22.7—217 mg d. wt · m^{-2} (Table VII). About 50—60% of this biomass was exchanged each year as a result of production and mortality ($P : \bar{B}$ = 0.45—0.67, and occasionally 0.04 in the habitat grazed by sheep at a high rate, where ant colonies were destroyed).

Food intake by ants in these habitats varied from 190 to 7257 mg d, wt · m^{-2}. The food of animal origin accounted for 50% and it mostly consisted of larvae and adults of the orders Diptera, Auchenorrhyncha, and Aranea (80—90%) (P ę t a l et al. 1971, K a j a k et al. 1972). The biomass of animal food intake ranged from 4.41 to 39.24% of the prey available on the average per season, being much higher in poor than in fertile habitats. The application of mineral and organic fertilizers lowered these figures from 13.4 to 1.8% and from 4.4 to 0.4%, respectively. Ants took more matter than many invertebrates characterized by a high consumption. In

Table VII. Biomass of ants and food intake in different meadows
For explanation of symbols see Section 3.2.

Elements compared	Deschamp-sietum cae-spitosum (reserve)	Arrhenatheretum medio-europaeum (mown meadows)			Lolio-Cynosuretum cristati (pastures)	
	1	2		3	5	
		a	b		a	b
Ant biomass (mg d. wt $\cdot$ m^{-2})	217.0	241.7	23.1	190.0	52.9	22.7
$P : \bar{B}$	0.50	0.60	0.67	0.60	0.45	0.04
Food biomass (mg d. wt $\cdot$ m^{-2})	5425.0	7257.0	773.0	4750.0	477.0	190.0
Food of animal origin (mg d. wt $\cdot$ m^{-2})*	2712.0	3628.0	387.0	2375.0	239.0	95.0
Food intake in per cent of above-ground primary production	2.76	2.34	0.07	0.80	0.12	0.04
Food intake in per cent of available prey biomass	39.24	13.40	1.76	17.77	4.41	0.42

*Diptera, Auchenorrhyncha, Aranea.

the unfertilized Arrhenatheretum meadow, ants used $7.2 \, g \cdot m^{-2} \cdot$ season^{-1}, while the consumption by Orthoptera was 0.7, by Homoptera 0.8, and by Lepidoptera larvae $0.1 \, g \cdot m^{-2} \cdot$ season^{-1} (A n d r z e j e w s k a 1976).

The predation by ants was most intensive during the period of their maximum production, which was usually adjusted to the production of prey available. It has been found that the production of wandering spiders is reduced in 49%, leafhoppers in 43%, and Diptera in 32% over the growing season. In different years, however, various groups of animals dominated the diet of ants, depending on their abundance in the habitat; groups with a higher production were preyed upon a higher rate (P ę t a l et al. 1971, K a j a k et al. 1972, P ę t a l 1974).

If prey were in short supply during the maximum food requirements in ants, the organization of foraging was modified. In the populations of *Myrmica* spp. primarily the number of foragers increased and the diet was enriched with other groups, more available in the habitat. The dynamics of searching for food was adjusted to the actual state of resources in the habitat (P ę t a l 1967, 1968). Also the distribution of nests was shifted from clumped to almost uniform, which enabled ants a more efficient utilization of prey (P ę t a l 1977a, 1977b).

A continuous accumulation of large amounts of food and a high metabolism of ant colonies account for the accumulation of large amounts of organic matter, faeces, and metabolites in nests. This is of importance for the adaptation of the nest microhabitat through number regulation of particular groups of microflora which can influence soil processes, thus contribute to changes in physico-chemical, including thermal conditions of nests.

7. SOIL HABITAT OF ANT NESTS AND THE ASSOCIATED VEGETATION

7.1. INTRODUCTION

The effect of ants on soil is related to building nests. In meadows, ants build earth nests in the form of mounds made up of mineral particles and plant material. Other components of the nest are food remains and final products of metabolism, all these materials being bound with the secretion of mandibular glands of ants. The nest has a system of caves and galleries, where about 80% of all its inhabitants permanently stay, where food is stored, and where aphids associated with roots can be raised.

The temperature and humidity of nests are regulated by ants. They are relatively little dependent on the habitat type and even on the geographical location.

As a result, physico-chemical properties of soil and soil microorganisms are chan-
ged, this being followed by changes in vascular plants (P ę t a l, J a k u b c z y k and
W ó j c i k 1970, P ę t a l 1977a).

7.2. SURFACE AREA OCCUPIED BY ANT NESTS

Ant nests cover a rather large area in grasslands. On clay-gravel soils of Berkshire, *L. flavus* colonies occupied 10–11% of the whole area (W a l o f f and B l a c k i t h 1962). In pastures of Colorado only one species, *Pogonomyrmex occidentalis* (Cresson), occupied from 0.03 to 0.28% of the area at a nest density ranging from 0.0003 to 0.0031 · m^{-2} (R o g e r s 1972). *Atta vollenveideri* Forel occurring in the pastures of Paraguay occupied 12.8 ± 2.8% of the area at a nest density of 0.40 · m^{-2} (J a n-
k m a n 1976).

