Vertical Microdistribution of Drosophilidae (Diptera) within Various Forests in Hokkaido

III. The Tomakomai Experiment Forest, Hokkaido University

By

Masanori J. TODA*

北海道におけるいろいろな森林内のショウジョウバエ類の垂直分布

III. 北海道大学苫小牧演習林

戸 田 正 憲*

Abstract

1) Vertical stratification structure of a drosophilid community in a natural broad-leaved forest was regarded as consisting of two associations, Canopy Association and Floor Association, each of which was divided further into two subassociations, *i. e.*, the former into Cc and Cs, and the latter into Fs and Ff.

2) This stratification structure was relatively constant throughout the active season. However, in the spring the average distribution heights of component species showed a tendency to be higher, and in the autumn, contrarily, they tended to decrease.

3) The distribution range of the Cs Subassociation was lowered to the herbaceous layer at an artificial edge of a secondary broad-leaved forest. This edge-effect extended at least 5 m inside from the forest edge at the stage of two years after forest felling. This phenomenon suggests that the living space of forest animals is largely divided into two layers, the outer foliage layer and the inner floor layer.

4) The vertical stratification structure was less clear in the white fir artificial forest examined than in the deciduous broad-leaved forests, somewhat resembling the situation at the edge of the broad-leaved forest.

Key words: Drosophilid flies, Forest edge, Deciduous broad-leaved forest, Tomakomai, Vertical stratification.

Introduction

Although the existence of vertical stratification of plant and animal communities is a basic concept in forest ecology (SMITH, 1973), the canopy layer is still one of

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* Institute of Low Temperature Science, Hokkaido University, Sapporo 060, Japan.
北海道大学低温科学研究所

the least explored zones on land because of its height and inaccessibility. Up to the present, many attempts have been made to collect information on the invertebrates living in this zone by various kinds of indirect collecting techniques (*e. g.*, CORBET, 1961 a; MERRILL and SKELLY, 1968; NIELSEN, 1975; WOLDA, 1979; SUTTON, 1979; SUTTON and HUDSON, 1980; MÜNSTER-SWENDSEN, 1980; MOEED and MAEDS, 1984), or by methods of direct access (*e. g.*, DAVIDSON, 1930; PERRY, 1978).

The previous studies (TODA, 1977 b; BEPPU, 1980) of this series, using retainer-type traps set vertically from the ground to the canopy, revealed that clear stratification existed in the vertical distribution of drosophilid flies within a natural broad-leaved forest and a streamside forest. This paper discusses the results of similar surveys made in various forests in the Tomakomai Experiment Forest, putting special emphasis on the vertical distribution at the forest edge, and compares the vertical stratification structure in a natural broad-leaved forest with that of a previous report (TODA, 1977 b).

Methods

Surveys were carried out at the following seven stations (Fig. 1).

Station I was located in a natural deciduous broad-leaved forest. Data concerning the vegetational stratification in this forest are presented in Table 1. Approximately four layers were recognized: 1) canopy layer, *ca.* 12～22 m high; 2) subarboreal layer, *ca.* 6～10 m high; 3) shrub layer, *ca.* 2～6 m high; 4) herbaceous layer, *ca.* 0～0.7 m high, which was relatively sparse and composed of *Osmunda cinnamomea, Rhus ambigua, Maianthemum dilatatum*, etc. Six "retainer" type I traps (TODA, 1977 a) baited with fermenting bananas were set at different heights, 0.1, 1, 4, 7, 10 and 13 m, from the ground to the canopy (Photos 1, 2). The upper four traps were suspended by a rope hung from a bough of the canopy, and the lower two were hung from a tree branch or a trunk. Collections were made in four different periods: from July 10 to August 20 and October 2 to 16 in 1982; and from June 6 to 22 and July 14 to August 22 in 1983. During each survey period, trapped flies were removed and baits were renewed at weekly intervals.

Station II was made at the Forest Observation Tower. Seven traps were set at the heights of 23, 19, 14, 9, 4, 1 and 0.1 m (Photos 3～9). The upper five traps were suspended by a rope tied to the top arm of the Tower. The rope was situated between two large oak (*Quercus dentata ca.* 20 m high and *Q. mongolica* var. *grosseserrata ca.* 19 m high) trees at the edge of a natural deciduous broad-leaved forest. Collections were made from July 15 to August 13 in 1977.

Station III was located in a white fir (*Abies sachalinensis*, 40 years old, *ca.* 12～15 m high) artificial forest. A rope was hung from a bough of an oak (*Q. mongolica* var. *grosseserrata*) tree (*ca.* 9 m high). Four traps were set at the heights of 7, 4, 1 and 0.1 m. Collections were made from July 5 to August 4 in 1979.

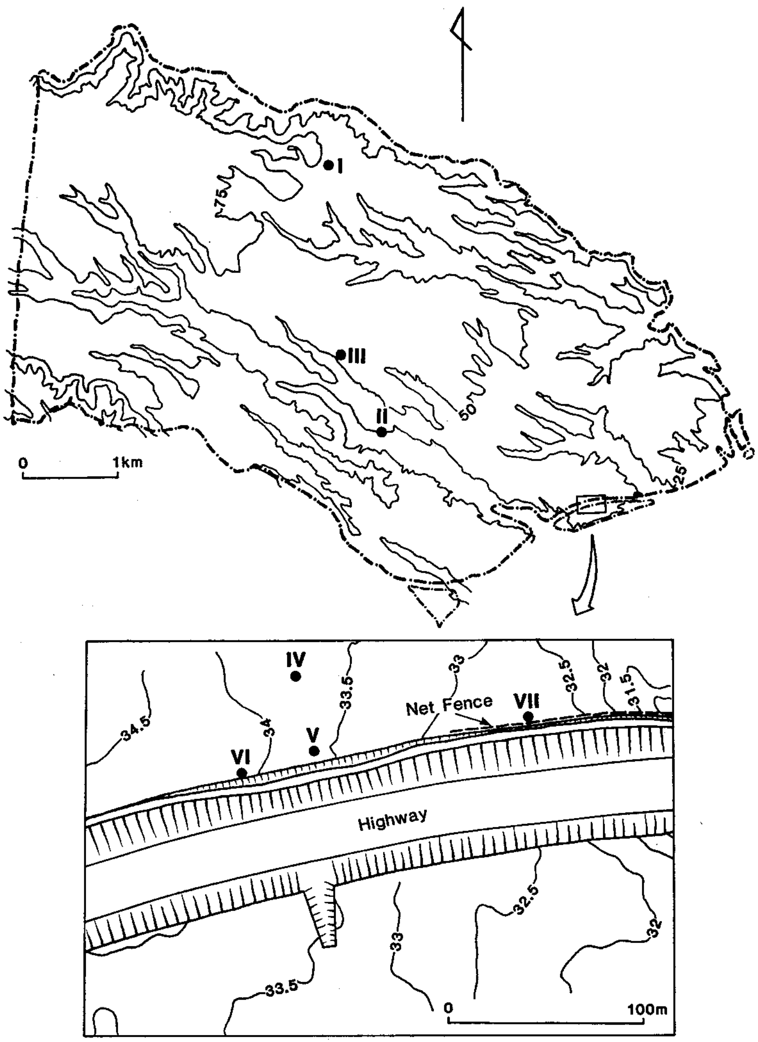

Fig. 1. Location of seven trapping stations in the Tomakomai Experiment Forest.

