SŁAWOMIR MAZUR

BEETLE SUCCESSION IN FEEDING SITES OF THE PINE SHOOT BEETLE *(TOMICUS PINIPERDA L., COLEOPTERA SCOLYTIDAE)* IN ONE-SPECIES AND MIXED PINE STANDS

ABSTRACT

The succession mentioned was studied in four phases: 1) foundation of galleries and laying of eggs, 2) development of bark beetle larvae, 3) phase of pupae and fresh incubated beetles, 4) light galleries. On all occasions 3 118 specimens of beetles were captured from 28 780 galleries.

It has been examined that in a process of the succession there are two main associations of beetles: the first, consisting of stenotopic predators, occuring in the first two phases (with *Rhizophagus depressus* as a dominant), and the second, containing eurytopic non-meat-eating beetles, occuring in the remaining phases (with *Phloeonomus pusillus* as a dominant). The number of species gradually becomes higher simultaneously with the development of galleries. It seems to be that neither forest habitat nor forest composition are of decisive value in the process of the succession of subcortical beetles.

INTRODUCTION

The study of beetle succession is a trial to find some regularities and correlations which give a foundation for investigations on the biology and ecology of the group of insects discussed. The study of the influence of the habitat may be useful for evaluation of the factors of natural environment resistance in various habitats. To date only two mentions are found in the Polish partinent literature on this subject: Karpiński [7] observed an increase in the number of predatory beetles occuring in the feeding galleries of *Ips typographus* and *Ips duplicatus* in richer habitats; Bałazy [2] noticed quantitative differences in the abundance of entomophages in managed and primeval forests. The influence of the specific composition of the stands, and thus the contribution of undergrowth has so far not been investigated. The influence of undergrowth was studied since it is generally considered rich ecosystems composed of a large number of components have a higher natural resistance. Hence the concept of biocoenotic enrichment of poor pine forests by the introduction of undergrowth. The present

paper, therefore, is also a trial of evaluation from the standpoint of certain aspects of biological forest protection, of the effects of undergrowth admixture as a factor enriching the biocoenosis.

MATERIAL AND METHODS

As basis for the present work served material collected during field work.

Succession was investigated in 4 phases: 1) the stage of female gallery boring and oviposition by the pine shoot beetle, 2) its larval stage, 3) the stage of pupa and immature beetles and 4) the stage of abandoned feeding sites. This division was adopted for practical reasons, in order to reach conclusions concerning the occurence of the particular species in the successive developmental stages of the bark beetle, and on the other hand, to allow sufficiently long intervals between the successive observations that the changes would be noticeable. This gradation does not differ much from that in similar works where the number of steps in succession studies varies from 3 [13] to 6 [8].

Since the present paper is a part of group studies on the influence of the habitat and the specific composition of the stands on some useful groups of forest insects, conduced in the Institute of Forest and Wood Protection of the Warsaw Agricultural University. The field work was performed on the same experimental areas as the previous studies of J. Szyszko. The criteria for the choice of the experimental surface and its precise characteristic are given in the paper by this author [21].

The investigations included the following habitats: fresh deciduous forest (FDF), moist mixed coniferous forest (MMCF) and fresh coniferous forest (FCF) including pine stands with undergrowth (U) (FDFU, MMCFU and FCFU) and without undergrowth in what used to be Forest District Gościeradów (Lublin) in 1971 and habitats of fresh mixed coniferous forest (FMCF) and fresh coniferous forest (FCF) in the Forest District Smolniki (Olsztyn) in 1972 (variants with undergrowth denoted FMCFU and FCFU). Each habitat and each tree stand were represented by 3 study areas. Thus, in Gościeradów 18 and in Smolniki 12 such areas were established. On each of them 5 pine tree traps were set. On each pine an 8 m segment was marked and divided into 2 m sections. Observations were made after barking in each phase a 0.5 m segment from each section and counting the number

of feeding sites of the pine shoot beetle (number of female galleries) and collection of beetles present in them. Only imagines were collected with omission of immature forms for the following reasons:

1) the purpose in view was investigation of the succession in the occurrence of various beetle species in the galleries of the pine shoot beetles. For this the counting of larval forms was not necessary. No causes are known — with the exception of species of the genus *Thanasimus* Latr. (and in a certain sense, some *Lycidae, Elateridae* and *Pyrochroidae,* but these belong rather to the succession in rotting wood) — of the presence of exclusively larval stages of the studied beetles in the subcortical environment.

2) young development stages of most species are not known, and this would make identification of species impossible.

3) the aim of the present paper was not the usefulness of certain beetles (this would have required studies on the nutrition of the larvae).

These reservations caused some inconvenience since the imagines of the checkered beetles do not belong to the subcortical fauna, only their larvae. However, since the latter beetles are the best known useful insects, only their imagines were collected in the bark scales, in all other calculations it is omitted.

The dates of observation depended on the developmental stage of the feeding site and were fixed in the following periods: phase I April 23 — May 5, phase II May 29 — June 16, phase III July 10—23, phase IV the beetles were collected in the period September 10 — November 22.

In Gościeradów the traps on the study surface were arranged in quadrangles (the 5th one as diagonal) situated equally in reference to cordial points. In Smolniki the traps were arranged randomly. On the surfaces in Smolniki the moisture of the subcortical substrate was also determined by the drier method.

A total of 150 trees were examined and 571.31 m² of bark were removed. Material was collected from 28 780 feeding sites in which 3 118 specimens were caught belonging to 68 beetle species.

The average diameter of the trap-trees at mid length, the frequency of the pine shoot beetles and subcortical beetles in various habitats are listed in Table 1.

The described procedure does not differ from the methods applied in other studies of this type. They all consist in barking tree segments of various length chosen according to the adopted criterion. The advantage of these methods is the possibility of determining the true frequency of the subcortical beetles, its drawback, however, is the fact that barking destroys the environment this making the uncom-

http://rcin.org.pl

Table 1. The average diameter of the trap-trees at mid length as well as the frequency of the pine shoot beetles and subcortical beetles in various habitats

Habitat	Average diameter	Mean density of the pine shoot beetle per 1 m^2	Density of the subcortical beetles per 1 feeding site
FDF	18.5	60.18	0.10
FDFU	17.4	50.91	0.16
MMCF	14.7	46.70	0.10
MMCFU	16.2	63.29	0.07
FCF	14.3	46.88	0.07
FCFU	14.7	51.22	0.09
FMCF	16.0	38.07	0.09
FMCFU	15.5	38.72	0.09
FCF	18.0	41.98	0.13
FCFU	18.7	45.34	0.08

parable in a certain sense. Moreover the material may prove too scant for statistical elaboration.

For each beetle species found under the bark the extent of attachment to the subcortical environment and the trophic relations were established. The degree of attachment to the environment was determined according to the classification of Szujecki [19]:

F_3 — characteristic species belonging exclusively to the subcortical fauna and not found as a rule in other environments;

F_2 — characteristic selective species most numerous on trees but finding also favourable conditions in other environments;

F_1 — associated species occuring in smaller or larger numbers on trees and in other environments;

F_0 — foreign species characteristic for other environments accidentally included in the subcortical fauna.

The classes of attachment of the particular species were determined on the basis of the literature [14, 15, 17, 18, 19].

The trophic relations were established after Szujecki [20]. Two groups were distinguished: euzoophages and the remaining beetles comprising hemizoophages, and parazoophages including also sapro-, phyto- and microphages. To euzoophages were classified the exclusively meat-eating species. As hemizoophages were considered species predatory in principle but which were found to be able to live periodically on food other than meat. Species eating plant remnants or lower flora material were classified as sapro- and microphages. Many of these are no doubt parazoophages which also consume meat.

The material was also analysed from the zoogeographical point of view with the assumption of following elements according to Pawłowski [16] and Kostrowicki [9]: cosmopolitic, holarctic, palearctic, eurosiberian, eurocaucasian, european, subpontomediterranean. As base for zoo-

geographic analysis served the works of Pawłowski [16], Palm [14] and Saalas [17].

A list of species classified to trophic groups is given in Table 2, with the degree of attachment to the environment and zoogeographic analysis.

Comparison of the beetle groups in the particular developmental phases in all habitats is based on the similarity of dominance.

The climatic data were obtained from the State Institute of Meteorology and Water Management, meteorological stations in Gościeradów, Zaklików, Kraśnik, Iława and Ostróda.

RESULTS

COURSE OF SUCCESSION OF SUBCORTICAL BEETLES

Communities in the particular phases of development of the feeding sites

Phase I

In this period on all surfaces 387 specimens were caught belonging to 12 species. The material was collected from 8 314 feeding sites. The subpontomediterranean *Rhizophagus depressus* proved to be dominant in this phase (D = 93.5%). It is most abundant in FDF habitats. Of the remaining species three represent european, four eurosiberian, one palearctic, two holarctic and one cosmopolitic elements. The average density in this period was 0.055 specimen per 1 feeding site (0.012 in MMCF habitat without undergrowth to 0.169 in FDF without undergrowth).

Characteristic for this period are specific conditions caused by the fact that the area accessible to the subcortical beetles is limited solely to the female galleries partly filled with wormdust. The only food are eggs and excrements of the bark beetles or sometimes imagines. The galleries are only accessible through the inlet holes, this determining the size of the incoming beetles (small or flat so that they avoid ejection with wormdust [24]. Specialized predators find optimal conditions of development here (Fig. 1, 2). Other eurytopic species (represented by holarctic and palearctic elements finding their way accidentally into the feeding sites during penetration of lying trees) do not play any major role.

