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THE ARTHROPOD COMMUNITIES OF CONIFEROUS FOREST TREES

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ABSTRACT. Canopy arthropod communities of four coniferous tree species, found in UK plantations, were examined using pyrethrum knockdown. The species selected were Scots pine (*Pinus sylvestris*), Corsican pine (*Pinus nigra* var. *maritima*), Sitka spruce (*Picea sitchensis*) and Norway spruce (*Picea abies*). Arthropods were often found in high densities, with figures up to 11,000 m^{-2}. These are higher densities than those previously recorded from other trees in temperate or tropical regions. Communities were dominated by Collembola and Acarina except where there were outbreaks of the Green spruce aphid (*Elatobium abietinum*). The dominance of epiphyte feeders and mites concurs with data from studies on conifers in Japan. Species richness of herbivorous orders was found to be lower than that for broadleafed trees, but the richness of other groups was generally comparable. Community variations between tree genera were greater than those between related species. This study suggests that the structure of canopy arthropod communities on coniferous trees differs from that on broadleafs. The differences may be attributable to the density and longevity of the foliage on the evergreen conifers.

INTRODUCTION

It has been suggested that the biological communities which forest canopies support make a major contribution to global diversity (Nadkarni & Parker 1994). Prior to the recent developments in canopy access and sampling techniques, the organisms in these communities were difficult to investigate quantitatively or comprehensively. Of the animals present in this important habitat, arthropods are particularly interesting since they play significant roles in food webs, in nutrient cycling, and may be useful indicators of environmental change (Erhardt & Thomas 1991).

To date there has been a strong focus on the arthropods associated with trees in the tropics (Basset *et al.* 1992, Kitching *et al.* 1993). Here, the communities have been found to be species-rich assemblages with complexity of structure and function (Stork 1987). There are fewer equivalent studies in temperate forests, but data from these may be of great significance in investigating the universality of community theories and in contributing to a greater knowledge of global biodiversity.

In 1987, Stork drew a comparison between the arboreal arthropods on broadleaf trees in the U.K. (Southwood *et al.* 1982) and trees in Borneo. Community parameters such as abundance and biomass were found to vary between tree genera and species. Overall, however, the temperate communities were found to be less species-rich, but had similar guild structures to those in the tropics. So, temperate broadleaf trees may bear comparison in some ways with those in the tropics, but what of coniferous trees?

Conifers are significant host plants in many parts of the world, either because they are native or because of their commercial value. In Britain, for example, they make up 70% of the closed forest area (seven % of total land area; Kreysa 1987). There is little information concerning the communities supported by these trees which may enable comparisons to be drawn with previous work. There are, however, obvious host plant differences between broadleaf and coniferous trees which are potentially important for invertebrate communities. For example, the chemical composition of foliage and phloem content are known to differ, particularly in relation to secondary or defensive plant chemicals and to seasonal availability of nutrients (Kramer & Kozlowski 1979).

Toughness, leaf shape and size, which differ markedly between these two groups of trees, have also been demonstrated to affect invertebrate phytophages (Coley 1983, Kennedy & Southwood 1984, Neuvonen & Niemala 1981). The effects of these parameters need to be explored.

In Britain trees in the genera *Pinus* and *Picea* are planted over the greatest land area (53% of area forested), while the dominant broadleaf trees, *Quercus, Betula* and *Fraxinus* species, make up only 25% of the forested area (Locke 1987). More information is, therefore, required about the arthropod communities of the dominant forest tree species in the UK.

The aims of this study were to gather baseline information on the abundance of arthropods in the canopies of four commercially important conifers, and to compare the faunas of two tree genera and four tree species over a two year pe-

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riod. Using this approach, comparisons with broadleaf trees could then also be drawn.

