Ecol. Res. 4: 243–260, 1989

ECOLOGICAL RESEARCH

Arthropod Communities in a Japanese Cedar (*Cryptomeria japonica* D. Don) Plantation: Abundance, Biomass and Some Properties

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Abstract

Arboreal arthropod communities were censused by insecticidal knockdown in a plantation of Japanese cedar, *Cryptomeria japonica*, in central Japan from April 1983 to February 1985 at intervals of two months. All arthropods sampled were allocated to higher taxonomic groups or guilds and the composition of the communities was analyzed with respect to abundance, biomass and their seasonal trends. The total densities fluctuated seasonally from 200 to 3500 m^{-2}; corresponding biomass values ranged from 7 to 600 mg fresh weight m^{-2}. Maximum density and biomass generally occurred in summer and were minimum in winter. The consistently dominant guild in terms of abundance were the detritivores, mostly comprising Collembola and oribatid mites, accounting for 36–93% of all arthropods; phytophages, predators and detritivores were major guilds in terms of biomass, showing average proportions of 27%, 23% and 20%, respectively.

Biomass ratios of predators to prey were generally high in some canopy communities, suggesting the importance of predation pressure in regulating the population levels of arthropods in forests. Average individual size of predators was approximately proportional to that of prey, irrespective of tree locality. Soil arthropod communities maintained densities approximately 10^2–10^3 times as large as the corresponding canopy communities throughout the year. The seasonal variations in abundance were much greater in canopy than in soil communities.

Key words: Abundance; Arthropod communities; Biomass; Canopy and soil strata; *Cryptomeria japonica* plantation.

Introduction

The canopy strata of forest ecosystems support myriads of arthropod species that are highly diversified because of the structural heterogeneity of the strata and the stable supply of manifold resources. Many such species coexist on trees, forming a distinctive community structure through various interactions, including competition and predation.

Considerable attention has been paid to arboreal communities because the structural complexity and spatial delimitation of trees provide useful model habitats for the study of community ecology (Southwood et al., 1982a). Previous studies of arthropod communities on trees have focused primarily on the structural aspects of the communities due to interactions among or within the component species (e.g. Moran and Southwood, 1982; Southwood et al., 1982a, b; Stork, 1987) and the herbivore-plant, or insect-forest interactions which reflect the functional and coevolutionary aspects of the communities (e.g. Southwood, 1973; Mattson and Addy, 1975; Wolda, 1978a, b; Ohmart, 1984).

Accepted 26 May 1989

Table 1. Outline of the survey plot

Altitude (above sea level)	980 m
Stand density	2200 ha^{-1}*
Mean tree diameter at breast height	14.1 cm*
Mean tree height	11.5 m*
Annual mean air temperature	10.2°C†
	9.8°C‡
Annual precipitation	2290 mm yr^{-1}†
	1655 mm yr^{-1}‡

*as of 1983; †April 1983–March 1984; ‡April 1984–March 1985

Because of the paucity of field studies, however, little has yet been clarified about the patterns of arthropod communities in forest canopy strata. Accordingly, a major objective of the present study was to outline the composition, dynamics and some other quantitative features of the arthropod communities in forest ecosystems, bringing together a variety of information obtained from an evergreen coniferous forest and some other types of tree (e.g. Southwood et al., 1982a; Hijii, 1983, 1984, 1986). The present paper deals mainly with: 1) seasonal trends in faunal composition in terms of numbers of individuals and biomass, 2) differences in the faunal formation among tree species, 3) predation pressure reflected by the biomass relationship between predators and prey animals, and 4) comparison of community dynamics between canopy and soil strata censused in the same forest stand (Hijii, 1987).

Study Area and Methods

The data collection was carried out in a 26-yr-old plantation of a typical conifer of Japan, the Japanese cedar (*Cryptomeria japonica* D. Don), situated in the experimental forest of Nagoya University, Aichi Prefecture, in central Japan (35°11'N, 137°33' E). Climatic conditions during the survey and some characteristics of the forest stand are given in Table 1 and by Hijii (1987). This stand had a poor understory, in which only five plant species were recorded; *Sasamorpha borealis*, *Parabenzoin trilobum*, *Carpinus laxiflora*, *Hydrangea hirta*, *Viburnum dilatatum*.

The main plot (about 50×50 m) was set in the survey area and divided into 12 subplots, each measuring about 10×10 m, for periodic sampling. The properties of this even-aged and monocultural forest stand, whose canopy was fully closed, were assumed to satisfy the conditions of homogeneity throughout the 12 sampling occasions with respect to biotic and abiotic aspects of trees inhabited by arthropods. Seasonal changes in the abundance and biomass of arboreal arthropods were assessed from 24 April 1983 to 20 February 1985 at intervals of about two months (12 times). These subplots were separated by 10–20 m so that each fogging operation would not affect every other one.

Chemical knockdown (Southwood, 1966; Yamashita and Ishii, 1977; Erwin, 1983) was used for collection of arthropods from trees. The collection efficiency of this sampling method has been evaluated elsewhere (Hijii, 1986). On each sampling occasion, all trees inside each subplot were fumigated with ten tins of the synthetic pyrethroid insecticide, Varsan P Jet (Chugai Pharmaceutical Co.), each containing 24 g Permethrin with quick-knockdown properties. Fumigation was undertaken in the morning under calm conditions with the aid of a rod about 3 m in length. Twenty cone-shaped collectors, each constructed of laminated film and three stainless steel pipes (0.5 m^2 in projection area and 0.4 m in depth), were layed out randomly under the trees inside each subplot. All the arthropods that dropped onto them during a period of 6 h after the fogging were collected and preserved by washing with 80% ethanol. Details of the collection procedure have also been described by Hijii (1983).

In parallel with each sampling from the canopy strata, soil micro-arthropods were extracted from the 0–15-cm soil layer in the corresponding subplot using a total of 20 tin samplers (each measuring 5×4×5 cm) and a Tullgren apparatus (Aoki, 1973), and their seasonal changes in abundance and spatial pattern in relation to some physical conditions of the soil habitat were also examined (Hijii, 1987).

The numbers of individuals collected were counted after classification: by family for insects and by order or suborder for Arachnida. The fresh biomass of each taxon was weighed directly on a microbalance (Sartorius 2474, Zeiss Co.) soon after sorting. The animals were also assigned to guilds (Root, 1967; Moran and Southwood, 1982; Erwin, 1983) on the basis of literature information on their feeding habits (e.g. Uchida, 1966, 1970; Aoki, 1973). A guild is defined as a group of species that exploit the same class of resource in a similar way (Root, 1967). In the present study, the category of 'omnivores' was added as a new guild to the following six guilds: phytophages (subdivided into chewers (defoliators and leaf miners) and sap-suckers such as Homoptera), epiphyte fauna (including fungivores exploiting fungi and lichens on the surface of trees), detritivores comprised of saprophagous animals, tourists that have no direct trophic relationship with the trees, predators and parasitoids. The omnivorous guild comprised Stenopelmatidae (*Tachycines* sp.), whose dietary menu in the field is little known. No ants appeared in canopy samples during the survey. All collembolan species were tentatively allocated to the detritivorous guild because it could not be determined whether their food habits were saprophagous or not although several species of the order are known to be pollen feeders and fungivores (Christiansen, 1964).

