Ecological Entomology (1981) 6, 217–238

Host plant associations, diversity and species–area relationships of mesophyll-feeding leafhoppers of trees and shrubs in Britain

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ABSTRACT. 1. Sixty-two British species of Typhlocybine leafhoppers are known to feed on the leaf-mesophyll tissue of trees and shrubs. British host records for fifty-five of these are given.

2. The leafhopper faunas of thirty-six species of native and introduced trees and shrubs are described.

3. The Shannon-Wiener equation was used to calculate species diversity for adult samples collected from twenty different species at sixteen different localities in Wales, southern England and northern Scotland.

4. Sϕrensen's coefficients were calculated for rearing data from Britain generally, and subjected to cluster analysis. Most trees have low similarities with respect to leafhopper faunas and are quite distinct. Taxonomic relationships of trees appear to be relatively unimportant in determining the similarities of their leaf-hopper faunas.

5. Using the same data, species–area relationships were calculated for thirty-four different tree and shrub species and their associated leaf-hoppers. A significant regression was obtained, but it explained only 16% of the variation. It is thus suggested that host plant range is relatively unimportant in determining the numbers of these species associated with different trees in Britain.

6. Some introduced species of trees, particularly the recently planted *Nothofagus*, have acquired large leafhopper faunas.

Introduction

We previously described the mesophyll-feeding guild of leafhoppers associated with woodland canopy habitats in South Wales (Claridge & Wilson, 1976). In the present study, we present comprehensive host plant data, and analyses of diversity and species–area relationships for these insects more widely in Britain.

Mesophyll-feeding leafhoppers

All of the mesophyll-feeding leafhoppers in Britain, so far as is known, are members of the distinctive subfamily Typhlocybinae. Claridge & Wilson (1976) reviewed the feeding habits and general biology of this group. Only some species of *Empoasca* appear not to feed on mesophyll. *E.vitis* (Göthe) was mistakenly treated by us previously as a mesophyll-feeder. We now believe it to be primarily a phloem feeder and have excluded it from this study. All remaining species feed by piercing the leaf lamina of the host plant and removing the green contents, especially of the palisade mesophyll cells, leaving patches of empty cells which show up as characteristic pale stippling marks on the upper surfaces of leaves (Figs. 1 and 2, and Figs. 1–7 in Claridge & Wilson, 1976).

Of the eighty-eight species of Typhlocybinae listed as British by Le Quesne (in Kloet & Hincks, 1964), fifty-six, including *E.vitis*,

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0307-6946/81/0800-0217 $02.00

are thought to be primarily associated with trees or shrubs (Ribaut, 1936; China, 1943; Claridge & Wilson, 1976). A further eight species are now known to be British: *Edwardsiana diversa* Edwards and *E.fraterculus* Edwards were omitted in error from Le Quesne's list, *Alebra coryli* Le Quesne was added by Le Quesne (1977), *Eurhadina kirschbaumi* (Wagner) by Woodroffe (1971), *Eurhadina ribauti* (Wagner) and *Edwardsiana rosaesugans* (Cerutti) by Claridge & Wilson (1978b) and *Kyboasca bipunctata* (Oshanin) by Wilson (1979). A further species of *Edwardsiana* has been collected, but not previously listed. Dr W. J. Le Quesne believes that it may be *E.ishidai* (Matsumura), and we shall here refer to it as *E.ishidai* (?). Günthart (1979) recently reduced the list by one, by synonymizing *Zygina pruni* (Edwards) with *Z.flammigera* (Fourcroy).

We have collected information on fifty-five of the sixty-two mesophyll-feeding species now known from British trees. Major difficulties remain only with species of *Zygina* (= *Erythroneura* part). Le Quesne (in Kloet & Hincks, 1964) listed eight species, including *Z.pruni*, but we have only been able to recognize three, the identity of one of which is uncertain, and we here refer to it as *Zygina* species. The latter probably represents more than one biological species. For generic and specific nomenclature, we follow Nast (1972), with minor exceptions.

Methods

Two distinct methods of sampling were used:

1. Quantitative adult samples were obtained by the use of a sweep net on the lower branches of trees and shrubs (Claridge & Wilson, 1976). Sites sampled in this manner are given with national grid references in Table 2. The localities in the north-west Highlands of Scotland were described by Claridge *et al.* (1968), and most of those in south Wales by Claridge & Wilson (1976).
2. Hand sampling of nymphs and rearing of adults on a large scale were used to determine precise host plant associations: we have previously stressed the importance of rearing data for establishing host plant associations of these active flying insects (Claridge & Reynolds, 1972; Claridge & Wilson, 1976). Such hand collecting was done at all sites sampled above (Table 2), but also more casually at others in south-west, central, south-east and north-west England, north Wales and central Scotland. The only regions from which we have no personal data are north-east England and southern Scotland.

Results and analyses of samples

Trees and associated leafhoppers

A summary of rearing data and host plant records for the fifty-five mesophyll-feeding species we have studied is given in Table 1. For all species more than five individuals were reared from each host. For some oligophagous and polyphagous bivoltine species considerable differences in host plants may occur between generations (Claridge & Wilson, 1978c). Such generation differences are not noted in the following account, but are indicated in Table 1. The validity of our host plant associations for Britain is strengthened and broadly confirmed from previous records summarized in China (1943) and from unpublished records by W. J. Le Quesne (personal communication).

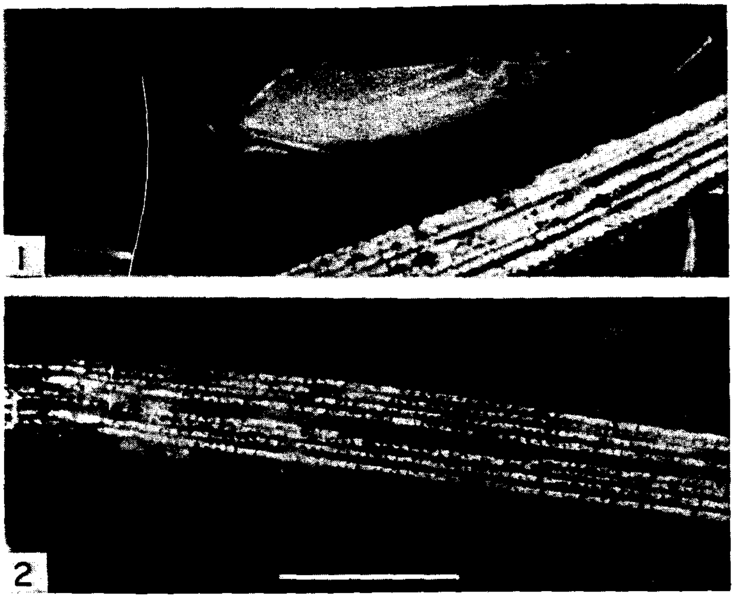
Of thirty-six species of trees and shrubs studied by us two were Gymnosperms and the remainder Angiosperms. The leafhoppers associated with these species in our samples are described more fully below. Detailed data given previously by Claridge & Wilson (1976) are not repeated here. The insects are given in the nomenclature, taxonomic sequence, and under the family names of Clapham *et al.* (1962).

GYMNOSPERMAE

Pinaceae

Pinus sylvestris L. (Scots pine)

Only one species, *Aguriahana germar* (Fig. 1), was found. Nymphs and adults were collected from pines at Thursley Common (SU9041) and Yagden Hill (SU8842), Surrey, and adults from Beinn Eighe National Nature Reserve, W. Ross (NG9866), Scotland (4.viii. 1963, M.F.C.). Feeding damage is characteristic (Fig. 2).



FIGS. 1 and 2. ***Aguriahana germari***: 1, adult; 2, feeding damage on ***Pinus sylvestris***. Scale line approximately 2 mm.

Taxaceae

Taxus baccata L. (yew)

No nymphs or adults were found and no feeding damage has been seen.

ANGIOSPERMAE

Tiliaceae

Tilia cordata Mill. (small-leaved lime)

Samples from Taf Fechan and Craig-y-Cilau in South Wales produced only one species, *Alnetoidia alneti*. However, collections from Juniper Hall, Surrey, produced adults and nymphs of five species: *Alebra wahlbergi*, *Fagocyba cruenta*, *Aguriahana stellulata*, *Edwardsiana lethierryi* and *A.alneti*. In these samples, *Fagocyba cruenta* and *E.lethierryi* were the commonest species.

Aceraceae

Acer campestre L. (field maple)

Two species, *Alnetoidia alneti* and *Alebra wahlbergi*, were dominant in South Wales (Claridge & Wilson, 1976). Three other species were also found: *Fagocyba cruenta*, *Edwardsiana frustrator* and *E.lethierryi*. Dr M. A. Jervis (*in litt.*) informs us that he has also reared *Lindbergina aurovittata*.

Acer pseudoplatanus L. (sycamore)

Sampled through the summer of 1974 in South Wales (Claridge & Wilson, 1976), and a single 3 min sample was taken at Taf Fechan in 1976. At each site the same species were represented. Most abundant in the samples were *Fagocyba cruenta* and *Alnetoidia alneti*. *Eurhadina loewii*, *Ossiannilssonola callosa* and *Edwardsiana nigriloba* were also commonly represented. Less common were *Edwardsiana frustrator* and *Alebra wahlbergi*.

Hippocastanaceae

Aesculus hippocastanum L. (horse chestnut)

No routine sampling was done but hand collecting at Juniper Hall, Surrey, and large sweep-net samples from Bute Park, Cardiff, were used to establish species associations. Nymphs of three species were found: *Fagocyba cruenta*, *Edwardsiana lethierryi* and *Alebra wahlbergi*, of which *F.cruenta* was the most abundant.

TABLE 1. Host plants confirmed by more than five separate rearings for mesophyll-feeding leafhoppers in Britain. *Fraxinus, Ilex* and *Taxus* are not included as no species were recorded as breeding on them. * indicates host for second (summer) generation only.