The relative moisture of the subcortical substrate was on the average 53.7 to 60.7 per cent.

Phase II

A total of 817 specimens were caught belonging to 31 beetle species. The material was collected from 5 666 feeding sites. In this stage the
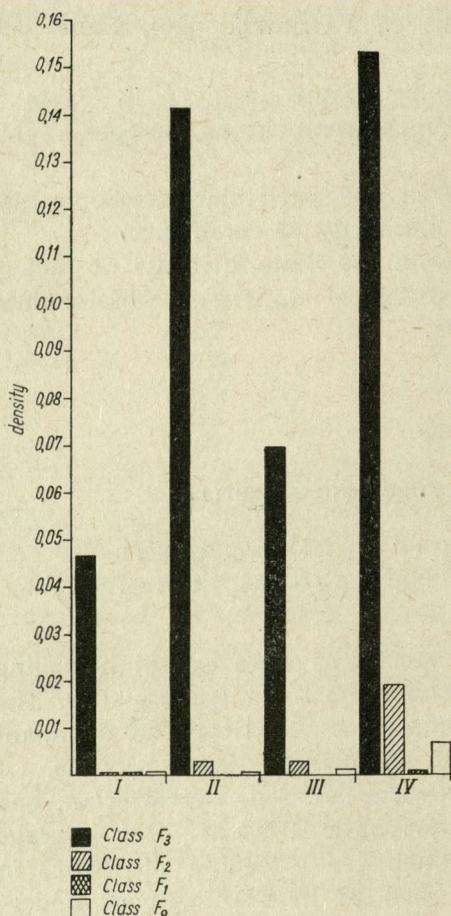
Fig. 1. Participation of beetles of various attachment classes in the particular succession phases.
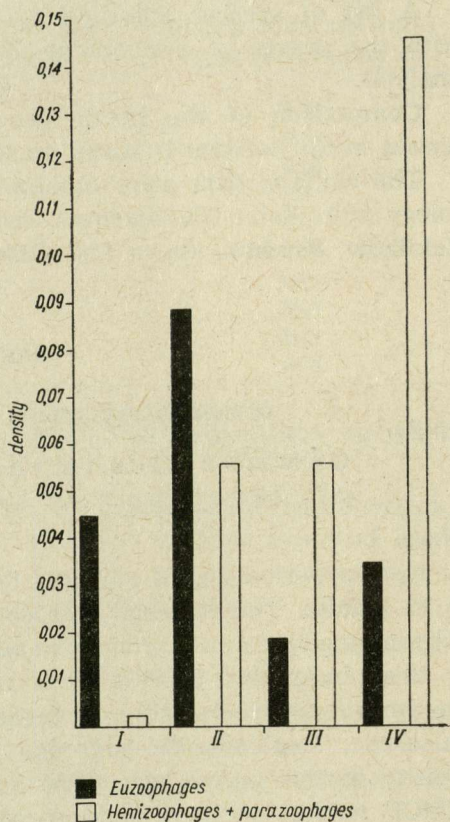
Fig. 2. Participation of non-meat-eating and meat-eating beetles in the particular succession phases.

subpontomediterranean *Rhizophagus depressus* was dominant (D = = 54.5%) with the accompanying holarctic species *Phloeonomus pusillus* (D = 29.4%). *Rh. depressus* was most abundant on FCF and MMCF habitats in Smolniki. Of the remaining species four represent holarctic, five palearctic, eight eurosiberian, nine european, one eurocaucasian and two subpontomediterranean elements. The average density was 0.152 specimen per one feeding site (from 0.036 in the FCF habitat in Gościeradów to 0.221 in the FCF habitat in Smolniki, both without undergrowth). In this period important changes occur in the feeding sites. Their surface increases owing to the galleries drilled by larvae, various moulds develop on the wormdust and excrements, mites, *Collembola* and other insects penetrate into the galleries. The larvae of

the pine shoot beetle contribute to the enlargement of the nutritional basis. As compared with the preceding period the number of species present increases and so does the density of beetles belonging to the highest attachment classes living at the cost of the larvae, as well as the number of non-meat-eating species (Figs 1 and 2). Relative moisture of the subcortical substrate was 56.6—61.9 per cent.

Phase III

At this stage 7 591 feeding sites were examined and 560 specimens collected belonging to 27 species. In this period the holarctic *Phloeonomus pusillus* (D = 48.3%) dominates. From among the remaining species seven represent palearctic, four eurosiberian, six european, two subpontomediterranean and two eurocaucasian elements. The average density was 0.075 species per feeding site (from 0.043 in a MMCF habitat to 0.136 in FCF without undergrowth in Smolniki). In this period conditions for specialized beetles become much worse: the nutritional base diminishes, the feeding sites are only accessible through the inlet holes and slits in the bark, moisture increases. Relative moisture of the subcortical substrate was on the average 66.1—70.7 per cent.

Phase IV

In this period 7 012 feeding sites were examined and a total of 1 258 beetle specimens were found belonging to 51 species. Dominant at this time is *Phloeonomus pusillus* (D = 54.6%). The remaining species represent the following elements: one — cosmopolitic, eight — holarctic, four — palearctic, eleven — eurosiberian, nine — european, four — subpontomediterranean and three — eurocaucasian. Average density was 0.179 specimen per one feeding site (from 0.111 in MMCF habitat to 0.295 in FDF with undergrowth).

The subcortical environment is at this time accessible to many foreign accidental eurytopic species, some of which are euzoophages (Figs 1 and 2). The subwood dies back completely and the structure of the feeding sites is obliterated. Average relative moisture was 75.3—78.6 per cent.

General characters of the succession

A general regularity in the succession of subcortical beetles is the transition from a small number of specialized predators to a large number of non-meat-eating ones less and less attached to the subcortical environment (Figs 1 and 2).

The predatory species appear as early as the oviposition phase of the pine shoot beetle and the optimum of their requirements corresponds to the conditions in the feeding sites of *Hylurgops palliatus* Gyll. [13]. The species appearing together with these beetles are either eurytopic

or accidental, foreign to the environment. The highest density of predatory species falls to the stage of larvae development of the pine shoot beetle. Food is most profuse and the surface of the feeding sites largest. With further development of the feeding sites the nutrition basis shrinks and the environmental conditions deteriorate. Foliation of the trees, particularly in rich habitats, reduces the amount of light penetrating to the forest floor, and moisture increases. The specialized species disappear and non-meat-eating ones begin to dominate which only occasionally supplement their feeding requirements with larvae or pupae of the pine shoot beetle. These species are mostly eurytopic, with a wide range, sciophilous and hygrophilous. Only exceptionally heliophilous species may occur in larger numbers (e.g. *Phloeopora angustiformis* in a FCF habitat).

A turning point in the succession is the period of pupae development and emergence of young pine shoot beetles. Owing to the lack of food and deformation of the feeding site structure the stenotopic predatory species are almost completely eliminated, but invasion of hygrophilous non-meat-eating species does not occur yet. Hence the relatively low density of beetles in the feeding sites. Their density increases only as large numbers of beetles of various species appear, seeking mostly shelter inder the bark.

Analysis of Czekanowski's verified diagram and other diagrams allows the conclusion that in the succession of subcortical beetles we are dealing essentially with two communities. The first occurs in phase I and partly in phase II. It comprises stenotopic predatory species, as example of which may be quoted *Rhizophagus depressus*. As seen, this community is associated with the presence of eggs and larvae of the pine shoot beetle and the specific structure of the feeding sites in these phases. The second community is characterized by the dominance of eurytopic hemi- and parazoophages appearing sometimes as early as phase II and dominating in phases III and IV. A typical example is *Phloeonomus pusillus*. This community is associated with the usually already empty galleries and its influence on the abundance of the pine shoot beetle is slight. As compared with the first community the latter comprises a larger number of species many of which have been to date classified to predators exterminating the pine shoot beetle. Thus, the fact of their dominance in the end phases of beetle succession "degrades" their usefulness.