For each of the major animal groups and all the arthropods sampled, seasonal variability in abundance throughout the two years was evaluated by coefficient of variation (CV) (Usher et al., 1979) in order to describe the differences in the population dynamics as a whole between the canopy and the soil strata.

Results

Seasonal changes in density, biomass and proportional distribution of major animal groups

All insect families were grouped under major taxa, whose abundances (number m^{-2}) and corresponding biomass values (mg fresh weight m^{-2}) are given in Appendices 1 and 2, respectively. Figure 1 shows the seasonal changes in total abundance and total biomass of arthropods over the sampling periods. The total abundance fluctuated with season, ranging from about 200 to 3500 m^{-2}, with a marked increase in June and August. The seasonal pattern of fluctuation was similar in both years. The general trend of seasonal changes in abundance was almost synchronized with that of monthly mean air temperature measured in the present area (Hijii, 1987). Over the study periods, Collembola and Acarina (oribatids) were the most abundant groups among the canopy fauna and their combined abundance constituted 36–93% of the total.

The total biomass, on the other hand, ranged from about 7 to 600 mg fresh weight m^{-2}, and showed a pattern of seasonal change similar to that of the total abundance. Maximum values of biomass recorded in June of both years showed a striking similarity. The dominant

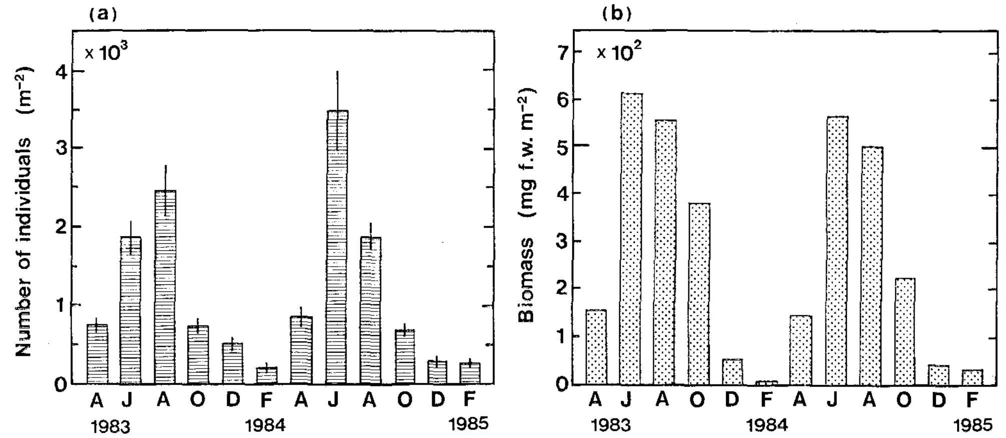

Fig. 1. Seasonal changes in (a) abundance and (b) biomass of all arthropods sampled from the canopies. Vertical bars for abundance indicate ±95% CL. Each biomass value was determined by weighing the animals sampled from 20 collectors together.

taxa with regard to biomass were lepidopteran larvae, Hemiptera and Araneae throughout almost the entire study periods.

Community composition and its seasonal trends

The abundances (number m^{-2}) and biomass values (mg fresh weight m^{-2}) of arthropods arranged by guilds are also given in Appendices 1 and 2, respectively. Seasonal changes in the abundance and biomass of each guild are illustrated in Fig. 2. Almost all the guilds, as this figure shows, reached maximum values of density and biomass in June or August. Figure 3 demonstrates the percentage proportions of the various guilds in terms of total abundance and to total biomass on each sampling occasion. With regard to abundance, the guild of deteritivores was consistently dominant, constituting 36–93% of the total count over the study periods. On the other hand, the patterns of proportional distribution in biomass were less similar to those in abundance and varied with the season. Phytophages, predators and detritivores were major guilds in terms of biomass, constituting on average 27%, 23% and 20% of the total biomass, respectively.

The relative proportions in terms of both abundance and biomass of the taxonomic groups were also evaluated for the three major guilds of phytophages, detritivores and predators. In terms of number, more than 90% of phytophages were sap-suckers (Hemiptera (Cercopidae, Psyllidae); Thysanoptera). Chewers (lepidopteran larvae; Coleoptera (Chrysomelidae)) exceeded sap-suckers in terms of biomass in June of both years. One characteristic of the present Japanese cedar plantation was that no aphids, which are often representative phytophagous insects in many trees, were obtained from the canopies throughout the study periods. Since high numbers of aphids were obtained previously from a Japanese larch (*Larix leptolepis*) plantation in the same region between spring and summer (Hijii, unpublished), the presence/absence of aphids would appear to be dependent on differences in the palatability of leaves to sap-sucking insects. This absence of aphids in the present Japanese cedar canopies might also have been related to the absence of ants, which feed on aphid honey-dew.

In terms of abundance, the guild of detritivores was consistently dominated by two micro-

