The Bark of Trees: Thermal Properties, Microclimate and Fauna

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The bark of trees: thermal properties, microclimate and fauna

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Summary. The thermal properties of four different types of bark were investigated on twentyfour central European tree species using thermocouples. Tree species with white bark avoid overheating of their surface by reflection of the radiation. Species with fissured and scaly barks shade inner parts of their bark. Some tree species with fissured barks show high insulation across the bark. Smooth and thin barks show no adaptation to avoid overheating. These tree species (in central Europe e.g. *Fagus sylvatica*) have to form closed stands and are not able to occur in open stands as tree species with structured or white bark types.

The arthropod fauna of the same bark types was studied on six tree species using three collecting methods. The microclimate on the bark determines the number per cm^2 of some species, some are active during winter, and other tend to aptery and reproduce parthenogenetically. On smooth bark one species dominates, whereas a highly diverse fauna lives on fissured barks. The occurrence of species on bark is determined by the microstructure, microclimate and consistence of the epiphyts. If tree species alter within forest ecosystems the dominant species on bark will persist. Specialists of fissured barks will die out if tree species with smooth bark (*Fagus sylvatica*) form the central European forest.

Little attention has been paid to an important component of the forest ecosystem – the trunks, and especially the bark, of trees. Different bark types have different physiological properties, related to the ecology of different tree species, and provide different habitats for bark-living arthropods. Bark microclimates will depend on general climatic conditions, and on the location of individual trees (e.g. stand centre or edge). The varying climates within forests, forest edges, and clearings within woods have been extensively investigated (e.g. Geiger 1961; Kiese 1971; Jaeger and Kessler 1980), as have the tree trunk microclimates (e.g. Krenn 1933; Aichele 1950; Lieberum 1961). The thermal properties of bark, which depend on its structure, will also affect the tree trunk microclimate.

Forest soil faunas (Thiede 1973; Altmüller 1979; Schaefer 1980) and arthropods which shift from one forest stratum to another during their life cycle (Funke 1971a, 1973, 1979; Funke and Sammer 1980) have been well studied. There is some information on crown faunas (Hesse 1940; Höregott 1960; Klomp and Teerink 1973). Tree trunks are important elements of forest ecosystems, e.g. 57% of the spider fauna living in a central European forest were only found on trunks (Albert 1976). For many arthropods living in forests, tree trunks are of importance to egg laying and larval development, orientation in pairing, mating area, resting area during day and night, overwintering, hunting ground and miration zone (Funke and Sammer 1980). However, little is known about arthropods which exclusively inhabit the bark of trees (Pschorn-Walcher and Gunhold 1957; Wunderlich 1982). Bark living arthropods, like arthropods which live inside the wood of trees (Annila 1977) are likely to respond strongly to microclimatic factors. Variations in the distribution of species around a trunk, species communities and reproduction biology may correspond to differences in the microclimates provided by different tree species. These in turn will depend on bark structure, which may itself represent part of a tree's suite of adaptations to climatic conditions in general, and on its particular location within the forest.

Materials and methods

Microclimate

All investigations were carried out near Marburg (Federal Republic of Germany) 50° 48′ 18″ N, 8° 48′ 16″ E, at about 300 m sealevel. The bark of central European trees may be separated into four different types: smooth, white, fissured and scaly barks. I investigated the thermal properties of twentyfour tree species: on smooth bark of *Prunus avium* L., *P. cerasus* L., *P. persica* B., *P. domestica* × *cerasifera, Sorbus aucuparia* L., *Carpinus betulus* L., *Alnus rugosa* (DU Roi) and *Fagus sylvatica* L.; on white bark of *Betula pendula* R.; on fissured bark of *Pyrus communis* L., *Malus domestica* B., *Tilia cordata* M., *Populus canadensis* M., *Salix alba* L., *Alnus glutinosa* G., *Quercus robur* L., *Juglans regia* L. and *Fraxinus excelsior* L.; on scaly bark of *Picea abies* K., *Pinus sylvestris* L., *Larix decidua* M., *Acer pseudo-platanus* L., *A. platanoides* L. and *Aesculus hippocastanum* L.

Bark temperatures at different positions were measured every 20 seconds and recorded using thermocouples (Cu/Konstantan, ∅ 0.1 mm), which were put in or on the bark of the trees at a standard 1.5 m above groundlevel. The errors in temperature measurements due to solar radiation were checked using a radiometer and found to be negligible. Global radiation was measured every 2 minutes and recorded using a pyranometer (300–3,000 nm), which was put on the trunks of the trees.