In meadows and pastures of Poland the dominant species (*Myrmica* spp., *L. niger, L. flavus*) occupied from 0.1 to 1% of the area at a nest density of 0.1–0.3 · m^{-2} (C z e r w i ń s k i, J a k u b c z y k and P ę t a l 1971, P ę t a l et al. 1977).

7.3. PHYSICO-CHEMICAL PROPERTIES AND MICROFLORA OF SOIL IN ANT NESTS

Physical properties of soil in ant nests are an effect of changes in soil profile. When building their nests, ants remove small mineral particles from deeper soil layers and de-
posit them on the surface. In opposite direction they carry organic matter. The amount of earth removed, which is used for mound building, is large. According to L y f o r d (1963), ants transferred into the surface about 60 g of soil per m^2 in a season. S u d d (1969) has found that during only one day ants of the genus *Myrmica, Lasius niger, Formica lemani* Bondr. and *F. lugubris* Zetterstedt carried onto the surface from 0.04 to 0.40 g of soil in one nest.

The system of galleries and caves increases soil porosity. In this relation soil is better aerated and water can move more readily through it. Large amounts of organic matter also increase the water capacity of soil in ant nests. As a result the weight of this soil by volume drops.

Chemical changes in the soil of ant nests result from the accumulation of organic matter and its subsequent decomposition. The pH of ant nests is modified. In the nests built on alkaline soils pH drops, while it increases in nests on acid soils. In nests on soils characterized by more or less neutral reaction, changes in pH are small (P ę t a l 1977a).

In ant nests the contents of nutrients readily available for plants, such as K_2O and P_2O_2, and exchangeable cations such as Ca^{++}, Mg^{++}, K^+, Na^+, are usually higher than in the surrounding habitat (C z e r w i ń s k i, J a k u b c z y k and P ę t a l 1969, 1971, P ę t a l, J a k u b c z y k and W ó j c i k 1970, G a s p a r 1972). The differences become larger when the surrounding soil is poor in these nutrients. They also occur when soil is supplied with mineral and organic fertilizers. The increased concentrations of these substances are maintained for a longer time even in abandoned nests, reaching a level characteristic of a given habitat after two years (C z e r w i ń s k i, J a k u b c z y k and P ę t a l 1969).

The studies quoted above also show that chemical changes in the soil of ant nests are accompanied by changes in the abundance of some microflora groups. This is particularly the case of ammonifying bacteria and fungi, the number of which in ant nests is higher than in the surrounding soil. Instead, the number of Actinomycetes is usually lower in ant nests.

7.4. CHANGES IN CHEMICAL PROPERTIES AND MICROFLORA OF SOIL IN ANT NESTS AFTER THE APPLICATION OF MINERAL FERTILIZERS

Mineral fertilizers have an effect on soil processes not only in the habitat but also in ant nests (Z. Czerwiński, H. Jakubczyk and J. Pętal — unpublished data). As an example a meadow located on the black muck soil supporting the Arrhenatheretum association (habitat 4) can be taken, where experimental plots were minerally fertilized with N, P_2O_5, and K_2O at a rate of 200 kg · ha^{-1} for 25 years and compared with unfertilized plots.

The application of mineral fertilizers was followed by an increase in the level of K_2O and P_2O_5, changes in the content of exchangeable cations (Ca^{++}, Mg^{++}, K^+) and carbon (Table VIII). There were also changes in the abundance of microflora. Mineral fertilizing was followed mostly by a decrease in the number of ammonifying bacteria, while the number of fungi and Actinomycetes was only slightly affected. Similar tendencies occurred also in ant nests, where they were more strongly pronounced (Table VIII). The ratio of the number of ammonifying bacteria to the number of Actinomycetes, which according to H. Jakubczyk (personel communication) can be considered as an index characterizing early stages of mineralization in relation to humification, is symptomatic here. After the application of mineral fertilizers the value of this index dropped insignificantly in the habitat and more than 20 times in ant nests. Thus mineral fertilizers lowered the differences in chemical properties and microflora between soil of ant nests and the soil of surrounding habitat, on the one hand, and increased the differences in the rate of organic matter mineralization, on the other.