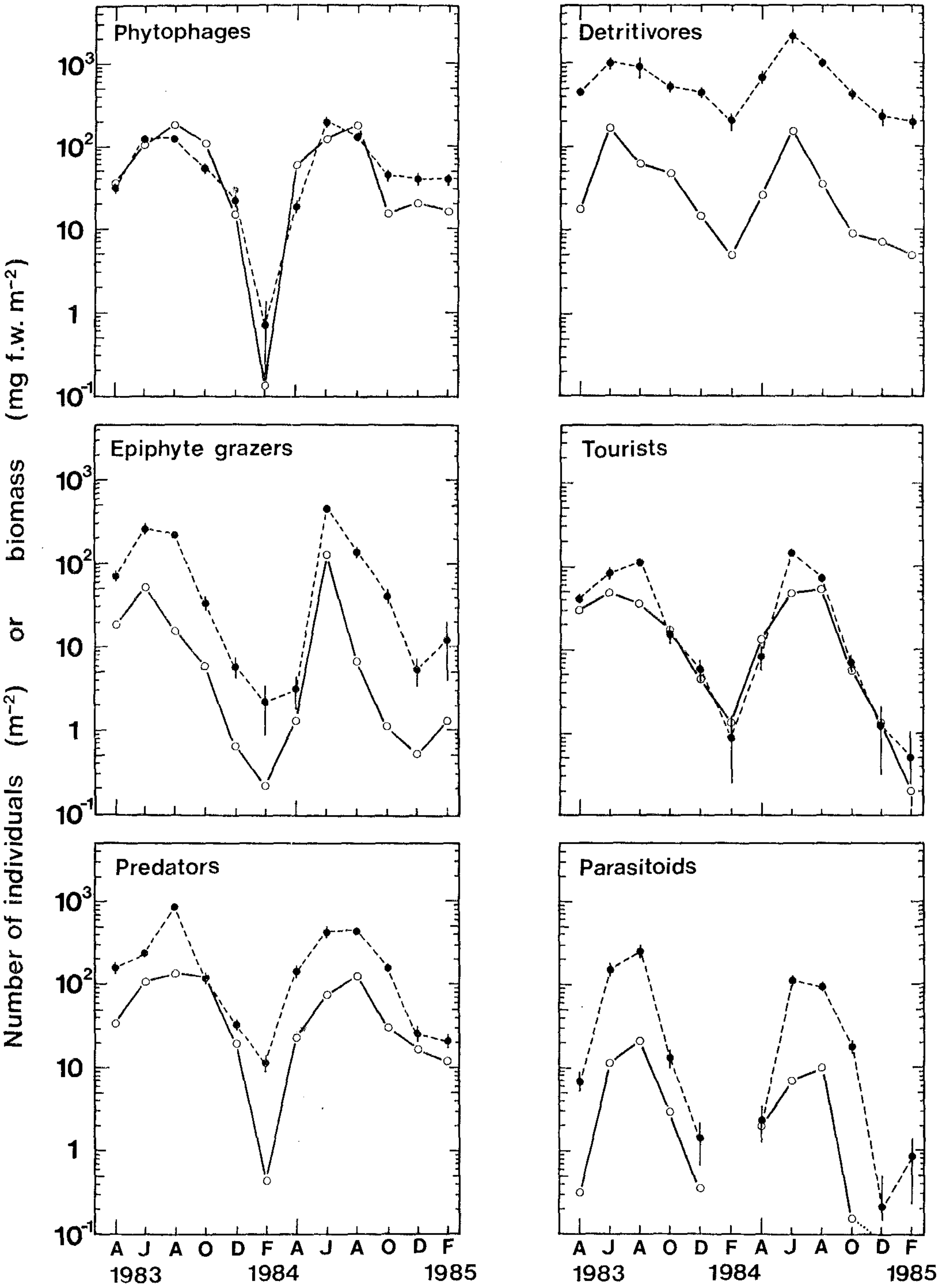

Fig. 2. Seasonal changes in abundance (●) and biomass (○) of major guilds. Vertical bars for abundance indicate ±95% CL.

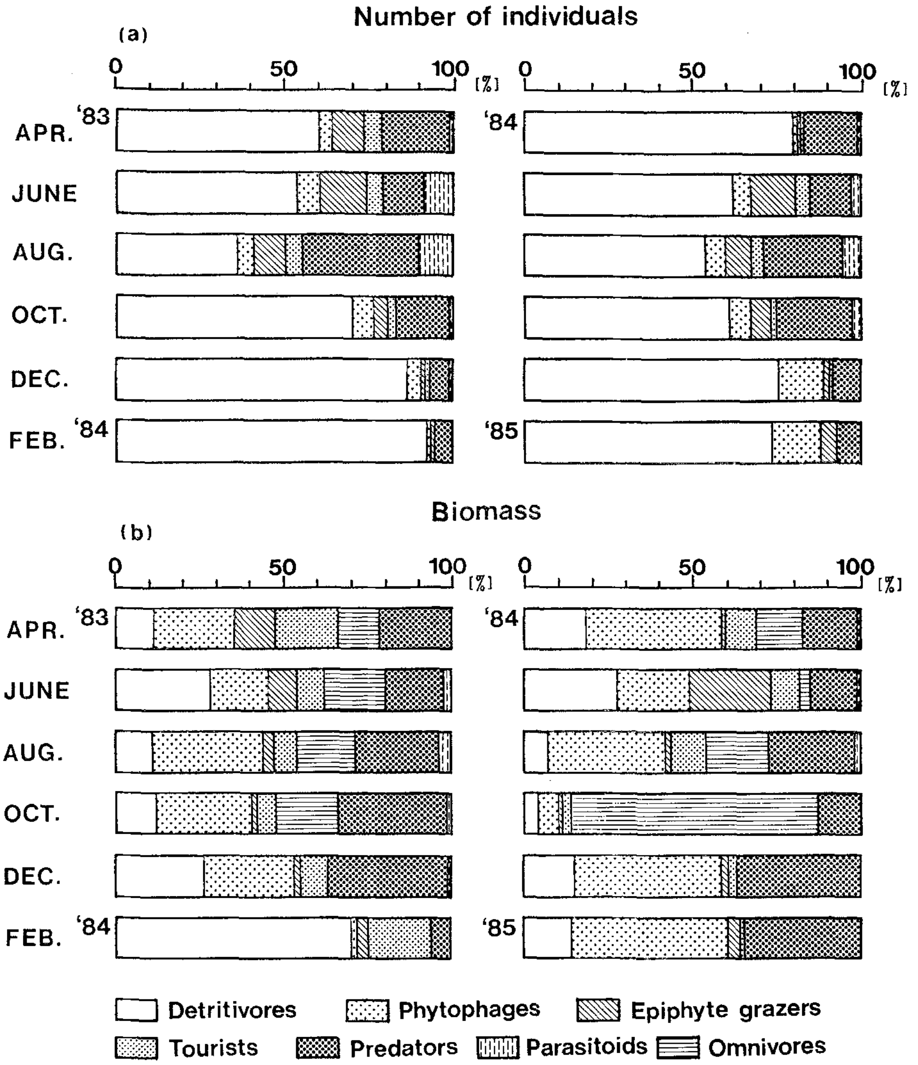

Fig. 3. Seasonal trends of percentage proportions in (a) abundance and (b) biomass of guilds.

arthropod groups, Collembola and oribatid mites (Cryptostigmata), and a similar trend of dominance held also for biomass over the study period, except for June in both years. Major component groups of the predatory guild were carnivorous mites (mainly Mesostigmata and Prostigmata) in abundance, and Araneae in biomass. Particularly in the winter, Araneae was the taxon most represented in the guild of predators in terms of biomass.

Biomass relationship between predators and prey

The biomass relationship between predators and prey was traced over the two years on simple assumptions for the allocation of animals into both categories. The predators and prey as categorized here were defined in the same manner as that proposed by Hijii (1986): the guilds of predators and parasitoids were all allocated to predators; phytophages,

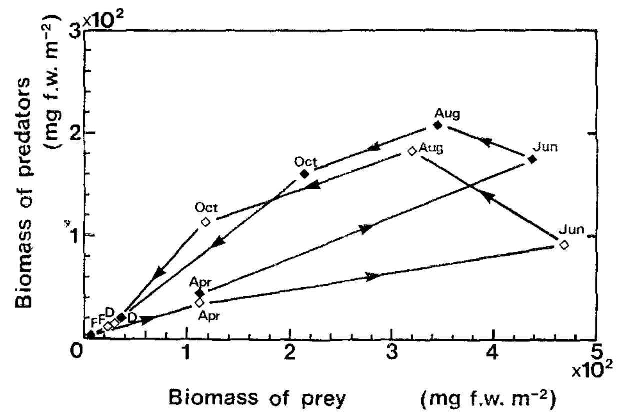

Fig. 4. Biomass relationship between predators and prey represented by a phase diagram (◆: April 1983–February 1984, ◇: April 1984–February 1985). See text for allocation of animals between predators and prey.