Four stations were made in a secondary deciduous broad-leaved forest dominated by *Q. mongolica* var. *grosseserrata*. The forest stratification was represented approximately by three layers: 1) canopy layer, *ca.* 4~8 m high, composed of *Q. mongolica* var. *grosseserrata*, *Prunus maximowiczii*, *P. sargentii*, *Acer mono*, *Sorbus alnifolia*, *Kalopanax pictus*, *Fraxinus lanuginosa*, *Tilia japonica*, *Phellodendron amurense* var. *sachalinense*, *Acer palmatum* var. *matsumurae*, etc.; 2) shrub layer, *ca.* 0.5~2 m high, saplings of the canopy tree species, *Euonymus oxyphyllus*, *Magnolia obovata*, *Morus bombycis*, *Pourthiaea villosa*, *Hydrangea paniculata*, *Viburnum opulus* var. *calvescens*, etc.; 3) herbaceous layer, *ca.* 0~0.5 m high, *Carex lanceolata*, *Maianthemum dilatatum*, *Pachysandra terminalis*, *Dryopteris crassirhizoma*, *Rhus ambigua*, *Vitis coignetiae*, *Schisandra chinensis*,

Table 1. Number of trees (more than 2 m high) of different species in each height grade within a quadrat (30×30 m^2) at Station I

Height (m):	2 ~ 4	4 ~ 6	6 ~ 8	8 ~ 10	10 ~ 12	12 ~ 14	14 ~ 16	16 ~ 18	18 ~ 20	20 ~ 22	26 ~ 28	Total
Sorbus alnifolia	32	12	8	3	—	4	—	—	2	—	—	61
Fraxinus lanuginosa	19	10	3	1	1	3	—	—	—	—	—	37
Quercus mongolica var. *grosseserrata*	14	6	6	1	1	—	2	1	1	—	—	32
Carpinus cordata	2	1	—	14	3	4	1	1	—	—	—	26
Acanthopanax sciadophylloides	12	8	3	—	—	—	—	1	—	—	—	24
Ostrya japonica	1	5	5	1	1	—	3	3	1	1	—	21
Magnolia obovata	9	2	3	—	1	—	1	2	1	—	—	19
Acer japonicum	14	2	1	—	—	—	—	—	—	—	—	17
Prunus sargentii	6	7	3	—	—	—	—	—	—	—	—	16
Tilia japonica	4	4	1	2	2	—	—	1	—	—	1	15
Magnolia praecocissima var. *borealis*	7	3	—	—	—	—	—	—	—	—	—	10
Acer ornatum var. *matsumurae*	1	—	—	—	2	2	1	2	—	—	—	8
Aralia elata	2	2	3	—	—	—	—	—	—	—	—	7
Pourthiaea villosa	4	2	—	—	—	—	—	—	—	—	—	6
Acer mono	4	—	1	—	—	—	—	—	—	—	—	5
Cercidiphyllum japonicum	3	1	1	—	—	—	—	—	—	—	—	5
Picea jezoensis	—	—	3	—	—	—	—	—	—	—	—	3
Euonymus oxyphyllus	3	—	—	—	—	—	—	—	—	—	—	3
Kalopanax pictus	3	—	—	—	—	—	—	—	—	—	—	3
Prunus maximowiczii	1	—	1	—	—	—	—	—	—	—	—	2
Hydrangea paniculata	2	—	—	—	—	—	—	—	—	—	—	2
Acer mono var. *mayrii*	2	—	—	—	—	—	—	—	—	—	—	2
Alnus hirsuta	—	—	—	—	—	—	1	—	—	—	—	1
Cornus controversa	—	—	—	—	—	—	1	—	—	—	—	1
Morus bombycis	—	—	1	—	—	—	—	—	—	—	—	1
Tilia maximowicziana	—	—	1	—	—	—	—	—	—	—	—	1
Phellodendron amurense var. *sachalinense*	—	1	—	—	—	—	—	—	—	—	—	1
Total	145	66	44	22	11	13	10	11	5	1	1	329

etc. A part of the forest was felled in the autumn of 1977 to construct a highway. In order to study the influence of forest felling on drosophilid flies, especially on the vertical distribution at the forest edge, collections were made from July 5 to August 4, 1979 at the following four stations.

Station IV (Photos 10, 14), the control, was located at Meteorological Tower Station C, situated 45 m inside from the forest edge. Five traps were set at the heights of 8, 6, 4, 1 and 0.1 m.

Station V (Photos 11, 15) was made at Meteorological Tower Station B, situated 5 m inside from the forest edge. Trap heights were the same as in Station IV.

Station VI was located at an artificial forest edge with poor mantle vegetation (Photo 12). Four traps were set at the heights of 7.8, 4, 1 and 0.1 m.

Station VII was located at another forest edge, where a windbreak net fence (0.5~5.9 m high) was constructed in 1978 to protect forest edge trees from strong wind and sunshine (Photo 13). Four traps were set at the heights of 5.8, 4, 1 and 0.1 m, inside the fence (Photo 16).

Results and Discussion

1. Natural broad-leaved forest

Based upon the results of summer (July 14 to August 22, 1983) collections at Station I, vertical distribution patterns in a natural broad-leaved forest were compared among drosophilid species by cluster analysis (UPGMA: unweighted pair-group method using arithmetic average, SNEATH and SOKAL, 1973). The similarity between two species was evaluated by a niche overlap index according to COLWELL and FUTUYMA's (1971) relative circular weighting method. Some "rare" species, which were defined as species with a total number of individuals less than the

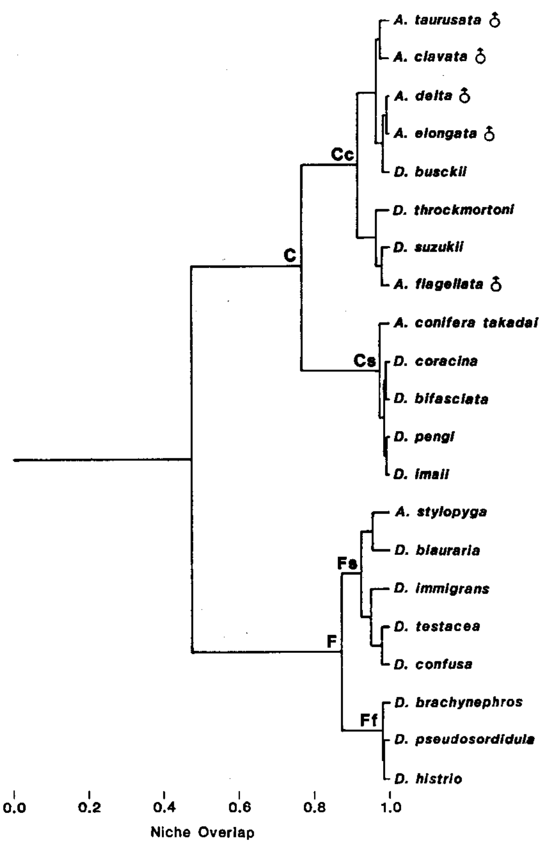

Fig. 2. Niche overlap dendrogram (by UPGMA) for the similarity of vertical distribution in drosophilid species collected at Station I (natural broad-leaved forest) in the summer, 1983.

Table 2. Number of drosophilid flies collected at Station I from July 14 to August 22, 1983, with indication of the results of the correspondence analysis (solid enclosure: primary correspondence, broken enclosure: secondary one, *cf.* TODA and TANNO, 1983) and average distribution heights. "Rare" species excluded from the cluster analysis are shown in parentheses