Host plant Typhlocybinae	*Pinus sylvestris*	*Tilia cordata*	*Acer campestre*	*Acer pseudoplatanus*	*Aesculus hippocastanum*	*Frangula alnus*	*Prunus avium*	*Prunus padus*	*Prunus spinosa*	*Prunus domestica*	*Crataegus monogyna*	*Sorbus aria*	*Sorbus aucuparia*	*Malus sylvestris*	*Rosa* species	*Rubus* species	*Thelycrania sanguinea*	*Ulmus glabra*	*Ulmus procera*	*Betula pubescens/pendula*	*Alnus glutinosa*	*Corylus avellana*	*Carpinus betulus*	*Nothofagus obliqua/procera*	*Fagus sylvatica*	*Castanea sativa*	*Quercus robur*	*Quercus petraea*	*Quercus cerris*	*Quercus ilex*	*Populus* species	*Salix* 'Willows'	*Salix* 'Sallows'	Total
Alebra albostriella (Fallén)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	●	—	—	—	—	3
A.coryli Le Quesne	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	1
A.wahlbergi (Boheman)	—	●	●	●	●	—	●	—	—	—	—	●	—	—	—	—	—	●	●	●	●	—	●	—	—	●	—	—	—	—	—	—	—	12
Kybos betulicola (Wagner)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	1
K.butleri (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	1
K.populi (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	1
K.smaragdula (Fallén)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	1
K.strigilifer (Ossiannilsson)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	1
K.virgator (Ribaut)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	1
Kyboasca bipunctata (Oshanin)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Fagocyba carri (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	—	—	—	—	—	2
F.cruenta (H.-S.)	—	●	●	●	●	—	●	—	—	—	●	●	●	—	—	—	—	●	●	●	—	●	●	●	●	●	—	—	—	—	—	—	—	16
Ossiannilssonola callosa (Then)	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Edwardsiana alnicola (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	1
E.avellanae (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	1
E.bergmani (Tullgren)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E.candidula (Kirschbaum)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	1
E.crataegi (Douglas)	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E.diversa (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E.flavescens (Fabricius)																							●		●									2
E.frustrator (Edwards)			●	●								●										●		●			●	●						7

E.geometrica (Schrank)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	1
E.hippocastani (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	—	●	●	—	—	—	—	—	—	—	—	—	—	—	4
E.ishidai Matsumura ?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E.lanternae (Wagner)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	1
E.lethierryi (Edwards)	—	●	●	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
E.nigriloba (Edwards)	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E.plebeja (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E.prunicola (Edwards)	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E. rosae (L.)	—	—	—	—	—	—	●*	—	—	—	—	●*	●*	●*	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
E.rosaesugans (Cerutti)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
E.salicicola (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	1
E.spinigera (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	1
E.tersa (Edwards)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	1
Eupterycyba jucunda (H.-S.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	1
Linnavuoriana decempunctata (Fallén)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	1
L.sexmaculata (Douglas)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	1
Lindbergina aurovittata (Hardy)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	●*	●*	●*	●*	●*	●*	—	●*	●*	●*	●	—	—	—	11
Ribautiana debilis (Douglas)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
R.tenerrima (H.-S.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	2
R.scalaris (Ribaut)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	●	—	—	—	—	3
R.ulmi (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Typhlocyba bifasciata (Boheman)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	2
T.quercus (Fabricius)	—	—	—	—	—	—	●	●	●	●	—	—	—	—	—	—	—	—	—	—	—	●	●	●	●	●	●	●	—	—	—	—	—	11
Eurhadina concinna (Germar)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	—	—	●	●	—	●	●	—	—	—	—	—	6
E.kirschbaumi (Wagner)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	●	—	—	—	—	—	2
E.pulchella (Fallén)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	—	—	—	—	—	2
E.ribauti (Wagner)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	●	—	—	—	—	—	2
E.loewii (Then)	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Aguriahana germari (Zetterstedt)	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
A.stellulata (Burmeister)	—	●	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Alnetoidia alneti (Dahlbom)	—	●	●	●	—	—	●	●	●	—	●	●	●	●	—	—	●	●	—	●	●	●	●	—	●	—	—	—	—	—	—	—	—	17
Zygina species	—	—	—	—	—	—	●	—	●	●	●	●	●	●	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Z.suavis (Rey)	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Z.tiliae (Fallén)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	●	—	—	—	—	—	—	—	—	—	—	—	—	1
Total	1	5	5	7	3	1	7	2	4	2	4	5	5	3	3	3	2	7	6	8	11	9	7	6	6	3	9	10	3	1	2	2	4	

Aquifoliaceae

Ilex aquifolium L. (holly)

No nymphs or feeding damage were found, though adults of some species of *Zygina* may use the evergreen foliage as an overwintering site.

Rhamnaceae

Frangula alnus Mill. (alder buckthorn)

Only one associated species was found: *Zygina suavis.* Nymphs were taken commonly at Blackmill, Glamorgan, but few adults were seen on the plant.

Rosaceae

Prunus species

Four *Prunus* species were sampled: *Prunus avium* L. (cherry), *P.spinosa* L. (blackthorn), *P.domestica* L. (bullace/plum), and *P.padus* L. (bird cherry). More species were found on cherry than on other *Prunus* species: *Alnetoidia alneti, Fagocyba cruenta, Typhlocyba quercus, Edwardsiana rosae* and *Zygina* species were all frequent. Samples from cherry at Box Hill, Surrey, included also large numbers of *Aguriahana stellulata* and *Alebra wahlbergi,* two species rarely collected from this tree in South Wales. Only two of these species were collected from bird cherry: *A.alneti* and *T.quercus.* Five species were collected from blackthorn: *F.cruenta, T.quercus, A.alneti, Zygina* species and *Edwardsiana prunicola,* the latter has not yet been recorded on other *Prunus* species. Two species were recorded on plum/bullace: *T.quercus* and *Zygina* species. Only *T.quercus* was found on all four *Prunus* species.

Crataegus monogyna Jacq. (hawthorn)

Samples were taken in South Wales in 1974 (Claridge & Wilson, 1976) and Taf Fechan in 1976, as well as hand collecting for nymphs at various sites. Four species were reared: *Alnetoidia alneti, Fagocyba cruenta, Edwardsiana crataegi* and *Zygina* sp. *A.alneti* was always the most abundant.

Sorbus species

Samples were collected from three *Sorbu* *S.aucuparia* L. (rowan), *S.aria* (L.) Crant (whitebeam) and *S.intermedia* (Ehrh.) Per (Swedish whitebeam). Five leafhoppers wer reared from rowan: *Fagocyba cruenta* *Edwardsiana frustrator, E.rosae, Alnetoidi* *alneti* and *Zygina* species. With the exceptio of *E.frustrator,* these species were also foun on whitebeam. In addition, samples fro Swedish whitebeam at Box Hill produce both adults and nymphs of *Alebra wahlbergi.*

Malus species (apple)

Alnetoidia alneti was very common in al samples. *Edwardsiana rosae* was also commo and *Zygina* species has been reared. Chiswel (1964) found *Edwardsiana crataegi* (=*froggati* abundant, but we have not found it on apple.

Rosa species (rose)

The commonest species was *Edwardsian* *rosae. Rosa* species are the only known host for the first generation (Claridge & Wilson 1978c). At Taf Fechan, nymphs and adults o *Edwardsiana rosaesugans* were found. N other British localities are known for thi species.

Rubus species (bramble)

Ribautiana tenerrima and *Lindbergin* *aurovittata* are common in South Wales. A further species of *Ribautiana, R.debilis* wa found with *R.tenerrima* at Worms Head Rhossili, Glamorgan (SS384877).

Cornaceae

Thelycrania (=*Cornus*) *sanguinea* (L.) Four (dogwood)

Alnetoidia alneti and *Edwardsiana divers* were commonly found.

Ulmaceae

Ulmus species (elms)

The majority of samples were collected from *Ulmus glabra* Huds. (wych elm), but a single large sample was also taken from *U.procera* Salisb. (English elm) at Mitcham, Surrey.

Samples from Wales contain up to six species: *Ribautiana ulmi* (often extremely abundant), *Fagocyba cruenta, Alnetoidia alneti, Edwardsiana hippocastani, E.plebeja* and *Typhlocyba bifasciata.*

The collection from *U.procera* in Surrey differed from those taken from *U.glabra.* No *A.alneti, T.bifasciata* or *E.plebeja* were found although the collection was large (> 700 individuals). *Ribautiana ulmi* was abundant and *Fagocyba cruenta* and *E.hippocastani* were also present. In addition, *Alebra wahlbergi* was common: it occurs only occasionally on *U.glabra* in South Wales. *Edwardsiana ishidai* (?), close to *E.lanternae,* was also collected from *U.procera.* In addition almost ninety individuals (48♀, 40♂) of *Kyboasca bipunctata* were found. It is not yet clear whether these differences between the elms represent geographical variation in the fauna or differences between the species as hosts for leafhoppers.

Betulaceae

Betula species (birch)

Betula pubescens Ehrh. was sampled more regularly than *B.pendula* Roth. Samples were taken in 1974 (Claridge & Wilson, 1976), and single samples were later obtained from Taf Fechan and Roath Park. Large numbers of individuals are rarely obtained despite the fact that eight species have been reared. At Coed-y-Bedw, *Fagocyba cruenta* and *Edwardsiana bergmani* were the most abundant species. Other collections have been dominated by *Alnetoidia alneti.* Other species associated with birch are *Alebra wahlbergi, Kybos betulicola, Linnavuoriana decempunctata, Lindbergina aurovittata* and *Eurhadina concinna.*

Alnus glutinosa (L.) (alder)

Of the eleven associated species, the commonest are *Fagocyba cruenta* and *Alnetoidia alneti.* Others are *Kybos smaragdula, Alebra wahlbergi, Edwardsiana geometrica, E.alnicola, E.hippocastani, Eupterycyba jucunda, Lindbergina aurovittata, Eurhadina concinna* and *Zygina tiliae.* The proportion of the samples made up by *Alnetoidia alneti* varies considerably at different sites. At Roath Park and Taf Fechan, up to 95% was of this species. At Coed-y-Bedw and Fforest Ganol, *A.alneti* accounted for only about 35% of the total adults.

Corylaceae

Corylus avellana L. (hazel)

The commonest associated leafhoppers are *Fagocyba cruenta, Edwardsiana avellanae* and *Alnetoidia alneti.* Others less common are *Edwardsiana frustrator, E.hippocastani, Lindbergina aurovittata, Ribautiana tenerrima* and *Typhlocyba quercus.* Few specimens of *Alebra coryli* were identified from South Wales, but it was common in samples from Surrey. *Edwardsiana spinigera* is similarly common in samples from Surrey, but has yet to be found in South Wales.