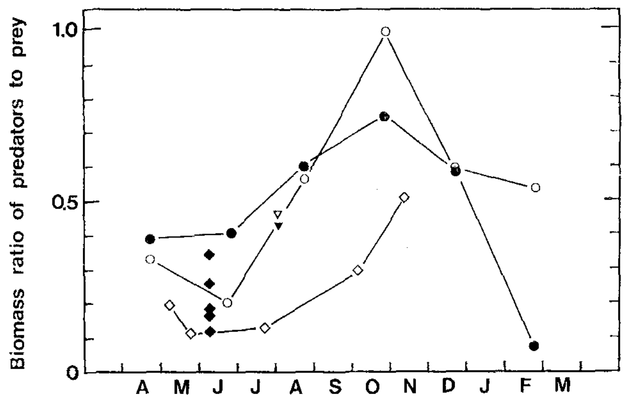

Fig. 5. Seasonal trends in the biomass ratio of predators to prey for some tree species surveyed: 26-yr-old plantation of *Cryptomeria japonica* (CJ-26) for 1983–1984 (●) and for 1984–1985 (○), 15-yr-old plantation of *Cryptomeria japonica* (◆; CJ-15: Hijii, 1986), 24-yr-old plantation of *Chamaecyparis obtusa* (◇; CO-24: Hijii, 1983) for 1979–1981, average values of six species of broad-leaved tree in South Africa (▼) and in the United Kingdom (▽) shown in Table 2 (Moran & Southwood, 1982). The period of Jan.–Feb. in S.A. is assumed to be seasonally equivalent to that of July–Aug. in the U.K. and Japan.

deteritivores, epiphyte grazers and tourists constituted prey. No predatory animals were found in the guild of tourists. Each of the prey guilds appeared to consist of species that had the possibility of being captured or parasitized, either specifically or accidentally, by predators on trees. The biomass of omnivores was evenly divided between predators and prey.

The seasonal changes in biomass values of predators (B_{pred}) and prey (B_{prey}) are shown in Fig. 4 in the form of a phase diagram as a function of time. The general seasonal trends of B_{pred} and B_{prey} and their maximum values were similar over the two years (about 200 mg fresh weight m^{-2} for "predators" and 450 mg fresh weight m^{-2} for "prey"). Seasonal changes in the biomass ratio (γ) of predators to prey are superimposed in Fig. 5. As

Table 2. Total abundance (number m^{-2}) and total biomass (mg d.w. m^{-2}) of arboreal arthropods in various forest stands censused by chemical knockdown.

Forest stands	Country	Age of stand (years)	Date	Abundance (m^{-2})	Biomass (mg d.w. m^{-2})	Author
Cryptomeria japonica plantation	Japan	26	25 June 1983	1898.1	175.2	This study
			27 June 1984	3537.3	161.1	
Cryptomeria japonica plantation		15	9 June 1984	3754.8*	165.9*	Hijii (1986)
Chamaecyparis obtusa plantation		24	22 July 1980	1227.7	179.4	Hijii (1983, 1984)
Larix leptolepis plantation		16	22 July 1980	957.8	72.5	Terakawa (1982)
Pinus densiflora & *Pinus thunbergii* mixed			31 May 1974	680.5	396.6†	Watanabe (1976)
Pinus thunbergii			24 June 1964	179.6		Ochi et al. (1968)
Pinus densiflora			1–27 Aug. 1971	132.0		Yamashita and Ishii (1976)
Pinus densiflora		35	July 1966	600.0	114.3†	Kikuzawa and Shidei (1967)
Fagus crenata			13 May 1965	87.5	42.9†	Kikuzawa and Shidei (1966)
Betula pendula	U.K.		24 July–2 Aug. 1979	1290.3	1402.5‡	Moran and Southwood (1982)
Buddleia davidii				186.2	295.1‡	
Quercus robur				591.3	600.2‡	
Robinia pseudoacacia				42.3	57.3‡	
Salix cinerea				139.6	275.7‡	
Salix alba				83.5	144.1‡	
Betula pendula	S.A.		28 Jan.–12 Feb. 1979	57.7	372.9‡	Moran and Southwood (1982)
Buddleia davidii				85.5	486.7‡	
Quercus robur				41.4	498.3‡	
Robinia pseudoacacia				120.4	324.1‡	
Erythrina caffra				120.7	461.9‡	
Salix capanensis				30.7	271.7‡	

(Note) All data are expressed as m^{-2}; *calculated values; †converted from fresh weight to dry weight assuming d.w. = f.w./3.5 (cf. Peters, 1983; Kitazawa, 1977); ‡calculated from the allometric regression of average individual weight on body length; U.K. = the United Kingdom, S. A. = South Africa; the period of Jan.–Feb. in S.A. is assumed to be seasonally equivalent to that of July–Aug. in U.K. and Japan.

the figure shows, the ratios increased in late summer to autumn, reaching their maximum values in October of both 1983 ($\gamma \doteqdot 0.75$) and 1984 ($\gamma \doteqdot 1.00$).

Discussion

Comparison of community composition between coniferous plantations and broad-leaved trees

Part of the present data are compared in Table 2 with other knockdown-sample data taken from various types of forest during similar seasons, with respect to abundance (number m^{-2}) and biomass (mg dry weight m^{-2}). This table indicates that arthropod communities were relatively denser in the coniferous plantations as a whole than in broad-leaved forests. The difference in faunal abundance or biomass among tree species, however, may reflect no more than one aspect of the community structure because the amount of arboreal arthropods

Table 3. Relationship between leaf- and arthropod biomasses in three coniferous plantations situated in the same region.