SUBCORTICAL BEETLE SUCCESSION IN REFERENCE TO HABITAT CONDITIONS AND SPECIFIC COMPOSITION OF STAND

The course of succession for the chosen beetle species in all habitats and in all forest stand variants is shown in diagrams.
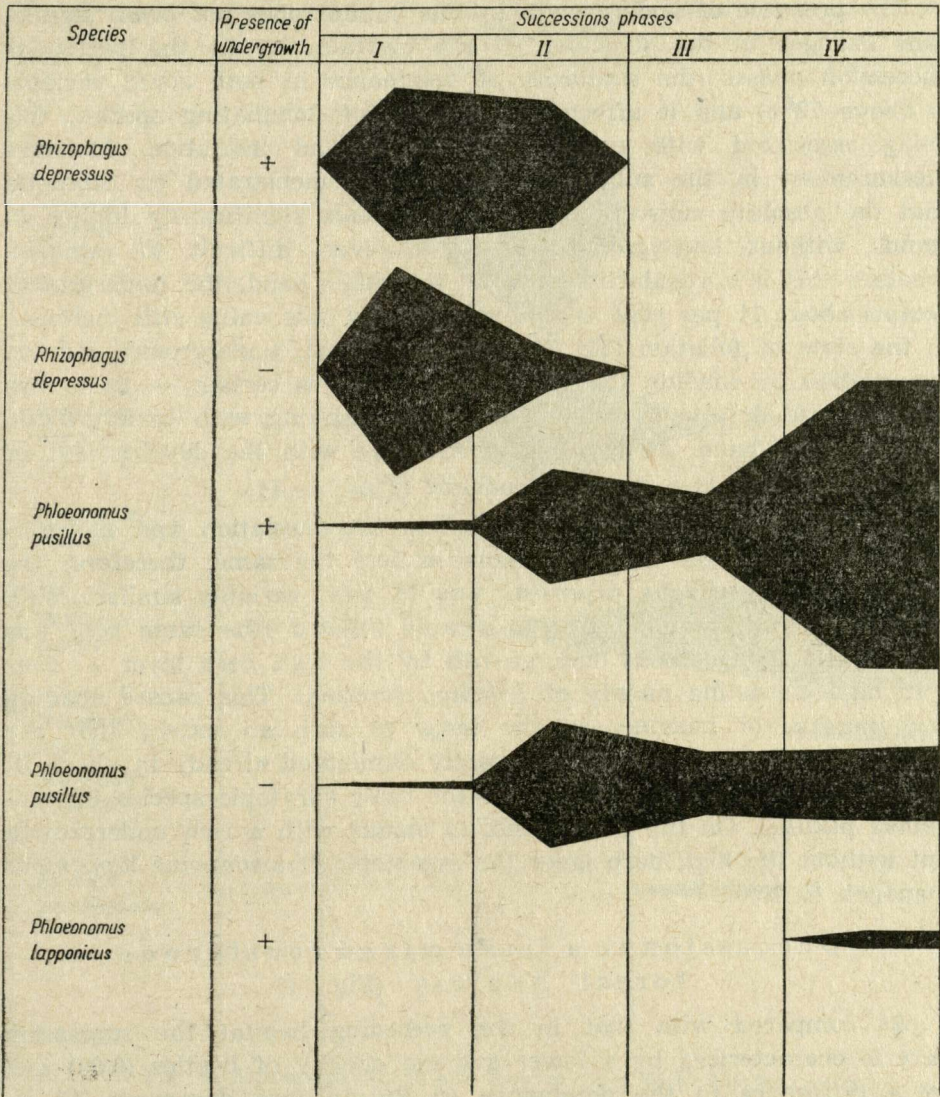
Fig. 3. Succession of chosen species in FDF habitat.

Succession in a fresh deciduous forest habitat (Fig. 3)

This habitat is characterized by a high abundance and density of subcortical beetles (on 6 surfaces, i.e. 20%, 1 134 specimens were caught, that is more than 30 per cent of the total caught with average density 0.14). Numerous is both the thermophilous euzoophage *Rhizophagus depressus* and the eurytopic parazoophage *Phloeonomus pusillus*. The contribution of other species was low and they did not play any role in the structure of the community.

The presence of undergrowth in this habitat does not cause significant changes in the structure of the communities in the particular succession phases (the similarity of dominance in both stand variants is above 72%) and it affects the number of dominating species, this being associated with moisture conditions and insolation. Moisture measurement in the subcortical substrate demonstrated in Smolniki that the absolute moisture of this substrate is significantly higher in stands without undergrowth. It is, however, difficult to establish whether this is a regularity since on the other hand, the undergrowth retains about 11 per cent of the rainfall and this value still increases in the state of foliation [23]. On the other hand, undergrowth reduces evaporation by shading the ground. One thing is certain — these two relations are dependent on the degree of covering with undergrowth. On the other hand, an increase of moisture with the development of the feeding sites is a general tendency (Figs. 8—11).

At first, when the trees are leafless the insolation and moisture conditions under the bark are more or less the same, therefore, the density of *Rhizophagus depressus* was in both variants similar. With time, however, the undergrowth became foliated (the same role was played in stands without undergrowth by the high herb layer — over 1 m high consisting mainly of *Solidago serotina*). This caused shading and increase of moisture in the traps to such an extent that the thermophilous *Rh. depressus* was partly eliminated already in phase II, and so was in the end phases even the most eurytopic species *Phloeonomus pusillus*. On the other hand, in stands with a rich undergrowth but without the high herb layer the stenotopic *Phloeonomus lapponicus* managed to live.

Succession in a fresh mixed coniferous forest habitat (Fig. 4)

As compared with that in the preceding habitat the succession here is characterized by a lower average density of beetles (0.09) and by a difference in the dominance of *Rhizophagus depressus*. If we compare the dominance of this species in the FDF habitat in Gościeradów and its dominance in the FMCF and FCF habitats in Smolniki, it was seen that in the FDF habitat this beetle dominated in phase I, whereas in Smolniki in phase II. The attractive factor for this species are the terpenes volatilized during female gallery boring by the pine shoot beetles. The temperature eliciting flight of the pine shoot beetle is 10—12°C [1], the intensity being more dependent on the maximal temperatures that on the diurnal average ones [3]. For gallery boring a temperature of 12°C is sufficient. In Gościeradów, however, the maximal temperature remained above this value during almost the whole of April (11 days with diurnal mean above 10°C). In Smolniki,
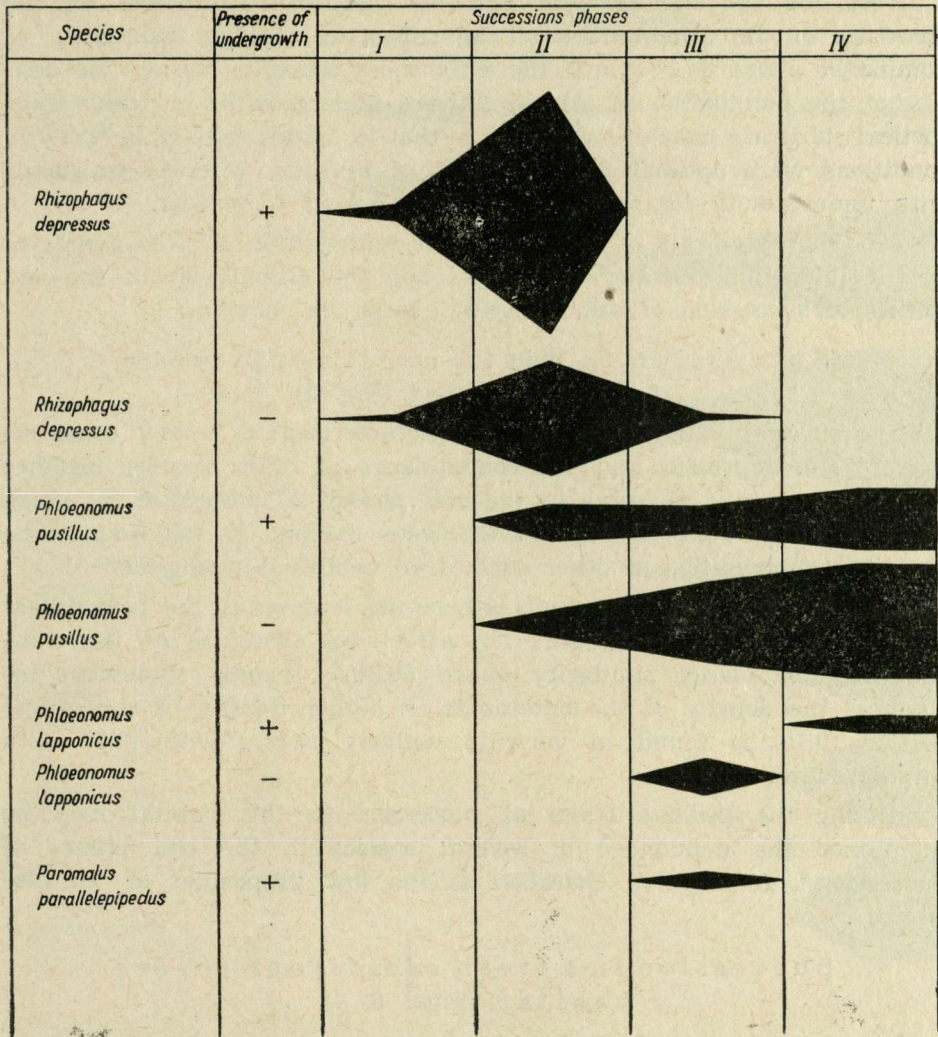
Fig. 4. Succession of chosen species in FMCF habitat.

on the other hand, after second 10 days the temperature fell and hoar-frost and snow occured (3 days with diurnal temperature above 10°C). In both localities pine shoot beetle flight had already started and the beetles bored female galleries, but in Smolniki a rise of temperature set in as late as the first half of May (number of days with mean diurnal temperature above 10°C was 11 in the period May 1—15). This probably influenced the date of flight of *Rhizophagus depressus* and its dominance in phase II.

The density of *Phloeonomus pusillus* was much lower that in the previously described habitat.

Here too the undergrowth had no significant influence on the structure of the communities of the subcortical beetles (similarity of dominance above 60.2%), and the differences concerns mainly the density of the dominants. In stands without undergrowth, in which subcortical substrate moisture was higher that in stands with undergrowth, conditions were optimal for *Phloeonomus pusillus,* whereas in stands with undergrowth *Ph. lapponicus* also managed to subsist.

A favourable trait is here the high contribution of *Rh. depressus* in the initial phases, and a negative one the elimination in the end phases of succession of other species except *Ph. pusillus.*

Succession in mixed moist coniferous forest habitat (Fig. 5)

The succession in this habitat is characterized by a low contribution of *Rh. depressus* and the codominance of other species together with *Phloeonomus pussillus* in the end phases of succession in which the euzoophage *Paromalus parallelepipedus* reached its maximum density. The contribution of other subcortical beetles is negligible.