MATERIALS AND METHODS

TREE SPECIES. The tree species chosen for this study were Scots pine (*Pinus sylvestris*), Corsican pine (*Pinus nigra* var. *maritima*), Norway spruce (*Picea abies*) and Sitka spruce (*Picea sitchensis*). All were the same age (25 years) and were planted in monospecies stands. The pines were located in the New Forest on the Southern Coast of Britain and the spruces in South Wales, where rainfall levels are suitable for optimal growth.

These species were selected for several reasons. Firstly, they occupy large areas of the forested land in Britain and form a significant habitat type. Secondly, comparisons between species in the same genus and a comparison between two genera were possible. All four tree species share the factors associated with "coniferousness" which might influence the arthropod faunas they support. These factors include photosynthetically efficient needles; high levels of secondary chemicals; continuous needle abscission ("evergreeness"); cone production and the retention of a high proportion of dead branches in the canopy. Any differences between the canopy communities can be attributed to structural and chemical differences between genera and species.

INVERTEBRATE SAMPLING. Arthropod samples were collected from three replicate canopy units (the canopy between four tree boles) within the stand of each tree species, on four occasions in 1986 and five in 1987. Samples were usually taken at six week intervals from May to October and were evenly spaced across the time when arthropods were expected to be most abundant and active. Where possible, trees at the two locations were sampled on consecutive days to minimize variation.

The samples were collected by pyrethrum knockdown, using a mistblower (Hurricane Major-Cooper-Pegler) to project the chemical (Pybuthrin 2/16 (Roussel UCLAF); a mixture of natural pyrethins synergized with piperonyl butoxide) into the canopy (Ozanne *et al.* 1988). The canopy units were each sprayed for one minute under still air conditions. The arthropods were allowed to fall onto a 1 m^2 sheet for one hour and were then removed and stored in alcohol. All density figures are therefore standardized to 1 m^2 ground area. Samples were initially sorted to the level of order. Five orders were selected for identification to species level: Homoptera, Coleoptera, Psocoptera, Hymenoptera (morphotyped) and the Araneae. These were chosen to represent a range of trophic levels.

ANALYSES. Analyses were carried out to investigate variations in total arthropod abundance, the abundance of each order collected and the species richness of the five selected orders.

Several sets of analyses were undertaken using a split-plot anovar design to take into account possible site differences and the Newman-Keuls test. Data were transformed using log $(x+1)$ transform unless they were analyzed non-parametrically (usually due to lack of variance within cells). The latter data sets were investigated using Kruskal Wallis or Friedman's analysis (Sokal & Rohlf 1981, Snedecor & Cochran 1970). The first form of analysis carried out was between the tree species for each season separately. Subsequently, a comparison between seasons was made for the four tree species. Similar analyses were carried out both for densities and for species richness.

RESULTS

The study found that conifer canopies supported high mean densities of arthropods (160–1323 m^{-2} over 1 year (TABLE 1)), with peak means of over 11,000 m^{-2} in some months. The most abundant orders were always the Collembola and Acarina, except where the Homoptera were found in outbreak densities (Green spruce aphid: *Elatobium abietinum,* on Sitka spruce). Thus the canopy communities were normally dominated by organisms feeding on epiphytes and organic debris. However, a large number of orders were represented in the canopy samples and these are known to exhibit a wide range of feeding strategies.

Species richness for some of the groups examined (TABLE 2), was lower than that found for tropical samples. For example, Stork (1988) gives figures of 30 species of Coleoptera 20 m^{-2} ground area. However, for orders such as the Homoptera the richness of 12 species 20 m^{-2} ground area given by Stork is very similar to that on Scots pine. Species richnesses are also comparable with those for equivalent canopy volumes in broadleaf trees in Britain (TABLE 3). For example, the richness of Araneae on Scots pine was greater than, or virtually equal to, figures given for oak, birch and willow by Southwood *et al.* (1982) (TABLE 3). The species richness of the Psocoptera was again of the same order as for the four broadleafs and even those for the Coleoptera bear comparison with those for willow. The richness of more specialist herbivores such as the Homoptera, was lower than that on the broadleafs.