Forest stands	Age (yr)	Leaf biomass (kg d.w. m^{-2})	Arthropod biomass* (mg d.w. m^{-2})	Author
Chamaecyparis obtusa	24	1.4	179.4	Hijii (1984)
Cryptomeria japonica	15	1.2	165.9	Hijii (1986)
Larix leptolepis	16	0.4	74.3	Terakawa (1982)

*Maximum values observed

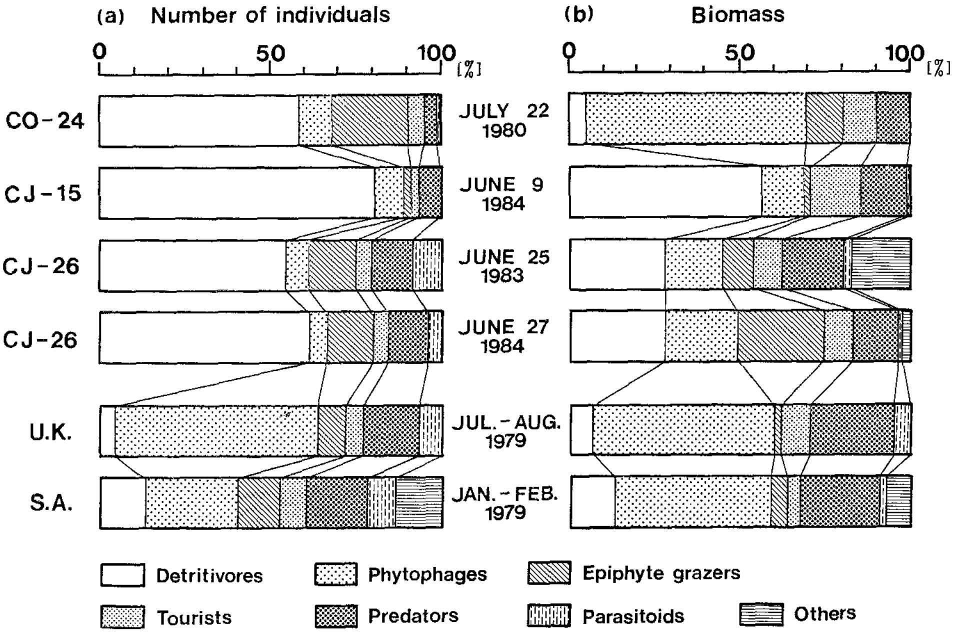

Fig. 6. Comparison of the proportional distributions of guilds by (a) abundance and (b) biomass among some tree species. All data are assumed to be recorded at almost the same season and average values of the six tree species shown in Table 2 are used for the U.K. and S.A. For explanation of forest stand codes, see the caption of Fig. 5.

is likely to be dependent on the organic resources of trees (see Table 3 for an example of the biomass relation).

One distinctive feature of the community composition was that many of the arthropod communities in these plantations were significantly dominated by the guild of detritivores. Figure 6 illustrates the proportional distributions of guilds by abundance (number m^{-2}) and by biomass (mg dry weight m^{-2}) recorded from those coniferous plantations situated in the same region (Hijii, 1983, 1984, 1986) and from broad-leaved trees in the United Kingdom and South Africa (Moran and Southwood, 1982).

Figure 6 shows that in all the coniferous plantations, i.e. 15-yr-old (Hijii, 1986) and 26-yr-old (this study) *Cryptomeria japonica* and 24-yr-old *Chamaecyparis obtusa* (Hijii, 1984), more than 50% of the individuals were detritivores, mostly Collembola and oribatid mites; these constituted a strikingly higher proportion in terms of both abundance and biomass, than was the case in communities on the broad-leaved trees. In contrast, phytophages in the coniferous plantations accounted for a much smaller proportion than in the broad-leaved trees.

Phytophage insects, which appear to be closely associated with trees, occasionally have a critical influence on the growth and survival of forest trees through their disruptive grazing (Mattson and Addy, 1975). At endemic population levels, however, they do little serious damage to the growth and structure of forest trees. In most forest ecosystems, only about 1–10% of the leaf biomass per year is utilized by these foliage grazers (e.g. Ohmart et al., 1983; Wint, 1983; Mattson and Addy, 1975). In coniferous forests in Japan, grazing loss of leaves is no more than 1% of total leaf biomass (e.g. Furuno and Saito, 1982).

On the other hand, the overwhelming dominance in abundance of detritivores in conifers could be related to one of the biological properties characteristic of this tree type: dead leaves and dead branches remain attached to the trees for considerable periods of time. In a *Cryptomeria japonica* plantation, for example, these periods of attachment were estimated to be about 0.5 yr for dead leaves and 4 yr for dead branches (Katsuno et al., 1984). Extension of habitat to the canopy strata would be one explanation for the dominant abundance of detritivorous animals on the above-ground parts of these evergreen coniferous trees. Furthermore, some of these detritivores may be involved in the fragmentation of dead plant organs, or their mechanical degradation into smaller pieces, facilitating microbial colonization, not only in the A_0 layer but also in the canopy strata.

Another characteristic difference of arboreal communities between forest types was observed in the average body size of the arthropod fauna. As summarized in Table 4, the average individual body weight of every guild member was markedly lower in the Japanese coniferous plantations than in broad-leaved trees in the United Kingdom and South Africa (Moran and Southwood, 1982); only in the case of chewing phytophages was the difference in average individual body size not so large between those from these three plantations and those from the broad-leaved trees in the U.K. This table also shows that average individual weight for each guild differed little among the three plantations situated in the same region, irrespective of the tree species or stand age.

Regulative effects of predation on the population levels of arboreal arthropods deduced from the predator/prey biomass relation

For arthropod communities, particularly phytophage communities, it has been pointed out that interspecific competition plays a smaller evolutionary role than has been assumed

Table 4. Average individual weight (mg d.w.) with range for arboreal arthropods in coniferous plantations in Japan and broad-leaved trees in the United Kingdom (U.K.) and South Africa (S.A.) (Moran and Southwood, 1982), arranged by guild.

Guild	CO-24	CJ-15	CJ-26			U.K.	S.A.
	Average Range	Average Range	1983	1984	Average Range	Average Range	Average Range
Phytophages		0.07 (0.03–0.17)	0.35	0.25	0.29 (0.05–0.93)	1.02 (0.66–2.35)	7.67 (1.59–30.29)
(chewers)		1.19 (0.66–2.97)	2.26	2.05	2.15 (0.10–3.91)	3.43 (2.72–6.93)	20.82 (4.38–48.23)
(sap-suckers)		0.02 (0.01–0.03)	0.25	0.15	0.19 (0.05–0.92)	0.91 (0.49–1.83)	3.26 (1.14–12.55)
Epiphyte grazers		0.01 (0.01–0.02)	0.04	0.06	0.05 (0.01–0.12)	0.33 (0.13–0.38)	2.36 (0.17–12.21)
Detritivores		0.03 (0.03–0.04)	0.03	0.01	0.02 (0.01–0.05)	2.72 (0.28–2.80)	8.57 (0.34–29.73)
Tourists		0.39 (0.32–0.55)	0.15	0.15	0.15 (0.09–0.45)	2.52 (1.28–4.39)	2.82 (1.17–3.61)
Predators		0.10 (0.05–0.12)	0.09	0.07	0.08 (0.01–0.30)	2.34 (1.72–5.03)	8.50 (1.35–31.44)
(Araneae)	0.83 (0.55–1.51)	0.81 (0.66–1.36)	0.39	0.40	0.39 (0.15–0.70)		
Parasitoids		0.08 (0.06–0.10)	0.02	0.02	0.02 (0.002–0.24)	1.16 (0.24–2.02)	1.35 (0.85–2.08)
Total	0.07 (0.03–0.15)	0.04 (0.04–0.05)	0.08	0.06	0.07 (0.01–0.14)	1.19 (1.02–1.98)	5.29 (2.69–12.04)
Predators	0.13 (0.07–0.88)	0.10 (0.05–0.12)	0.09	0.09	0.09 (0.01–0.35)	1.19 (1.74–4.59)	6.20 (1.24–21.56)
Prey	0.07 (0.02–0.14)	0.04 (0.03–0.05)	0.07	0.05	0.06 (0.01–0.10)	2.08 (0.83–2.14)	5.03 (1.85–15.39)

Note: Average values and ranges are calculated based on data from12 (CJ-26: 26-yr-old *Cryptomeria japonica*) and five (CO-24: 24-yr-old *Chamaecyparis obtusa*) sampling occasions, from five individual trees with different sizes in CJ-15 (15-yr-old *Cryptomeria japonica*) and from six tree species both in U.K. and in S.A.