Daily temperature sums (temperatures were read from the recorded values every 2 h, and summed for each day), minimum and maximum temperatures of air and each bark recording position were read. Due to the microclimatic effect on bright days readings were made every 15 minutes and only days with low wind speed (<2 m s^{-1}) were compared).

Infrared absorptivity of bark was measured with a multipurpose spectrophotometer in the laboratory (700–1,600 nm) using pieces of bark collected in the field.

The length of vegetative period of *Fagus sylvatica, Quercus robur* and *Betula pendula* was recorded during spring and in autumn. I recorded whether the leaves were fully expanded, green, or fallen, and leaf size was calculated using 100 randomly selected leaves per tree and 10–20 individuals per tree species.

Fauna

The bark living fauna was investigated on the same bark types on six tree species in typical stands: on smooth bark of *Fagus sylvatica*, on white bark of *Betula pendula*, on fissured bark of *Quercus robur, Ulmus glabra* and *Salix alba*, and on scaly bark on *Acer pseudo-platanus*. Only adult trees were examined, since typical bark surfaces are only formed by older trees. Several methods were used to examine the fauna living on the barks:

a) Hand collections. From 20 cm above the ground up to 2.5 m all animals on the trunk around the whole tree were collected in a pooter and preserved in 70% ethanol in the laboratory. Tree species, time of day, weather conditions, girth and position of the tree, and behaviour of the bark fauna were noted. At least four trunks were examined per collection and tree species. By night sampling was carried out using a torch.

b) Collections using a vacuum cleaner. To investigate the fauna classified as 'microarthropoda' living in the epiphytic vegetation, which could not be collected by hand, pooters were fitted on a vacuum cleaner and marked areas on the trunk surface were cleaned of all epiphytic vegetation including the microarthropoda. The areas examined, at a standard 1.5 m above groundlevel, were previously marked (10 × 10 cm or 15 × 10 cm) and arranged to face north, east, west and south. The size of the marked areas on fissured barks were measured following the idges and hollows on the bark, so that the number of animals per cm^2 collected from the different tree species would be comparable. The composition of the epiphytic vegetation was noted and the microarthropoda sorted out under a microscope in the laboratory and preserved in 70% ethanol.

The epiphytic material was dried at 65° C to constant weight, burned at 800° C in a muffel-oven and weight again (organic and inorganic masses).

c) Arboreal photo-eclectors. Investigations with arboreal photoeclectors were carried out during two seasons (1982 and 1983) on one individual of *Fagus sylvatica* (smooth bark) and *Quercus robur* (fissured bark) each and on two individuals of *Betula pendula* (white bark) in typical stands. This method is described by Funke (1971 b). Four funnels per trunk were connected, forming a complete sleeve around the trunks, at 1.85 m above groundlevel. The collecting boxes faced north, west, south and east. On *Betula pendula* one funnel per trunk was used because of the small girth, which was comparable within the other tree species. Formaldehyde (4% mixed with a detergent) was used as a fixative and changed weekly. The animals collected in the different collecting boxes were preserved in 70% ethanol in the laboratory. The animals obtained by each collecting method were sorted, identified, and counted.

Statistical analysis followed Sachs (1969) and Mühlenberg (1976).

d) Birds. Certhia familiaris L. (Short-toed tree creeper), *C. brachydactyla* B. (Tree creeper) and *Sitta europaea* (L.) (Nuthatch) are known to feed on arthropods living on the bark of trees (Berndt 1977). Dead individuals of these birds ($n=8$) were collected in the field during summer, and stomach contents investigated. The time the birds spent on the barks searching for food was observed with field glasses and measured using a stop watch.

