Studies on the invertebrate fauna on branches of spruce (*Picea abies*) (L.) during winter

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The invertebrate fauna on branches of spruce (*Picea abies* (L.)) was studied monthly from November to March near Oslo. The following average density and dry biomass per m² foliage was recorded for the five months: 47.9/14.2 mg, 37.6/13.0 mg, 34.4/10.3 mg, 41.1/12.0 mg and 21.6/8.6 mg. In numbers, Araneida and Psyllidae were about equally represented, and together made up 56 to 78 % of the total material, and respectively 57 to 71 % and 6 to 31 % in biomass. The spiders, almost exclusively immature, were represented by at least 10 species. *Philodromus* sp. (*aureolus* – group) dominated with 33 to 45 % of the total spider number. Among the 19 species of psyllids, *Trioza urticae* (L.) and *Psylla klapaleki* Sulc. made up respectively 70 to 84 % and 10 to 16 % of the material. The density and biomass of psyllids decreased significantly in March.

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This investigation had two main aims. The first was to study the composition and density of the overwintering invertebrate fauna on the branches of spruce (*Picea abies* (L.)), listing the actual groups and species. Very little is known about this fauna in spruce woods during winter. The second aim was to study whether the density of invertebrates on the branches decreases markedly during winter. Such a reduction may be caused by bird predation. The density may also decrease due to invertebrates leaving the branches, either actively or passively. As for the first factor, several overwintering passerine birds in the Norwegian spruce woods prey on the invertebrate fauna on branches (e. g. Palmgren 1932, Haftorn 1956). Gibb (1960) showed that tits (Paridae) and goldcrests (*Regulus regulus* (L.)) depend to a large extent on this kind of food for their survival during winter in English pine woods. He found that during severe winters the birds may strongly reduce the density of invertebrates on branches of pines, and the winter survival of tits and goldcrests depends on the invertebrate density.

MATERIAL AND METHODS

The material was collected from spruce wood at Øverland, Bærum, near Oslo during the winter 1970/71. The trees from which the samples were taken were 10 – 20 m high, mostly 14 – 18 m, and were chosen at random. Each sample consisted of the outer half of one or several branches midway up the tree. Both goldcrests and several species of tits visited this part of the trees during food-seeking in winter.

A method modified after Palmgren (1932) and Gibb (1960) was used in collecting and sorting out the material. A plastic bag, about 50 cm in diameter and 120 cm deep, was fastened to a metal ring on a handle, and the bag was gently placed around the branch and closed. The branches were then cut off the tree. The bags were stored at – 20° C. Each month, 18 – 20 samples were taken. The sampling dates were as follows: 9 November, 16 and 19 December, 11 January, 12 February, and 11 March. The branches were covered with snow only at the first sampling. In January, the branches were collected in

Fig. 1. Degree of cover used when the area of spruce foliage from the samples were measured. The picture covers 50 × 50 cm.

rainy weather. The rest of the samples were either a little wet, or dry.

The further handling of the samples was rather tedious. When ice and snow had melted, the branches were cut in smaller pieces and beaten against the inside wall of a metal bucket (about 30 cm in diameter and 35 cm deep) with a plastic bag on the inside. Because the twigs were often wet, implying that invertebrates might still stick to their surface, the twigs were always afterwards gently stirred under water in a white tray. Invertebrates washed off in this way were easily detected.

The contents of the bucket were then carefully examined by placing small bits in a white tray with water. Most invertebrates were found on the water surface. The remains in the original sample bag were treated in the same way.

Of the total material of Araneida, 5.3 % were found by stirring the beaten twigs under water, 40.1 % were found in the metal bucket, and 54.5 % in the sampling bag. Corresponding values for Psyllidae were 4.8 %, 28.4 %, and 66.8 %, and for the rest of the material treated together (excluding Thysanoptera, which were too small to be picked out systematically) 11.7 %, 37.0 %, and 51.3 %.

The sample size was expressed in m^2 by spreading the foliage evenly on a measured background. The degree of cover used is illustrated in Fig. 1. Mean size of samples ± SD from November to March was, respectively: 0.46 ± 0.10, 0.87 ± 0.33, 0.83 ± 0.20, 1.00 ± 0.20, and 0.84 ± 0.30 m^2.