(e.g. Connell, 1983; Roughgarden, 1983) because, as found in several sets of field data, the density or biomass of arthropods at their endemic population levels is strongly regulated below the carrying capacity in spite of the quantitative richness of resources. Interactions with host plants, the physical environment, chance and/or natural enemies such as predators and parasites are assumed to be potential exogenous factors which can affect the population levels and community structure of phytophagous animals (e.g. Connell, 1983; Strong, 1983). Although possibly acting as a crucial factor, the regulative effects of predation or parasitism on the population levels of herbivores and other taxa have seldom been confirmed in field investigations.

The biomass ratio of predators to prey could be a useful index for evaluating the degree of predation pressure in forest canopy communities. Figure 5 demonstrates the biomass ratio calculated for the three coniferous plantations in Japan and for broad-leaved trees in the United Kingdom and South Africa (Moran and Southwood, 1982), each being plotted for the corresponding months in which the samples were collected.

It is noticeable that the ratios are generally high, especially in the period from summer to autumn, almost reaching 1.0. For the 26-yr-old *Cryptomeria japonica* plantation, the seasonal trends were similar in both years. These large predator/prey biomass ratios imply that the predation pressure in forest canopy communities may be a major factor of negative feedback regulation, affecting herbivore reproduction and survival.

It has been argued from the standpoint of energetic theory that predators in general should not exceed prey animals by more than 0.1 times the biomass (Phillipson, 1966). The present larger estimates of this ratio would have been affected by differences in the pattern of seasonal fluctuation and in the life cycle between predators and prey animals; lepidopteran larvae, for

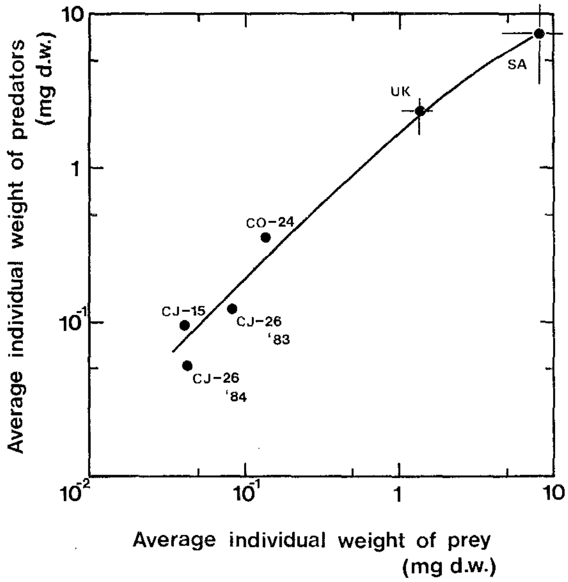

Fig. 7. Relationship between average individual weight of predators and that of prey for some tree species. All data used for regression are calculated from the same data sets as those used in Fig. 6 and the data for the 26-yr-old *Cryptomeria japonica* plantation are converted from fresh to dry weight assuming d.w. = f.w./3.5 (Peters, 1983; Kitazawa, 1977). Average values with ±1 SE for the six tree species shown in Table 2 are used for the U.K. and S.A.

example, were significantly decreased on canopies from autumn to winter, whereas spiders were still active on the surfaces of trees at that time. Diurnal and/or seasonal movements between soil and canopy strata observed for some animal groups (e.g. Bowden et al., 1976) would also be an additional factor having a direct effect on the ratio. However, we do not have enough information on the turnover of predator and prey animals to determine the actual level of predation pressure in forest arthropod communities.

Another distinctive feature was recognized with regard to the relationship of average individual weight (biomass/number) between predators and prey (Fig. 7), which is given by the hyperbolic formula:

$$1/W_{\mathrm{pred}} = 0.50/W_{\mathrm{prey}}+0.071$$

where W_{pred} and W_{prey} denote average individual weight (mg d.w.) of predators and prey of each forest stand, respectively. All the data used (the average values of data from six tree species were used for both the United Kingdom and South Africa) were assumed to have been obtained in almost similar seasons. Figure 7 also indicates that both W_{pred} and W_{prey} in broad-leaved trees in the U.K. and S.A. were about 10–100 times larger than those in the coniferous plantations in Japan. These relations imply that some biological or evolutionary factor affects the size relationship between predators and prey in canopy communities, irrespective of tree type and location.

Community dynamics on the canopy and soil strata

For forest arthropod communities, canopy strata differ strikingly from soil strata in both their structural properties and functional roles. Compared with the canopy, the soil environment would be expected to show much less variation in physical conditions, since it is buffered against extremes of temperature and moisture (e.g. Usher et al., 1979). The predictable properties of a soil environment with respect to habitat utilization and food availability would also be a factor affecting the community structure and dynamics (e.g. Takeda, 1987).

The environmental differences between the two habitats would exert effects on the community composition and population dynamics of the major taxa concerned. Figure 8 is a simple example of a comparison of community dynamics between canopy and soil strata. The data for the soil strata were collected simultaneously with those for the canopy strata at the corresponding subplots (Hijii, 1987). Communities of Collembola, oribatid mites and carnivorous mites (which were common animal groups in both strata) and total arthropods are compared with respect to their seasonal changes in abundance per unit ground area (number m^{-2}).

Two clear differences are apparent from the environmental heterogeneity of these strata; differences in both the population level and stability of seasonal fluctuation of each animal group. Figure 8 reveals that the soil arthropod communities maintained densities approximately 10^2–10^3 times larger than those of the canopy communities. As demonstrated in Fig. 9, the $\log_{10}$-transformed canopy/soil ratios in terms of abundance for oribatid and carnivorous mites decreased remarkably in winter, which means that the differences in abundance between the two strata would become larger in winter. The ratios for the collembolan community, on the other hand, were rather constant in comparison with the other two groups.