The influence of undergrowth is here the same as in the precedingly discussed sites, that is it does not affect the structure of the communities (dominance similarity above 60.2%), it only somewhat influences the density of the dominants. A higher density of subcortical beatles (0.10) is found in variants without undergrowth (0.07 with undergrowth).

Among the positive traits of succession in this habitat may be mentioned the dominance of several species in the end phases of succession[1]. A negative character is the low proportion of *Rh. depressus.*

Succession in a fresh coniferous forest habitat (Figs. 6, 7)

Investigations on succession were performed in this habitat on 12 study areas in Gościeradów and Smolniki. The density of subcortical beetles was found to be low and a characteristic feature is the codominance of several species in the end phases. It is also interesting that the thermophilous species *Phloeopora angustiformis* occured in Gościeradów. On the studied surfaces in this locality *Rh. depressus* was present in small numbers whereas in Smolniki reached its maximal abundance in phase II.

---

[1] The codominance of several species is considered as a positive quality from the point of view of the possibility of colonization of the subcortical environment by beetles. It is, namely, evidence of the diversity of the environmental conditions and this does not lead to the elimination of species. Practical problems arising owing to increases competition are omitted.

Species	Presence of undergrowth	Successions phases			
		I	II	III	IV
Rhizophagus depressus	+				
Rhizophagus depressus	−				
Phloeonomus pusillus	+				
Phloeonomus pusillus	−				
Phloeonomus lapponicus	+				
Placusa depressa	+				
Placusa depressa	−				
Paromalus parallelepipedus	−				
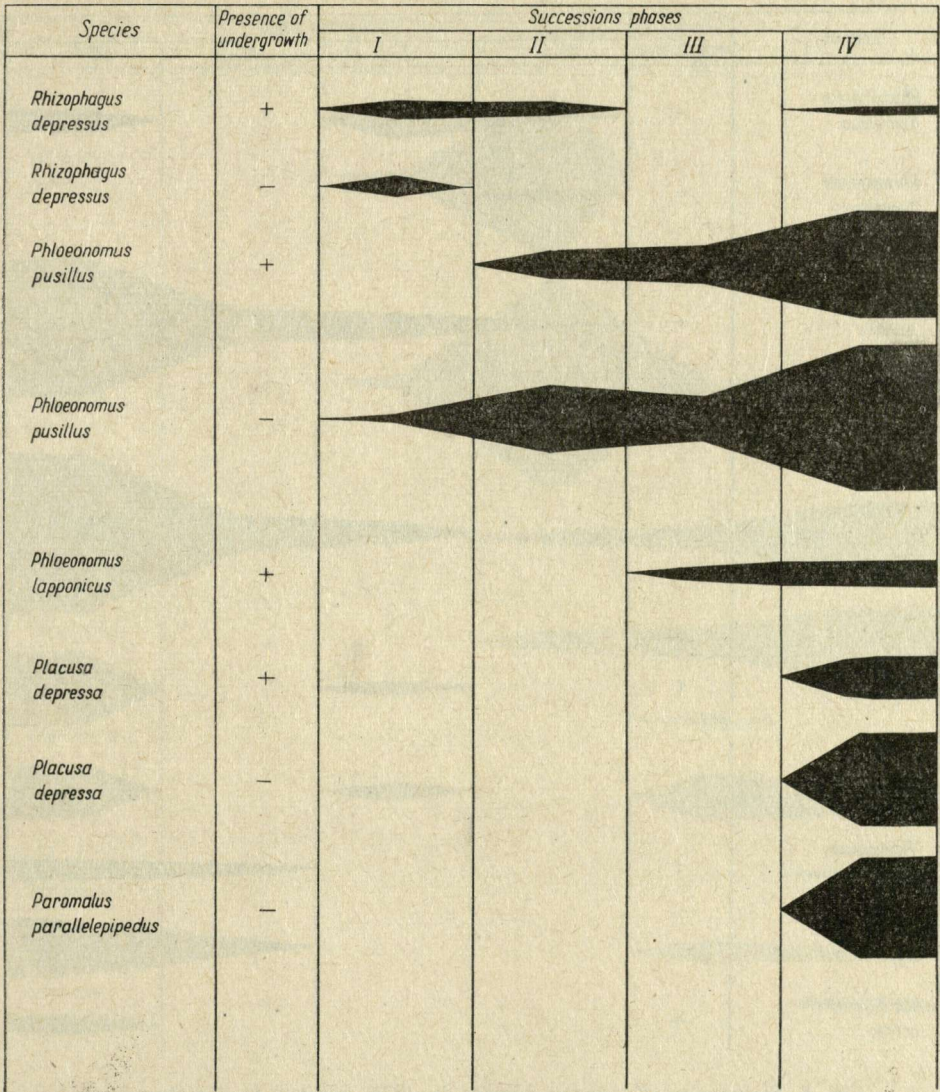
Fig. 5. Succession of chosen species in MMCF habitat.

It is difficult to evaluate the influence of undergrowth in this habitat on account of the low number of beetles. At any rate significant changes were not found in the structure of the beetles communities. The similarity of dominance in Smolniki between the two variants was above 70 per cent and in Gościeradów 68.3 per cent (with the exception of phase II in which it was 49.0).

A positive trait here is the codominance of several species in the end phases of succession and a negative one the low density of subcortical beetles.

Species	Presence of undergrowth	Successions phases			
		I	II	III	IV
Rhizophagus depressus	+				
Rhizophagus depressus	−				
Phloeonomus pusillus	+				
Phloeonomus pusillus	−				
Phloeopora angustiformis	+				
Phloeopora angustiformis	−				
Phloeonomus lapponicus	+				
Phloeonomus lapponicus	−				
Placusa atrata	+				
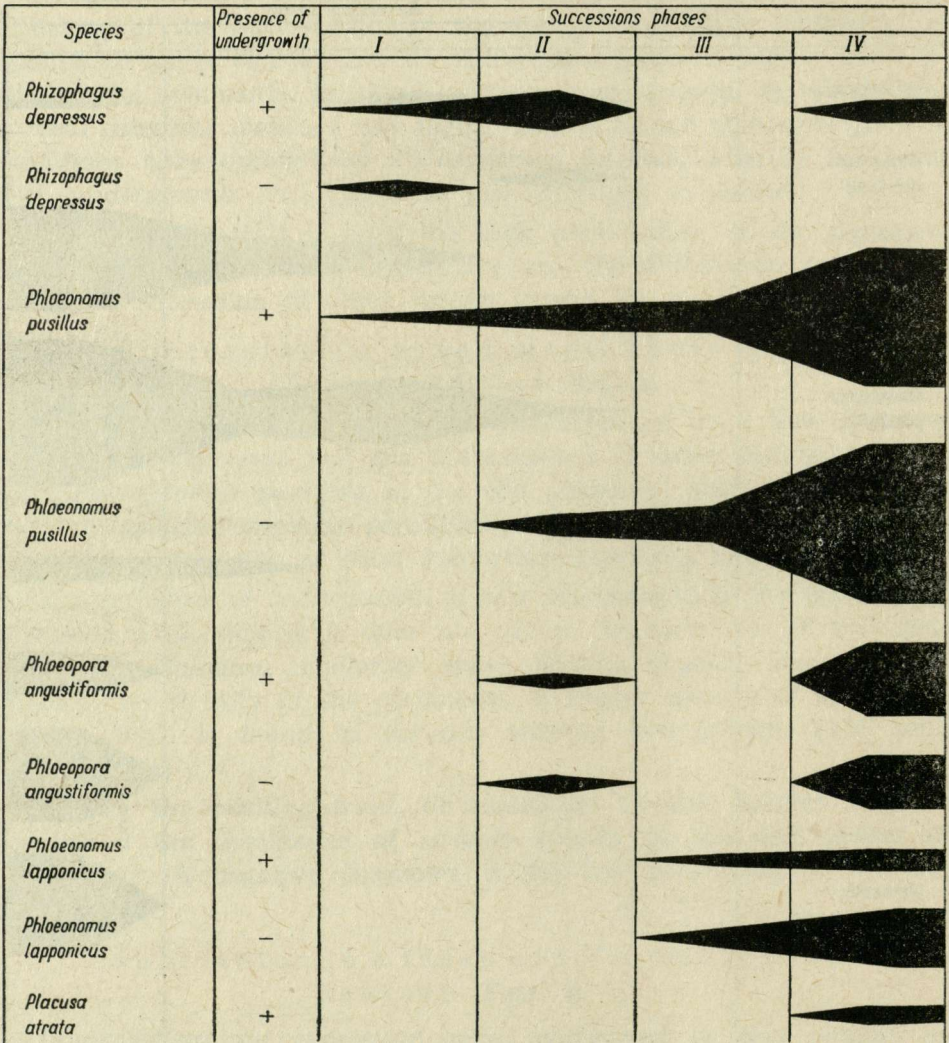
Fig. 6. Succession of chosen species in FCF habitat in Gościeradów.