Trap height (m):	13	10	7	4	1	0.1	Total	Average height (m)
Cc Subassociation								
(*Amiota* spp. ♀*)	34	18	3	—	—	—	55	
(*A. furcata* ♂)	1	—	—	—	—	—	1	(13.0)
(*A. dispina* ♂)	1	—	—	—	—	—	1	(13.0)
A. taurusata ♂	13	1	—	—	—	—	14	12.8
A. clavata ♂	5	2	—	—	—	—	7	12.1
A. delta ♂	10	2	1	—	—	—	13	12.1
(*A. trifurcata*)	3	2	—	—	—	—	5	(11.8)
(*A. trochlea* ♂)	2	2	—	—	—	—	4	(11.5)
(*A. albilabris*)	1	1	—	—	—	—	2	(11.5)
A. elongata ♂	8	2	2	—	—	—	12	11.5
D. busckii	7	1	1	1	—	—	10	11.2
D. throckmortoni	4	4	1	—	—	—	9	11.0
D. suzukii	6	7	—	1	—	—	14	10.9
A. flagellata ♂	6	8	1	2	—	—	17	10.2
Cs Subassociation								
A. conifera takadai	22	8	11	6	6	—	53	8.9
D. coracina	28	36	12	12	12	—	100	8.7
D. bifasciata	399	313	204	107	152	17	1,192	8.7
(*D. multispina*)	—	1	1	—	—	—	2	(8.5)
D. pengi	10	8	5	6	5	—	34	8.1
(*A. okadai*)	1	1	—	—	1	—	3	(8.0)
D. imaii	62	72	57	37	42	1	271	7.8
(*D. trilineata*)	—	—	1	—	—	—	1	(7.0)
Fs Subassociation								
A. stylopyga	2	1	2	—	3	—	8	6.6
D. biauraria	12	7	4	11	16	2	52	6.0
D. immigrans	1	4	3	4	4	—	16	5.9
(*L. quinquemaculipennis*)	—	—	1	1	—	—	2	(5.5)
D. testacea	11	27	10	10	63	10	131	4.5
D. confusa	7	15	14	20	53	—	109	4.3
(*D. moriwakii*)	—	1	—	1	2	—	4	(4.0)
Ff Subassociation								
D. brachynephros	—	1	2	2	8	1	14	2.9
D. pseudosordidula	—	2	2	6	26	—	36	2.3
D. histrio	1	6	3	10	66	7	93	2.2
(*D. nigromaculata*)	—	—	—	—	1	—	1	(1.0)
(*D. curvispina*)	—	—	—	—	—	1	1	(0.1)
Total	657	553	341	237	460	39	2,287	

* Female specimens of most species of the subgenus *Amiota* are not identified to species.

number of traps (6 in this case), were excluded from the analysis.

The resulting dendrogram is shown in Fig. 2. Twenty-one species subjected to the analysis were classified first into two clusters, C and F, each of which was divided further into two subclusters. As a result, four different groups, Cc, Cs, Fs and Ff, were distinguished for the vertical distribution pattern in the natural forest. Cc included 8 species (*Amiota taurusata, A. clavata, A. delta, A. elongata, Drosophila busckii, D. throckmortoni, D. suzukii* and *A. flagellata*); Cs, 5 spp. (*A. conifera takadai, D. bifasciata, D. pengi* and *D. imaii*); Fs, 5 spp. (*A. stylopyga, D. biauraria, D. immigrans, D. testacea* and *D. confusa*); Ff, 3 spp. (*D. brachynephros, D. pseudosordidula* and *D. histrio*). The distribution patterns of these species were further examined by the correspondence analysis of TODA and TANNO (1983) and the correspondence is shown with square enclosures in Table 2. Average distribution heights calculated by the formula given by TODA (1985) is also shown in the table. The "rare" species excluded from the analyses were assigned to appropriate groups on the basis of their distributions. From the results of the correspondence analysis, the vertical distribution patterns of the four groups were characterized as follows: Cc was confined almost exclusively to the canopy layer, Cs occupied the canopy layer but was also distributed down to the shrub layer, Fs was distributed primarily in the shrub layer but was also found in the subarboreal or canopy layer, and Ff was more or less confined to the shrub or herbaceous layer.

The vertical range covered by the above survey did not extend above the tree top layer. To survey drosophilid distribution at and above the uppermost layer of

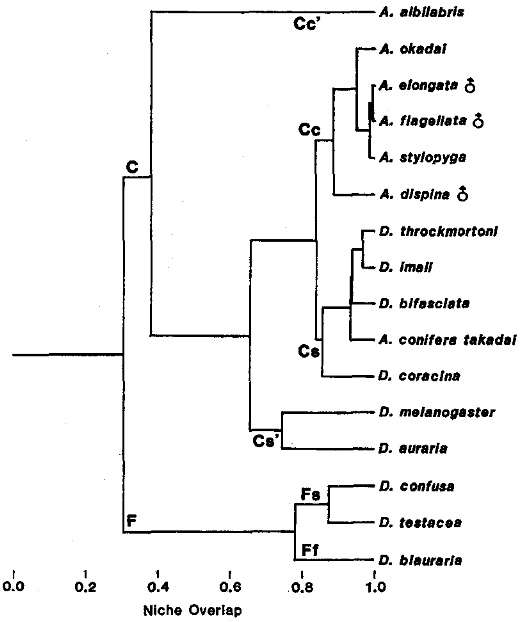

Fig. 3. Niche overlap dendrogram (by UPGMA) for the similarity of vertical distribution in drosophilid species collected at Station II (Forest Observation Tower) in the summer, 1977

Table 3. Number of drosophilid flies collected at Station II from July 15 to August 13, 1977 (*cf.* the explanation of Table 2)

Trap height (m):	23	19	14	9	4	1	0.1	Total	Average height (m)
Cc′ subcluster									
A. albilabris	1	5	—	1	—	—	—	7	18.1
Cc subcluster									
(*Amiota* spp. ♀)	—	13	19	3	—	—	—	35	
A. okadai	4	3	7	2	—	—	—	16	16.6
(*A. delta* ♂)	—	2	2	—	—	—	—	4	(16.5)
(*A. trifurcata*)	—	1	1	—	—	—	—	2	(16.5)
(*L. quinquemaculipennis*)	—	2	4	—	—	—	—	6	(15.7)
A. elongata ♂	—	3	7	1	—	—	—	11	14.9
A. flagellata ♂	1	7	20	5	—	—	—	33	14.6
A. dispina ♂	—	3	2	3	—	—	—	8	14.0
(*L. maculata*)	—	—	3	—	—	—	—	3	(14.0)
(*A. clavata* ♂)	—	—	1	—	—	—	—	1	(14.0)
(*A. balaenodentata* ♂)	—	—	1	—	—	—	—	1	(14.0)
A. stylopyga	—	3	17	5	—	—	—	25	13.6
(*A. subfurcata* ♂)	—	1	2	2	—	—	—	5	(13.0)
(*A. furcata* ♂)	—	1	2	2	—	—	—	5	(13.0)
Cs subcluster									
D. throckmortoni	1	1	4	3	1	—	—	10	12.9
(*D. busckii*)	—	1	2	—	1	—	—	4	(12.8)
D. bifasciata	8	30	41	25	29	2	1	136	12.3
(*D. triauraria*)	1	—	—	1	1	—	—	3	(12.0)
D. imaii	1	1	12	5	7	—	—	26	10.9
A. conifera takadai	1	1	4	4	4	—	1	15	10.0
D. coracina	—	13	40	12	22	14	1	102	10.0
Cs′ subcluster									
D. melanogaster	4	13	8	8	4	9	10	56	9.8
(*D. lacertosa*)	—	—	—	1	—	—	—	1	(9.0)
(*Leucophenga* sp. 1)	—	—	—	1	—	—	—	1	(9.0)
D. auraria	—	2	1	—	2	—	2	7	8.6
Fs subcluster									
D. confusa	—	—	1	2	14	5	—	22	4.2
(*D. ezoana*)	—	—	—	—	2	—	—	2	(4.0)
(*D. pengi*)	—	—	—	—	2	—	—	2	(4.0)
(*D. moriwakii*)	—	—	—	—	1	—	—	1	(4.0)
(*A. taurusata* ♂)	—	—	—	—	1	—	—	1	(4.0)
(*D. multispina*)	—	—	—	—	1	—	—	1	(4.0)
D. testacea	—	—	—	1	4	1	1	7	3.7
Ff subcluster									
(*D. histrio*)	—	—	—	1	1	1	2	5	(2.8)
(*D. immigrans*)	—	—	—	—	2	—	2	4	(2.1)
D. biauraria	—	5	2	8	49	158	65	287	1.9
(*D. brachynephros*)	—	—	—	—	1	4	—	5	(1.6)
(*D. sordidula*)	—	—	—	—	—	1	1	2	(0.6)
(*D. nigromaculata*)	—	—	—	—	—	1	2	3	(0.4)
Total	22	111	203	96	149	196	88	865	