The coefficient of variation (CV) for seasonal fluctuation in abundance can be used as an index to indicate the stability of the population level in each habitat. The CV values through-

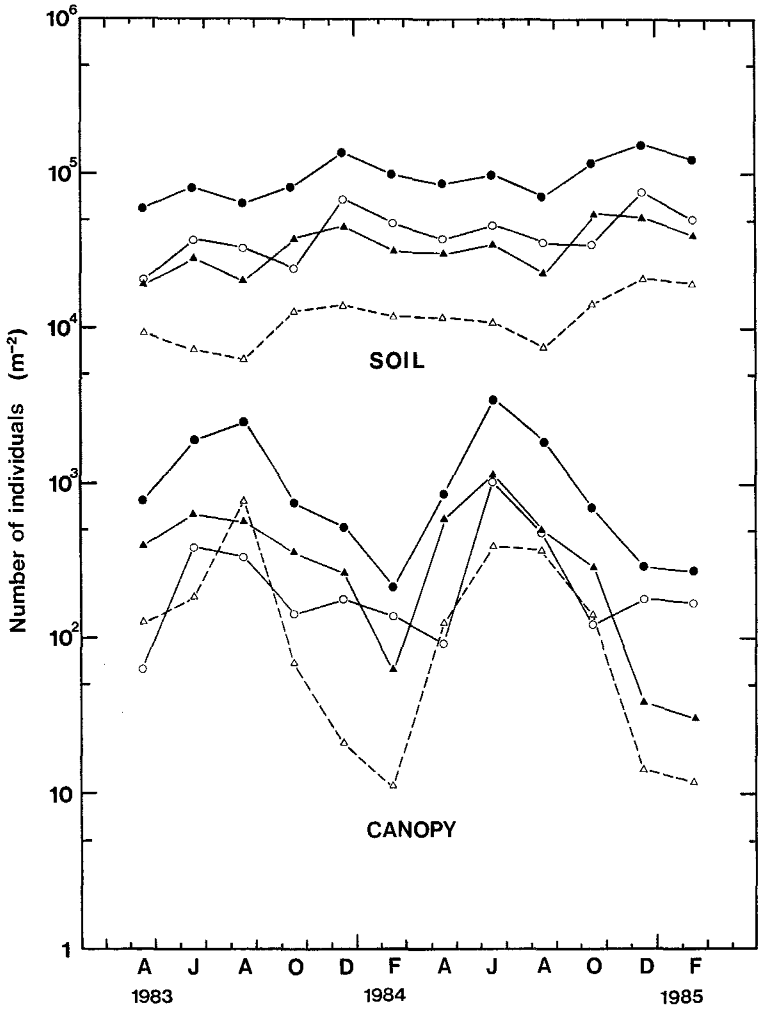

Fig. 8. Comparison of seasonal patterns of fluctuation in abundance (number m^{-2} on log scale) between soil and canopy strata for some major animal groups. The data for soil strata are from Hijii (1987). ●: all arthropods; ○: Collembola; ▲: oribatid mites; △: carnivorous mites.

out the two years calculated using log-transformed data were significantly lower in soil than in canopy communities; 2.9% (soil): 13.4% (canopy) for total arthropods, 3.6%: 14.5% for Collembola, 3.4%: 20.1% for oribatid mites and 4.0%: 32.2% for carnivorous mites. These results suggest that soil arthropod communities maintained more stable population levels throughout the two years than canopy communities. Thus, these two features may also support the hypothesis that with respect to population dynamics, the soil strata provide arthropod communities with a more physically stable and persistent habitat with a more predictable food supply than the above-ground canopy strata. The population dynamics of the species common to both canopy and soil strata and the temporal migration of animals between the two habitats in relation to changes in environmental conditions should also be investigated in future studies on the structure and function of forest arthropod communities.

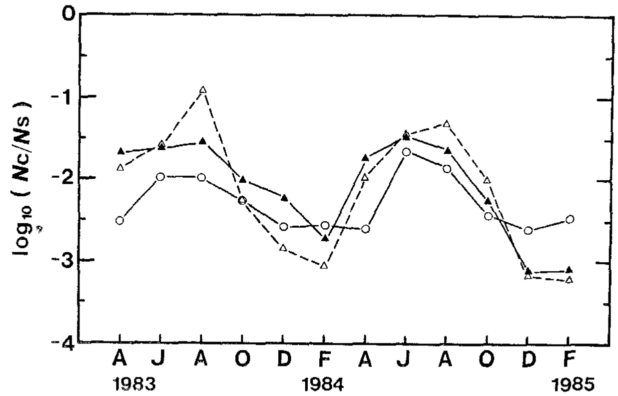

Fig. 9. Seasonal changes in the ratio of N_C to N_S, where N_C and N_S denote the abundance of each animal group in the canopy and in the soil strata, respectively. All data are expressed as $\log_{10}(N_C/N_S)$. ○: Collembola; ▲: oribatid mites; △: carnivorous mites.

Acknowledgments

I am indebted to Prof. K. Hozumi, Nagoya University, for his helpful suggestions and continuous encouragement during the study. I am also grateful to Prof. T. R. E. Southwood, Oxford University, for his many invaluable suggestions for improvement of the manuscript. Thanks are also extended to the members of the Inabu Experimental Forest and the Laboratory of Silviculture of Nagoya University for their facilities and helpful assistance during the field work.

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*Titles are tentative translations for original titles in Japanese by the author.

Appendix 1. Numbers of individual arthropods (number m^{-2}) sampled from the canopies of a 26-yr-old *Cryptomeria japonica* plantation, arranged by guild and major taxonomic group.