To control the efficiency of the method, fractions from eight samples were carefully studied with binoculars after beating. Only two Araneida, one Aphididae, and one nymph of Homoptera were discovered from altogether 1.63 m^2 studied in this way. This made up 8.3 % of the mean total density recorded in the eight samples, when Thysanoptera were disregarded. This indicates that stirring under water is effective in detecting those animals which are left on the twigs after beating. Studying twigs with binoculars did not reveal any groups which were so firmly attached that they would not be released in water.

The invertebrates were frozen, and later dried at 75° C and weighed. Then they were kept for one day in a moist chamber and preserved in alcohol. Araneida and Psyllidae, being the dominant groups, were then as far as possible identified to species.

Some Acarina and Collembola were observed, but these groups were not taken into account in this investigation. Thysanoptera were picked out as far as possible, but the density of this group is obviously underestimated.

Table I gives mean monthly temperature and precipitation, compared with average conditions (Det norske meteorologiske insti-

Table I. Mean monthly temperature (°C) and precipitation (mm) during the winter of 1970/71, compared with normal conditions.

	Nov.	Dec.	Jan.	Feb.	March
Temperature					
1970/71	-0.8	-1.4	-2.4	-0.5	-2.0
Normal	1.1	-2.0	-4.7	-4.0	-0.5
Precipitation					
1970/71	180	24	61	40	72
Normal	69	63	49	35	26

Table II. Composition and density of the invertebrate fauna on branches of spruce (Picea abies) during winter. The density of Thysanoptera is underestimated. $\bar{x}$= mean number per m^2 (see Fig. 1), S.E.=standard error, k= number of samples of the total number (n), in which the group was present.

	November n=19			December n=20			January n=18			February n=18			March n=18		
Group	$\bar{x}$	S.E.	k	$\bar{x}$	S.E.	k	$\bar{x}$	S.E.	k	$\bar{x}$	S.E.	k	$\bar{x}$	S.E.	k
Araneida	13.3	3.3	17	10.3	2.0	18	8.7	1.7	18	13.3	3.2	18	10.0	1.9	17
Psocoptera				0.04		1	0.05		1						
Hemiptera															
Heteroptera				0.1		2	0.06		1	0.06		1	0.04		1
Cicadidae	0.4		4	0.4		4	0.2		2	0.4		2	0.7		4
Psyllidae	13.8	5.9	14	13.8	4.3	16	18.8	5.5	16	14.5	4.4	14	3.9	1.3	10
Aphididae	6.3		13	3.0		14	1.0		9	1.9		8	0.3		3
Homoptera nymph	0.1		1							0.06		1			
Thysanoptera	11.9		13	8.0		16	4.4		9	9.1		10	5.2		8
Coleoptera															
Staphylinidae							0.04		1						
Chrysomelidae				0.06		1									
Col.imago indet.	0.09		1							0.04		1			
Col.larva "	0.1		1	0.04		1	0.08		1	0.04		1			
Hymenoptera															
Tenthredinidae													0.03		1
Parasitica	0.8		5	0.8		7	0.4		3	0.6		6	0.07		1
Hym.imago indet.										0.04		1	0.4		4
Diptera															
Bibionidae	0.2		1	0.1		2				0.1		1			
Nematocera indet.	0.2		2	0.1		2				0.2		4			
Cyclorrhapha	0.4		4	0.5		4	0.4		4	0.4		3	0.3		4
" pupa				0.04		1									
Syrphidae larva				0.1		1	0.1		2						
Dipt. imago indet.	0.2		1				0.04		1	0.2		3	0.06		1
Lepidoptera															
Geometridae larva							0.04		1						
Lep.imago indet.										0.05		1			
Lep. pupa "				0.1		1				0.09		1			
Lep. larva "	0.08		1												
Insect imago indet.													0.03		1
" pupa "				0.08		2	0.07		1	0.05		1	0.5		4
" larva "													0.09		2
Total (except Thysanoptera)	47.9			37.6			34.4			41.1			21.6		

tutt 1971, 1972). This particular winter was obviously rather mild. Much of the precipitation was rain, and the amounts of snow were smaller than usual. The data were measured at Blindern, about 10 km away from the sampling localities, but measurements have shown that climatic conditions are very similar at these two localities (O. Hogstad, pers. comm.).