the forest canopy, vertical trap collections were made at Station II in the summer (July 15 to August 13) of 1977, with the aid of the top arm of the Forest Observation Tower. The top trap (23 m high) was set *ca.* 3∼4 m above the tree tops, and the second one (19 m high) was set in the uppermost layer of the canopy. The obtained data were subjected to the same analyses as in the first case, and the resulting dendrogram and correspondence table are shown in Fig. 3 and Table 3, respectively. In this case, too, component drosophilid species were classified first into two major clusters, C and F. Cluster C was divided further into four subclusters, Cc, Cc′, Cs and Cs′, and cluster F into two, Fs and Ff. Cc included 5 *Amiota* species, which were distributed exclusively in the canopy layer. Of the 5 species, *A. stylopyga* changed its distribution considerably from Fs at Station I to Cc at Station II. Cc′ included only one species, *A. albilabris*, which was most abundant in the uppermost layer of the canopy. The species composition of Cs differed less between Station I and II, *i.e.*, 4 out of the 5 component species were common to both stations. Two species of Cs′, *D. melanogaster* and *D. auraria*, tended to be distributed evenly from the canopy to the ground. Almost all the species belonging to cluster C were limited to below the tree top layer, not extending above the canopy as some insects in tropical rain forests (CORBET, 1961 a, 1964; HADDOW and CORBET, 1961; HADDOW and SSENKUBUGE, 1965; SUTTON and HUDSON, 1980). The total number of individuals collected at the top trap was much smaller than that at other traps. Two species of Fs, *D. confusa* and *D. testacea*, did not change their distribution patterns radically from those observed at Station I, being centered in the shrub layer. *D. biauraria*, which belonged to Fs at Station I, lowered its average distribution height from 6.0 m to 1.9 m and were more or less confined to the shrub or herbaceous layer. Thus, the vertical distribution patterns of most species were nearly identical between the two stations, except for the above-mentioned small changes in some species. The small changes may be due partly to the fact that Station II was located at the forest edge facing the Observation Tower.

In general, the above results are consistent with those obtained at Misumai, near Sapporo (TODA, 1977 b). TODA recognized five different patterns of vertical distributions, Types 1 to 5, and classified component species of a drosophilid community in a natural broad-leaved forest into two major associations, floor association (combined Types 1+2) and canopy association (combined Types 4+5), and one minor group, which was distributed in the subarboreal layer (Type 3). However, this classification was made more or less subjectively. Therefore, to make a reliable comparison between the two localities, it is necessary to reclassify component species of the Misumai community by the same method as in the present study. Application of UPGMA cluster analysis to the data obtained in the summer (July 3 to August 1, 1974) resulted in complete agreement with the afore-mentioned results at Station I. That is, component species were classified first into two major clusters, C and F, each of which was divided further into two subclusters, the former into Cc and Cs, and the latter into Fs and Ff. Cc included the species of Type 5, Cs

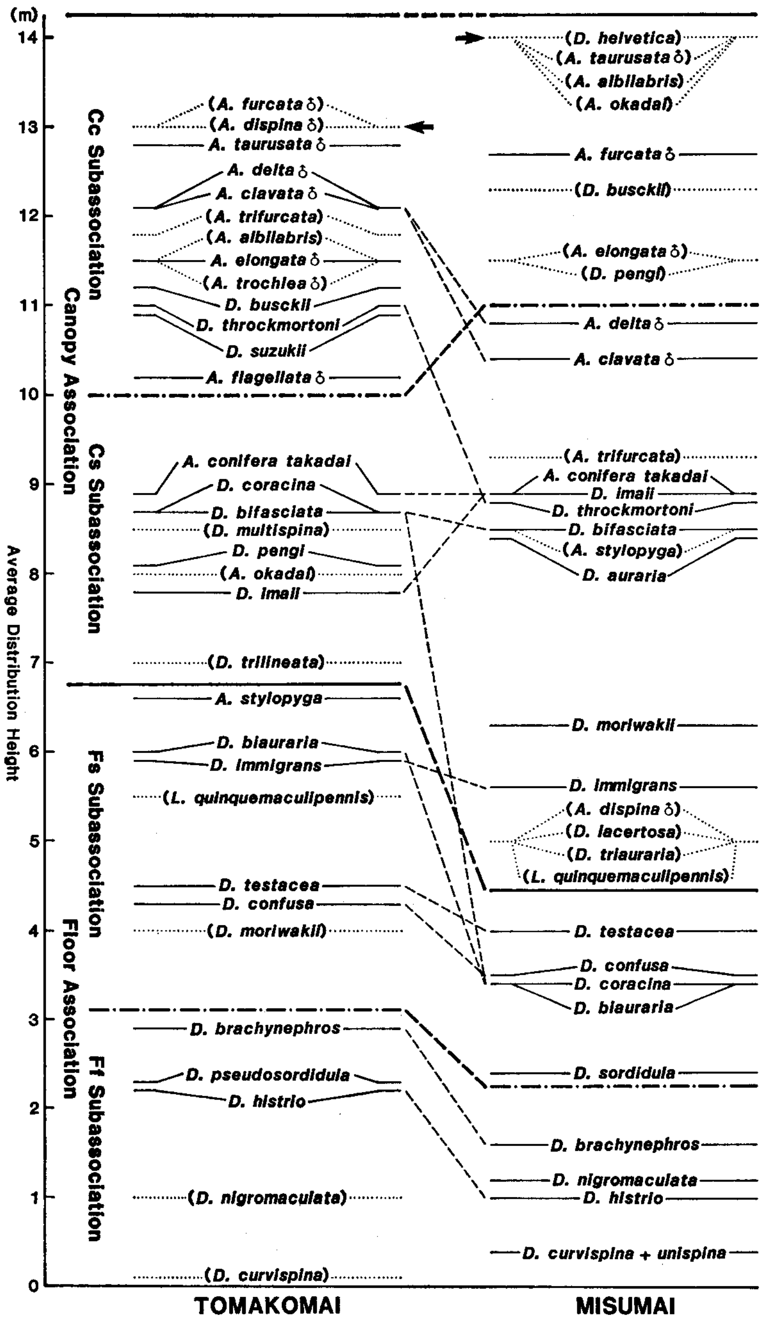

Fig. 4. Comparison of vertical stratification structure between two drosophilid communities in natural forests at Tomakomai and at Misumai, including the average distribution height of each component species. "Rare" species are shown in parentheses and by a dotted line. Arrow indicates the height of the top trap.

those of Types 5 to 3, Fs mainly those of Type 2, and Ff mainly of Type 1. Here, these clusters and subclusters are renamed as follows: C — Canopy Association, including Cc and Cs Subassociations, and F — Floor Association, including Fs and Ff Subassociations. In Fig. 4 component species of these associations or subassociations are compared between the two natural forest drosophilid communities at Tomakomai and Misumai, together with the average distribution height of each species. The change in average height is shown only for non-"rare" species at both localities. Although the average heights of these species tended to be higher at Tomakomai than at Misumai and there were some changes in components of subassociations, the main components of the two associations were quite constant between the two localities, with only two exceptions, *D. coracina* and *D. immigrans*. *D. coracina* belonged to Cs Subassociation (distributed 8.7 m high in average) at Tomakomai but to Fs Subassociation (3.8 m) at Misumai. The changeable nature of this species in vertical distribution has been repeatedly pointed out in other studies (TODA, 1977 b, 1985; TODA and FUKUDA, 1985). On the other hand, the difference observed in *D. immigrans*, which belonged to Fs at Tomakomai but to Cs at Misumai, may be of no significance. The Type 3 species distributed mainly in the subarboreal layer are sometimes classified into different subassociations, Cs or Fs, according to their relation to other species, in spite of no changes in the distribution height. Although the average height of *D. immigrans* did not change locally in the present study, it has been empirically confirmed that most species of Type 3, which are sporadic migrants or invaders from other habitats (TODA, 1977 b), are more or less changeable in their vertical distribution patterns (TODA, 1985; TODA and FUKUDA, 1985).