Results

1 Microclimate and thermal properties

1.1 Factors determine bark temperatures

Temperature is a thermometric property which describes the energy content of matter. Energy is transferred by radia-

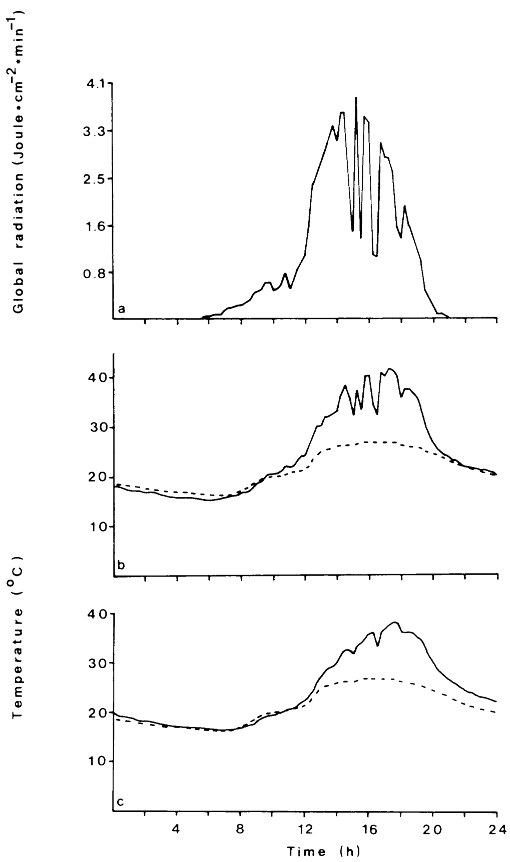

Fig. 1 a–c. Microclimate of the bark of *Fagus sylvatica* L. Global radiation (Joule cm^{-2} min^{-1}), bark temperatures —— (°C) and air temperature - - - (°C) 1,5 m above the ground on a man-made border of a forest (21.5.1981) facing south west. **a** global radiation; **b** surface temperature; **c** cambial temperature

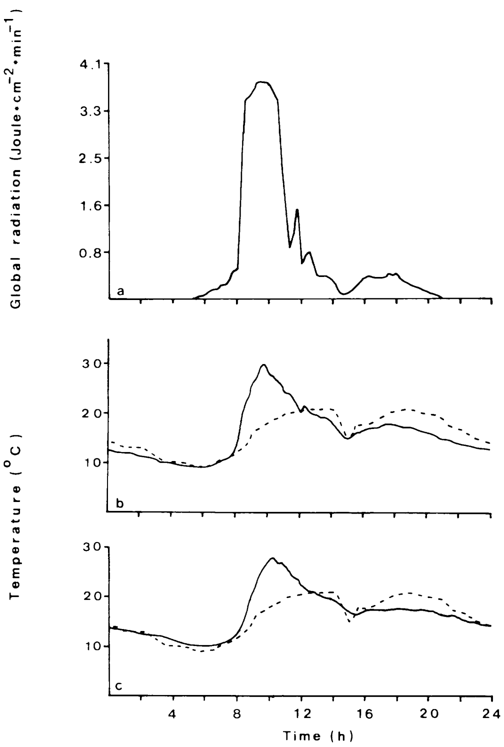

Fig. 2a–c. Microclimate of the bark of *Betula pendula* R. Global radiation (Joule cm^{-2} min^{-1}), bark temperatures —— (°C) and air temperature – – – (°C) 1,5 m above the ground on a trunk standing singly (15.6.1981). **a** global radiation facing east; **b** surface temperature facing east; **c** cambial temperature facing east

tion, convection, conduction, evaporation or condensation, and by electrical, chemical, and mechanical means. Generally the last three play a minor role in determining plant temperatures (Precht et al. 1973). Plant temperature and transpiration rate are functions of radiation, air temperature, wind speed, and humidity, which describe the environment near the plant. The temperature of small plant parts (e.g. small leaves) is tightly coupled to air temperature by virtue of large convective heat-transfer coefficients. The temperature of large plant parts (e.g. large leaves and tree tunks) can depart considerably from air temperature in a strong radiation field on days with low wind speed (Figs. 1–4) because of the relatively small convective heat-transfer coefficients (Precht et al. 1973). Inside the bark (cambium) convection, evaporation, and condensation are not very efficient in heat transfer.

1.2 Global radiation and temperatures on different types of bark

1.2.1 Smooth bark. Fagus sylvatica, which is widespread in Europe, provides an example of a tree with smooth bark. Figure 1 presents the microclimate of an individual standing on a man-made border of a forest, facing south-west. The trunk was not shaded by leaves. The high surface temperatures on the bark are due to high solar radiation onto the same spot of the trunk. Cambial temperatures reach values of up to 40° C and the temperature difference between cambium and air shows high values.