Carpinus betulus L. (hornbeam)

Alnetoidia alneti and *Fagocyba cruenta* are the commonest species. Others are *Alebra wahlbergi, Edwardsiana flavescens, Lindbergina aurovittata, Typhlocyba bifasciata* and *Typhlocyba quercus.*

Fagaceae

Nothofagus species (southern beeches)

Various species of *Nothofagus* have been introduced to Britain from South America and Australasia, mostly for specimen trees. However, in recent years (since about 1930) the deciduous *N.obliqua* (Mirb.) Bl. and *N.procera* (Poepp. & Endl.) Oerst. from Chile have been planted more widely as forest trees (Nimmo, 1971). We have collected from these mostly in South Wales. Dr R. C. Welch, Monks Wood Experimental Station, has also sent us large samples collected mostly in England and has very kindly allowed us to use his data here. It is clear from our combined data that at least six species of mesophyll-feeders have established breeding populations on these *Nothofagus* in Britain: *Lindbergina* *aurovittata, Edwardsiana frustrator, Fagocyba cruenta, Typhlocyba quercus, Eurhadina concinna* and *E.kirschbaumi.*

Fagus sylvatica L. (beech)

At Coed-y-Bedw, Roath Park and Taf Fechan, *Fagocyba cruenta* made up 80% of the samples. At Fforest Ganol in 1974 *F.cruenta* made up 50% of the total, with *Alnetoidia alneti* accounting for another 35%. Other less common species are *Edwardsiana flavescens, Lindbergina aurovittata, Typhlocyba quercus* and *Eurhadina concinna.*

Castanea sativa Mill. (sweet chestnut)

A few samples were taken in Surrey and Glamorgan. Numbers of individuals collected were generally low. Three were reared and appear to be associated with the plant: *Fagocyba cruenta* and *Alebra wahlbergi* were the commonest, but *Typhlocyba quercus* was also found.

Quercus species (oaks)

Four species of oaks were sampled: the native *Quercus robur* L. (common oak) and *Q.petraea* (Matt.) Liebl. (sessile oak), and the introduced *Q.cerris* L. (turkey oak) and *Q.ilex* L. (holm oak). Most sampling was done on *Q.robur,* from which nine species were reared. The commonest were *Alebra albostriella, Typhlocyba quercus, Ribautiana scalaris, Eurhadina concinna, E.pulchella* and *Lindbergina aurovittata.* Less common were *Edwardsiana frustrator, Fagocyba carri* and *Eurhadina ribauti.* All of these species were also collected from *Q.petraea.* At Blackmill, Glamorgan, also large numbers of *Eurhadina kirschbaumi* were taken. Further sampling from other sessile oak woodlands revealed further populations (Claridge & Wilson, 1978b), but none were found on common oak. Adults of *E.kirschbaumi* were collected also from *Q.cerris,* which is known as a host on the mainland of Europe (R. Remane, *in litt.*).

Three species were reared from *Q.cerris*: *Alebra albostriella, Ribautiana scalaris* and *Lindbergina aurovittata,* all found also on common and sessile oaks. The numerical distribution of *Alebra* and *Ribautiana* among these oak species is interesting. *Alebra albostriella* was collected in similar numbers from comparable samples from each of the three species. However, *R.scalaris* was much more abundant on turkey oak than on either common or sessile oaks.

Only one species, *Lindbergina aurovittata,* was collected in very low numbers from the evergreen *Q.ilex.*

The American red oak, *Q.borealis* Michx., was searched in Cardiff, but despite some feeding damage, no leafhoppers were found.

Salicaceae

Populus species (poplars)

Two species were collected from *Populus* species in South Wales: *Kybos populi* from *P.alba* L. (white poplar), *P.tremula* L. (aspen), *P.nigra* L. (black poplar) and *P.canescens* (Ait.) Sm. (grey poplar); and *Edwardsiana candidula* from *P.canescens* only, at Roath Park, Cardiff.

Salix species (sallows and willows)

From the point of view of describing leafhoppers, *Salix* species are conveniently divided into those commonly known as 'sallows' and 'willows', a division which is reflected in the subgeneric grouping of species by Clapham *et al.* (1962). Sallows, such as *S.capraea* L., *S.cinerea* L., *S.repens* L. and *S.aurita* L., were sampled and four leafhoppers found: *Kybos butleri, K.strigilifer, Edwardsiana salicicola* and *Linnavuoriana sexmaculata.* Usually, only very low numbers of these species were encountered and samples were never large. Willows, such as *Salix fragilis* L. and *S.alba* L., produced two species–also only in low numbers: *Kybos virgator* and *Edwardsiana tersa.*

The *Salix* feeding species probably show greater specificity than we have shown here. For example *K.rufescens* seems to be restricted to *S.purpurea* in Britain and northern Europe (W. J. Le Quesne, R. Remane and M. Asche, personal communications).

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The Shannon–Wiener equation was used to calculate the species diversity and evenness for adult samples from twenty tree species (Table 2). Samples from Coed-y-Bedw, Roath Park and Fforest Ganol in 1974 were combined for each tree species at each locality. The species-diversity of samples collected in north-west Scotland (Claridge *et al.*, 1968) was also calculated. No systematic sampling was done on *Salix* species or *Pinus sylvestris*, and these trees are not included. Also *Fraxinus* is excluded because such low numbers of leafhoppers were found. For elm, only samples from *U.glabra* were considered. The mean species diversity and mean evenness for each tree species may be arranged in rank order (highest to lowest mean species diversity) together with richness (Fig. 3). Evenness and diversity were not significantly correlated ($r = 0.365$, $P = 0.12$), because of the great variation between those tree samples that have a high diversity and low evenness, and those that have a low diversity and relatively high evenness.

If the species richness of each included tree is considered it can be seen that *Alnus* has most species and *Populus* has least. It is apparent that the rank order of trees given by species richness does not correspond with that given by species diversity. This is due to species diversity being a combination of both species richness and evenness. Samples from *Quercus robur* have the highest mean species diversity, although not the greatest number of associated species. In the *Q.robur* samples no one species was very much commoner than any other. The great variation in diversity and evenness of *Alnus* samples is due to the variation in numbers of *Alnetoidia alneti*. In many samples it was by far the commonest species. When it is only as common as other species the calculated diversity is high. Similarly, *Fagus* samples are always dominated by large numbers of *Fagocyba cruenta*, and although six species are associated with *Fagus*, the calculated species diversity is always low. Trees with fewer associated species, such as *Sorbus*

Oleaceae

Fraxinus excelsior L. (ash)

Careful collecting revealed only a few adults of *Zygina* species. *Empoasca vitis* is no longer regarded as a mesophyll-feeder (see above).

Leaf-hopper species diversity of tree species samples

Tree species was taken as a unit of habitat within the woodland canopy in this study. In order to investigate the distribution patterns of the leafhopper community within the woodland canopy, the species diversity of leafhoppers on different tree species was measured, and differences between tree species were investigated in terms of species diversity and shared leafhopper species.

The diversity of a sample (the alpha diversity of Whittaker, 1972) may be expressed most easily merely by stating the number of species present. This measure, useful as it is, ignores the relative abundance of the species present. This aspect of diversity has been widely investigated by the use of diversity indices. Morris (1971) reviewed the use of such indices for the study of grassland Auchenorrhyncha, and their general properties are discussed by Peet (1974), Pielou (1975) and Whittaker (1972). The Shannon–Wiener index (Shannon & Weaver, 1949) was chosen for this study.

Two components of diversity are combined in the Shannon–Wiener equation: (i) the number of species (species richness), and (ii) the evenness of allotment of individuals among the species. A greater number of species increases species diversity, as also does a more even distribution of numbers between species. The equation for the Shannon–Wiener function is given by:

$$H = -\sum_{i=1}^{s} p_i(\log p_i),$$

where H = index of species diversity, s = species number, and p_i = proportion of total sample belonging to ith species. Evenness may be obtained from the ratio: $E = H/H_{\max}$, where E = evenness (range 0–1), H = observed species diversity and $H_{\max} = \log s$ = maximum species number in sample (from Pielou, 1975). The antilog form of H is recommended by Peet (1974) to simplify interpretation and is used here. Exp. (H) (antilog) is a measure of the number of equally common species which produce the same diversity as the unequally common species in the sample (MacArthur, 1965). In this form evenness becomes $E = \exp(H)/S$.