2. Seasonal changes

Based on the results of surveys made in different seasons at Station I, seasonal changes in the vertical stratification structure of a drosophilid community in the natural forest are shown in Fig. 5. The structure in the summer did not change radically between two successive years, 1982 and 1983, although the number of species collected was smaller, especially in Cc Subassociation, in 1982 than in 1983. Of 14 species which were not "rare" in either year, only 3 species belonged to different subassociations between the two years: *A. stylopyga* belonged to Cs in 1982 but to Fs in 1983; *D. testacea* to Ff in 1982 but to Fs in 1983; *D. suzukii* to Cs in 1982 but to Cc in 1983. The structure in the spring was characterized by the virtual lack of components of Ff Subassociation and relatively higher average distribution heights of component species. It should be noted that *D. confusa*, *D. histrio* and *A. conifera takadai* belonged to Cs, Fs and Cc Subassociation, respectively. All the non-"rare" species decreased their average distribution heights from the spring to the summer. On the contrary, the autumn structure was characterized by the scarcity of Cc Subassociation and the abundance of Floor Association. As mentioned by TODA (1977 b), the main components of the Floor Association were fungivorous species, which should have prospered due to the richness of food resources on the forest floor in the autumn.

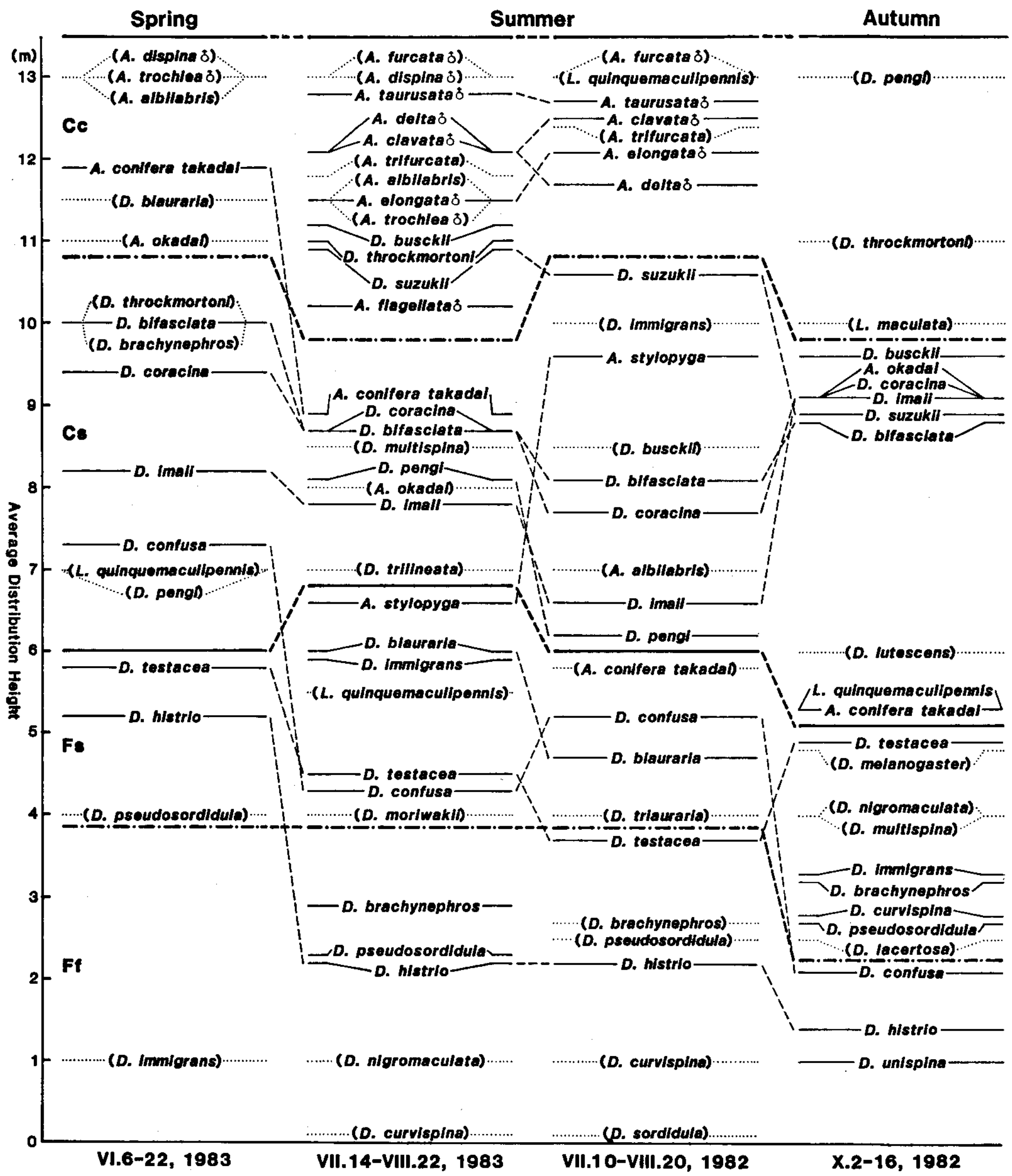

Fig. 5. Comparison of vertical stratification structure of a drosophilid community at Station I in different seasons. (*cf.* the explanation of Fig. 4).

3. Secondary broad-leaved forest

The samples collected in the 18 traps at Stations IV to VII in or at the edge of a secondary broad-leaved forest were compared with one another by the UPGMA cluster analysis. The similarity of sample composition was evaluated by HORN's (1966) measurement of overlap. From the resulting dendrogram (Fig. 6-A), the 18 traps, each of which is shown with Station No. and trap height, were classified