1.2.2 White bark. There are some tree species in Central Europe with white barks, one of which is *Betula pendula*.

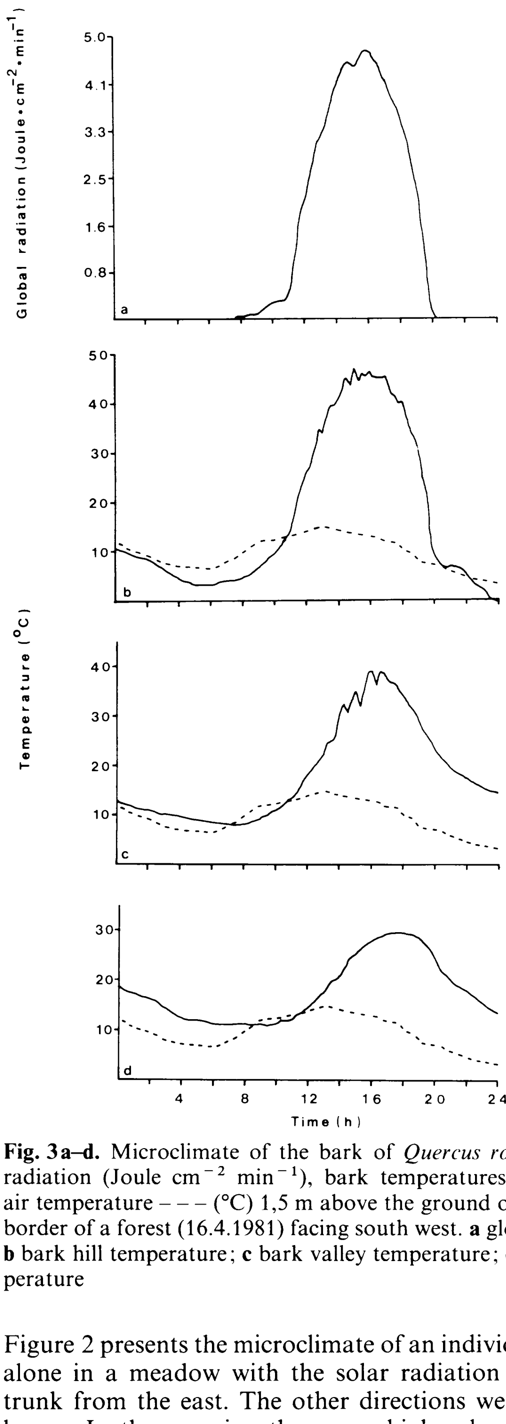

Fig. 3a–d. Microclimate of the bark of *Quercus robur* L. Global radiation (Joule cm^{-2} min^{-1}), bark temperatures —— (°C) and air temperature – – – (°C) 1,5 m above the ground on a man-made border of a forest (16.4.1981) facing south west. **a** global radiation; **b** bark hill temperature; **c** bark valley temperature; **d** cambial temperature

Figure 2 presents the microclimate of an individual standing alone in a meadow with the solar radiation reaching the trunk from the east. The other directions were shaded by leaves. In the morning there was high solar radiation on the trunk and the white surface reached temperatures of up to 30° C. Air and bark temperature show a depression between 14.30 h and 15.30 h due to a storm.

1.2.3 Fissured bark. Many tree species have fissured barks. The terms bark hills (the idges) and bark valleys (the hollows) are used to describe winged cork (Esau 1965). The microclimate of a fissured bark of *Quercus robur* standing on a man-made border of a forest facing south-west is shown in Fig. 3. Bark hills show extreme temperatures due to solar radiation and are heated considerably above air temperature. Typically bark valley temperature values are less extreme in spite of proximity to the bark hill. Also