Table VIII. Nutrient content and microflora of the soil in *Myrmica* spp. nests and of the surrounding soil covered with Arrhenatheretum medioeuropaeum (habitat 4) minerally fertilized in 1972 and unfertilized

Elements compared	Fertilized meadow		Unfertilized meadow	
	environment	ant nest	environment	ant nest
$K_2O + P_2O_5$ in mg $\cdot$ 100 g of soil^{-1}	20.9	30.1	6.7	10.6
$Ca^{++} + Mg^{++} + K^+$ in mval. $\cdot$ 100 g of soil^{-1}	23.6	20.3	23.0	25.6
Per cent C	3.9	4.5	3.3	4.2
Ammonifying bacteria in millions $\cdot$ g d. wt of soil^{-1}	13.2	10.4	15.5	228.2
Fungi in millions $\cdot$ g d. wt of soil^{-1}	0.4	4.7	0.5	2.0
Actinomycetes in millions $\cdot$ g d. wt of soil^{-1}	4.9	2.9	5.0	3.2
Bacteria $\cdot$ Actinomycetes^{-1}	2.8	3.2	3.1	71.3

7.5. THE EFFECT OF ANT NESTS ON VASCULAR PLANTS

Changes in the soil of ant nests are followed by a characteristic plant succession. First, plants with rhizome covered mounds of the nests. In the Deschampsietum meadow these were *Carex panicea* L. and *Poa pratensis* L. (Pętal, Jakubczyk and Wójcik 1970). Then the species characteristic of fertile habitats, requiring moist and warm soil entered. Short-lasting nests of *Myrmica* spp. did not caused an advanced succession. Within two years after the abandoning of the nests by ants, the vegetation returns to the original state. Considerable floristic differences occurred on long-term nests of *L. flavus*. Gaspar (1972) has found that these nests were inhabited by a lower number of plant species than the surrounding habitat, and they were largely favourized. These plants included *Festuca rubra* L. and *Thymus* sp. They did not occur in the nest surroundings. Similarly King (1976) found that on ant nests built in meadows of southern Cornwall the number of seedlings was about 30% lower than in the surrounding habitat, and one species, *Aira praecox* L. was preferred. Also the production of seeds in plants covering ant nests was four times lower than in surrounding plants.

Ant nests have also an effect on plant production. Near the nests of American species of the genus *Pogonomyrmex,* plant cover was better developed and the standing crop of biomass was higher by 63% as compared with the area beyond the zone of nest influence (Rogers 1972). According to Jankman (1976), the nests of *Atta vollenveideri* in pastures of Paraguay are starting points for forest succession.

8. MODIFICATION OF SOIL PROCESSES IN ANT NESTS

8.1. INTRODUCTION

It is known (D u t h i l 1971, D i c k i n s o n and P u g h 1974) that the main factor responsible for the direction of decomposition is the quality of organic matter. It determines the activity of different microflora groups, such as ammonifying bacteria, fungi, and Actinomycetes. The dominance of one of these groups is followed by changes in the amount of exchangeable cations released and in pH. The development of ammonifying bacteria is related to alkaline reaction and, at the same time, it increases pH. This enhances the exchange of cations in the soil absorbing complex. The development of fungi, instead, is related to the acidification of soil, which increases the chance of leaching exchangeable cations. Actinomycetes, which take part in the synthesis of humic acids, account for an increase in the exchange capacity of soil, thus also for retaining of exchangeable cations. These three groups of microflora have a positive or negative effect on each other, of various degrees. They also depend on the effect of soil fauna on both their number and activity.

Quantitative changes in basic chemical properties and microflora of ant nests result from both organic matter decomposition characteristic of the habitat and direct or indirect influences of ants. As it has been noted above, the effect of ants consists of changes in physical soil properties related to the nest structure and of chemical changes re-

Table IX. Chemical properties and microflora of the soil in ant nests and surrounding habitats Meadows and pastures as in Tables I–III. A — ant nest, B — surrounding habitat. S is the sum of exchangeable cations ($Ca^{++} + Mg^{++} + K^+ + Na^+$) per 100 g of soil

Variables		Myrmica spp.		Lasius niger	
		mean	range	mean	range
pH	A	5.90 ± 0.18	$4.05-7.20$	5.97 ± 0.19	$4.9-7.4$
	B	5.68 ± 0.20	$4.20-6.8$	5.60 ± 0.24	$4.3-7.2$
S(meq $\cdot$ 100 g d. wt soil^{-1})	A	18.53 ± 2.43	$1.02-35.66$	11.05 ± 1.77	$1.07-21.63$
	B	16.60 ± 2.59	$9.82-33.63$	11.18 ± 1.81	$0.95-24.20$
C (%)	A	4.37 ± 0.31	$0.54-6.16$		
	B	3.14 ± 0.19	$1.07-4.47$		
Bacteria ($10^6 \cdot$ g d. wt soil^{-1})	A	209.25 ± 60.93	$6.3-686.5$	125.41 ± 65.89	$10.90-846.0$
	B	38.51 ± 10.38	$7.6-140.8$	20.96 ± 3.70	$2.69-55.8$
Fungi ($10^6 \cdot$ g d. wt soil^{-1})	A	2.12 ± 0.24	$0.40-4.70$	1.49 ± 10.37	$0.18-4.70$
	B	1.46 ± 0.37	$0.40-6.70$	1.14 ± 0.29	$0.12-4.90$
Actinomycetes ($10^6 \cdot$g d. wt. soil^{-1})	A	2.18 ± 0.37	$0.18-4.80$	3.51 ± 0.74	$0.40-9.42$
	B	3.98 ± 0.76	$1.19-12.8$	6.46 ± 1.53	$0.40-4.90$
Number of ants per nest		999.70 ± 90.14	$185-1662$	1019.10 ± 263.25	$48-3361$
$P : \bar{B}$		0.36 ± 0.04	$0.001-0.28$	0.42 ± 0.06	$0.02-0.63$