In 1986, Corsican pine supported the greatest density of arthropods over the season. Abundance of arthropods on this species was greater than that on the two spruces, with Scots pine

TABLE 1. Mean densities of arthropods per 1 m² ground area, for four conifer species. The mean is taken across the whole season, May to October. (Arth−Arach. = Arthropods minus arachnids)

	Tree species			
	Norway spruce	Sitka spruce	Scots pine	Corsican pine
1986				
Arthropods	159.59	218.69	435.09	597.42
Arth−Arach.	118.58	159.92	347.66	512.34
Collembola	57.63	10.76	214.21	392.14
Psocoptera	16.25	2.67	3.83	11.08
Hemiptera	9.42	324.83	55.42	31.58
Thysanoptera	0.25	0.00	4.75	1.67
Neuroptera	0.08	0.58	0.92	0.83
Mecoptera	0.00	0.08	0.08	0.00
Lepidoptera	4.08	2.17	1.00	1.58
Trichoptera	0.00	2.67	4.83	0.00
Diptera	6.18	4.92	14.61	10.43
Hymenoptera	9.75	3.92	9.25	4.42
Coleoptera	7.69	2.38	3.79	4.19
Araneae	6.91	3.42	6.11	10.59
Opiliones	0.17	0.50	4.33	2.50
Acarina	53.25	20.00	151.50	124.08
1987				
Arthropods	730.29	1322.45	1046.31	616.30
Arth−Arach.	411.62	871.55	457.47	405.32
Collembola	220.20	166.11	333.09	192.36
Psocoptera	26.44	16.39	10.72	16.45
Hemiptera	28.72	193.06	20.19	48.79
Thysanoptera	0.47	2.20	7.93	4.33
Neuroptera	1.91	3.64	2.82	3.20
Mecoptera	0.00	0.27	0.00	0.00
Lepidoptera	3.93	3.73	1.53	1.08
Trichoptera	0.07	0.13	0.07	0.73
Diptera	20.87	17.87	20.87	23.07
Hymenoptera	8.13	8.28	11.10	7.33
Coleoptera	10.60	4.80	4.07	4.53
Araneae	29.18	15.43	14.37	20.18
Opiliones	0.47	1.73	2.87	2.27
Acarina	150.76	145.22	502.28	164.69

supporting intermediate numbers ($p<0.05$). The Collembola were numerically dominant on three of the four tree species, the exception being Sitka spruce, on which there was an outbreak of *E. abietinum*. The Acarina were the second most abundant order and the Homoptera the third for all but Sitka spruce.

Of the epiphyte feeders, the Collembola were significantly more abundant on the pines than the spruces ($p<0.001$). The carnivores were dominated by the Araneae, which were significantly more abundant on Corsican pine than on the other trees ($p<0.05$). The only other group to show significant variations in abundance between tree species in this year was the Diptera which showed higher densities within the canopy of Scots pine ($p<0.001$). Scots pine also supported the greater species richness of Araneae ($p<0.01$) and Heteroptera ($p<0.001$), whereas the Coleoptera were more species rich on Scots pine and Norway spruce ($p< 0.01$).

In 1987, Sitka spruce supported the greatest densities of arthropods, with significantly greater numbers than Corsican pine or Norway spruce ($p<0.001$) and once again this could be attributed to *E. abietinum*. The total densities were also very high on Scots pine ($p<0.001$) and when the figures were adjusted to take *E. abietinum* into account (by largely removing them), this tree supported the highest densities of arthropods in 1987. Scots pine supported the greatest densities of Acarina ($p<0.001$) and Collembola ($p<0.01$), so the dominant orders were as in the previous year, reinforcing the described patterns.

There were significant variations in the densities of some orders with tree species. The her-

TABLE 2. Species richness of canopy arthropods per 1 m^2 ground area, for four species of conifer.