RESULTS

The composition and density of the invertebrate fauna on spruce branches during winter are given in Table II. Although a comparatively large number of groups was present, the spiders and psyllids dominated in number, followed by the aphids. Thysanoptera are listed to illustrate that their density is not insignificant, but because of underestimation (see Material and Methods), this group will not be discussed further.

The spiders were present in nearly every sample (k = 17 – 18), indicating a rather uniform distribution as a group on the branches. Their average density was almost the same throughout the winter. The highest density recorded in a single sample was 64 per m^2, but 87 % of the samples with spiders contained less than 20 individuals per m^2.

Psyllids were found in about 75 – 90 % of the samples from November to February (k = 14 – 16). In March they were found in 56 % of the samples (k = 10), and their density dropped in this month from about 14 – 19 per m^2 to 4 per m^2. The maximum density of psyllids in one sample was 108 per m^2. The density of this group showed greater variation from sample to sample than was found for the spiders. 69 % of the samples with psyllids contained less than 20 per m^2.

The aphids also decreased in number and constancy during March. These insects, together with the remaining groups in Table II,

Table III. Monthly percentage distribution of spider species on branches of spruce (Picea abies) from November 1970 to March 1971. n=number of specimens.

	Nov.	Dec.	Jan.	Feb.	March
Dictyna sp.	14	10	7	4	15
Philodromus sp. (aureolus-gr.)	33	45	35	45	38
Tibellus sp.	1	2	3		
Thomisidae indet.		1	1		1
Theridion tinctum (Walck.)			2		2
T. pallens Blackw.	6	1		1	6
Theridion sp.	3	2	6	1	1
Tetragnatha sp.				1	1
Araneus cucurbitinus Clerk	3		2	1	1
Araneus sp. (tuberculatus-gr.)	12		2	2	
Araneus sp.	15	28	13	25	24
Cyclosa conica (Pallas)		1		1	1
Pityohyphantes phrygianus (C.L.Koch)	5	3	9	10	
Linyphiidae juv.	1	2			1
Juv.,indet.	7	6	19	10	11
n	104	116	127	222	132

occurred in low densities or with low constancies throughout winter, and accordingly S. E. is not estimated.

The total average number of invertebrates per m^2 of branches ranged between 34 and 48 during the first four months, dropping to 22 in March. This decrease was primarily due to the reduced psyllid density this month.

The spider fauna was dominated by Thomisidae (*Philodromus* sp., *Tibellus* sp. and Thomisidae indet. in Table III) and Araneidae (the genera *Araneus* and *Cyclosa* in Table III), these two families making up 68 % of the total material. Altogether at least 10 species of spiders were present.

All spiders were juveniles or subadults, except one adult of *Theridion tinctum* and four adults of *Theridion pallens*. Of the five species identified, only *Pityohyphantes phrygianus* occurred in such numbers that some information about the sex-ratio could be obtained. Of the 27 specimens, all subadults, in which the sex could be determined, 25 were females.

Nineteen species of psyllids were identified, representing three genera (Table IV). *Trioza urticae* was the dominating species, making up 70 – 84 % of the psyllids throughout the winter. 10 – 16 % of the psyllids belonged to *Psylla klapaleki* and 1 – 4 % to *Trioza curvatinervis*. The species composition and relative density did not show marked changes during winter. Whereas both sexes were quite evenly represented in *T. urtica* and *T. curvatinervis*, only one male was found (in February) among the 122 specimens of *P. klapaleki*.

Fig. 2 illustrates the average biomass of spiders, psyllids, the remaining invertebrates, and the total fauna during winter, given as dry weight per m^2. Except for the high mean weight of spiders in February, and therefore also of the total weight in this month, the general trends for all groups was either a fairly constant weight per m^2 from month to month, or a slight drop in weight. The high mean value for spiders in February was mainly caused by an unusually high value in one of the samples (38.65 mg). When this extreme is disregarded, the mean value for

spiders becomes 6.7, and for the total fauna 10.2. These values are similar to those of the preceding month. When this correction is taken into consideration, the general trend for the weight of the total fauna and for Araneida is a rather even and slow decrease throughout winter. The total weight per m^2 recorded in March is about 60 % of that recorded in November. The recorded biomass of spiders is also nearly halved. This drop in biomass is not followed by a corresponding drop in density (Table II).