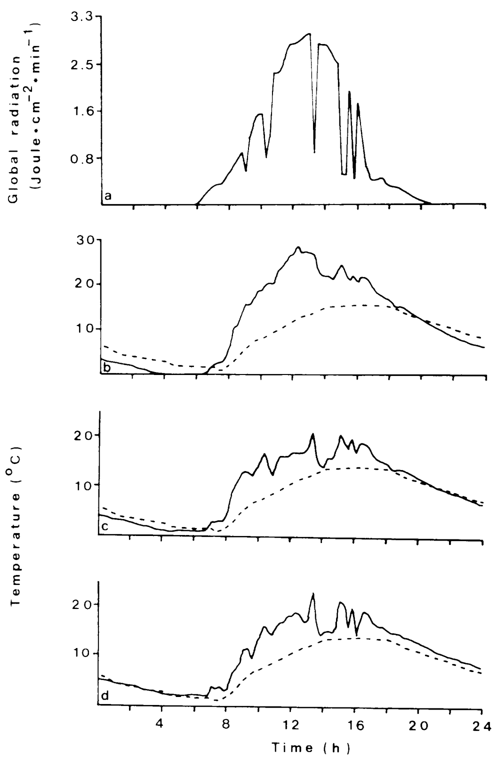

Fig. 4a–d. Microclimate of the bark of *Pinus sylvestris* L. Global radiation (Joule cm^{-2} min^{-1}), bark temperatures —— (°C) and air temperature – – – (°C) 1,5 m above the ground on a man-made border of a forest (5.5.1983) facing south. **a** global radiation; **b** surface temperature on a barkplate; **c** surface temperature under a barkplate; **d** cambial temperature

bark valley temperatures remain above air temperature for longer. On bright days bark hills may be exposed to solar radiation for 6 h or more while bark valleys are irradiated for only 1.5 h because they are shaded by the neighbouring bark hills. The cambial temperature never reaches values above 30° C (Fig. 3).

1.2.4 Scaly bark. Pinus sylvestris provides an example of a scaly bark type. Figure 4 shows the microclimate of this species standing on a man-made forest border facing south. On bark plates the temperature as well as the bark-air temperature difference reach high values due to solar radiation. The area beneath a plate is always shaded; there is less heating, and the cambium temperatures are similar to those just beneath the plates.

1.3 Insulation of bark

Insulation of bark is due to tiny air spaces of cork cells and this is responsible for the heat insulating property of bark (Cooke 1948). The insulating properties obviously differ between the different tree species and types of bark. If surface and cambial temperatures are measured at the same time, the temperature differences per mm bark and across the whole bark can be calculated. Figure 5 shows the insulation per solar radiation (average and standard deviation) (°C/Joule cm^{-2} min^{-1}) across the whole bark of different trees, with the tree species in an ordered sequence, and facing south (natural conditions, low wind speed). As the insulation of bark is a function of radiation,