	Tree species			
	Norway spruce	Sitka spruce	Scots pine	Corsican pine
1986				
Psocoptera	1.08	0.50	0.92	1.08
Homoptera	—	—	—	—
Heteroptera	0.33	0.08	1.25	0.00
Lepidoptera	0.58	0.50	0.75	0.33
Hymenoptera	0.22	0.92	1.83	1.67
Coleoptera	2.75	1.58	2.17	1.58
Araneae	2.17	1.08	3.75	2.42
1987				
Psocoptera	1.87	2.40	2.27	2.33
Homoptera	2.53	1.93	3.27	3.27
Heteroptera	—	—	—	—
Lepidoptera	—	—	—	—
Hymenoptera	5.80	4.53	7.73	7.33
Coleoptera	3.93	2.67	2.40	2.67
Araneae	4.53	4.00	5.60	5.73

bivores were notably variable. The Homoptera were, of course, most abundant on Sitka spruce ($p<0.001$) and the two spruces both supported significantly greater numbers of Lepidoptera than the two pines ($p<0.01$).

The carnivores also showed significant variation. Norway spruce supported greater numbers of Araneae than all but Scots pine ($p<0.05$) and a greater number of Coleoptera than all other trees ($p<0.001$). On Sitka spruce the carnivore community was dominated by Araneae and by Neuropteran larvae (mainly Hemerobiidae). The dynamics of this latter group appeared to follow that of the aphids. The pines supported significantly greater densities of Opiliones ($p<0.01$).

Although Homopteran densities were greatest on Sitka spruce the species richnesses were significantly greater on the pines ($p<0.05$). Norway spruce supported a greater number of species of Coleoptera than Scots pine ($p<0.001$), but fewer species of Psocoptera than the other trees ($p<0.01$). The Hymenoptera were more species-rich on the pines than the spruces ($p<0.05$).

Significantly greater numbers of insects were recorded in 1987 than in 1986 ($p<0.001$). In fact, significantly increased densities were found for eight out of fourteen orders, with only one, the Thysanoptera, decreasing. The three orders for which species richness was analysed, the Coleoptera, Araneae and Hymenoptera were all more rich in 1987.

Discussion

The data from this study illustrate, not surprisingly, that the patterns of arthropod abundance and species richness in tree canopies are complex. However, pyrethrum knockdown has enabled the collection of data on conifer canopy arthropods which may be important to ecologists and to forest managers. While the study found that the communities which the four conifer trees supported were varied and differed in structural detail between years, it was possible to detect some general patterns and to compare these with studies in other habitats.

The densities of arthropods found in this and in subsequent work (Ozanne *et al.* in press) were very high, from 3–20 times greater than those found on angiosperm trees in either temperate or tropical environments. The densities were, however, of the same order as those found on Hinoki cypress (*Chamaecyparis obtusa*), Japanese red cedar (*Cryptomeria japonica*) and Japanese red pine (*Pinus densiflora*) in Japan (Hijii 1983, Hijii 1989, Kikuzawa & Shidei 1967). It seems, therefore, that, per unit ground area, conifers support greater densities of arthropods than broadleafed trees.

What may account for this? There are a number of characteristics of coniferous canopies which could encourage high densities of arthropods. Firstly, conifers tend to have greater leaf area indices (LAI) than broadleaf trees (Tadaki 1966). Thus the higher densities of arthropods per square meter ground area may in part be explained by

TABLE 3. Species richness of canopy arthropods per 15 m^2 ground area. (Data for broadleafed trees taken from Southwood *et al.* 1982.)

	Tree species							
	Norway spruce	Sitka spruce	Scots pine	Corsican pine	Oak	Birch	*Salix alba*	*Salix cinerea*
Psocoptera	9	10	13	9	13	10	6	8
Homoptera	8	9	11	8	25	22	12	15
Heteroptera	2	1	6	1	25	23	12	15
Coleoptera	13	18	11	19	53	30	8	15
Araneae	19	14	24	9	25	23	8	19

greater surface area within the overhanging canopy column. This allows for reduced resource competition in terms of space and potential food supply.