SYNTHESIS OF RESULTS AND DISCUSSION

The factor decisive for the development of the complex of sub-cortical beetles is the microclimate of the subcortical environment [8] which largely depends on external conditions such as temperature and moisture of the surroudings. Particularly significant is here the influence of temperature and moisture of the subcortical zone on the beetles. As established by Zinovyev [25], specialization of subcortical beetles tends towards definite ecological conditions, particularly moisture, and not towards a trophic specialization. Most of the subcortical

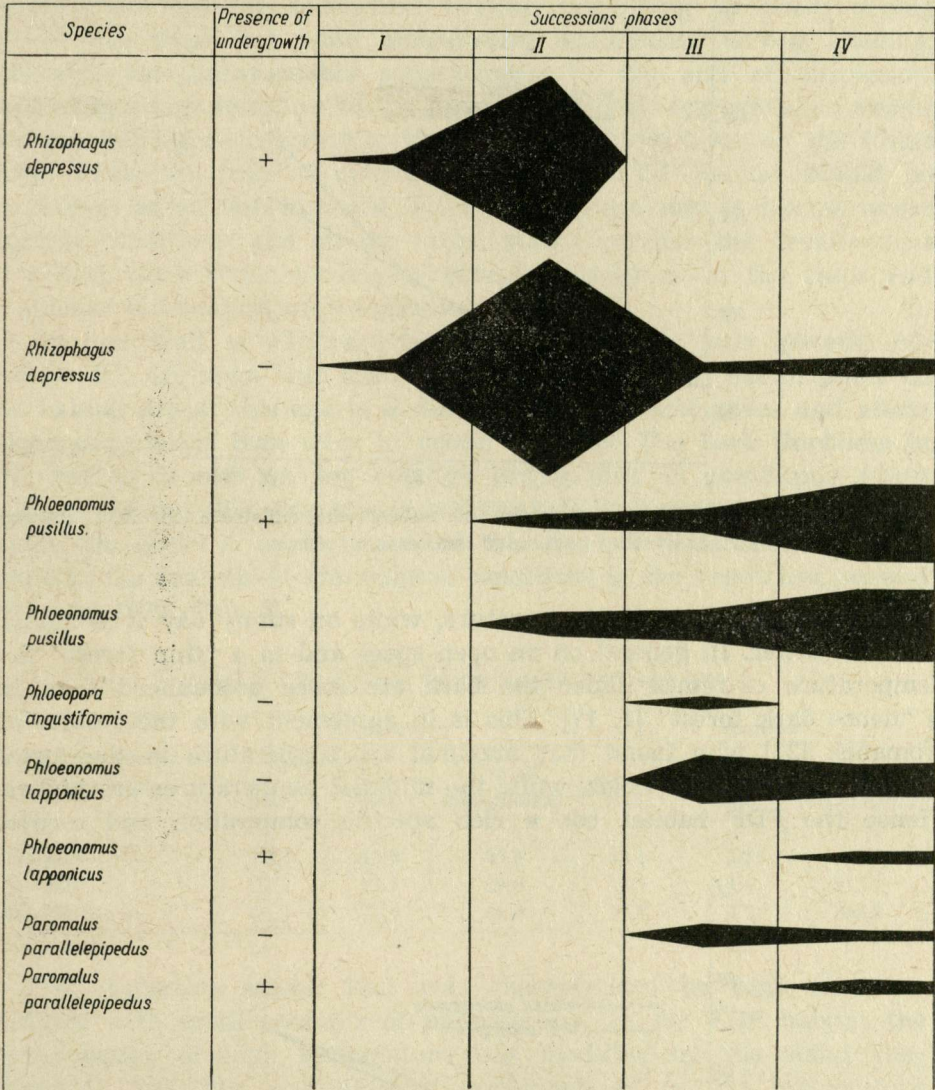| Species	Presence of undergrowth	Successions phases			
		I	II	III	IV
Rhizophagus depressus	+				
Rhizophagus depressus	−				
Phloeonomus pusillus.	+				
Phloeonomus pusillus	−				
Phloeopora angustiformis	−				
Phloeonomus lapponicus	−				
Phloeonomus lapponicus	+				
Paromalus parallelepipedus	−				
Paromalus parallelepipedus	+				

Fig. 7. Succession of chosen species in FCF habitat in Smolniki.

beetles have high requirements as regards moisture with simultaneous high temperature [13].

In the light of these findings the differences in the course of succession in the FDF habitat as compared with coniferous forest ones cannot be considered as accidental. The forest is an important factor modulating temperature and moisture distribution in the environment. On the other hand, the subcortical temperature is strictly dependent on external conditions. The temperature under the bark on an open space and in a "thin forest" has a similar course, and in the night it
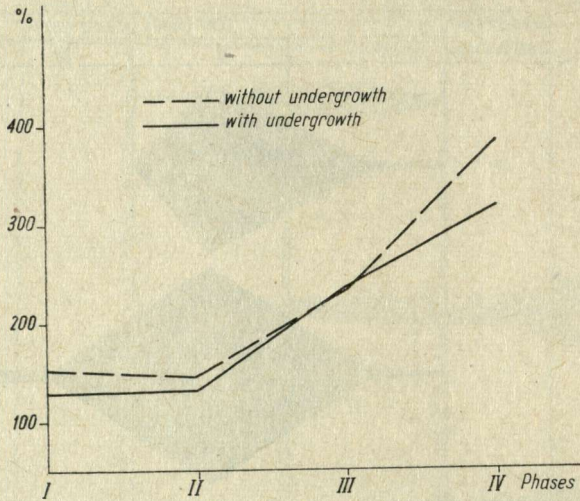
Fig. 8. Changes in absolute moisture of subcortical substrate in FCF habitat
in the particular succession phases.

is almost the same as air temperature, while on sunny day it is higher
than the latter. In general on an open space and in a "thin forest" the
temperature extremes under the bark are more pronounced than in
a "dense dark forest" [1, 17]. This is in agreement with the results of
Tomanek [22] who found that maximal air temperature in the forest
are lower than in the fields, while the minimal temperatures are higher.
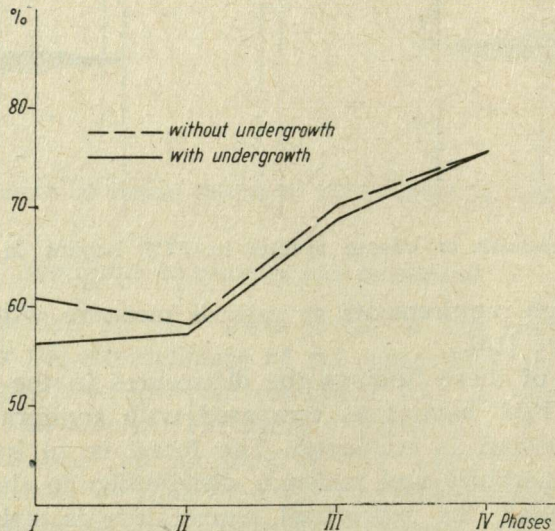Hence the FDF habitat has a rich specific composition and creates

Fig. 9. Changes in relative moisture of subcortical substrate in FCF habitat in
the particular succession phases.

better conditions for subcortical beetles, preventing excessive drying up of the traps and wide temperature differences. Strong shading, however, has unfavourable consequences in the end of succession, producing a high moisture in the traps. This is still aggravated in stands without undergrowth owing to the dense high herb layer on the forest floor. Thus, the lack of undergrowth in the FDF habitat should be considered as an unfavourable factor: on the one side it creates worse thermic conditions, and on the other, makes possible the development of a high herb layer, leading to excessive moisture in the traps and a quicker elimination of heliophilous predators.

Another trait of FDF are better conditions for pine growth. Although the age span was limited to class III (41—60 years), pines on the habitat are at this age in a different development phase and attain larger dimensions than trees in poorer habitats. The bark thickness in this habitat is also on the average larger than in coniferous forest habitats [6] and this also affects temperature and moisture distribution under the bark. A confirmation of the above considerations may be found in the analysis of atmospheric conditions in the vegetative seasons 1971 and 1972 (Tab. 3).

Table 3. Climatic data for the seasons 1971 and 1972

| Periods between the phases | Gościeradów | | | Smolniki | | |
| | temperature | | sum of precipitation | temperature | | sum of precipitation |
	max.	min.		max.	min.	
I—II	20.9	13.9	65.8	16.1	5.8	85.8
II—III	21.2	11.5	69.6	22.7	12.4	115.1
III—IV	21.3	11.3	67.0	17.3	8.7	262.1

The vegetative season 1971 was characterized by high air temperature with small amounts of precipitation. In the FDF habitat the drying action of high temperature was modified by the stand conditions [1, 22]. The possibility of occurrence of critical temperature (37.8°C) under the bark [5] what may occur at air temperature around 30°C [17] was much greater in the coniferous forest habitats. Together with a moisture deficit this could cause elimination of the beetles, particularly of *Rh. depressus*. It produced, however, under definite conditions, particularly on the lower side of the traps, favourable conditions for the occurrence of the thermophilous species *Phloeopora angustiformis*.

In 1972 high temperatures were noted only in July, whereas the amount of precipitation greatly exceeded that in 1971. This created better conditions for the subcortical beetles in Smolniki. For the differences between the FCF habitats in Gościeradów and Smolniki the

fact is not without significance that the stands in Gościeradów were only just entering the III age class (ca 37 years), whereas in Smolniki the corresponding stands were 52 years old (stands without undergrowth) and 61 years (stands with beech undergrowth), this being also associated with different average dimensions and bark thickness.