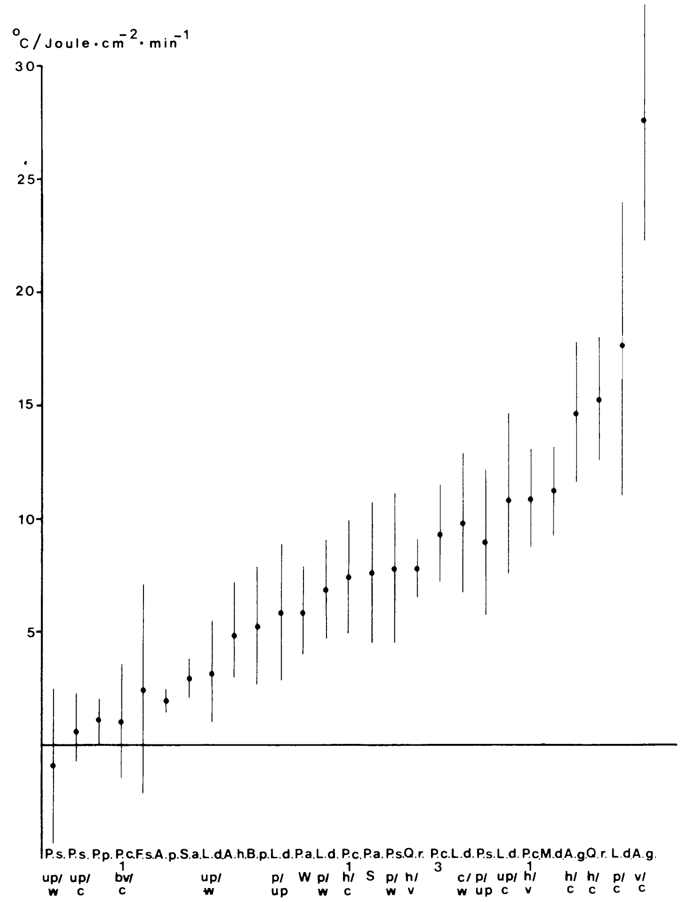

Fig. 5. Insulation of bark of different tree species. Temperature differences per solar radiation (°C/Joule cm^{-2} min^{-1}) (averages and standard deviation of all values >0.2 Joule cm^{-2} min^{-1}). All trees stand alone or on forest edges, facing south. *P.s. Pinus sylvestris, P.p. Prunus persica, P.c. Populus canadensis, F.s. Fagus sylvatica, A.p. Acer platanoides, S.a. Salix alba, L.d. Larix decidua, A.h. Aesculus hippocastanum, B.p. Betula pendula, P.a. Prunus avium* (*W.* winter, *S* summer), *Q.r. Quercus robur, P.c. 3 Prunus domestica* × *cerasifer, M.d. Malus domestica, A.g. Alnus glutinosa* Thermocouples are measuring temperature difference between: *up/w* under a plate/wood *up/c* under a plate/cambium, *bv/c* bark valley/cambium, *p/up* plate/under a plate, *p/w* plate/wood, *h/c* bark hill/cambium, *h/v* bark hill/bark valley, *c/w* cambium/wood, *p/c* plate/cambium

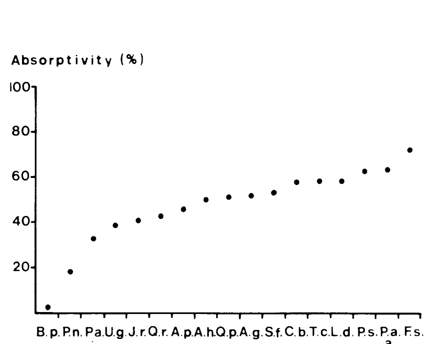

Fig. 6. Infrared absorptivity (%) of barks of different trees. (Mean of all values 700–1,600 nm.) *B.p. Betula pendula, P.n. Populus nigra, P.a. j Picea abies* (girth < 15 cm), *U.g. Ulmus glabra, J.r. Juglans regia, Q.r. Quercus robur, A.p. Acer pseudo-platanus, Q.p. Quercus petraea, A.g. Alnus glutinosa, S.f. Salix fragilis, C.b. Carpinus betulus, L.d. Larix decidua, P.s. Pinus sylvestris, P.a. a Picea abies* (girth > 50 xm), *F.s. Fagus sylvatica*

Table 1. Duration of the vegetative period of *Fagus sylvatica, Quercus robur* and *Betula pendula* standing alone, on forest edges or inside the forests

Tree species/position	Year							
	1982	days	1983	days	1984	days	∅	±
F.s. standing alone	30.4.–23.8.	115	22.4.–26.8.	126	25.4.–30.8.	127	122.6	6.6
F.s. on forest edges	30.4.– 8.10.	161	22.4.–26.8.	126	25.4.–30.8.	127	138.0	14.4
F.s. inside forest	7.5.–15.10.	161	26.4.–26.9.	156	7.5.–10.10.	156	157.6	2.8
Q.r. standing alone	12.5.–15.10.	156	2.5.– 3.10.	154	7.5.–10.10.	156	155.3	1.1
Q.r. inside forest	12.5.–15.10.	156	2.5.– 3.10.	154	7.5.–10.10.	156	155.3	1.1
B.p. standing alone	4.5.–15. 9.	134	21.4.–26.8.	127	25.4.–15.9.	143	134.6	8.0
B.p. inside forest	4.5.–15. 9.	134	21.4.–26.8.	127	25.4.–15.9.	143	134.6	8.0

F.s. = *Fagus sylvatica* L.; Q.r. = *Quercus robur* L.; B.p. = *Betula pendula* R.

the averages were calculated using all values >0.2 Joule cm^{-2} min^{-1}.

Tree species with thin and smooth bark types show little or no temperature differences per unit solar radiation between the surface and cambium. There is little thermal insulation between bark valleys and the cambium (or underneath bark plates) of tree species with fissured or scaly bark types: e.g. *Populus canadensis, Pinus sylvestris* and *Larix decidua;* but the bark hills (plates) shade the neighbouring bark valleys (under bark plates) so that these inner parts of the bark are not heated as much as the outer parts.

In addition, some tree species with fissured barks, e.g. *Quercus robur, Malus domestica* and *Alnus glutinosa*, show marked temperature differences between bark valleys and cambium. These tree species have structured barks with shading of the bark valleys plus high thermal insulation across the bark.

For *Betula pendula*, with its white bark, a medium value of insulation was calculated.

1.4 Absorptivity of bark

Infrared absorption (700–1,600 nm) was taken as an index for the absorptivity of the bark surface. On white barks of *Betula pendula* no absorption could be measured from 700–1,150 nm and the absorption from 1,200–1,600 nm is 6.9% at most.