lated to the accumulation of organic matter in nests, such as food, its remains, and metabolites of ants. These properties can have an effect on the quantitative differentiation of microflora and on its activity. Also the size of ant colonies should influence this.

Analysing soil processes, the effect of microflora on chemical properties of soil in ant nests and in their surroundings, then the effect of ant colonies and the properties of surrounding soil on soil properties in ant nests was estimated for *Myrmica* spp. and *L. niger* occurring in the lowland meadows and mountain pastures described above. The mean values and the range of the properties under study are given in Table IX.

8.2. THE EFFECT OF MICROFLORA ON CHEMICAL PROPERTIES OF SOIL IN ANT NESTS AND SURROUNDING HABITATS

To compare the effect of microflora on chemical properties of the soil in ant nests and in the surrounding habitat, a linear multiple regression was used:

$$y = a + b_1 x_1 + b_2 x_2 + b_3 x_3$$

Chemical properties of soil, such as (a) pH, (b) the content of exchangeable cations $(S = Ca^{++} + Mg^{++} + K^+ + Na^+)$, and (c) percentage of carbon were considered as the variables dependent on the following independent variables: (1) ammonifying bacteria, (2) fungi, and (3) Actinomycetes. The regression equations were calculated for each chemical property of the soil in ant nests and surrounding habitats. Coefficients a and b ($i = 1, 2, 3$) for pairs of these equations were compared by the F test (Table X). Statistically significant differences at a confidence levels of 0.05 and 0.01 were found for the effect of microflora on the pH and content of exchangeable cations in ant nests and the surrounding habitat; there were no significant differences in the con-

Table X. Coefficients of the multiple regression of chemical properties of soil on microflora in ant nests and surrounding habitats

b_i ($i = 1, 2, 3$) — increase in a soil character when x_i (x_1 — number of bacteria, x_2 — number of fungi, x_3 — number of Actinomycetes) increases by unit, independent of x_j ($j = 1, 2, 3$), $i \neq j$
I — *Myrmica* spp., II — *Lasius niger*, A — ant nest, B — surrounding habitat. In parentheses the level of significance. S — sum of exchangeable cations

	Dependent variables		Regression coefficient				Tests	
			a	b_1	b_2	b_3	Fb_i ($i = 1, 2, 3$)	Fa
I	pH (y_1)	A	5.1847	0.0010	−0.0440	0.2705	2.75 (0.05)	3.33 (0.05)
		B	6.5313	0.0047	−0.3357	0.1151		
	S^x (y_2)	A	3.1449	0.0266	1.6681	2.8754	6.42 (0.01)	4.90 (0.01)
		B	11.1447	0.1387	−3.1141	1.0939		
	%C (y_3)	A	2.7092	0.0030	0.3706	0.1067	1.14 (<0.05)	2.19 (<0.05)
		B	2.7725	0.0047	−0.1061	0.0854		

	pH (y_1)	A	5.7274	0.0032	−0.2175	0.0488	3.83 (0.05)	2.89 (0.05)
		B	5.5145	0.0333	−0.4159	−0.0185		
II	S (y_2)	A	4.2235	0.0213	−0.2621	1.2996	4.97 (0.05)	3.81 (0.05)
		B	6.4012	0.2766	−2.1264	0.2284		

tent of carbon. It follows from the significance of the difference between coefficients a that the changes in chemical properties of soil as an effect of microflora activity start from a higher level in the surrounding soil than in the nest soil. The differences in the coefficients b_i show that the microflora action on the pH and exchangeable cation content differs in intensity and direction in ant nests as compared with the surrounding habitat. Hence it may be suggested that ants can account for differences in the effect of microflora on organic matter decomposition in their nests.