Secondly, the high LAI and closed canopy may result in a more stable microclimate within the coniferous canopy than for more open broadleafed woodland. This stability would be significant in encouraging population growth, particularly in groups which are humidity sensitive due to poor cuticular waterproofing and high surface area to volume ratios. The arthropod communities of all four tree species contain high proportions of arthropods with small body sizes such as Acarina, Collembola and Psocoptera, which would indeed be sensitive to variable humidity.

Thirdly, the longevity of the canopy foliage is greater in evergreen trees than in deciduous trees. For example, Norway spruce often carries 5 years growth of foliage, and needle retention has been recorded up to 12 years (Savill & Evans 1986). This longevity allows the build up of microbial communities which will provide some arthropods with an enhanced food supply. Even though the needles of conifers are difficult to utilize, the overall biomass and percentage coverage of the phylloplane by microorganisms is high in comparison with the leaves of deciduous trees (Campbell 1985). Since the communities on at least three of the tree species in this study were dominated by epiphyte feeders and detritivores, needle longevity may make a significant contribution to the high densities of arthropods.

On all the conifers, except Sitka spruce, the two dominant groups of invertebrates for 1986 and 1987 were the Collembola and the Acarina. In Sitka spruce these two groups were second and third in density. These findings are broadly in agreement with those for Japanese red cedar (*Cryptomeria japonica*), on which Collembola and Acarina made up 60–90% of the individuals collected from the canopies (Hijii 1989). In the present study, the percentages were found to vary between tree species. However, for Norway spruce, Scots pine and Corsican pine figures remarkably similar to those in Japan were observed (51–90%). Work on natural Japanese conifer forests also indicated the dominance of these two orders (Yamashita & Ishii 1976), suggesting that it is not a phenomenon of closely spaced plantation trees. Recent work shows that on Norway spruce at some sites in Britain, the Psocoptera are also highly abundant (Ozanne *et al.* in press).

In both years of the study the percentage of the fauna made up by the Collembola and Acarina in the canopy of Sitka spruce was considerably below the 60–90% range: 1986 = 14%, 1987 = 24%. The times of year at which the densities of Collembola and Acarina were at their lowest, correspond with the peak numbers of Homoptera; that is June 1986 (Homoptera: 79%) and May 1987 (Homoptera: 98%). This suggests that the high densities of Homoptera have suppressed groups such as the Collembola and also the Psocoptera, which were notably low in numbers. Since the food sources differ, competition for other resources such as space or changes in the arboreal environment mediated by heavy attack must bring about this change in the abundance of other groups.

The data from this study concerning the proportional abundance of phytophages do not concur with those collected by Moran & Southwood (1982) for deciduous trees in Britain and South Africa. They found that when the mean number of individuals was considered, phytophages (particularly sap-feeders) were overwhelmingly dominant on all the trees sampled, giving a figure of 68%. This is clearly not the case for conifers.

The data collected for conifers show that the importance of each of the feeding guilds, as described by Moran & Southwood (1982), varies between months of the year. It is not satisfactory, therefore, to draw broad-ranging conclusions from samples taken on single dates. It was possible, however, to compare the data for the four conifers in August 1986 and August 1987 with that collected for the deciduous trees. For all conifer species, in both years, the sap-feeding phytophages comprised less than 32% of the total arthropod fauna (Corsican pine 1987 = 31.3%), most being below 10%. These figures correspond more closely with those found by Stork (1987) for trees in a Bornean tropical forest, where sap-feeders were 12.3% of the total fauna, than with those for temperate trees.