The psyllid biomass was rather constant during the first half of winter, but during the second half the value dropped to about one fifth of the original one. This drop was most obvious from February to March. The biomass of the remaining groups showed no obvious drops during winter.

DISCUSSION

The most characteristic feature of the invertebrate spruce fauna studied was the strong dominance of Araneida and Psyllidae. Only a few works have treated the invertebrate fauna on branches of conifers. Gibb's (1960) studies, covering several winters, revealed a rather constant relative composition of invertebrates on pine branches in England. Homoptera (aphids and chermids) usually made up 85–90 % of the total material. In some years, the aphids were heavily parasitized by Braconidae (Hymenoptera). Also in the present material, several aphids were evidently parasitized. Immature Thomisidae dominated among the spiders even in Gibb's (1960) studies on pine branches. However, psyllids, if present at all, were evidently of minor importance in his studies.

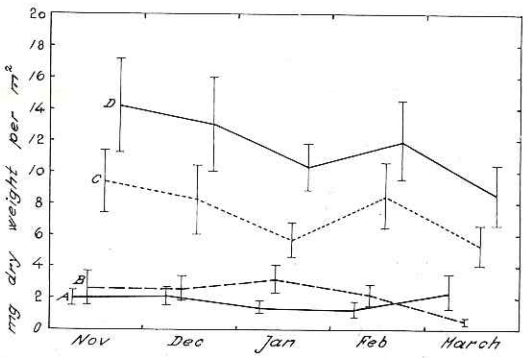

Fig. 2. Average monthly dry weight of invertebrates per m^2 spruce foliage during winter. Vertical lines: Standard error. A = Total except Araneida and Psyllidae, B = Psyllidae, C = Araneida, D = Total. Sampling was done once a month (18–20 samples); the values within each month have been displaced along the abcissa for practical reasons only.

Palmgren (1932) studied the invertebrate fauna on spruce branches during summer at Åland island in Finland. Psocoptera dominated in numbers (38 % of the material), followed by Araneida (28 %). Psyllidae, being represented by the genera *Psylla* and *Trioza*, made up only 0.6 % of the total. In the present winter study, only two specimens of Psocoptera were recorded. Because these insects usually pass the winter in the egg stage (Imms 1964), this result is quite reasonable.

No psyllid species develop on spruce (Ossiannilsson, pers. comm.). It is, however, typical that many of those psyllid species which hibernate as adults migrate to evergreen conifers during late summer and autumn to spend the winter in the trees (Ossiannilsson, pers. comm., Schaefer 1949). The host plant of *T. urticae* is *Urtica dioica* L., whereas *P. klapaleki* and *T. curvatinervis* are bound to *Salix* sp. As for the rest of the psyllid species, host plants of thirteen genera have been recorded (Ossiannilsson, pers. comm.).

The present results indicate that the migration to spruce had been completed in November. Palmgren (1932) found, in addition to the low psyllid density on spruce branches during summer, that the content of psyllids in stomachs of goldcrests was consistently higher in autumn than in summer. Both his observations are explained by the migration pattern of the psyllids.

P. klapaleki was represented almost exclusively by females. This can probably be explained by a high mortality rate of males (Ossiannilsson, pers. comm.). *A. affinis* has not earlier been recorded in Norway (Ossiannilsson, pers. comm.).

The density of psyllids in March is rather low compared with the preceding months. This may be due to increased activity as the temperature increases, causing parts of the psyllid population to leave the branches and prepare the migration back to their host plants. During several winters, the authors

Table IV. Monthly percentage distribution of psyllid species on branches of spruce (Picea abies) from November 1970 to March 1971. n=number of specimens. x denotes < 1%.