All other barks tested showed some absorption between 700 and 1,600 nm with widely differing values, but always a minimum at 900 nm. The absorptivity is a function of wavelength, but nevertheless the average absorptivity (%) of the bark from different trees can be calculated by the mean of all values (700–1,600 nm). In Fig. 6 average absorptivity is shown. One extreme is *Betula pendula* with very low absorptivity, the other is *Fagus sylvatica*, where nearly 80% of all tested wavelengths are absorbed. Reflection of radiation by the white bark of *Betula pendula* avoids heating of the surface and the cambium.

1.5 Vegetative period

Quercus robur and *Betula pendula* show no significant differences in the duration of the vegetative period between isolated individuals and individuals inside the forest (Table 1). Free-standing individuals of *Fagus sylvatica* show shorter durations of the growing period through all the years (t test, $P<0.01$). On an average, the growing period of free-standing individuals of *Fagus sylvatica* is 35 days shorter per year, and the leaves change colour and fall earlier in autumn.

Over 4–5 years free-standing individuals will have lost the equivalent of a whole year's vegetative period compared with individuals inside the forest.

2 Fauna of bark

2.1 Oribatei

The epiphytic vegetation on bark affects the arthropod community living there (Andre 1983, 1985). In this study on the bark of *Fagus sylvatica* only *Pleurococcus sp.* could be found, on *Quercus robur Pleurococcus sp.* and *Lecanora conizaeoides* in variable amounts, on *Acer pseudo-platanus Pleurococcus sp., Lecanora conizaeoides*, and *Usnea sp.*, whereas on the barks of *Salix alba* mosses of the genus *Mnium* were dominant, *Pleurococcus sp.* was present.

Of all microarthropoda (body size <1 mm) found in the epiphytic vegetation 96.9% were Oribatei ($n=23,652$). Other groups were rare (Collembola 1.1%, Psocoptera 0.9%).

On barks of all tree species *Carabodes labyrinthicus* (M.) was dominant (Table 2) with the exception of *Salix alba* (see below). *Carabodes labyrinthicus* is fungivorous and shows little tendency for migration (Wallwork 1983).

There are significant differences in the frequencies of *Carabodes labyrinthicus* per cm^2 on the different aspects of the trunk of *Fagus sylvatica* (X^2 test, $P<0.01$). There is no correlation between the organic and inorganic masses of the epiphytic vegetation (*Pleurococcus sp.*) and the frequency of *Carabodes labyrinthicus* on the trunk (multiple correlation test). During the whole year *C. labyrinthicus* was found as adults on the trunks in high numbers. There are different microclimates on different aspects of the trunk: significant differences exist in temperature sums, minimum and maximum temperatures every day around the trunk (X^2 test, $P<0.01$) even in closed stands. The average maximum temperatures (bark-air difference) per day calculated for every day for three months in winter (December 1982–March 1983) are exponentially correlated with the total number of *Carabodes labyrinthicus* found on the same positions on the trunk of *Fagus sylvatica* ($\ln y = 6.95 + 1.24\,x$, $r=0.95$, $P<0.001$). The same was found for the frequency of *C. labyrinthicus* on the bark of *Quercus robur*. The frequency of this Oribatid species on the different aspects on treetrunks is determined by their microclimatic conditions.

Table 2. Oribatei on trunks of different trees (mean number per collection)