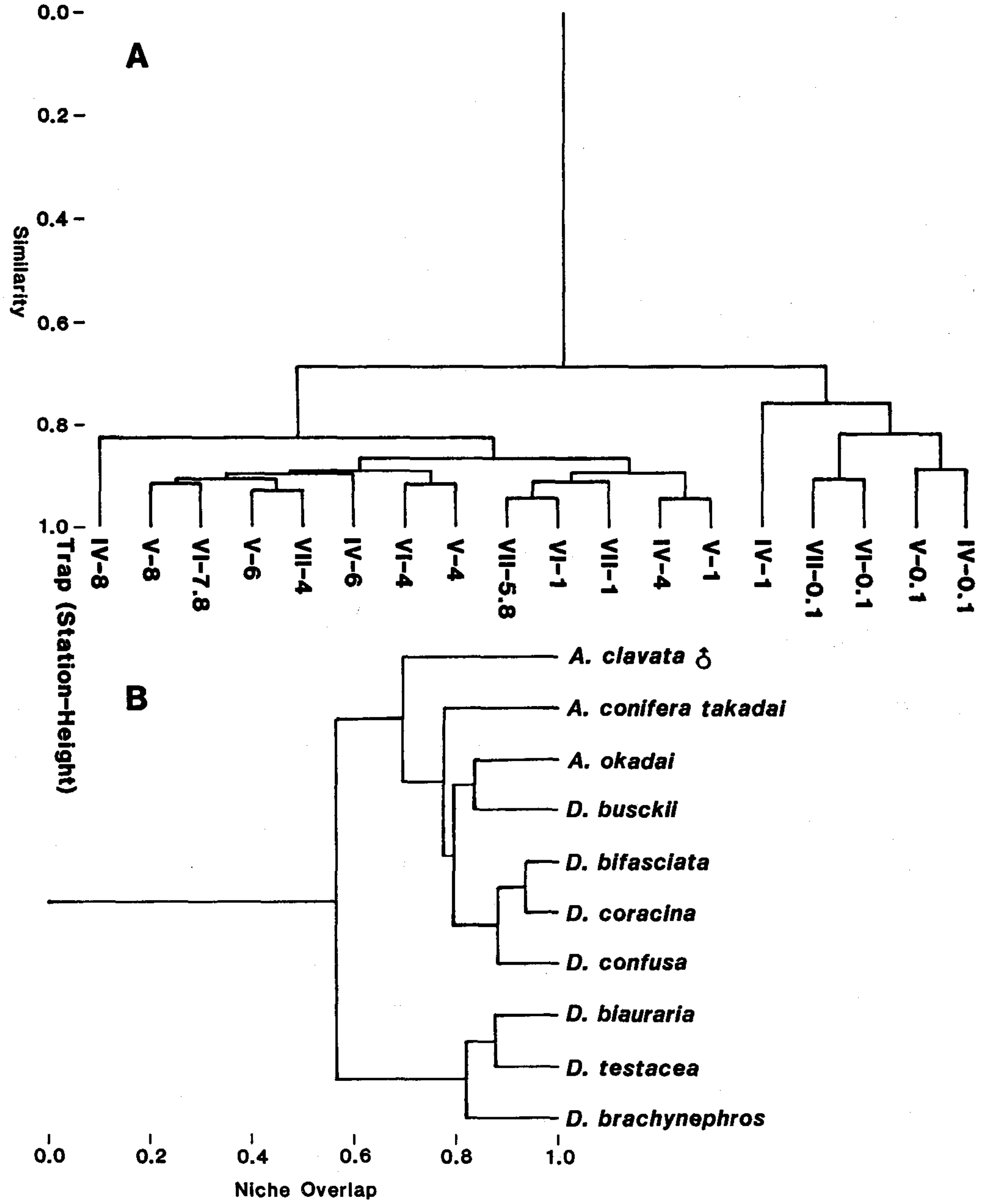

Fig. 6. Cluster analyses (UPGMA) of trap samples (A) and of drosophilid species (B), based on the results of collections at Stations IV to VII (secondary broad-leaved forest) in the summer, 1979.

into three clusters. The first cluster included 10 traps set 4 or more meters high and 3 traps set 1 m high at the forest edge (Stations V to VII). The second consisted of only one trap, IV-1. The 4 traps set on the ground (0.1 m heigh) made up the third cluster.

Table 4. Number of drosophilid flies collected at Stations IV to VII from July 5 to August 4, 1979 (*cf.* the explanation of Table 2)

Cluster:	1													2	3				
Station:	IV	V	VI	V	VII	IV	VI	V	VII	VI	VII	IV	V	IV	VII	VI	V	IV	Total
Trap height (m):	8	8	7.8	6	4	6	4	4	5.8	1	1	4	1	1	0.1	0.1	0.1	0.1	
(*Amiota* spp. ♀)	3	10	8	6	1	2	10	2	5	1	—	1	2	—	—	—	—	—	51
A. clavata ♂	7	7	6	3	2	1	10	4	2	1	—	1	—	1	—	—	—	—	45
(*A. delta* ♂)	1	—	1	4	—	4	1	1	—	—	—	—	—	—	—	—	—	—	12
(*A. stylopyga*)	2	—	1	—	—	1	3	—	1	—	—	—	—	1	—	2	—	—	11
(*A. elongata* ♂)	3	1	—	1	—	2	1	1	—	—	—	—	—	—	—	—	—	—	9
(*A. albilabris*)	1	1	—	1	1	1	—	—	—	—	—	1	—	—	—	—	—	—	6
(*L. quinquemaculipennis*)	—	—	—	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	3
(*A. subfurcata* ♂)	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
(*D. lutescens*)	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2
(*A. dentata* ♂)	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
(*A. taurusata* ♂)	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
A. conifera takadai	2	—	1	1	—	2	6	3	3	5	—	1	—	—	3	2	1	1	31
(*D. imaii*)	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	1	—	—	3
A. okadai	4	6	5	5	1	2	8	2	2	7	1	—	—	—	3	1	1	—	48
(*D. melanogaster*)	1	2	—	2	—	—	—	1	—	—	—	—	—	—	1	—	—	1	8
(*D. ezoana*)	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	2
D. busckii	9	7	8	4	3	10	8	7	13	21	19	5	8	—	5	1	—	—	128
(*Ch. costata*)	1	—	—	—	—	1	—	—	—	—	—	1	1	—	—	—	—	—	4
(*D. hydei*)	—	—	1	—	—	1	—	—	1	—	—	—	—	—	1	—	—	—	4
(*A. dispina* ♂)	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
D. bifasciata	34	43	63	38	30	40	53	49	34	51	30	24	41	25	37	32	13	—	637
(*D. suzukii*)	1	—	2	—	—	3	—	1	3	1	—	—	—	2	—	4	—	—	17
D. coracina	13	7	7	11	9	11	22	4	10	26	9	11	30	13	8	8	9	2	210
D. confusa	1	3	6	7	5	7	22	19	7	12	14	9	10	29	6	6	5	5	173
(*D. immigrans*)	—	—	1	—	—	—	1	—	—	2	—	—	—	2	—	2	—	—	8
(*D. pseudosordidula*)	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	2
(*D. pengi*)	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
D. biauraria	6	7	10	12	12	18	14	17	15	25	26	12	29	13	50	44	30	15	355
(*D. triauraria*)	—	—	—	—	1	—	1	—	—	—	2	1	—	—	1	1	1	—	8
(*D. sordidula*)	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	2	—	1	5
D. testacea	—	—	2	2	1	1	7	6	4	6	6	3	5	22	21	6	26	10	128
(*D. histrio*)	—	—	—	—	—	—	2	1	—	3	1	—	—	3	1	2	2	1	16
(*D. moriwakii*)	—	—	1	—	—	1	2	1	—	—	—	2	3	1	1	—	3	—	15
D. brachynephros	—	—	—	1	1	—	—	—	1	1	1	3	4	3	10	15	34	9	83
(*D. auraria*)	1	—	1	1	—	—	1	—	—	—	—	—	1	—	2	—	3	2	12
(*D. nigromaculata*)	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	2	—	3
(*D. unispina*)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2
Total	94	94	126	100	67	109	176	120	103	163	110	75	136	116	150	129	131	48	2,047

The distributions of 10 non-"rare" drosophilid species among the 18 traps were compared also by the UPGMA cluster analysis (Fig. 6-B). The 10 species were classified into two groups: the first included 6 species, which belonged to Canopy Association in the natural forest, and *D. confusa* of Fs Subassociation, while the second included 3 species of Floor Association.

The correspondence between these species and trap clusters is shown in Table 4. In general, the first cluster of traps corresponded to the species of Canopy Association and the third to those of Floor Association. In the sample composition IV-1 was intermediate between the two major clusters, characterized by the species of Cs and Fs Subassociations. However, closer inspection of the table revealed some differences in the distribution patterns at the forest edge between the species of Cc Subassociation and those of Cs. The species of the former subassociation, *e.g. A. clavata*, were more or less confined to the canopy layer even at the forest edge, whereas those of the latter, *e.g. A. conifera takadai* and *D. bifasciata*, lowered their distribution ranges as far as the herbaceous layer. The latter tendency was conspicuous at Station VII, which had a net fence. The distribution patterns of the Floor Association species at the forest edge did not change radically from those inside the forest.