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Roath Park	*N*	—	—	1248	—	—	—	—	—	—	—	—	2652	—	—	1951	—	1132	—	—	—
1974	*S*	—	—	8	—	—	—	—	—	—	—	—	12	—	—	6	—	10	—	—	—
ST 185803	*H*	—	—	4.72	—	—	—	—	—	—	—	—	1.96	—	—	1.41	—	7.11	—	—	—
7 samples	*E*	—	—	0.61	—	—	—	—	—	—	—	—	0.23	—	—	0.17	—	0.64	—	—	—
Roath Park	*N*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	206	—	66	—
1976	*S*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	3	—
1 sample	*H*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.08	—	2.37	—
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.82	—	0.44	—
Roath Park	*N*	—	—	—	—	20	—	—	68	—	—	—	—	—	—	—	—	—	—	—	—
1977	*S*	—	—	—	—	4	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—
1 sample	*H*	—	—	—	—	3.21	—	—	3.08	—	—	—	—	—	—	—	—	—	—	—	—
	E	—	—	—	—	0.84	—	—	0.63	—	—	—	—	—	—	—	—	—	—	—	—
Roath Park	*N*	—	—	—	—	—	—	—	—	—	—	262	—	—	—	—	—	—	—	—	—
1978	*S*	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—	—	—	—	—	—
1 sample	*H*	—	—	—	—	—	—	—	—	—	—	4.10	—	—	—	—	—	—	—	—	—
	E	—	—	—	—	—	—	—	—	—	—	0.73	—	—	—	—	—	—	—	—	—
Taf Fechan	*N*	8	—	74	—	—	—	180	—	75	266	59	778	98	—	419	—	100	—	406	—
1976	*S*	1	—	5	—	—	—	3	—	3	5	5	6	3	—	3	—	7	—	5	—
SO 045095	*H*	1	—	4.54	—	—	—	1.91	—	2.25	3.04	2.28	1.22	2.06	—	1.82	—	5.15	—	1.87	—
1 sample	*E*	1	—	0.78	—	—	—	0.59	—	0.59	0.69	0.51	0.10	0.40	—	0.34	—	0.79	—	0.35	—
Wenallt	*N*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	553	—
1976	*S*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—
ST 153834	*H*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.98	—
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.38	—
WALES: BRECON																					
Craig-y-Cilau	*N*	30	—	—	—	—	55	58	—	—	205	—	—	—	—	—	—	—	—	—	—
1974	*S*	1	—	—	—	—	6	3	—	—	4	—	—	—	—	—	—	—	—	—	—
SO 190160	*H*	1	—	—	—	—	4.97	2.23	—	—	2.49	—	—	—	—	—	—	—	—	—	—
1 sample	*E*	1	—	—	—	—	0.74	0.58	—	—	0.66	—	—	—	—	—	—	—	—	—	—
Cwm Clydach	*N*	—	—	—	—	—	—	—	—	6	—	54	—	142	—	234	—	119	—	—	—
1974	*S*	—	—	—	—	—	—	—	—	4	—	5	—	9	—	4	—	9	—	—	—
SO 215125	*H*	—	—	—	—	—	—	—	—	3.78	—	4.35	—	5.04	—	1.55	—	5.08	—	—	—
1 sample	*E*	—	—	—	—	—	—	—	—	0.96	—	0.82	—	0.74	—	0.27	—	0.71	—	—	—
ENGLAND: SURREY																					
Box Hill	*N*	—	—	—	—	—	28	—	37	—	—	—	—	—	—	—	34	—	—	—	—
Headley Warren 1976	*S*	—	—	—	—	—	4	—	5	—	—	—	—	—	—	—	4	—	—	—	—
TQ 193542	*H*	—	—	—	—	—	4.37	—	3.21	—	—	—	—	—	—	—	2.73	—	—	—	—
1 sample	*E*	—	—	—	—	—	0.92	—	0.65	—	—	—	—	—	—	—	0.72	—	—	—	—

TABLE 2. Numbers of individuals (*N*), numbers of species (*S*), diversity (*H*) and evenness (*E*) of adult leafhopper samples from different localities in Britain.

Site	Host plant	*Tilia cordata*	*Acer campestre*	*Acer pseudoplatanus*	*Aesculus hippocastanum*	*Prunus avium*	*Prunus spinosa*	*Crataegus monogyna*	*Sorbus aria*	*Sorbus aucuparia*	*Ulmus glabra*	*Betula pubescens*	*Alnus glutinosa*	*Corylus avellana*	*Carpinus betulus*	*Fagus sylvatica*	*Castanea sativa*	*Quercus robur*	*Quercus petraea*	*Quercus cerris*	*Populus nigra*
WALES: GLAMORGAN																					
Blackmill 1976	*N*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	690	—	—
SS 935864	*S*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—
2 samples	*H*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4.27	—	—
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.70	—	—
Cathays Park	*N*	—	—	—	228	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1977	*S*	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ST 176772	*H*	—	—	—	1.73	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2 samples	*E*	—	—	—	0.50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cathays Park	*N*	—	—	—	96	—	—	—	—	—	—	—	—	—	—	—	83	—	—	—	—
1978	*S*	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—
1 sample	*H*	—	—	—	2.82	—	—	—	—	—	—	—	—	—	—	—	3.09	—	—	—	—
	E	—	—	—	0.64	—	—	—	—	—	—	—	—	—	—	—	0.58	—	—	—	—
Coed-y-Bedw	*N*	—	860	—	—	—	—	335	—	138	2189	120	636	425	—	2039	—	523	—	—	—
1974	*S*	—	4	—	—	—	—	5	—	8	6	5	12	4	—	4	—	11	—	—	—
ST 112826	*H*	—	2.12	—	—	—	—	3.84	—	7.69	3.04	6.62	6.85	5.26	—	1.67	—	7.72	—	—	—
8 samples	*E*	—	0.39	—	—	—	—	0.69	—	0.82	0.45	0.76	0.66	0.65	—	0.21	—	0.77	—	—	—
Fforest-Ganol	*N*	—	625	720	—	—	—	—	—	—	811	—	496	224	1165	1084	—	481	—	—	—
1974	*S*	—	6	9	—	—	—	—	—	—	9	—	16	6	7	8	—	12	—	—	—
ST 144835	*H*	—	4.20	4.77	—	—	—	—	—	—	4.01	—	8.89	4.42	3.23	2.58	—	8.93	—	—	—
7 samples	*E*	—	0.60	0.58	—	—	—	—	—	—	0.56	—	0.75	0.56	0.42	0.36	—	0.76	—	—	—
Merthyr Mawr	*N*	—	—	—	—	—	—	—	—	—	—	—	126	—	—	—	—	—	—	—	—
1974	*S*	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—	—	—	—	—	—
SS 870773	*H*	—	—	—	—	—	—	—	—	—	—	—	3.76	—	—	—	—	—	—	—	—
1 sample	*E*	—	—	—	—	—	—	—	—	—	—	—	0.64	—	—	—	—	—	—	—	—
Merthyr Mawr	*N*	—	—	—	—	—	—	—	—	—	—	—	653	—	—	—	—	—	—	—	—
1978	*S*												4								

ST 185803	*H*			4.72									1.96	–		1.41		7.11	–	–	
7 samples	*E*	–	–	0.61	–	–	–	–	–	–	–	–	0.23	–	–	0.17		0.64	–	–	–
Roath Park	*N*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	206	–	66	–
1976	*S*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	3	–
1 sample	*H*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.08	–	2.37	–
	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.82	–	0.44	–
Roath Park	*N*	–	–	–	–	20	–	–	68	–	–	–	–	–	–	–	–	–	–	–	–
1977	*S*	–	–	–	–	4	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
1 sample	*H*	–	–	–	–	3.21	–	–	3.08	–	–	–	–	–	–	–	–	–	–	–	–
	E	–	–	–	–	0.84	–	–	0.63	–	–	–	–	–	–	–	–	–	–	–	–
Roath Park	*N*	–	–	–	–	–	–	–	–	–	–	262	–	–	–	–	–	–	–	–	–
1978	*S*	–	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–
1 sample	*H*	–	–	–	–	–	–	–	–	–	–	4.10	–	–	–	–	–	–	–	–	–
	E	–	–	–	–	–	–	–	–	–	–	0.73	–	–	–	–	–	–	–	–	–
Taf Fechan	*N*	8	–	74	–	–	–	180	–	75	266	59	778	98	–	419	–	100	–	406	–
1976	*S*	1	–	5	–	–	–	3	–	3	5	5	6	3	–	3	–	7	–	5	–
SO 045095	*H*	1	–	4.54	–	–	–	1.91	–	2.25	3.04	2.28	1.22	2.06	–	1.82	–	5.15	–	1.87	–
1 sample	*E*	1	–	0.78	–	–	–	0.59	–	0.59	0.69	0.51	0.10	0.40	–	0.34	–	0.79	–	0.35	–
Wenallt	*N*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	553	–
1976	*S*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–
ST 153834	*H*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.98	–
	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.38	–
WALES: BRECON																					
Craig-y-Cilau	*N*	30	–	–	–	–	55	58	–	–	205	–	–	–	–	–	–	–	–	–	–
1974	*S*	1	–	–	–	–	6	3	–	–	4	–	–	–	–	–	–	–	–	–	–
SO 190160	*H*	1	–	–	–	–	4.97	2.23	–	–	2.49	–	–	–	–	–	–	–	–	–	–
1 sample	*E*	1	–	–	–	–	0.74	0.58	–	–	0.66	–	–	–	–	–	–	–	–	–	–
Cwm Clydach	*N*	–	–	–	–	–	–	–	–	6	–	54	–	142	–	234	–	119	–	–	–
1974	*S*	–	–	–	–	–	–	–	–	4	–	5	–	9	–	4	–	9	–	–	–
SO 215125	*H*	–	–	–	–	–	–	–	–	3.78	–	4.35	–	5.04	–	1.55	–	5.08	–	–	–
1 sample	*E*	–	–	–	–	–	–	–	–	0.96	–	0.82	–	0.74	–	0.27	–	0.71	–	–	–
ENGLAND: SURREY																					
Box Hill	*N*	–	–	–	–	–	28	–	37	–	–	–	–	–	–	–	34	–	–	–	–
Headley Warren 1976	*S*	–	–	–	–	–	4	–	5	–	–	–	–	–	–	–	4	–	–	–	–
TQ 193542	*H*	–	–	–	–	–	4.37	–	3.21	–	–	–	–	–	–	–	2.73	–	–	–	–
1 sample	*E*	–	–	–	–	–	0.92	–	0.65	–	–	–	–	–	–	–	0.72	–	–	–	–

TABLE 2. Numbers of individuals (*N*), numbers of species (*S*), diversity (*H*) and evenness (*E*) of adult leafhopper samples from different localities in Britain.