It is difficult to make comparisons of species richness between this study and those on broadleaf trees because of the lack of sampling unit standardization, (most figures for broadleafs are not given per 1 m ground area). It can be done, however, by merging the species lists from several of the 1 m^2 sample units collected under the conifers. Fewer species of specialist herbivores (such as Homoptera and Lepidoptera) were found, per unit ground area, on the conifers than have been recorded for broadleafs. However, other sectors of the community were found to be diverse and to contain woodland specialist species. That the species richness of the indicator orders was often comparable with that found for broadleaf trees, shows that conifers host more complex communities than had previously been thought. Some of the species present are woodland specialists, e.g., spiders in the genera *Cyclosa* and *Achaearanea*. This indicates that commercially grown conifers may be of value in conserving woodland species where broadleafed habitat is not now available.

The lower herbivore species-richness on conifers could be accounted for by lack of ecological opportunity (Fraser & Lawton 1994). In Britain the area planted with spruce and pine has increased dramatically in the last 90 years and there is strong evidence that number of herbivore species is increasing rapidly (Evans 1987). In spite of the chemical and physical barriers conifers put up against herbivory, it is likely that the number of herbivores associated with these trees will, in time, approach that on broadleafs.

The communities supported by the four conifer species differed both in the species composition and in the abundances between and within years. However, after outbreaks of spruce aphids were taken into account, some patterns emerged. In both years pines supported the greatest densities of arthropods. This could be attributed to either chemical or structural differences; the latter is currently under investigation. The differences in overall faunal densities were greater between genera than between species within genera, which might have been expected if the faunal composition was similar on related species. This was the case in some orders such as the Homoptera, but not in all.

Epiphyte feeders and detritivores, such as the Collembola and Psocoptera, were more abundant in the canopies of the pines than the spruces, contributing to the greater faunal densities, and were much more numerous as autumn approached. It is also clear from the data that, in 1987, the spruces supported a greater herbivore load than the pines, and may therefore have suffered greater productivity losses. Defoliating herbivores such as the Lepidoptera were notably more abundant on the spruces than on the pines in this year.

Species richness variations were also greater between genera than between tree species. However, in some orders such as the Coleoptera, the actual species composition did vary considerably between tree species. The richness was usually greatest on Scots pine which is native to parts of Scotland and has been introduced to parts of Southern Britain. Total species richness has been attributed to the length of time that a tree has been in the British flora (Kennedy & Southwood 1984). This concept does not necessarily extend to the richness per unit area as sampled in this study, but it is interesting that the data should support this hypothesis.

Conclusion

This study indicates that the arthropod communities supported by coniferous trees are more diverse than generally supposed and differ in several ways from those found on broadleafed trees. The data suggest that it is not possible to generalize about arboreal communities from sampling in tropical forests, since the communities may not be typical of all forested ecosystems. Indeed, further work in temperate forests is required in order to gain the understanding necessary to manage these habitats successfully. Greater access to quantitative data regarding canopy arthropod communities is required before their structure and function can be clearly understood.

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Literature Cited

Basset Y., H-P Aberlane, and G. Delvare. 1992. Abundance and stratification of foliage arthropods in a lowland forest of Cameroon. Ecological Entomology 17: 310–318.

Campbell R. 1985. Plant microbiology. Arnold. London. 191pp.

Coley P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs 53: 209–233.

Erhardt A. and J.A. Thomas. 1991. Lepidoptera as indicators of change in the semi-natural grasslands of lowland and upland Europe. *in* N.M. Colins and J.A. Thomas, eds., The Conservation of Insects and their Habitats. 15th Symposium of the Royal Entomological Society of London, Academic Press, London, pp. 213–236

Evans H.F. 1987. Sitka spruce insects: Past, present and future. Proceedings of the Royal Society, Edinburgh. Section B 93: 157–168.

Fraser S.M. and J.H. Lawton. 1994. Host range expansion by British moths onto introduced conifers. Ecological Entomology 19: 127–137.

Hijii N. 1983. Arboreal arthropod fauna in a forest I. Preliminary observation on seasonal fluctuations in density, biomass and faunal distribution in a *Chamaecyparis obtusa* plantation. Japanese Journal of Ecology 33: 435–445.