8.3. THE EFFECT OF ANT COLONIES ON SOIL PROPERTIES IN ANT NESTS

The relation of soil properties in ant nests to environmental factors and to the presence of ants was analysed by means of the linear multiple regression. Such soil properties in ant nests as (a) pH, (b) the content of exchangeable cations, (c) the number of ammonifying bacteria, and (d) the number of Actinomycetes were considered as the variables dependent on the following independent variables related to the soil surrounding the nests: (1) pH, (2) the content of exchangeable cations (S), (3) the number of ammonifying bacteria, and (4) the number of Actinomycetes; also two features of ant colonies are included here as independent variables: (5) the number of ants in a colony and (6) the turnover of ant biomass.

First it has been tested which properties of nest soil have a significant effect on ant societies independent of the effect of surrounding soil. For this purpose multiple correlation coefficients were calculated for the properties of nest soil $(y_i, i = a, b, c, d)$ taking into account only the effect of the properties of surrounding soil $(x_i, i = 1, 2, 3, 4)$. Then the joint effect of the surrounding soil and ant colony was calculated $(x_i, i = 1, 2, 3, 4, 5, 6)$. The correlation coefficients for the effect of surrounding soil (R_2) and for the joint effect of surrounding soil and ants (R_1) were statistically significant at confidence levels of 0.05 and 0.01, and their values ranged from 0.397 to 0.961 (Table XI). The F test for the significance of the difference between correlation coefficients R_1 and R_2 indicates that the size of ant colonies and the turnover of ant biomass have a highly significant effect on the pH, content of exchangeable cations, and number of ammonifying bacteria in the soil of *Myrmica* spp. nests, and on the pH in the soil of *L. niger* nests.

The next step was to analyse the effect of each environmental factor and ant colonies on the soil of nests. Using the formula already quoted:

$$R^2 = \beta_1 r_1 y + \beta_2 r_2 y + \ldots + \beta_6 r_6 y$$

the effect of each independent variable was calculated as a part of the variability of a given property of the nest soil which was explained by the second power of the multiple correlation coefficient (Table XII). The second powers of these coefficients involved from 35.7 to 92.35% of the variability in the nest soil.

Table XI. Comparison of the coefficients of multiple correlation R characterizing the effect of the environment (R_2) and the effect of the environment and ants (R_1) on the properties of the nest soil
In parentheses the confidence level. S is the sum of exchangeable cations

Ant groups	Properties of soil in ant nests	R_2	R_1	F test	
Myrmica spp.	pH	0.886	0.929	3.985	(0.01)
	S	0.886	0.918	2.384	(0.05)
	bacteria	0.881	0.961	12.516	(0.01)
	Actinomycetes	0.912	0.920	0.622	(<0.05)
Lasius niger	pH	0.938	0.957	2.068	(0.05)
	S	0.837	0.882	1.705	(<0.05)
	bacteria	0.898	0.911	0.727	(<0.05)
	Actinomycetes	0.397	0.594	1.508	(<0.05)

Table XII. Percentage contribution of some environmental factors and ant colonies to changes in the properties of the nest soil explained by the multiple correlation coefficients
S is the sum of exchangeable cations

Environmental factors and ants (independent variables)	Soil in ant nests (dependent variables)							
	Myrmica spp.				*Lasius niger*			
	pH	S	bacteria	Actino-mycetes	pH	S	bacteria	Actino-mycetes
pH	129.40	48.15	0.50	−5.96	63.38	4.72	−16.03	14.13
S	−14.18	28.81	−25.81	12.95	−3.41	−13.86	9.15	−3.73
Ammonifying bacteria	1.28	22.99	54.86	20.47	35.29	80.50	92.51	−11.17
Actinomycetes	−11.65	−9.66	5.21	57.12	1.30	1.09	9.70	−2.11
Number of ants per colony	0.44	−9.47	−26.19	1.06	−7.20	−8.20	−12.42	31.39
$P : \bar{B}$ of colony	−18.99	3.45	83.78	−1.00	2.19	13.47	0.17	6.76
R^2 = explained variability in per cent	86.30	84.27	92.35	83.64	91.55	77.72	83.08	35.27
$1 - R^2$ = unexplained variability in per cent	13.70	15.73	7.65	16.36	8.45	22.28	16.92	64.73

Each of the properties of the surrounding soil and ant colonies explained the variability either positively or negatively. Some properties of the nest soil were mostly determined by the properties of the surrounding soil. They include pH and the number of Actinomycetes in the nests of *Myrmica*, depending on the pH and the number of Actinomycetes in the surrounding soil in 129.40 and 57.12%, respectively. They also include pH and the number of bacteria in the nests of *L. niger*, which were influenced by the same features of the surrounding soil in 63.38 and 92.51%, respectively.