Site	Host plant	*Tilia cordata*	*Acer campestre*	*Acer pseudoplatanus*	*Aesculus hippocastanum*	*Prunus avium*	*Prunus spinosa*	*Crataegus monogyna*	*Sorbus aria*	*Sorbus aucuparia*	*Ulmus glabra*	*Betula pubescens*	*Alnus glutinosa*	*Corylus avellana*	*Carpinus betulus*	*Fagus sylvatica*	*Castanea sativa*	*Quercus robur*	*Quercus petraea*	*Quercus cerris*	*Populus nigra*
WALES: GLAMORGAN																					
Blackmill 1976	*N*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	690	–	–
SS 935864	*S*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–
2 samples	*H*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.27	–	–
	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.70	–	–
Cathays Park	*N*	–	–	–	228	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1977	*S*	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ST 176772	*H*	–	–	–	1.73	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2 samples	*E*	–	–	–	0.50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cathays Park	*N*	–	–	–	96	–	–	–	–	–	–	–	–	–	–	–	83	–	–	–	–
1978	*S*	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–
1 sample	*H*	–	–	–	2.82	–	–	–	–	–	–	–	–	–	–	–	3.09	–	–	–	–
	E	–	–	–	0.64	–	–	–	–	–	–	–	–	–	–	–	0.58	–	–	–	–
Coed-y-Bedw	*N*	–	860	–	–	–	–	335	–	138	2189	120	636	425	–	2039	–	523	–	–	–
1974	*S*	–	4	–	–	–	–	5	–	8	6	5	12	4	–	4	–	11	–	–	–
ST 112826	*H*	–	2.12	–	–	–	–	3.84	–	7.69	3.04	6.62	6.85	5.26	–	1.67	–	7.72	–	–	–
8 samples	*E*	–	0.39	–	–	–	–	0.69	–	0.82	0.45	0.76	0.66	0.65	–	0.21	–	0.77	–	–	–
Fforest-Ganol	*N*	–	625	720	–	–	–	–	–	–	811	–	496	224	1165	1084	–	481	–	–	–
1974	*S*	–	6	9	–	–	–	–	–	–	9	–	16	6	7	8	–	12	–	–	–
ST 144835	*H*	–	4.20	4.77	–	–	–	–	–	–	4.01	–	8.89	4.42	3.23	2.58	–	8.93	–	–	–
7 samples	*E*	–	0.60	0.58	–	–	–	–	–	–	0.56	–	0.75	0.56	0.42	0.36	–	0.76	–	–	–
Merthyr Mawr	*N*	–	–	–	–	–	–	–	–	–	–	–	126	–	–	–	–	–	–	–	–
1974	*S*	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–
SS 870773	*H*	–	–	–	–	–	–	–	–	–	–	–	3.76	–	–	–	–	–	–	–	–
1 sample	*E*	–	–	–	–	–	–	–	–	–	–	–	0.64	–	–	–	–	–	–	–	–
Merthyr Mawr	*N*	–	–	–	–	–	–	–	–	–	–	–	653	–	–	–	–	–	–	–	–
1978	*S*	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–
1 sample	*H*	–	–	–	–	–	–	–	–	–	–	–	1.38	–	–	–	–	–	–	–	–
	E	–	–	–	–	–	–	–	–	–	–	–	0.24	–	–	–	–	–	–	–	–

Roath Park	*N*	—	—	1248	—	—	—	—	—	—	—	—	2652	—	—	1951	—	1132	—	—	—
1974	*S*	—	—	8	—	—	—	—	—	—	—	—	12	—	—	6	—	10	—	—	—
ST 185803	*H*	—	—	4.72	—	—	—	—	—	—	—	—	1.96	—	—	1.41	—	7.11	—	—	—
7 samples	*E*	—	—	0.61	—	—	—	—	—	—	—	—	0.23	—	—	0.17	—	0.64	—	—	—
Roath Park	*N*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	206	—	66	—
1976	*S*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	3	—
1 sample	*H*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.08	—	2.37	—
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.82	—	0.44	—
Roath Park	*N*	—	—	—	—	20	—	—	68	—	—	—	—	—	—	—	—	—	—	—	—
1977	*S*	—	—	—	—	4	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—
1 sample	*H*	—	—	—	—	3.21	—	—	3.08	—	—	—	—	—	—	—	—	—	—	—	—
	E	—	—	—	—	0.84	—	—	0.63	—	—	—	—	—	—	—	—	—	—	—	—
Roath Park	*N*	—	—	—	—	—	—	—	—	—	—	262	—	—	—	—	—	—	—	—	—
1978	*S*	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—	—	—	—	—	—
1 sample	*H*	—	—	—	—	—	—	—	—	—	—	4.10	—	—	—	—	—	—	—	—	—
	E	—	—	—	—	—	—	—	—	—	—	0.73	—	—	—	—	—	—	—	—	—
Taf Fechan	*N*	8	—	74	—	—	—	180	—	75	266	59	778	98	—	419	—	100	—	406	—
1976	*S*	1	—	5	—	—	—	3	—	3	5	5	6	3	—	3	—	7	—	5	—
SO 045095	*H*	1	—	4.54	—	—	—	1.91	—	2.25	3.04	2.28	1.22	2.06	—	1.82	—	5.15	—	1.87	—
1 sample	*E*	1	—	0.78	—	—	—	0.59	—	0.59	0.69	0.51	0.10	0.40	—	0.34	—	0.79	—	0.35	—
Wenallt	*N*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	553	—
1976	*S*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—
ST 153834	*H*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.98	—
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.38	—
WALES: BRECON																					
Craig-y-Cilau	*N*	30	—	—	—	—	55	58	—	—	205	—	—	—	—	—	—	—	—	—	—
1974	*S*	1	—	—	—	—	6	3	—	—	4	—	—	—	—	—	—	—	—	—	—
SO 190160	*H*	1	—	—	—	—	4.97	2.23	—	—	2.49	—	—	—	—	—	—	—	—	—	—
1 sample	*E*	1	—	—	—	—	0.74	0.58	—	—	0.66	—	—	—	—	—	—	—	—	—	—
Cwm Clydach	*N*	—	—	—	—	—	—	—	—	6	—	54	—	142	—	234	—	119	—	—	—
1974	*S*	—	—	—	—	—	—	—	—	4	—	5	—	9	—	4	—	9	—	—	—
SO 215125	*H*	—	—	—	—	—	—	—	—	3.78	—	4.35	—	5.04	—	1.55	—	5.08	—	—	—
1 sample	*E*	—	—	—	—	—	—	—	—	0.96	—	0.82	—	0.74	—	0.27	—	0.71	—	—	—
ENGLAND: SURREY																					
Box Hill	*N*	—	—	—	—	—	28	—	37	—	—	—	—	—	—	—	34	—	—	—	—
Headley Warren 1976	*S*	—	—	—	—	—	4	—	5	—	—	—	—	—	—	—	4	—	—	—	—
TQ 193542	*H*	—	—	—	—	—	4.37	—	3.21	—	—	—	—	—	—	—	2.73	—	—	—	—
1 sample	*E*	—	—	—	—	—	0.92	—	0.65	—	—	—	—	—	—	—	0.72	—	—	—	—

TABLE 2 (continued)

Site		Host plant																			
		Tilia cordata	*Acer campestre*	*Acer pseudoplatanus*	*Aesculus hippocastanum*	*Prunus avium*	*Prunus spinosa*	*Crataegus monogyna*	*Sorbus aria*	*Sorbus aucuparia*	*Ulmus glabra*	*Betula pubescens*	*Alnus glutinosa*	*Corylus avellana*	*Carpinus betulus*	*Fagus sylvatica*	*Castanea sativa*	*Quercus robur*	*Quercus petraea*	*Quercus cerris*	*Populus nigra*
Juniper Hall/	*N*	54	–	–	22	50	–	–	45	–	–	–	–	–	–	–	–	–	–	–	–
Box Hill 1978	*S*	3	–	–	3	6	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–
TQ 180505	*H*	2.65	–	–	1.52	4.12	–	–	5.67	–	–	–	–	–	–	–	–	–	–	–	–
1 sample	*E*	0.07	–	–	0.30	0.79	–	–	0.89	–	–	–	–	–	–	–	–	–	–	–	–
Mitcham Common	*N*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	93
1976	*S*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
TQ 295675	*H*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.16
1 sample	*E*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.55
Mitcham Common	*N*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	23
1977	*S*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
1 sample	*H*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.77
	E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.83
SCOTLAND: WEST SUTHERLAND																					
Inverpolly	*N*	–	–	–	–	–	–	–	–	–	13	112	14	148	–	–	–	–	–	–	–
1968	*S*	–	–	–	–	–	–	–	–	–	3	4	2	2	–	–	–	–	–	–	–
NC 085163	*H*	–	–	–	–	–	–	–	–	–	2.75	2.73	1.82	1.35	–	–	–	–	–	–	–
2 samples	*E*	–	–	–	–	–	–	–	–	–	0.92	0.73	0.86	0.43	–	–	–	–	–	–	–
Ben Hope	*N*	–	–	–	–	–	–	–	–	39	–	149	28	–	–	–	–	–	–	–	–
1968	*S*	–	–	–	–	–	–	–	–	2	–	3	3	–	–	–	–	–	–	–	–
NC 465535	*H*	–	–	–	–	–	–	–	–	1.72	–	2.97	1.36	–	–	–	–	–	–	–	–
2 samples	*E*	–	–	–	–	–	–	–	–	0.78	–	0.99	0.28	–	–	–	–	–	–	–	–
Duartbeg	*N*	–	–	–	–	–	–	–	–	–	–	48	–	166	–	–	–	–	–	–	–
1968	*S*	–	–	–	–	–	–	–	–	–	–	4	–	2	–	–	–	–	–	–	–
NC 164396	*H*	–	–	–	–	–	–	–	–	–	–	2.93	–	1.11	–	–	–	–	–	–	–
2 samples	*E*	–	–	–	–	–	–	–	–	–	–	0.77	–	0.09	–	–	–	–	–	–	–
Mean diversity		1.55	3.15	4.67	2.02	3.66	4.67	2.66	3.99	3.86	3.06	3.71	3.40	3.20	3.23	2.26	2.91	6.68	4.27	2.07	1.96
Mean evenness		0.90	0.49	0.66	0.48	0.81	0.83	0.62	0.72	0.78	0.66	0.75	0.47	0.48	0.42	0.27	0.65	0.75	0.70	0.39	0.69