It is difficult to evaluate the role of undergrowth in the FCF habitat. The subcortical beetles find here rather unfavourable conditions on account of the readily drying up bark and wide temperature differences and their density and abundance in this habitat are low (on 12 surfaces, thus 40%, 1 071 specimens were found, i.e. ca 30% of the total, with average density 0.07—0.13). The influence of the undergrowth involves insolation and moisture regulation. This cannot, however, be expected where there is oak undergrowth on degraded habitats, covering 20—40 per cent of the surface. The dense beech undergrowth in Smolniki, however, covering about 70 per cent of the surface, did not significantly influence the course of beetle succession.
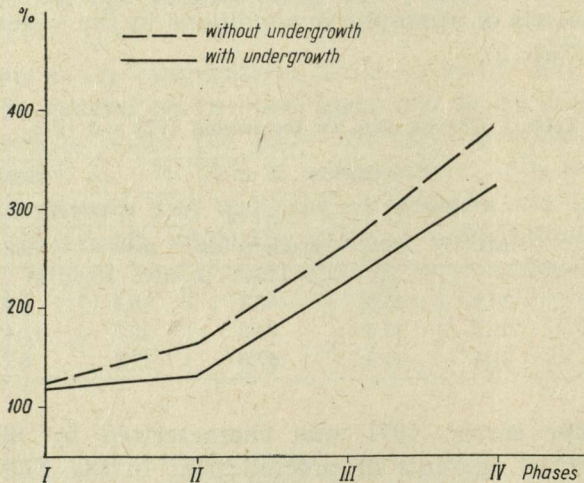
Fig. 10. Changes in absolute moisture of subcortical substrate in FMCF habitat in particular succession phases.

The situation is somewhat different in more fertile habitats such as FMCF and MMCF. The lack of undergrowth in the FMCF habitat caused a mass appearance of *Calamagrostis arundinacea* which plays a similar role as does *Solidago serotina* in FDF habitats — leading to the development of high moisture in the traps, as has been experimentally confirmed (Figs 10, 11). This found its reflection in the elimination of *Phloeonomus lapponicus* which subsisted, however, as subdominant in stands with undergrowth.

In the MMCF habitat in Gościeradów after a scarce appearance of *Rh. depressus* in the first phases of succession, probably owing to the

Table 2. List of collected species with their quality characters

No.	Species	Number of ex.	Occurence		Degree of attachm.	Trophic relations	Zoogeographical analysis						
			Gość.	Smoln.			cos.	hol.	pal.	eus.	euk.	eur.	subp.
1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	*Notiophilus biguttatus* F.	1		+	F_0	e			**+**				
2	*Calathus micropterus* Duft.	1		+	F_0	e				+			
3	*Pterostichus oblongopunctatus* F.	23	+	+	F_0	e			+				
4	*Cercyon flavipes* Thunb.	1	+		F_0	e		+					
5	*Amphicyllis globus* F.	1		+	F_2	p						+	
6	*Plegaderus vulneratus* Panz.	32		+	F_3	e			+				
7	*Paromalus parallelepipedus* Herbst	84	+	+	F_3	e			+				
8	*Cylister linearis* Er.	1		+	F_3	e			+				
9	*Cylister angustatus* Hoffm.	1	+		F_3	e			+				
10	*Pteryx suturalis* Heer	3	+		F^1	p						+	
11	*Orthopterus atomus* Gyll.	1	+		F_2	p						+	
12	*Siagonium quadricorne* Kirby	2	+		F_3	h						+	
13	*Phloeocharis subtilissima* Mann.	12	+	+	F_2	e						+	
14	*Phloeonomus planus* Payk.	25	+	+	F_3	h					+		
15	*Phloeonomus lapponicus* Zett.	176	+	+	F_3	h		+					
16	*Phloeonomus pusillus* Grav.	1 198	+	+	F_3	h		+					
17	*Phloeonomus punctipennis* Thoms.	19	+	+	F_3	h				+			
18	*Oxytelus tetracarinatus* Block	6	+	+	F_0	p		+					
19	*Trogophleus corticinus* Grav.	2	+	+	F_0	p	+						
20	*Stenus humilis* Er.	3	+	+	F_0	e		+					
21	*Stenus impressus* Germ.	2	+		F_0	e							+
22	*Medon brunneus* Er.	2		+	F_0	e						+	
23	*Lathrobium brunnipes* F.	1	+		F_0	e				+			
24	*Rugilus rufipes* Germ.	1	+		F_0	h						+	
25	*Nudobius lentus* Grav.	25	+	+	F_3	h				+			
26	*Xantholinus linearis* Ol.	4	+	+	F_0	e		+					
27	*Gabrius splendidulus* Grav.	46	+	+	F_2	h				+			
28	*Quedius xanthopus* Er.	5	+	+	F_2	e				+			
29	*Euryporus picipes* Payk.	1	+		F_0	p			+				
30	*Conosoma littoreum* L.	3	+	+	F_2	p		+					
31	*Conosoma testaceum* F.	2	+		F_2	p		+					
32	*Bryocharis formosus* Grav.	1		+	F_0	h						+	
33	*Bolitobius thoracicus* F.	1		+	F_1	h		+					
34	*Phloeopora testacea* Mann.	32	+	+	F_3	h					+		
35	*Phloeopora angustiformis* Baudi	106	+	+	F_3	h							+
36	*Ischnoglossa prolixa* Grav.	1		+	F_1	h			+				
37	*Atheta aequata* Er.	39	+	+	F_3	h				+			
38	*Homalota plana* Grav.	21		+	F_3	h		+					
39	*Dadobia immersa* Er.	6	+	+	F_3							+	
40	*Eurysa castanoptera* Kryn.	1	+		F_2	h						+	
41	*Leptusa angusta* Aube	7	+	+	F_3	h						+	
42	*Leptusa haemorrhoidalis* Heer	4	+	+	F_3	h		+					
43	*Leptusa ruficollis* Er.	1	+		F_3	h						+	
44	*Anomognathus cuspidatus* Er.	9	+	+	F_3	h					+		
45	*Placusa depressa* Markl.	62	+	+	F_3	h					+		
46	*Placusa atrata* Sahlb.	99	+	+	F_3	h				+			
47	*Placusa tachyporoides* Waltl.	2		+	F_3	h			+				
48	*Thanasimus formicarius* L.	73	+	+	F_3	e				+			
49	*Thanasimus rufipes* Brahm	1		+	F_3	e						+	
50	*Laemophloeus alternans* Er.	2	+		F_3	e	+						
51	*Silvanus bidentatus* F.	4	+		F_3	e			+				
52	*Cerylon histeroides* F.	3	+		F_3	e			+				
53	*Cyphon variabilis* Thoms.	1		+	F_1	h					+		
54	*Rhizophagus bipustulatus* F.	4	+	+	F_3	e							+
55	*Rhizophagus depressus* F.	875	+	+	F_3	e							+
56	*Rhizophagus dispar* Payk.	7	+	+	F_3	e			+				
57	*Rhizophagus ferrugineus* Payk.	3	+	+	F_3	e				+			
58	*Rhizophagus nitidulus* F.	6	+	+	F_3	e					+		
59	*Epurea pusilla* Ill.	11	+	+	F_3	h				+			
60	*Glischrochilus quadripustulatus* L.	9	+	+	F_3	e				+			
61	*Pityophagus ferrugineus* L.	9	+		F_3	e				+			
62	*Nemosoma elongatum* L.	8		+	F_3	e						+	
63	*Hypophloeus linearis* F.	4		+	F_3	e				+			
64	*Phyllodecta vittata* F.	1		+	F_0	p		+					
65	*Phyllodecta nemorum* L.	9	+		F_0	p			+				
66	*Crypturgus cinereus* Herbst	2	+	+	F_3	p			+				
67	*Crypturgus hispidulus* Thoms.	5	+	+	F_3	p			+				
68	*Crypturgus pusillus* Gyll.	5	+		F_3	p			+				
	Total	3.118	53	50			2	12	16	14	6	14	4

Abbreviations:

Gość. — Gościeradów   hol. — holarctis
Smoln. — Smolniki   pal. — paleartic
e — euzoophage   eus. — eurosiberian
h — hemizoophage   euk. — eurocaucasian
p — parazoophage   eur. — european
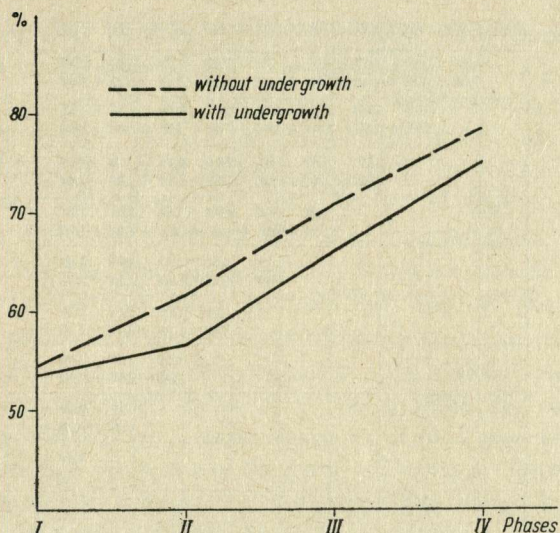cos. — cosmopolitic   subp. — subpontomediterranean

Fig. 11. Changes in relative moisture of subcortical substrate in FMCF habitat in particular succession phases.

unfavourable climatic conditions, the density of subcortical beetles increased consistently. In general the beetles found better conditions in the stands lacking undergrowth, perhaps this was due to better insolation conditions. This seems to be confirmed by the appearance of the heliophilous *Paromalus parallelepipedus*.

It is possible that the habitat conditions dependent on temperature and moisture influence the appearance of a new *Rh. depressus* generation. In FDF habitats and FMCF where the latter species was most dense, it was found no more in the traps in larger numbers in the end phases of succession. On the other hand, on all surfaces of MMCF and FCF this species was present also in phase IV. This may indicate that after developing in the soil *Rh. depressus* finds in the same traps conditions for hibernation, whereas traps in richer habitats are too moist and eliminate this species.