The content of exchangeable cations in the nest soil mostly depended on the general type of organic matter decomposition in the surrounding soil. It was primarily determined by pH (in 48.15% for *Myrmica* spp. nests and in 4.72% for *L. niger* nests) and by the number of ammonifying bacteria (in 22.99% for *Myrmica* spp. nests and in 80.5% for *L. niger* nests). In the habitats under study, where the absorbing complex of soil was filled with exchangeable cations (V)[1] in 50—98%, the value of pH was positively correlated with the content of exchangeable cations $(r = 0.86, p = 0.01)$, while the number of ammonifying bacteria was related to the decomposition of organic matter, thus also to the rate of release of exchangeable cations.

The abundance of microflora in nests was mainly determined by ants. Differences were found in the effect of the ant species under study on various microflora groups. *Myrmica* spp. determined the number of ammonifying bacteria in 57.59%, while *L. niger* determined the number of Actinomycetes in 38.15%. The positive effect of ants on changes in the abundance of these microflora groups, explained by the factors considered, was related either to the biomass turnover, like in *Myrmica* spp. nests, or to the number of ants in colonies, like in *L. niger* colonies. The size of the societies of these ants limited the abundance of ammonifying bacteria.

The reasons for which various ants have different effects on microflora are probably related to their diet and biology. In *Myrmica* spp. nests, where the development of young generation is continued throughout the growing season, there is a continuous inflow of the animal food rich in proteins. Hence, the effect of these ant species on ammonifying bacteria is related to the biomass turnover of the colony. The diet of *L. niger* includes animal food only in the first half of the growing season, when the young generation develops. Then the carbohydrate food rich in carbon prevails. The remains of this food stored in the nest can promote the development of Actinomycetes. This development is firstly conditioned by the colony size and not by the turnover of biomass, the latter being much lower in *L. niger* than in *Myrmica* spp.

Ants have also a negative effect on the size of the properties of the nest soil. It could be an effect of relationships between particular chemical properties of soil and the microflora of ant nests, which are difficult to explain now.

9. CONCLUSIONS

Ants occupy an important position in the trophic structure of meadows since their biomass is high in relation to the biomass of other invertebrates and because they use large amounts of organic matter as food.

The development of ant populations mostly depends on intrapopulation factors. In the meadow habitats not subjected to intensive management the density of ant nests shows a high stability, and their distribution depends on the size of the society. The size of the society is largely regulated by internal factors. Biomass production of new

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[1] $V = \dfrac{S \cdot 100}{T}$, where S is the sum of exchangeable cations, T is the capacity to exchange cations, i.e., the maximum content of different cations which can be absorbed by 100 g of soil.

individuals is in direct proportion to the number of workers from earlier generations. The factor limiting the growth of a colony is the production of sexuals, which has a negative effect on the colony size and on its production in successive years. The production of sexuals depends on such environmental factors as temperature and available food supply, but first of all on the age structure of the workers; it is higher in the years following those in which the elimination rate of old workers was high. The number of currently produced workers has also a limiting effect on the size of the society, since at the end of the growing season the ratio of the biomass of young to old workers is maintained at a stable level.

Ants constructing nests have an effect on changes in soil processes. They modify the abundance of different microflora groups. Changes in the abundance of microflora in ant nests depend on the size of ant colonies and on their biomass turnover. The size of a colony has an inhibiting effect on the abundance of ammonifying bacteria and stimulates the abundance of Actinomycetes. The turnover of biomass has a positive effect on the number of ammonifying bacteria. When the joint effect of the colony size and biomass turnover is considered, *Myrmica* spp. colonies have a stimulating effect on the development of bacteria, while *L. niger* colonies promote the development of Actinomycetes. In this relation these ant species have different effects on the pH and the content of exchangeable cations in the soil of nests.

10. SUMMARY

The role of ants in meadow habitats is analysed with reference to their contribution to the trophic structure, amount of organic matter used, and effects on soil processes. The role of ants is determined by their social organization and the related high metabolic costs, as well as by their number dynamics, the latter being mostly controlled by intrapopulation factors.

During the 11-year period of the study conducted in eight types of meadows and pastures, unmanaged or managed more or less intensively, ant biomass ranged from 0.02 to 0.24 g. d. wt $\cdot$ m^{-2}, which accounted for 0.10–3.0% of the biomass of all invertebrates (Table I). The number of species varied from one to 14, *Myrmica* spp. and *L. niger* being dominants. The management of the habitat was followed by a reduction in the number of species and by a decrease in the number of colonies, at small changes in the number of individuals in colonies and a little increased biomass turnover (Table II).

The food intake of the dominant ant species varied from 0.190 to 7.257 g d. wt $\cdot$ m^{-2}, a half of this amount being of animal origin (Table VII).