———. 1989. Arthropod communities in a Japanese cedar (*Cryptomeria japonica* D Don.) plantation:

abundance, biomass and some properties. Ecological Research 4(3): 243–261.

KENNEDY C.E.J. AND T.R.E. SOUTHWOOD. 1984. The number of species of insects associated with trees; a re-analysis. Journal of Animal Ecology 53: 455–478.

KIKUZAWA K. AND T. SHIDEI. 1967. On the biomass of arthropods of the Japanese red pine forest in the vicinity of Kyoto. Bulletin Kyoto University Forest 39: 1–8.

KITCHING R.L., J.M. BERGELSON, M.D. LOWMAN, S. MCINTYRE, AND G. CARRUTHERS. 1993. The biodiversity of arthropods from Australian rainforest canopies. Australian Journal of Ecology 18 (2): 181–191

KRAMER P.J. AND T.T. KOZLOWSKI. 1979. Physiology of Woody Plants. Academic Press. New York; London. 811pp.

KREYSA J. 1987. The forest resource of the EEC-12: A Statistical Analysis. EEC-FAST Occasional Paper 162.

LOCKE G.M. 1987. Census of woodlands and trees 1979–1982. Forestry Commission Bulletin 63. HMSO. London.

MORAN V.C. AND T.R.E. SOUTHWOOD. 1982. The guild composition of arthropod communities in trees. Journal of Animal Ecology 51: 289–306.

NADKARNI N.M. AND G.G. PARKER. 1994. A profile of forest canopy science and scientists—who we are, what we want to know and obstacles we face: results of an international survey. Selbyana 15 (2): 38–50

NEUVONEN S. AND P. NIEMALA. 1981. Species richness of macrolepidoptera on Finnish deciduous trees and shrubs. Oecologia 52: 364–428

OZANNE C.M.P. 1991. The arthropod fauna of coniferous plantations. D.Phil. thesis. St. Anne's College. Oxford University.

———, M.R. SPEIGHT, AND H.F. EVANS. 1988. Spray deposition and retention in the canopies of five forest tree species. Aspects of Applied Biology 17, Part 2. Environmental Aspects of Applied Biology: 245–246.

———, C. HAMBLER, A. FOGGO, AND M.R. SPEIGHT. (in press) The significance of edge-effects in the management of forests for invertebrate biodiversity. *in* J. ADIS, R. DIDHAM AND N. STORK eds., Canopy arthropods. International Congress of Ecology VI, Manchester, England. 20–26th August, 1994. Chapman & Hall.

SAVILL P.S. AND J. EVANS. 1986. Plantation silviculture in temperate regions with special reference to the British Isles. Clarendon Press. 246pp.

SNEDECOR G.W. AND W.G. COCHRAN. 1970. Statistical Methods. 7th Edition. Iowa State University Press. Iowa USA.

SOKAL R.R. AND F.J. ROHLF. 1981 Biometry. 2nd Edition. Freeman & Co. Oxford.

SOUTHWOOD, T.R.E., V.C. MORAN, AND C.E.J. KENNEDY. 1982. The richness, abundance and biomass of the arthropod communities on trees. Journal of Animal Ecology 51: 635–649.

STORK N. 1987. Guild structure of arthropods from Bornean rain forest trees. Ecological Entomology 12: 69–80.

———. 1988. Insect diversity: facts, fiction and speculation. Biological Journal of the Linnean Society 35: 321–337.

TADAKI Y. 1966. Some discussions on the leaf biomass of forest stands and trees. Bulletin of Government Forest Experimental Station, Meguro 84: 135–61.

YAMASHITA Z. AND T. ISHII. 1976. Ecological studies of the arboreal arthropod fauna I. Basic structure of the arboreal arthropod fauna in the natural forest of Japan. Rep. Environ. Sci. Mie Univ. 1: 81–111.