	Nov.	Dec.	Jan.	Feb.	March
Aphalara affinis (Zett.)					1
A. exilis (Web. & Mohr)		x		1	
A. rumicicola Loginova			1		
Aphalara sp.		1		1	
Psylla corcontum Šulc		x			3
P. klapaleki Šulc	12	16	11	10	12
P. nigrita (Zett.)	1	1	x		
P. pyrisuga Foerst.		x	x		
Psylla sp.		x	1		
Trioza abdominalis Flor			x		3
T. acutipennis (Zett.)	1				
T. apicalis Foerst.				x	
T. cerastii (L.)			x		1
T. curvatinervis Foerst.	3	3	4	1	3
T. dispar Löw		x	x	1	
T. femoralis Foerst.				x	
T. nigricornis Foerst.		x		x	
T. rhamni (Schrnk.)				1	1
T. salicivora Reuter				1	1
T. striola Flor		1	1	1	4
T. urticae (L.)	84	76	81	83	70
Trioza sp.		x			
n	110	279	252	281	74

have recorded invertebrates on the snow surface of the forest floor in spruce woods around Oslo. Psyllids may be found throughout the winter, but are most common in the later part. Depending on the weather, they may be more or less active. Parts of this psyllid material were identified. As on spruce branches, *T. urticae* and *P. klapaleki* dominated, and mainly females were recorded of the latter species. Also *T. curvatinervis, T. striola, P. cornutum* and *P. nigrita* were found.

The increased activity of hibernating psyllids in spring, combined with periods with strong winds, may result in considerable spreading of the individuals. In several cases large numbers of psyllids have been observed on snow-covered lakes in March and April, evidently blown off from surrounding conifer forests.

In Palmgren's (1932) study, *Philodromus aureolus* (Cl.) dominated among the spiders. The dominant spider group in the present material could not be identified further than to the *P. aureolus* group. *P. phrygianus* was found in both studies. Among the other spiders listed by Palmgren (1932), the following should be mentioned, as the same genera

were recorded in the present study: *Dictyna arundinacea* (L.), *Aranea* sp., *Theridion* sp., *Theridion simile* C. L. Koch and *Tetragnatha obtusa* C. L. Koch.

Waaler (1972) studied the spider fauna on branches of spruce in the beginning of August at Ringsaker, south Norway, visiting three different habitats. Of the species and groups listed in Table III, the following were recorded: *P. phrygianus, C. conica, Dictyna* sp., *Tetragnatha* sp., *Araneus* sp. and Linyphiidae indet. All were juveniles, except a few of the *P. phrygianus* specimens.

Contrary to the psyllids, the spiders probably stay on the branches during their life cycle. It is typical that they hibernate as immatures and become fully developed during spring and summer (Dahl 1926, Dahl 1931, Reimoser 1937, Locket & Millidge 1953).

No serious reduction in total dry biomass could be demonstrated during winter. The biomass of spiders was somewhat reduced, but this was not followed by a corresponding reduction in density. Analysis of stomach contents of goldcrests by Palmgren (1932) support the assumption that mainly the larger invertebrate specimens are eaten.

The overwintering psyllids represent a significant contribution to the invertebrate biomass on the branches and clearly improve the food supply for goldcrests and tits. Roughly 20 % of the total invertebrate biomass recorded on the branches during winter was made up by psyllids (Fig. 2). A similar migration of chermids to pine trees during autumn was recorded by Gibb (1960).

Both goldcrests and tits feed on invertebrates on spruce branches during winter (Palmgren 1932, Haftorn 1956). Gibb (1960) found that the density and biomass of invertebrates on pine branches varied greatly from one winter to another; in some winters the density was greatly reduced, while in others it was quite constant.

Probably the invertebrate density on spruce branches also varies much from one winter to another. It is therefore difficult to say how representative the present results are. Whether the recorded density might have been a limiting factor for the overwintering populations of goldcrests and tits cannot be ascertained, as data on bird density are lacking. In this connection it should be mentioned that for birds, the amounts of snow on the branches may be even more important than the invertebrate density itself (Hogstad, pers. comm.). Thus total invertebrate density does not always correspond with the available amounts of food.

Because of only little snow on the spruce branches in the winter in question, smaller amounts of the invertebrates than usual had fallen down together with snow dropping from the branches. This may in part explain the modest reduction in total density.

Gibb (1960) measured the caloric content of invertebrates on pine branches during winter and recorded values between 5.83 and 6.13 cal/mg dry matter. If 6 cal/mg is used as a mean value in the present study, the mean caloric content of invertebrates per m^2 of spruce foliage varied between 51 and 85 cal.

It is interesting that the spiders dominating the biomass seem to be relatively evenly distributed, occurring on almost every branch. This is probably due to their high moving ability and to their predatory feeding habits. For birds, this distribution pattern is an advantage as they evidently seek food quite unsystematically on the branches.

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