The density of ant nests was relatively stable in the habitats not subjected to drastic changes. For eight years the density of nests in the *M. lemanica* ssp. *jacobsoni* population in the reserve meadow ranged from 0.14 to 0.17 per m^2 in spring and from 0.15 to 0.25 per m^2 in summer, when larger colonies were divided (Table IV). But large changes were observed in the distribution of nests, which ranged from clumped to uniform. Larger aggregations of colonies occurred in the years when they were large. One of the reasons for transition from a clumped to uniform nest distribution was intraspecific competition for food. The density of nests was less variable than the num-

ber of their inhabitants and was not correlated with it. This probably protected ants from excessive fluctuations and enabled them to colonize the habitat in a permanent way.

Ant production is more related to population than to environmental factors. A multiple correlation analysis shows that the total biomass production largely depends on the number of old workers in a colony. All the factors analysed had a differentiating effect on the production of castes. While the number of workers produced was most dependent on the number of old workers in the colony, the production of sexuals was most influenced by ambient temperature; at the same time temperature had a negative effect on worker production. Similarly, but to a lesser degree, the available food supply had an effect on the production of castes. The density of nests and the number of foragers had different effects on the production of castes. In *Myrmica* spp. they largely determined the production of workers, while in *L. niger* the production of sexuals. This can be explained by differences in the ecology of these species; the colonies of *Myrmica* spp. form aggregations within a population, while they are dispersed in the populations of *L. niger*.

The regulation of the number of individuals in *M. lemanica* ssp. *jacobsoni* is density-dependent. The production of new individuals was in direct proportion to the number of workers from earlier generations (Fig. 1). The factors limiting the exponential growth of colonies was the production of sexuals, also influencing the colony size and production in next years. In turn, the production of sexuals was determined by environmental conditions such as temperature and food supply, and on the age structure of workers. It was higher after the years with a high reduction in the number of old workers (Fig. 3), and this reduction was largely determined by foraging (Fig. 2). A high elimination of old workers probably disturbed the age-related labour division in the colony and intensified the care for larvae, particularly for the larvae of sexuals, absorbing more attention of young workers. At the end of the growing season a constant proportion was established between the biomass of currently produced workers and the biomass of workers from earlier generations (Fig. 4).

The effect of ants on soil resulted from building nests of earth and storing organic matter in them. As a result, physico-chemical soil properties were changed in nests and they were covered with specific plants. Ants had an effect on basic soil processes carried out by different microflora groups such as ammonifying bacteria, fungi, and Actinomycetes (Table X). The changes in soil processes depended on the size of a colony and biomass turnover, and were less concerned with direct effects on soil chemical properties than with the microflora of nests (Table XII). The colony size had a reducing effect on the number of ammonifying bacteria and a stimulating effect on the number of Actinomycetes, while biomass turnover had a positive effect on the number of bacteria. *Myrmica* spp. had a different effect on microflora than *L. niger*.

Taking into account the joint effect (stimulating and inhibiting) of the number of individuals in a colony and biomass turnover, *Myrmica* spp. promoted the development of bacteria, while *L. niger* stimulated the development of Actinomycetes and reduced the development of bacteria. In this relation the effect of these ant species on the pH and exchangeable cations in soil was different. Stimulation of the development of various groups of microflora by these species could result from differences in their diet, thus from the quality of organic matter stored in the nests. It could be also conditioned by the metabolites of colonies.

11. POLISH SUMMARY

Rozpatrywana jest rola mrówek w środowiskach łąkowych w aspekcie ich udziału w strukturze troficznej, ilości użytkowanej materii organicznej, oraz w zmianach procesów glebowych. O znaczeniu mrówek decyduje organizacja społeczna i związane z nią wysokie koszta metabolizmu oraz — zależna głównie od czynników wewnątrzpopulacyjnych — dynamika liczebności.

Na badanych w okresie 11 lat ośmiu typach łąk i pastwisk nie uprawianych oraz uprawianych mniej lub bardziej intensywnie biomasa mrówek wynosiła 0.02–0.24 g s. m. · m^{-2}, co stanowiło 0,10–3,0% biomasy wszystkich bezkręgowców (tab. I). Stwierdzono występowanie od 1 do 14 ga-

tunków mrówek. Dominowały gatunki *Myrmica* spp. i *L. niger*. Zabiegi gospodarcze powodowały redukcję liczby gatunków, zmniejszenie liczebności kolonii przy małych zmianach liczebności osobników w koloniach i nieco podwyższonej rotacji biomasy (tab. II).

W badanych środowiskach ilość pobranego pokarmu przez dominujące gatunki mrówek wyncsiła od 0,190 do 7,257 g s.m. · m^{-2}, w czym około połowę stanowił pokarm pochodzenia zwierzęcego (tab. VII).