According to the above results, the distribution of drosophilid flies in the secondary forest, especially at the artificial forest edge, is shown schematically in Fig. 7. The influence of forest felling extended at least 5 m inside from the forest edge, particularly in the species of Cs Subassociation. Even at the stage of the present survey, when the mantle vegetation was still undeveloped, the distribution ranges were lowered to the herbaceous layer at the forest edge. If the conditions at Station VII, where the forest edge was protected from strong wind and sunshine by a net fence, are regarded as representing a more advanced stage in the vegetational changes at the forest edge, the tendency mentioned above will be reinforced

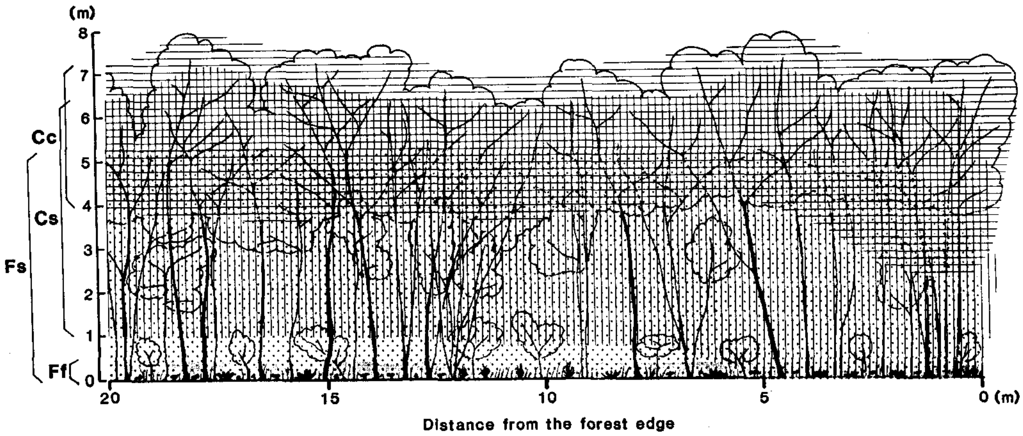

Fig. 7. Schematic representation of the vertical stratification structure in a drosophilid community of a secondary broad-leaved forest, with special reference to effects of forest felling on the structure at the forest edge.

in the process of the development of mantle vegetation. In this connection, CORBET (1961 b) mentioned, "from a microclimatic point of view, the canopy is similar to the forest margin near the ground", and "the canopy is to be regarded as presenting a simple forest-edge situation..." Furthermore, he cited two cases of epiphytic plant distribution reflecting this microclimatic situation: "Thus SCHIMPER (quoted by PITTENDRIGH, 1948) recognized as a distinct community a group of epiphytes which occurred on low bushes of savannah and also at the top of the forest canopy; and PITTENDRIGH (1948) has shown that certain bromeliads, ..., occur both in the canopy and also at the forest edge near ground level." The frequent occurrence of forest canopy dwellers in foliage layers of forest edge environments near the ground was also observed in other animals, *e.g.* titmice (NAKAMURA, 1970), larvae of a weevil, *Rhynchaenus fagi* (NIELSEN and EJLERSEN, 1977) and an ichneumonid wasp, *Pimplopterus dubius* (MÜNSTER-SWENDSEN, 1980). In conclusion, the living space of forest animals is largely divided into two layers, the outer foliage layer and the inner floor layer. This habitat stratification corresponds to the separation between production space and decomposition space in a forest ecosystem.

4. White fir artificial forest

The results of the cluster and correspondence analyses for the data obtained at Station III are shown in Fig. 8 and Table 5, respectively. Three clusters were recognized from the dendrogram for the similarity of vertical distribution in 9 non-"rare" species. The first cluster included 3 species (*A. conifera takadai*, *D. bifasciata* and *D. coracina*) of Cs Subassociation in the natural broad-leaved forest, 2 spp. (*A. stylopyga* and *D. confusa*) of Fs and 1 sp. (*D. pseudosordidula*) of Ff. These species were most abundant at the height of 1 m. The second cluster was composed of 2 species of Floor Association, *D. testacea* and *D. histrio*, which were more or less confined to the floor layer also in the white fir artificial forest. The third cluster included only one species, *D. biauraria*, which was collected at the

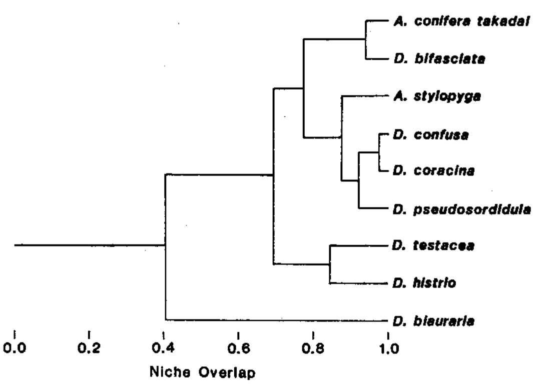

Fig. 8. Niche overlap dendrogram (by UPGMA) for the similarity of vertical distribution in drosophilid species collected at Station III (white fir artificial forest) in the summer, 1979.

Table 5. Number of drosophilid flies collected at Station III from July 5 to August 4, 1979 (*cf.* the explanation of Table 2)

Trap height (m):	7	4	1	0.1	Total	Average height (m)
(*A. clavata* ♂)	3	—	—	—	3	(7.0)
(*A. dispina* ♂)	1	—	—	—	1	(7.0)
A. conifera takadai	2	1	3	—	6	3.5
D. bifasciata	35	41	83	17	176	2.8
(*D. brachynephros*)	—	1	1	—	2	(2.5)
A. stylopyga	—	2	3	—	5	2.2
(*D. imaii*)	—	1	2	—	3	(2.0)
D. confusa	5	33	93	8	139	1.9
D. coracina	1	6	44	2	53	1.4
D. pseudosordidula	—	1	53	5	59	1.0
(*D. sordidula*)	—	—	2	—	2	(1.0)
(*A. elongata* ♂)	—	—	1	—	1	(1.0)
(*D. lutescens*)	—	—	1	—	1	(1.0)
(*D. immigrans*)	—	—	1	—	1	(1.0)
D. biauraria	—	2	—	3	5	1.7
D. testacea	1	5	6	10	22	1.6
D. histrio	—	—	2	2	4	0.6
Total	48	93	295	47	483	

heights of 4 and 0.1 m. Although no species of Cc Subassociation exceeded 4 specimens in sample size, *i. e.*, the limit value for the cluster analysis, *A. clavata* and *A. dispina* were collected exclusively at the top trap (7 m high), while one specimen of *A. elongata* was collected at the height of 1 m.

Thus, the vertical stratification structure was less clear in the white fir artificial forest than in the deciduous broad-leaved forests, and was characterized by the lowered distribution ranges in some species of Cs Subassociation. This situation resembled that at the edge of the broad-leaved forest.

Acknowledgements

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要　　約

北海道大学苫小牧地方演習林のいろいろな種類の森林で，果物トラップを林床から林冠まで垂直的に設置して，ショウジョウバエ類の垂直分布を調査した。

1) 広葉樹天然林内のショウジョウバエ群集は，林冠集団と林床集団によって構成され，さらに，両集団はそれぞれ2つの多少とも垂直分布型の異なる亜集団（林冠集団は Cc と Cs に，林床集団は Fs と Ff）に区分された。

2) この成層構造は，季節を通して比較的安定に維持されたが，春には構成種の分布高度がやや上がり，秋にはやや下がる傾向が見られた。

3) 高速道路に隣接する広葉樹二次林の林縁では，Cs 亜集団の分布帯が草本層にまで引き下げられた。隣接する林が皆伐されたことにより現出した人為的林縁における，このような成層構造の変化は，伐採後2年の段階で，林縁から少なくとも の5 m の所にまで及んでいた。林縁で林冠性種の分布帯が下がる傾向は，他の動物あるいは着生植物などにも共通に見られる現象で，一般に，森林性動物の生活空間は，外側の葉群層と内側の林床層に大きく2分されているとみなすことができる。

4) トドマツ人工林内でのショウジョウバエ群集の成層構造は，広葉樹林内でのそれと比べて不明瞭で，多少とも林縁における状況と似ていた。

Explanations of photographs

Photo 1. Upper three traps (13, 10 and 7 m high) at Station I.

Photo 2. Two traps (4 and 1 m high) at Station I.

Photo 3. Top trap (23 m high) at Station II.

Photo 4. Trap of 19 m height at Station II.

Photo 5. Trap of 14 m height at Station II.

Photo 6. Trap of 9 m height at Station II.

Photo 7. Trap of 4 m height at Station II.

Photo 8. Trap of 1 m height at Station II.

Photo 9. Trap on the ground (0.1 m high) at Station II.

Photo 10. Station IV at Meteorological Tower Station C.

Photo 11. Station V at Meteorological Tower Station B.