Guild	1983					1984						1985
Taxon	Apr	Jun	Aug	Oct	Dec	Feb	Apr	Jun	Aug	Oct	Dec	Feb
Phytophages	30.7	125.1	123.6	53.2	22.4	0.7	18.4	197.2	130.0	44.5	40.0	40.0
Lepidoptera (larvae)	1.5	5.3	2.7	2.0	0.3	0	0.8	3.5	7.5	1.1	0.2	0.3
Coleoptera	1.7	6.6	0.5	0	0	0	1.1	8.7	0.6	0	0	0
Hemiptera	5.1	26.9	21.8	41.3	15.6	0.2	6.0	31.4	28.9	2.1	32.9	21.8
Thysanoptera	22.4	86.3	98.6	9.9	6.5	0.5	10.5	153.6	93.0	41.3	6.9	17.9
Epiphyte fauna	72.7	263.2	221.7	33.5	5.9	2.2	3.1	468.6	141.2	42.5	5.3	12.5
Psocoptera	59.3	257.0	214.5	15.6	1.1	0.8	0.8	449.1	133.1	41.6	4.1	2.3
Coleoptera	13.4	6.2	7.2	17.9	4.8	1.4	2.3	19.5	8.1	0.9	1.2	10.2
Detritivores	458.6	1031.0	909.1	521.2	451.8	200.2	685.5	2186.9	1018.0	422.9	224.2	204.4
Acarina (oribatids)	393.6	639.8	572.7	366.6	271.7	61.7	591.9	1157.9	513.0	295.4	39.2	30.8
Collembola	62.7	383.9	327.9	143.1	179.6	138.2	92.4	1014.3	499.1	126.0	184.8	172.7
Diplopoda	0	1.7	0.2	0	0	0	0	4.2	0	0	0	0
Diptera	2.3	5.4	7.8	11.3	0.5	0.3	1.2	10.2	5.9	1.5	0.2	0.9
Others	0	0.2	0.5	0.2	0	0	0	0.1	0	0	0	0
Tourists	40.7	85.1	117.1	16.0	5.9	0.9	8.5	147.7	73.4	7.1	1.2	0.5
Lepidoptera (adults)	0	0.8	1.5	0.2	0	0	0.1	0.2	0.4	0	0	0
Diptera	36.8	82.2	113.7	14.7	5.9	0.9	6.2	146.1	70.7	6.0	1.2	0.5
Coleoptera	2.6	1.4	1.2	1.1	0	0	0.2	1.1	1.8	1.1	0	0
Plecoptera	1.2	0.5	0.2	0	0	0	2.0	0.3	0.5	0	0	0
Hymenoptera	0.1	0.2	0.5	0	0	0	0	0	0	0	0	0
Omnivores	0.2	4.8	1.4	0.6	0	0	0.2	3.3	1.1	1.4	0	0
Orthoptera	0.2	4.8	1.4	0.6	0	0	0.2	3.3	1.1	1.4	0	0
Predators	159.0	237.5	867.2	118.1	33.6	11.5	143.7	422.3	437.5	156.7	25.8	21.4
Araneae	21.0	46.2	86.7	47.8	12.3	0.2	14.1	14.3	50.1	8.1	11.1	9.5
Acarina (carnivorous)	127.8	183.9	777.9	68.1	20.9	11.3	128.6	399.3	382.7	147.6	14.7	11.9
Chilopoda	1.4	1.8	1.5	1.8	0.2	0	0.5	5.6	1.4	0.2	0	0
Opiliones	8.3	4.1	0.9	0.2	0	0	0.5	2.0	3.0	0.3	0	0
Hemiptera	0	0.9	0	0	0	0	0	0.8	0	0	0	0
Coleoptera	0.5	0.1	0	0	0	0	0	0.2	0.1	0.2	0	0
Hymenoptera	0	0.3	0	0	0	0	0	0.1	0	0	0	0
Diptera	0	0	0	0	0	0	0	0	0	0.3	0	0
Neuroptera	0	0.2	0.2	0.2	0.2	0	0	0	0.2	0	0	0
Parasitoids	7.1	151.4	259.2	13.1	1.4	0	2.3	111.3	95.6	18.2	0.2	0.8
Hymenoptera	7.1	151.4	259.2	13.1	1.4	0	2.3	111.3	95.6	18.2	0.2	0.8
Total	769.0	1898.1	2499.3	755.7	521.0	215.5	861.7	3537.3	1896.8	693.3	296.7	279.6

Appendix 2. Biomass of arthropods (mg f.w. m^{-2}) sampled from the canopies of a 26-yr-old *Cryptomeria japonica* plantation, arranged by guild and major taxonomic group.

Guild Taxon	1983					1984						1985
	Apr	Jun	Aug	Oct	Dec	Feb	Apr	Jun	Aug	Oct	Dec	Feb
Phytophages	37.2	105.0	184.5	109.3	14.5	0.2	59.6	120.9	177.4	15.3	20.3	16.1
Lepidoptera (larvae)	9.1	53.4	43.2	14.2	0.1		3.7	62.4	75.6	7.5	0	4.0
Coleoptera	9.1	33.0	0.6				3.1	13.9	0.7			
Hemiptera	18.8	14.8	139.0	94.7	14.2	0.1	52.6	36.0	100.2	7.5	20.1	11.9
Thysanoptera	0.2	3.8	1.7	0.4	0.2	0.1	0.2	8.6	0.9	0.3	0.2	0.2
Epiphyte fauna	18.8	52.8	15.2	5.9	0.6	0.2	1.4	134.1	7.0	1.1	0.6	1.3
Psocoptera	1.6	45.6	14.6	2.3	0.1	0.1	0.1	100.4	5.3	1.0	0.4	0.1
Coleoptera	17.2	7.2	0.6	3.6	0.5	0.1	1.3	33.7	1.7	0.1	0.2	1.2
Detritivores	17.7	174.0	62.3	48.7	14.7	5.0	26.0	156.3	34.8	8.7	6.8	4.9
Acarina (oribatids)	10.7	28.5	19.2	6.0	9.3	1.2	8.4	35.1	13.7	5.1	1.3	0.8
Collembola	4.4	18.2	18.6	42.7	5.4	3.8	17.6	74.0	21.1	3.6	5.5	4.1
Diplopoda		112.6	15.4					42.9				
Diptera and Others	2.6	14.7	9.1	0	0	0	0	4.3	0	0	0	0
Tourists	28.8	49.5	36.3	18.4	4.5	1.3	13.5	48.1	53.4	5.7	1.3	0.2
Lepidoptera (adults)	0	0.3	3.0	0.2			0.3	0.3	0.7			
Diptera	17.7	24.1	31.2	15.0	4.5	1.3	2.6	33.0	46.6	4.6	1.3	0.2
Coleoptera	7.3	24.1	1.6	3.2			0.2	13.3	3.5	1.1		
Plecoptera	3.8	1.0	0.5				10.4	1.5	2.6			
Hymenoptera	0	0	0									
Omnivores	19.3	111.4	98.5	71.8			21.0	21.6	93.4	167.9		
Orthoptera	19.3	111.4	98.5	71.8			21.0	21.6	93.4	167.9		
Predators	34.2	109.4	137.5	124.0	19.8	0.5	23.5	76.0	126.7	30.5	16.9	12.2
Araneae	10.7	59.1	107.5	93.6	18.8	0.5	16.8	35.0	51.8	17.3	16.9	12.2
Acarina (carnivorous)	0.5	1.4	3.1	0	0	0	0.4	2.0	1.2	0.7	0	0
Chilopoda	18.8	9.7	8.6	23.3	0		4.9	19.1	7.6	1.5		
Opiliones	1.1	33.7	16.7	5.5			1.4	15.5	63.7	0.9		
Hemiptera		1.8						1.8				
Coleoptera	3.1	1.1						1.6	0.9	1.1		
Hymenoptera		1.1						1.0				
Diptera										9.0		
Neuroptera		1.5	1.6	1.6	1.0				1.5			
Parasitoids	0.3	11.5	22.2	2.9	0.4		2.0	6.8	9.9	0.2	0	0.1
Hymenoptera	0.3	11.5	22.2	2.9	0.4		2.0	6.8	9.9	0.2	0	0.1
Total	156.3	613.6	556.5	381.0	54.5	7.2	147.0	563.8	502.6	229.4	45.9	34.8