Zagęszczenie gniazd mrówek jest stosunkowo mało zmienne w środowiskach nie podlegających drastycznym zmianom. W ciągu 8 lat zagęszczenie gniazd w populacji *M. lemanica* ssp. *jacobsoni* na łące rezerwatowej wahało się od 0.14–0,17 na m^2 w okresie wiosennym i 0,15–0,25 w okresie letnim, kiedy następował podział większych kolonii (tab IV). Znacznym zmianom podlegała natomiast struktura przestrzenna gniazd, od skupiskowej do równomiernej. Większe skupienia występowały w latach gdy kolonie były większe. Jedną z przyczyn zmiany rozkładu przestrzennego mrowisk ze skupiskowego na równomierny była konkurencja wewnątrzgatunkowa o zasoby pokarmowe środowiska. Zagęszczenie gniazd zmieniało się w mniejszym stopniu niż liczebność ich mieszkańców i nie było z nim skoordynowane. Zabezpieczało to prawdopodobnie populacje mrówek przed nadmiernymi fluktuacjami i zapewniało im stałe opanowanie środowiska.

Produkcja mrówek w większym stopniu zależy od czynników populacyjnych niż środowiskowych. Analiza korelacji wielokrotnej wykazała, że całkowita produkcja biomasy zależała przede wszystkim od liczebności starych robotnic w kolonii. Wszystkie analizowane czynniki wpływały różnicująco na produkcję kast. Podczas gdy liczba wyprodukowanych robotnic zależała w największym stopniu od liczby starych robotnic w kolonii, to na produkcję osobników płciowych największy wpływ miała temperatura środowiska, która jednocześnie ujemnie wpływała na produkcję robotnic. Podobnie jak temperatura, lecz w mniejszym stopniu, różnicował produkcję kast potencjalnie dostępny pokarm. Zagęszczenie gniazd i liczebność furażerek wykazały różny wpływ na produkcję kast badanych gatunków. Podczas gdy u gatunków *Myrmica* określały w wysokim stopniu produkcję robotnic, to u *L. niger* determinowały głównie produkcję osobników płciowych. Tłumaczy się to różnicami w ekologii tych gatunków – tworzeniem skupień w populacjach *Myrmica* spp. oraz ich dyspersję w populacjach *L. niger*.

Regulacja wielkości kolonii mrówek *M. lemanica* ssp. *jacobsoni* ma charakter zagęszczeniozależny. Produkcja nowych osobników była wprost proporcjonalna do stanu robotnic z poprzednich generacji (rys. 1). Czynnikiem limitującym wzrost eksponencjalny kolonii była produkcja osobników płciowych, która odbijała się także na wielkości kolonii i jej produkcji w latach następnych. Z kolei produkcja form płciowych zależała od warunków środowiskowych, jak temperatura i pokarm oraz od struktury wiekowej robotnic. Była ona większa po roku z dużą eliminacją starych robotnic (rys. 3), która w dużej mierze uwarunkowana była furażowaniem (rys. 2). Duża eliminacja starych robotnic naruszała prawdopodobnie związany z wiekiem podział pracy w kolonii i nasilała pracę nad pielęgnacją larw, zwłaszcza larw osobników płciowych bardziej absorbujących uwagę młodych robotnic. Na koniec sezonu wegetacyjnego ustalała się jednak wysoka wprost proporcjonalna zależność między biomasą nowo wyprodukowanych robotnic i robotnic z poprzednich generacji (rys. 4).

Wpływ mrówek na środowisko glebowe wynikał z budowy gniazd ziemnych i gromadzenia w nich materii organicznej. Dało to w efekcie zmiany fizyczne i chemiczne gleby mrowisk i specyficzną strukturę roślinności. Mrówki wpływały na zmiany podstawowych procesów glebowych prowadzonych przez różne grupy mikroflory: bakterie amonifikujące, grzyby i promieniowce (tab. X). Zmiany te zależały od wielkości kolonii oraz rotacji ich biomasy i w mniejszym stopniu dotyczyły bezpośredniego oddziaływania mrówek na właściwości chemiczne niż na mikroflorę mrowisk (tab. XII). Wielkość kolonii wpływała hamująco na liczbę bakterii amonifikujących i stymulowała liczebność promieniowców, natomiast rotacja biomasy wpływała dodatnio na liczebność bakterii. Gatunki *Myrmica* oraz *L. niger* różnie oddziaływały na mikroflorę.

Biorąc pod uwagę łączny wpływ (sumujący i znoszący) liczebności osobników w kolonii oraz rotacji biomasy, *Myrmica* spp. stymulowała rozwój bakterii, natomiast *L. niger* rozwój promieniowców wpływając ujemnie na bakterie. Wiązała się z tym różna intensywność oddziaływania mrówek na pH i metaliczne kationy wymienne. Stymulowanie rozwoju różnych grup mikroflory przez te gatunki mogło wynikać z różnic ich diety, a więc jakości nagromadzonej w mrowiskach materii organicznej i mogło być także uwarunkowane przez metabolity kolonii.

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