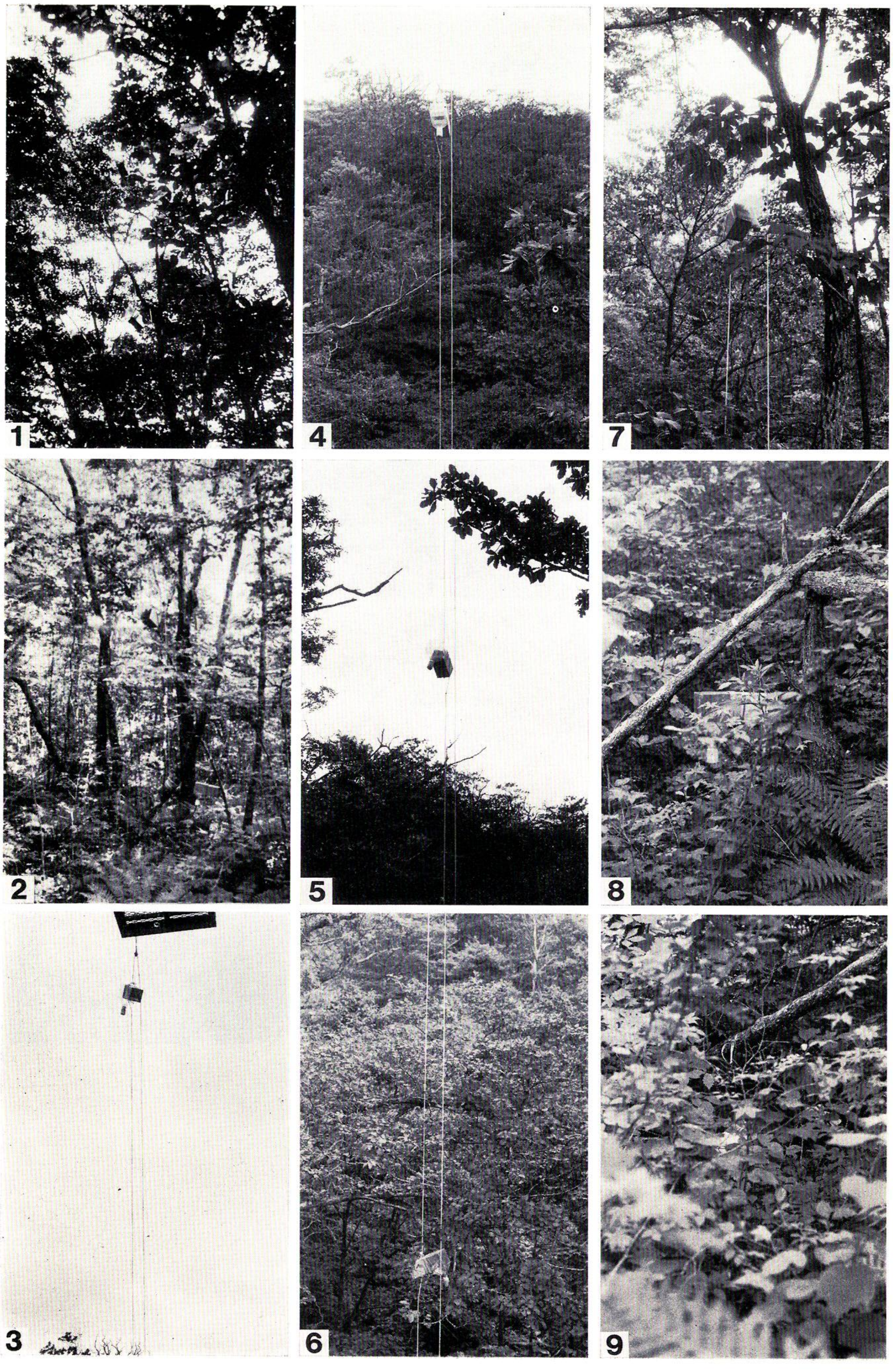
Photo 12. Artificial forest edge with poor mantle vegetation, where Station VI was located.

Photo 13. Forest edge with a windbreak net fence, where Station VII was located.

Photo 14. Station IV.

Photo 15. Station V.

Photo 16. Upper two traps at Station VII.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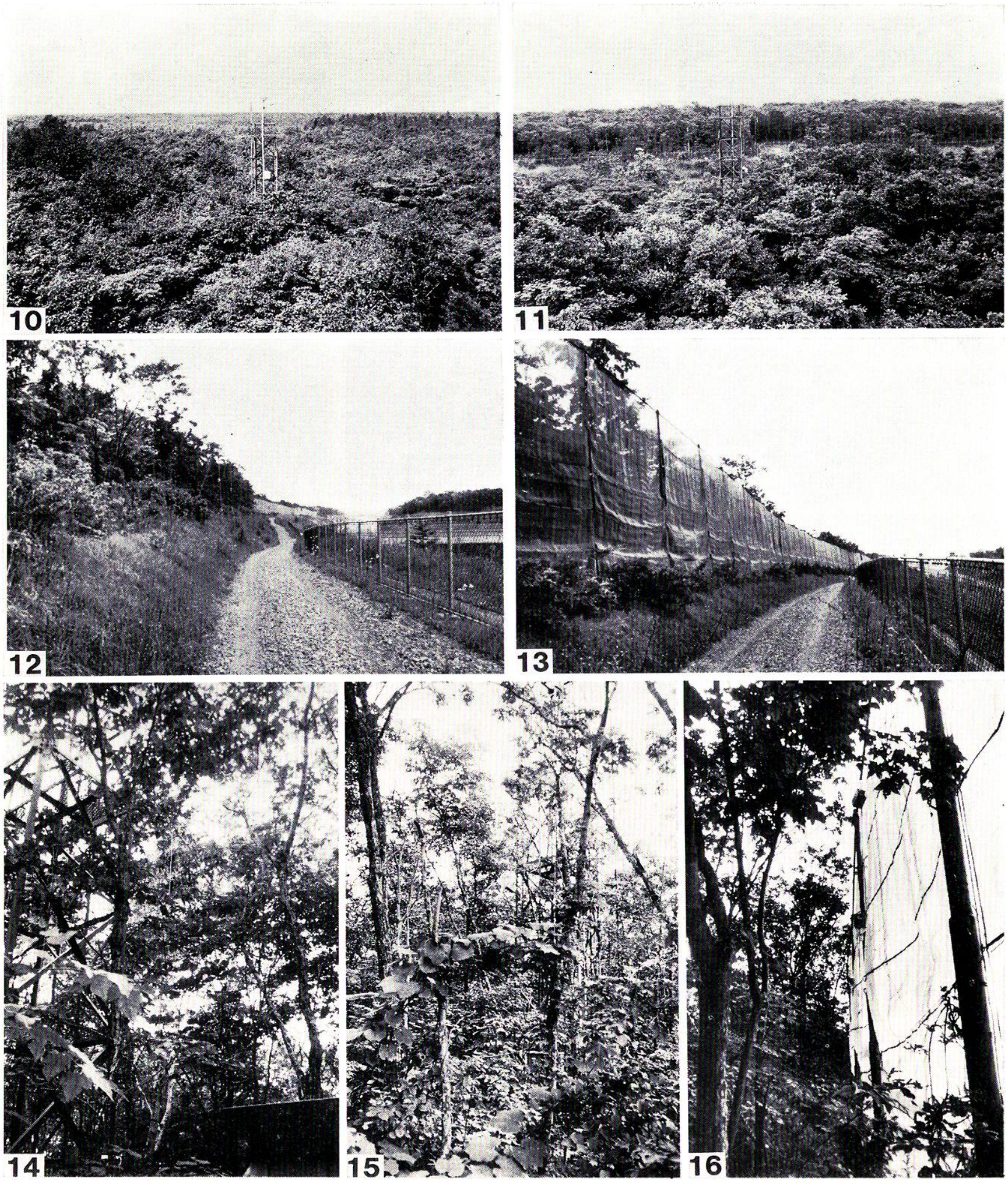
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