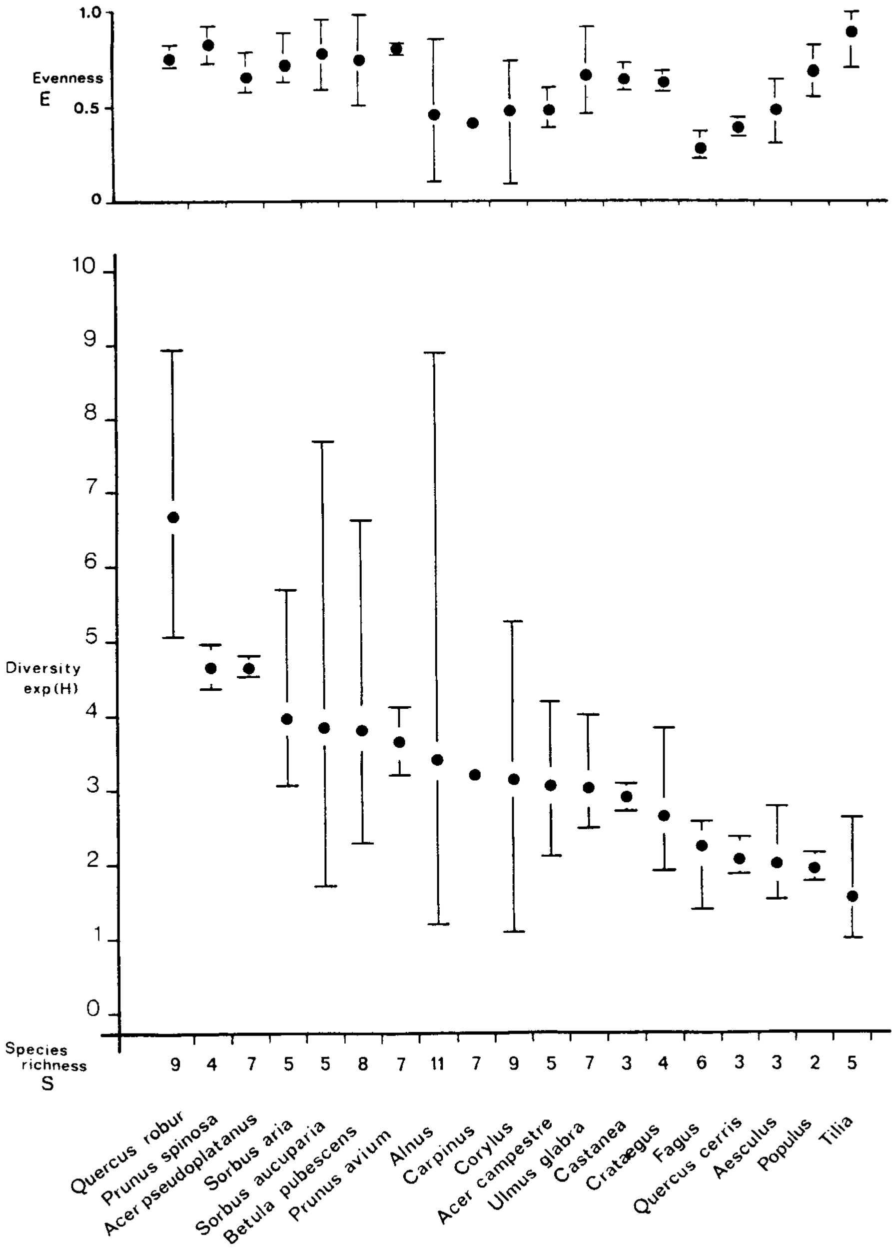


FIG. 3. Measures of diversity of mesophyll-feeding leafhoppers for adult samples from nineteen trees in S. Wales, S.E. England and N.W. Scotland. Data from Table 2. Vertical bars represent total range of measurements for each tree.

aucuparia, S.aria and *Acer campestre,* have a higher evenness and as a result a higher species diversity. The diversity of Scottish samples is mostly lower than that of samples from South Wales.

This approach to the comparison of tree species samples has the disadvantage that the identity of leafhopper species is ignored and that quantitative population samples are required. One way to take account of species identity is to measure the relative similarity of samples based on the ratio of shared species. Here only data on presence or absence of particular species in any habitat are required. Such a measure is given by Sφrensen's coefficient of similarity (Southwood, 1978), which is given by $100 \times 2c/(a + b)$, where c = number of shared species, a = number of species in habitat A, and b = number of species in habitat B. This coefficient tends to emphasize the importance of species common to both habitats. Both Sφrensen's coefficient and the coefficient of Percentage Similarity (Southwood, 1978) were employed by Claridge & Wilson (1976).

More complete leafhopper data are now available (Table 1) and similar analyses were made on the wider range of tree species. In practice it was found that there was little to choose between Sφrensen's Coefficient and that of Percentage Similarity, and so only the former is used here (Table 3).

Four relatively close associations may be recognized with 75% or more similarity between the component species. These are between: (1) *Tilia, Acer campestre* and *Aesculus*; (2) the more closely allied *Malus, Sorbus aucuparia* and *S.aria* (family Rosaceae); (3) *Carpinus* and *Fagus*; and (4) *Nothofagus* and *Fagus.* Most other trees have much less similarity with each other with respect to their leafhopper faunas. *Frangula, Populus, Salix fragilis, S.cinerea* and *Pinus* have no similarity with each other or with any other trees. The relatively polyphagous species *Alnetoidia alneti* and *Fagocyba cruenta* have the effect of increasing the levels of similarity calculated between tree species. They were removed from some analyses by Claridge & Wilson (1976) and the levels of similarity were then very low.

The host overlap of pairs of leafhopper species was calculated by using an analogue of Sφrensen's Coefficient. This is given by:

$$\frac{2M_c}{M_h + M_i} \times 100,$$

where M_c = number of tree species in which both occur together, M_h = number of tree species in which species h occurs, and M_i = number of tree species in which species i occurs (after Whittaker, 1972).

Cluster analysis was used to produce a dendogram (Fig. 4). Most obvious are the groups of species linked together at the 100% level of similarity. The levels of similarity reflect the host ranges of leafhopper species. The groups of species at the 100% level represent monophagous species associated with the same tree. These distinct groups are responsible for the low similarity values of tree species with respect to their shared leafhopper species (Table 3). For example, groups consisting of the following species: *Kybos populi* and *Edwardsiana candidula*; *Kybos virgator* and *Edwardsiana tersa*; *Kybos butleri, K.strigilifer, Edwardsiana salicicola* and *Linnavuoriana sexmaculata*; and the single species *Aguriahana germari* correspond to the species groups confined to *Populus, Salix fragilis, S.cinerea* and *Pinus* respectively. These leafhopper groups have no similarity to each other or to the other woodland Typhlocybinae with respect to host plants. Those tree species which have close associations based on their leafhopper faunas, such as *Carpinus* and *Fagus*, and *Tilia, Acer campestre* and *Aesculus*, have only oligophagous species associated with them, and no monophagous species.

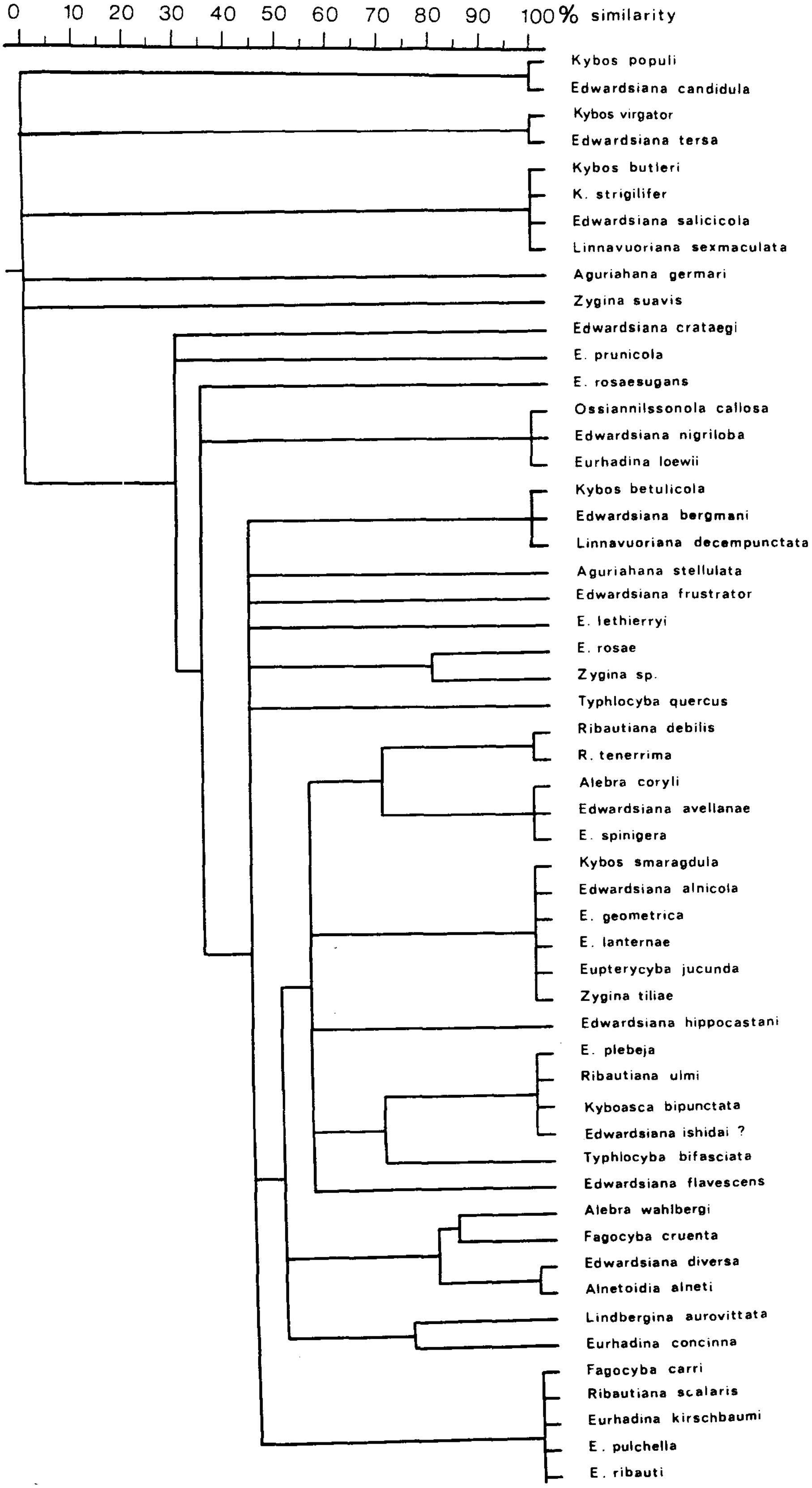
The conclusion to be drawn from these analyses is that most trees are quite distinct in their associated leafhopper species, and taxonomic affinity of the trees appears relatively unimportant (Table 3). The two *Acer* species differ markedly in their associated leafhoppers. Four species are shared, but *A.pseudoplatanus* has three specific to it. Different *Prunus* species may have very different numbers of associated leafhoppers. *Alnus* and *Betula* in the family Betulaceae, *Corylus* and *Carpinus* in the family Corylaceae, *Fagus, Quercus* and *Castanea* in the family Fagaceae all show marked differences in their leafhopper species in spite of relatively close taxonomic relationship. However, some unrelated trees are hosts for oligophagous leafhoppers, e.g. *Fagus* and *Carpinus* for *Edwardsiana flavescens*, *Tilia* and *Prunus avium* for *Aguriahana stellulata*, and *Ulmus* and *Carpinus* for *Typhlocyba bifasciata.*

Species–area relationships

Among the tree and shrub associated Typhlocybinae there are striking differences in the numbers of species found on different

TABLE 3. Sørensen's coefficient for leafhoppers from trees in Britain using rearing data from Table 1.