It was also essential to establish whether the occurrence of subcortical beetles is dependent on the abundance of the pine shoot beetle. It is true that, according to numerous authors, the subcortical beetles are not closely associated with a definite bark beetle species or tree [8, 10, 11], however, for the beetles of the first community the feeding sites of the pine shoot beetle supply, beside nutrition, conditions for development. Thus, there exists a certain relation between the number of female galleries and the number of subcortical beetles. This problem was investigated by calculating the mean number of female galleries per 1 m² of bark and then computing the significance of the differences between the particular habitats in various stand variants. The results are presented in diagrams (Figs 12, 13).

6

FDF	FDFU	MMCF	MMCFU	FMCF	FMCFU	FCF	FCFU	FCF	FCFU
	3,843 2,048+	0,703 2,064+	2,427 2,048+	3,891 2,048+	3,242 2,048+	2,295 2,048+	1,203 2,048−	0,914 2,048−	0,061 2,048−
		3,515 2,064+	0,949 2,048−	8,856 2,048+	7,659 2,048+	4,869 2,048+	6,599 2,048+	4,744 2,048+	3,325 2,048+
			2,356 2,064+	2,030 2,064−	1,593 2,064−	0,909 2,064−	0,215 2,064−	0,030 2,064−	0,647 2,064−
				6,048 2,048+	5,400 2,048+	4,583 2,048+	3,393 2,048+	3,277 2,048+	2,965 2,048+
					0,274 2,048−	1,539 2,048−	1,647 2,048−	2,689 2,048+	3,199 2,048+
						1,035 2,048−	2,031 2,048−	2,159 2,048+	2,784 2,048+
							0,811 2,048−	1,256 2,048−	2,008 2,048−
								0,331 2,048−	1,124 2,048−
									0,861 2,048+

Fig. 12. Significance of differences in density of pine shoot beetles per 1 m² between habitats and stand variants.

| FDFU	FDF	FCFU	FCF	MMCFU	MMCF	FCF	FCF	FMCFU	FMCF
	3,000 2,776+	3,500 2,776+	4,500 2,776+	4,500 2,776+	2,000 2,776−	1,875 2,776−	5,000 2,776+	5,000 2,776+	2,692 2,776−
		0,416 2,776−	1,364 2,776−	1,364 2,776−	0,000 2,776−	1,500 2,776−	1,00 2,776−	0,555 2,776−	0,357 2,776−
			0,952 2,776−	0,952 2,776−	0,312 2,776+	2,222 2,776−	0,555 2,776−	0,000 2,776−	0,000 2,776−
				0,000 2,776−	0,937 2,776+	3,158 2,776−	0,516 2,776−	1,176 2,776−	1,176 2,776−
					0,937 2,776−	3,158 2,776−	0,528 2,776−	1,176 2,776−	1,176 2,776−
						1,000 2,776−	0,666 2,776−	0,933 2,776−	0,333 2,776−
							3,750 2,776+	2,857 2,776+	1,538 2,776−
								0,714 2,776−	0,386 2,776−
									0,000 2,776−

Fig. 13. Significance of differences in subcortical beetles density per 1 feeding site between habitats and stand variants.

It may be in general affirmed that the presence of undergrowth is significantly correlated with the increase of FDF habitat with the decrease and in the MMCF habitat with the increase of abundance of the pine shoot beetle, whereas in the FMCF and FCF habitats the presence of undergrowth did not affect the size of the pine shoot beetle population. The increase in abundance of the pine shoot beetle in the FDF habitats without undergrowth did not lead to an increased

density of subcortical beetles, on the contrary, their density was higher in stands with undergrowth and the difference was significant. In the MMCF habitat, in spite of significant differences in the density of the pine shoot beetle, differences were not noted in the density of the subcortical beetles when undergrowth was introduced. On the other hand, significant differences in the density of the pine shoot beetle were noted in the FCF habitat in Smolniki, whereas the density of the subcortical beetles was significantly higher in stands without undergrowth. These deviations may possible be due to the environmental conditions and not the number of feeding sites of the pine shoot beetle and simple correlations are not probable. The occurrence of subcortical beetles is of concentrated type and the availability of food has no major influence of it [12]. Moreover, as has been established even typical predators *(Hypophloeus linearis, Nudobius lentus)* supplement their diet with detritus from the feeding sites since their survival in cultures with subcortical substrate added increased 2—3 times [25]. In general, therefore, one may speak of a relation between the number of pine shoot beetles only in the case of beetles of the first community (and only in the sense in which we say that for the occurrence of cavernicolous species caves are necessary). For the second community, in view of the obliteration of the structure of the feeding sites this problem does not exist.

It results from the analysis of the similarity of dominance (Czekanowski's diagram, Fig. 14) that, as already found earlier, we are dealing with two types of communities. This means that neither the habitat nor the specific composition of the stand affect the composition of the beetle communities in the succession. Several species are responsible for this succession, the most important role being played here by *Rhizophagus depressus* and *Phloeonomus pusillus*. The modifying role of the habitat or undergrowth consists in that a complex of variable microenvironmental characters enables in a higher or lesser degree the occurrence of the most important species or also of other accompanying species. Some habitats have a permanent complex of these characters as for instance the fresh deciduous forest, while in others it is less stable. No type of habitat or stand, however, has a specific complex of subcortical beetles. Hence the seemingly accidental character of similarity in the diagram of Czekanowski. The phases of succession are more essential for the communities than the type of habitat or the presence of undergrowth in the stand. A certain more distinct concentration of similarities involves FCF and FMCF habitats and results from the specifity of appearance of *Rh. depressus* in them. The more intensive appearance of this species in the FMCF and FCF habitats in Smolniki in phase II found its reflection in the high similarity with the FDF habitat where this species dominated in
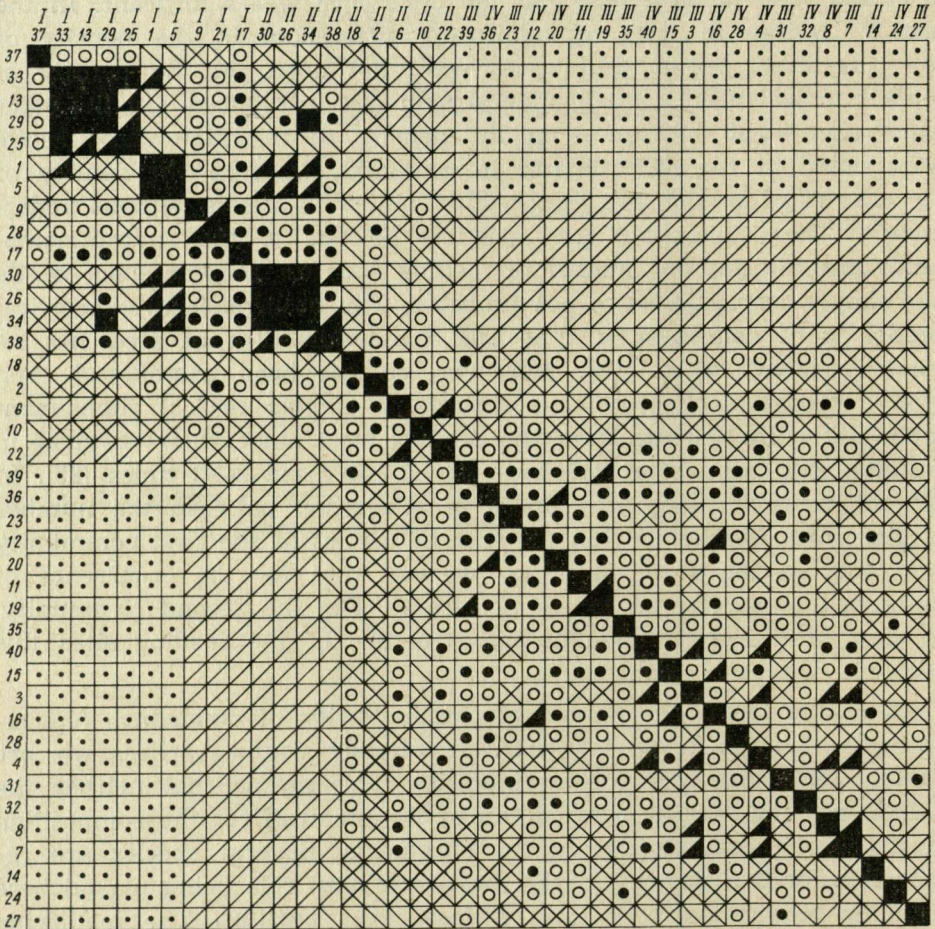
Fig. 14. Similarity of dominance in the particular habitats and stand variants in all succession phases. I, II, III, IV — succession's phases, 1—4 — FDF habitat with undergrowth, 5—8 — the same without undergrowth, 9—12 FCF habitat in Gościeradów with undergrowth, 13—16 — the same without undergrowth, 17—20 — MMCF habitat with undergrowth, 21—24 — the same without undergrowth, 25—28 — FCF habitat in Smolniki without undergrowth, 29—32 — the same with undergrowth, 33—36 — FMCF habitat with undergrowth, 37—40 — the same without undergrowth.

phase I, hence the second group of more distinct similarities including also MMCF habitats. The second community, beginning as early as phase II, is much more differentiated since it includes much larger number of species many of which are foreign elements in the subcortical environment. Therefore the composition of groups with highest similarity is highly fortuitous.