		1 Pinus	2 Tilia cordata	3 Acer campestre	4 A.pseudoplatanus	5 Aesculus	6 Frangula	7 Prunus avium	8 P.spinosa	9 P.domestica	10 P.padus	11 Crataegus	12 Sorbus aria	13 S.aucuparia	14 Malus	15 Rosa	16 Rubus	17 Thelycrania	18 Ulmus glabra	19 Betula pubescens	20 Alnus	21 Corylus	22 Carpinus	23 Nothofagus	24 Fagus	25 Castanea	26 Quercus petraea	27 Q.cerris	28 Q.ilex	29 Populus canescens	30 Salix fragilis	31 S.cinerea
1	*Pinus*	X																														
2	*Tilia cordata*	0	X																													
3	*Acer campestre*	0	80	X																												
4	*A.pseudoplatanus*	0	50	67	X																											
5	*Aesculus*	0	75	75	40	X																										
6	*Frangula*	0	0	0	0	0	X																									
7	*Prunus avium*	0	67	67	43	40	0	X																								
8	*P.spinosa*	0	22	22	18	0	0	54	X																							
9	*P.domestica*	0	0	0	0	0	0	44	67	X																						
10	*P.padus*	0	29	29	22	0	0	44	67	50	X																					
11	*Crataegus*	0	44	44	36	29	0	54	50	33	33	X																				
12	*Sorbus aria*	0	60	60	50	50	0	83	44	29	29	67	X																			
13	*S.aucuparia*	0	40	60	50	25	0	67	44	29	29	67	80	X																		
14	*Malus*	0	25	25	20	0	0	60	57	40	40	57	75	75	X																	
15	*Rosa*	0	0	0	0	0	0	40	29	40	0	29	50	50	67	X																
16	*Rubus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X															
17	*Thelycrania*	0	28	28	22	0	0	22	33	0	50	33	29	29	40	0	0	X														
18	*Ulmus glabra*	0	50	50	43	40	0	43	18	0	22	36	50	33	20	0	0	22	X													
19	*Betula pubescens*	0	46	46	40	36	0	40	17	0	18	33	46	31	18	0	18	20	40	X												
20	*Alnus*	0	25	25	22	14	0	22	13	0	15	13	25	12	14	0	14	15	33	42	X											
21	*Corylus*	0	28	43	37	17	0	25	15	0	18	31	29	43	17	0	33	18	37	35	30	X										
22	*Carpinus*	0	50	50	43	40	0	57	36	22	44	36	50	33	20	0	20	22	57	53	33	37	X									
23	*Nothofagus*	0	55	55	46	22	0	31	40	25	25	40	36	55	22	0	22	25	15	57	35	53	61	X								
24	*Fagus*	0	36	36	31	22	0	46	40	25	50	40	36	36	22	0	22	25	30	57	35	40	77	83	X							
25	*Castanea*	0	50	50	40	67	0	60	29	40	40	29	50	25	0	0	0	0	40	36	14	17	60	44	44	X						
26	*Quercus petraea*	0	0	13	12	0	0	12	14	17	17	0	0	13	0	0	15	0	0	22	19	21	23	62	37	15	X					
27	*Q.cerris*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	18	14	17	20	22	22	0	46	X				
28	*Q.ilex*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	22	17	20	25	28	29	0	18	50	X			
29	*Populus canescens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X		
30	*Salix fragilis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	
31	*S.cinerea*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X


0
10
20
30
40
50
60
70
80
90
100 % similarity
Kybos populi
Edwardsiana candidula
Kybos virgator
Edwardsiana tersa
Kybos butleri
K. strigilifer
Edwardsiana salicicola
Linnavuoriana sexmaculata
Aguriahana germari
Zygina suavis
Edwardsiana crataegi
E. prunicola
E. rosaesugans
Ossiannilssonola callosa
Edwardsiana nigriloba
Eurhadina loewii
Kybos betulicola
Edwardsiana bergmani
Linnavuoriana decempunctata
Aguriahana stellulata
Edwardsiana frustrator
E. lethierryi
E. rosae
Zygina sp.
Typhlocyba quercus
Ribautiana debilis
R. tenerrima
Alebra coryli
Edwardsiana avellanae
E. spinigera
Kybos smaragdula
Edwardsiana alnicola
E. geometrica
E. lanternae
Eupterycyba jucunda
Zygina tiliae
Edwardsiana hippocastani
E. plebeja
Ribautiana ulmi
Kyboasca bipunctata
Edwardsiana ishidai ?
Typhlocyba bifasciata
Edwardsiana flavescens
Alebra wahlbergi
Fagocyba cruenta
Edwardsiana diversa
Alnetoidia alneti
Lindbergina aurovittata
Eurhadina concinna
Fagocyba carri
Ribautiana scalaris
Eurhadina kirschbaumi
E. pulchella
E. ribauti

hosts (Table 1). Using our earlier more limited host-plant data (from Claridge & Wilson, 1976) we previously examined the relationship between numbers of leafhopper species and the geographical range of each host plant (Claridge & Wilson, 1978). No statistically significant relationships were found. Many of our abundant trees carried fewer leafhoppers than might have been expected and many of the rarer ones more. We have now examined the effect of geographical range on species number using the above more extensive data.

For a measure of geographical range of a host tree the number of 10 km squares occupied by each species in Great Britain (excluding Ireland) was taken from Perring & Walters (1962). Previously we used the ranges computed by Strong (1974a, b) from the same source. However, for tree genera with more than one British species, Strong added together the individual ranges for each species within that genus. Here we have treated separately all tree and shrub species for which we have comprehensive leafhopper data. For the purposes of calculation we have used the range of *B.pubescens* for *Betula* and *P.canescens* for *Populus*. Within the genus *Salix* we took *S.cinerea* as a measure for 'Sallows' and *S.fragilis* for 'Willows'. *Pinus* is omitted from the statistical analyses (as did Strong, 1974a, b) since only the supposed native range is given by Perring & Walters (1962) and not the real range including widespread plantings and seminatural areas. The introduced *Nothofagus* were not included by Perring & Walters (1962), but Nimmo (1971) gave the estimated geographical range of these trees in terms of 10 km squares as 65.

The relationship between the number of leafhoppers (S) associated with each host species and their geographical range in 10 km squares (A) from our data, but excluding *Nothofagus*, is given by the following regression equation:

$$\log_e(s+1) = 0.343 \log_e A - 0.869 \text{ (Fig. 5).}$$

This relationship is statistically significant ($F_{1,30} = 5.94$, $P < 0.02$), but the predictive value of the independent variable (geographical range) is low ($r = 0.4$). If *Nothofagus* is included, the level of significance is reduced ($F_{1,32} = 4.41$, $P = 0.04$) and the predictive value of range further reduced ($r = 0.35$).

Previously we were unable to obtain a significant relationship between numbers of associated leafhoppers and host geographical range (Claridge & Wilson, 1978a), but with larger numbers both of hosts and insects we now have a significant regression. However, a maximum of 16% ($r^2 = 0.16$) of the variation in leafhopper numbers about the regression is explained by geographical range. When *Nothofagus* is included the proportion is reduced to 12% ($r^2 = 0.12$).

A possible criticism of our previous analysis was that we used host data from only a small part of Britain, but plant distributions from the whole country (Claridge & Wilson, 1978a). However, there is no evidence to suggest that changes in host plant preferences occur in different parts of the country. Also collectors records from other areas agree generally with our conclusions (China, 1943; W. J. Le Quesne, personal communication). Our present data derive more widely and differ most particularly from the earlier set in that more host plants (thirty-six as compared to twelve) are included. What is known of host records on the mainland of northern Europe indicates no major differences from Britain in host plant associations (Günthart, 1971, 1974; Ribaut, 1936). We are therefore confident that our data form a representative list of host plant associations for these insects in Britain.

Discussion

In discussing the food specificity of herbivores, the terms monophagous, oligophagous and polyphagous are widely used. However, they cannot usefully be defined exactly since they are relative terms, representing degrees of specificity in a continuum. If monophagy is used strictly to mean feeding on only one species of host plant, then a monophagous species which feeds on a single taxonomically isolated host is not to be compared with a monophagous species which attacks only one species amongst several available closely related ones. Monophagy in the latter extreme sense, used recently by Connor *et al.* (1980), is very

FIG. 4. Dendrogram of leafhopper associations based on single linkage cluster analysis of shared host trees.

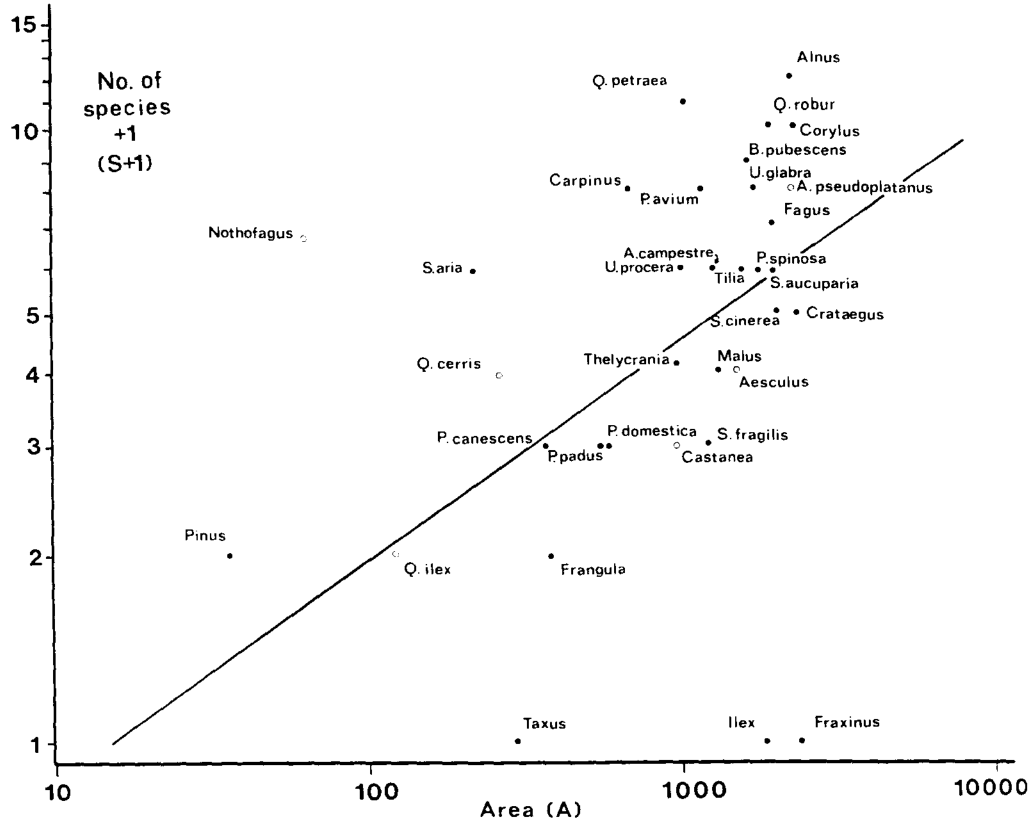


FIG. 5. The relationship between number of mesophyll-feeding leafhopper species associated with trees and the present range of each tree in Britain (computed as the number of 10 km squares from which each tree has been recorded). Points for *Pinus* and *Nothofagus* are shown, but were not used in the calculation of the regression line (see text). Open circles represent introduced plants.

rare. We prefer to use the term more inclusively (as does Cates, 1980) for species which feed either on one taxonomically very distinct species, or on a few closely related ones; the latter often being plants so similar that they regularly hybridize in nature. Examples of such closely related species from this study are *Quercus robur* and *Q.petraea,* and the 'sallow' and 'willow' groups of *Salix* species. The tree and shrub associated Typhlocybinae considered here are largely monophagous, with few oligophagous and polyphagous species (Fig. 6). Most trees have relatively distinct associated leafhopper faunas. Other tree associated leafhoppers are also mostly monophagous (Claridge & Reynolds, 1972). By contrast, leafhoppers of grassland habitats are usually said to be mostly polyphagous (for review see Waloff, 1980), though detailed studies on foodplant specificity in the field are few and difficult to undertake. However, at least one such study of grass feeding species does show considerable specificity (Drosopoulos, 1977).

The close association of tree feeding forms with particular host plants is well shown in some oligophagous bivoltine species, such as *Edwardsiana rosae* and *Lindbergina auro-vittata,* which have clear-cut differences in host preferences between generations (Claridge & Wilson, 1978c). Vidano (1960) showed a similar alternation of hosts in *Ficocyba ficaria* (Horvath).

In recent years considerable interest has developed in explaining the variation in numbers of insect species associated with different species of plants. Good general correlations between numbers of insects and the ranges of food-plants (species–area effects) have been demonstrated for many areas and

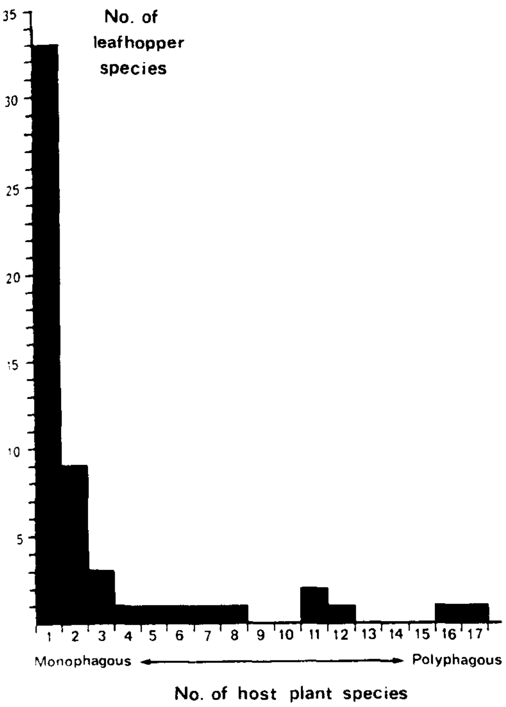


FIG. 6. **Histogram to show spectrum of host specificity of mesophyll-feeding leafhoppers. Data from** Table 1.

communities, including insects and trees in Britain (for review see Strong, 1979). It is widely agreed that the more abundant a plant in an area the larger the associated insect community is likely to be. However, though species–area correlations have been widely demonstrated, they rarely account for as much as 70% of the variance and usually for less. Particular attention has been paid to investigating the roles of such factors as plant form, chemistry and taxonomic affinity in accounting for the remaining variation in such correlations (Lawton, 1978; Strong & Levin, 1979).

An alternative approach to studying complete faunas associated with plants has been to concentrate on smaller and ecologically more uniform groups, or guilds (Root, 1973). Such guilds may sometimes be taxonomically uniform, as in the examples of the mesophyll-feeding leafhoppers described here and the gallforming guild on oaks (Cornell & Washburn, 1979), or quite diverse, as in the leafmining (Opler, 1974) and leafchewing guilds (Futuyma & Gould, 1979). Lawton & Price (1979) investigated the relationships between two taxonomic groupings: agromyzid flies and Umbelliferae in Britain. These flies are leaf- and stem-miners and approximate to a guild, as few other mining insects are associated with these plants.

Species–area effects have been demonstrated in many such guilds, though that part of the total variance around the regression, which is accounted for by the effects, is very variable – from 90% for leafminers on oaks (Opler, 1974) to 16% for mesophyll feeders in the present study. Lawton & Price (1979) attempted to account for the residual variance (68%) in their regression for agromyzid flies and British umbellifers, by considering plant factors other than range, such as size, leaf-form and taxonomic isolation, and also the effects of other insects. In this way it was possible to account for about 50% of the variation in their data. In the present study we tested for the importance of taxonomic isolation of host plants using the method of Lawton & Schröder (1977), in which the residuals from the species–area curve are plotted against the number of plant species in each genus in Britain. The effects are negligible. A weak positive relationship was found which was not statistically significant ($r = 0.31$, $F_{1,30} = 3.35$, $P = 0.7$, N.S.). Other characteristics investigated by Lawton & Price are not applicable here. Plant form and size were essentially similar as all plants were perennial trees or shrubs.

We have suggested that chemical differences between trees may be an important factor determining differences in the richness of herbivore faunas (Claridge & Wilson, 1978a). Lawton (1978) considered that clear effects of plant chemistry were very difficult to demonstrate and that the evidence for them was small or obscured by inadequacies in the data. May (1979) recently added weight to the view that host plant chemistry is unimportant in this context. However, it still seems probable to us that plant chemical factors are likely to account for some of the 84% unexplained variation in our species–area regression.

Previously we argued that the group of closely related plants studied by Opler (1974) may be more uniform chemically than the taxonomically more diverse flora with which we had been concerned. It is relevant that Cornell & Washburn (1979), in their study of gall-forming Cynipidae on oaks and related trees in California, could explain only 33% of the variation by species–area effects. However, when they excluded the non-*Quercus* oaks – that is reduced the taxonomic (and possibly chemical?) diversity – the regression was greatly improved and accounted for 72% of the variation. Thus it seems that when taxonomically, and therefore probably chemically, similar plants are studied, species–area effects are more apparent. We suggest therefore that in taxonomically more diverse floras, species-area effects may be reduced by other effects: plant chemistry is probably one of these. Much information exists to show that plants in general and trees in particular do differ in many features of secondary plant chemistry (see Hegnauer, 1962–73). Other related factors which may also be important are microanatomical ones, such as hairiness, thickness of cuticle, etc. However, we agree with Lawton (1978) that such effects are difficult to measure and to establish beyond doubt.

A further feature to emerge from our study, in agreement with Strong (1974a, b), is that recently introduced plants do not necessarily have less associated species than do related native ones. Connor *et al.* (1980) have also recently demonstrated the importance of the presence of closely allied trees in the accumulation of herbivores by an introduced tree.

Of the introduced species included in our regression (Fig. 5), *Acer pseudoplatanus* (sycamore) has the largest number of species. This may not be surprising as it is now widely abundant and was probably introduced about 1800 years ago, but it is more surprising that the associated fauna is larger than that of the native *A.campestre* and includes species not found on *A.campestre.* The more recently introduced to Britain and by no means widely planted, deciduous species of *Nothofagus* have rapidly attracted a leafhopper fauna almost as large as that of *Acer pseudoplatanus* (Table 1).

The *Nothofagus* fauna in Britain is drawn exclusively from those associated with the related *Fagus* and *Quercus* species (Fagaceae), some of which are otherwise monophagous. Leafhoppers of these trees undoubtedly have a degree of predilection (Southwood, 1973) for *Nothofagus,* probably based on physical and chemical similarities. It is tempting also to suppose that these trees may lack some feeding deterrents which prevent an otherwise quite specific species, such as *Eurhadina kirschbaumi,* from feeding regularly on plants other than *Quercus petraea* and *Q.cerris.*

Thus, we conclude that though species–area effects play a part in determining species richness of these leafhoppers on trees in Britain, other, presently unknown, but possibly physico-chemical factors, are often of overriding significance.

Acknowledgments

We wish to thank the many individuals who have helped us in field work, especially Mr G. A. Nixon. We are indebted to Dr H. Price for assistance in the preparation of tables and figures, Dr W. J. Le Quesne for his helpful advice on taxonomic matters and comments on our rearing data, Dr R. C. Welch for allowing us to use his unpublished host records for *Nothofagus,* Professor Dr R. Remane and Mr M. Asche, Philipps Universität, Marburg, Federal Republic of Germany, for information on host records in Europe, and Dr M. A. Jervis for access to his leafhopper data. Dr M. A. Jervis, Mr G. A. Nixon and Mr A. J. A. Stewart kindly read a draft of this paper.

We are deeply indebted to the Natural Environment Research Council for financial support for this project over many years.

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Accepted 15 December 1980