In the light of the foregoing considerations at the beginning of this chapter this state of things should be assumed as normal. Evolution of subcortical beetles advanced towards specialization for definite ecological conditions, and not for trophic conditions or tree species. Nearly all the beetles caught in the feeding sites of the pine shoot beetle occur on other coniferous or even deciduous trees and are found in the feeding sites of a number of bark beetles and other secondary pests. The areas of penetration of these beetles are not large as a rule [12] and are frequently limited to the size of one feeding site. Their high sensivity to temperature and moisture changes causes them to aggregate frequently on small areas (e.g. in the lower part of the traps, under pieces of thicker bark, etc.) whereas whole areas of the subcortical zone are empty. Therefore the general trend of changes in the structure of the subcortical beetles can only be predicted if the external action of various factors is radical, for instance high moisture in the traps, as was the cause when the herb layer was higher, or the drying up action of sun in poor pine stands, etc. Any intermediate action as for instance introduction of undergrowth shading 20—40 per cent of the surfaces produces unpredictable changes.

Akademia Rolnicza,
Instytut Ochrony Lasu i Drewna
ul. Rakowiecka 26/30, 02-528 Warszawa
Polska

REFERENCES

1. B a k k e, A. 1968. Ecological studies on bark beetles (*Coleoptera: Scolytidae*) associated with Scots pine (*Pinus silvestris* L.) in Norway with particular reference to the influence of temperature. Medd. Norsk. Skogforsk, 21: 443—602.

2. B a ł a z y, S. 1968. Analysis of bark beetle mortality in spruce forests in Poland. Ekol. Pol., A, 16: 657—687.

3. F r a n z, J. 1948. Ökologische Beobachtungen am Buchdruckers (*Ips typographus* L.). Teil I. Zool. Jb. Abt. Syst. Ökol. Geogr., 77: 426—442.

4. F r o g a t t, J. L. 1928. Introduction of the *Coleoptera*. Queens. Agr. Journ., 30: 530—541.

5. G r a h a m, S. A. 1924. Temperature as a limiting factor in the life of subcortical insects. J. Econ. Ent., 17: 377—383.

6. G r o c h o w s k i, J. R y m e r ó w n a, T. 1961. Badania nad udziałem kory w miąższości strzał w drzewostanach sosnowych. Fol. For. Pol., A, 7: 153—174.

7. K a r p i ń s k i, J. J. 1935. Przyczyny ograniczające rozmnażanie się korników (*Ips typographus* L. i *Ips duplicatus* Sahlb.) w lesie pierwotnym. Rozpr. Spraw. IBLP, 15: 1—86.

8. K h a r i t o n o v a, H. 1972. Entomofagi koroedov khvojnykh porod. Moskva, 128 pp.

9. K o s t r o w i c k i, A. S. 1953. Studia nad fauną motyli wzgórz kserotermicznych nad dolną Nidą. Fragm. Faun. Mus. Zool. Pol., 6: 263—447.

10. N i k i t y u k, A. J. 1951. Khishchnye i paraziticheskie nasekomye kak regulatory vrednonosnoj deyatelnosti i rasprastraneniya koroedov khvojnogo lesa. Bull. Mosk. Obshch. Isp. Prir., N. S., Ot. Biol., 56: 58—63.

11. N u o r t e v a, M. 1956. Über den Fichtenstamm-Bastkäfer, *Hylurgops palliatus* Gyll., und seine Insektenfeinde. Acta Ent. Fenn., 13: 7—118.

12. N u o r t e v a, M. 1964. Über den Einfluss der Menge des Brutmaterials auf die Vermehrlichkeit und die natürlichen Feinde des Grossen Waldgärtners, *Blastophagus piniperda* L. (*Col., Scolytidae*). Ann. Ent. Fenn., 30: 1—17.

13. O k o ł ó w, Cz. 1963. Materiały do fauny żerowisk korników — *Scolytidae* Puszczy Boreckiej. Pol. Pismo Ent., B, 20—30: 15—20.

14. P a l m, Th. 1952. Die Holz- und Rinden-Käfer der nordschwedischen Laubbäume. Medd. Skogs-Forskn. Inst., 40, 1951, 242 pp.

15. P a l m, Th. 1959. Die Holz- und Rinden-Käfer der süd- und mittelschwedischen Laubbäume. Opusc. Ent., Suppl. 16, 374 pp.

16. P a w ł o w s k i, J. 1967. Chrząszcze (*Coleoptera*) Babiej Góry. Acta Zool. Cracov., 12: 419—665.

17. S a a l a s, U. 1917. Die Fichtenkäfer Finnlands. I. Ann. Acad. Sc. Fenn., A, 8, xx + 547 pp.

18. S a a l a s, U. 1923. Die Fichtenkäfer Finnlands. II. Ann. Acad. Sc. Finn., A, 22, x + 746 pp.

19. S z u j e c k i, A. 1967. Kusakowate (*Staphylinidae, Col.,*) różnych środowisk leśnych Szerokiego Boru w Puszczy Piskiej. Fol. For. Pol., A, 13: 237—256.

20. S z u j e c k i, A. 1971. Wpływ rębni zupełnej na zgrupowanie ściółkowych kusakowatych (*Col., Staphylinidae*) borów sosnowych świeżych. Fol. For. Pol., A, 18: 5—45.

21. S z y s z k o, J. 1974. Relationship between the occurrence of epigeic carabids (*Coleoptera, Carabidae*), certain soil properities, and species composition of a forest stand. Ekol. Pol., 22: 237—274.

22. T o m a n e k, J. 1959. Mikroklimatyczne badania nad pionowym rozkładem ekstremalnych temperatur powietrza w borze mieszanym Lasów Doświadczalnych SGGW w Rogowie. Zesz. Nauk. SGGW, Leśn., 2: 83—120.

23. T o m a n e k, J. 1965. Wpływ podrostu i podszytu na wielkość intercepcji opadu w borze mieszanym (*Pineto-Quercetum* Kozł.). Zesz. Nauk. SGGW, Leśn., 7: 7—38.

24. W i c h m a n n, H. E. 1967. Die Wirkungsbreite des Ausstosreflex bei Borkenkäfer. Anz. Schadl., 40: 184—187.

25. Z i n o v y e v, Z. A. 1959. O znachenii kompleksa entomofagov v ogranichenii rozmnozhenia koroedov khvojnogo lesa. Moskva—Leningrad, 9—10; 62—86.

SUKCESJA CHRZĄSZCZY W ŻEROWISKACH CETYŃCA WIĘKSZEGO (*TOMICUS PINIPERDA* L., *COLEOPTERA*, *SCOLYTIDAE*) W JEDNOGATUN-KOWYCH I MIESZANYCH DRZEWOSTANACH SOSNOWYCH

STRESZCZENIE

Sukcesywny charakter występowania chrząszczy podkorowych w żerowiskach *Tomicus piniperda* L. polega na przechodzeniu wraz z rozwojem żerowiska od niewielkiej liczby gatunków wyspecjalizowanych drapieżców do dużej liczby gatunków o coraz słabszym powiązaniu ze środowiskiem podkorowym. Decydująca rola w sukcesji przypada zaledwie kilku gatunkom, większa część gatunków podkorowych pojawia się w niewielkich ilościach. W rozwoju sukcesji można wyróżnić dwa zasadnicze typy zgrupowań: pierwsze, składające się z wyspecjalizowanych, stenotopowych drapieżców (*Rhizophagus depressus*), które pojawia się w fazie rozwoju jaj i larw cetyńca i drugie, pojawiające się już pod koniec rozwoju larwalnego, obejmujące eurytopowe gatunki niemięsożerne (*Phloeonomus pusillus*). Siedliska lasowe w porównaniu z siedliskami borowymi odznaczają się większym zagęszczeniem chrząszczy podkorowych jak również szybką eliminacją w końcowych fazach sukcesji stenotopowych gatunków. Decydującymi dla kształtowania się zgrupowań chrząszczy podkorowych okazały się fazy rozwojowe żerowisk, a nie warunki siedliskowe czy drzewostanowe. Wprowadzenie domieszek biocenotycznych na siedliska borowe nie wywołuje ściśle ukierunkowanych zmian w przebiegu sukcesji.

СУКЦЕССИЯ ЖУКОВ В КОРМЕЖКАХ БОЛЬШОГО ЛЕСНОГО САДОВНИКА (*TOMICUS PINIPERDA* L., *COL. SCOLYTIDAE*) В БОРАХ И СМЕШАННЫХ СОСНОВЫХ ЛЕСАХ

РЕЗЮМЕ

Сукцессивный характер встречаемости короедов в кормежках *Tomicus piniperda* L. заключается в переходе, по мере развития кормежки, от небольшой группы специализированных хищников к большому количеству видов, все менее связанных с данной средой. Решающую роль играют в сукцессии лишь несколько видов, большинство видов жуков появляется в небольших количествах. В развитии сукцессии можно выделить два основные типа группировок: первая состоит из специализированных стенотопных хищников (*Rhizophagus depressus*), которые появляются в фазе развития яиц и личинок большого лесного садовника; вторая появляется под конец периода личиночного развития и состоит из эвритопных не хищных видов (*Phoeonomus pusillus*). Лесные биотопы по сравнению с борами характеризуются большей плотностью жуков, а также быстрым исчезновением стенотопных видов в конечных фазах сукцессии. Решающими для формирования комплексов короедов оказались фазы развития кормежек, а не условия среды или древостои. Введение биоценотических примесей в биотопы боров не имеет строго направленного влияния на изменения в ходе сукцессии.