	F.s.	Q.r.	B.p.	A.p.	S.a.	U.g.
Phthiracarus spec. Petry		0.01	0.01	0.3		0.07
Camisia spinifer (C.L. Koch)	0.005	0.01	0.01			
Camisia horrida (Hermann)	0.06	0.05	0.05	2.03		
Camisia segnis (Hermann)			0.38		1.0	
Camisia spec.	0.005			0.75		
Belba gracilipes Kulcz.	0.06	0.01	0.02	0.28	0.12	0.07
Belba spec.	0.005	0.09	0.06			
Eremaeus hepaticus C.L. Koch		0.09	0.02	0.43	43.62	0.03
Eremaeus oblongus C.L. Koch		0.02				
Ceratoppia bipilis (Hermann)				0.08		
Oribata geniculatus (L.)				0.97	1.06	
Xenillus clypeator Rob.-Desv.		0.04				0.07
Xenillus tegeocranus Hermann		0.02				0.07
Carabodes labyrinthicus (Mich.)	90.70	24.91	10.36	71.02	143.76	0.62
Cepheus dentatus (Mich.)	0.01					
Tectocepheus velatus (Mich.)	0.03	0.08		0.23	151.85	
Caleremaeus monilipes (Mich.)		0.5		0.1		
Cymberemaeus cymba (Nic.)	0.63	1.03		5.93	5.18	0.03
Micreremaeus brevipes (Mich.)					1.5	
Phauloppia lucorum (C.L. Koch)		0.06				
Oribatula exilis (Nic.)	0.005			0.05	11.0	0.07
Oribatula tibialis (Nic.)	0.01					
Eporibatula rauschenensis (Sell.)		0.14		13.67	54.76	
Scheloribates laevigatus (Koch)	0.02	0.01			2.0	
Scheloribates latipes (Koch)					2.0	0.03
Trichoribates trimaculatus (Koch)		0.01				
Chamobates spinosus Sell.		0.02				
Chamobates subglobosus (Oudem.)		0.01		0.08		
Chamobates lapidarius (Lucas)		0.14				
Chamobates schützi (Oudem.)					13.5	
Oribatella calcarata (C.L. Koch)		0.03	0.02	0.13	0.5	
Oribatella reticulata Berl.		0.07				
Parachipteria punctata (Nic.)		0.03				
Pelops plicatus (C.L. Koch)				0.17		
N	15747	2279	919	1330	929	32
mean number per collection	45.6	13.0	10.9	41.5	48.9	1.1
total number of species	10	22	8	15	14	9
diversity (Shannon Weaver)	0.06	0.42	0.28	0.96	1.59	1.62
evenness (Shannon Weaver)	0.02	0.14	0.13	0.34	0.60	0.70

F.s. = *Fagus sylvatica* L.; Q.r. = *Quercus robur* L.; B.p. = *Betula pendula* R.; A.p. = *Acer pseudo-platanus* L.; S.a. = *Salix alba* L.; U.g. = *Ulmus glabra* HUDS

The dominant species (Table 2) are quite similar on the bark of *Fagus sylvatica, Quercus robur* and *Betula pendula*, and there are only few species of Oribatei, which coexist besides *Carabodes labyrinthicus*. On bark of *Acer psuedoplatanus, Salix alba* and *Ulmus glabra* different Oribatid species and different epiphyts were found (Table 2). Despite of that, the values of diversity and evenness (Shannon Weaver), calculated for Oribatei living on the trunks, on richly structured barks (fissured and scaly) differ markedly from the values on smooth and white bark types (Table 2).

The microclimate on different aspects of the trunks of *Fagus sylvatica* and *Quercus robur* is important for the distribution of *Carabodes labyrinthicus*. The structure of the bark determines the species community of Oribatei on tree trunks.

2.2 Araneae

There are some spider species living exclusively on bark of trees (Wunderlich 1982). One of them is *Drapetisca socialis* (S.), the most important predator in European forest ecosystems (Funke 1973). Until now it has been recorded from the bark of *Fagus sylvatica* (Kullmann 1961; Albert 1976; Funke 1979), but I found it living on the bark of all trees (Table 3) and it is four times more frequent on the bark of *Betula pendula* than on the bark of *Fagus sylvatica* (Fig. 7).

As a rule the adult stage of most spider species in central Europe is found during summer (Toft 1976). *Agyneta innotabilis* and *Entelecara penicillata* live mainly on trunks of trees with fissured or scaly barks. Subadults of both species were found during January, adults from May–August and subadults were found again in September. This suggests that *A. innotabilis* and *E. penicillata* use the favourable microclimatic conditions of bark valleys to reproduce even in early spring and in late autumn.

Only few species were found on the smooth bark of *Fagus sylvatica* and on white bark of *Betula pendula*. Here *Drapetisca socialis* was dominant, whereas on the fissured bark of *Quercus robur Entelecara penicillata* was dominant and *D. socialis, Micaria subopaca* and *Agyneta innotabilis* were also found. The spiders showed preferences for the structure of the bark: summed over the whole year more species and individuals were found on trunks of *Quercus robur* than on any other tree species. On richly structured bark types (fissured and scaly) the indices of diversity and evenness (Shannon Weaver) calculated for Araneae showed higher values than on smooth and white bark types (Table 3).

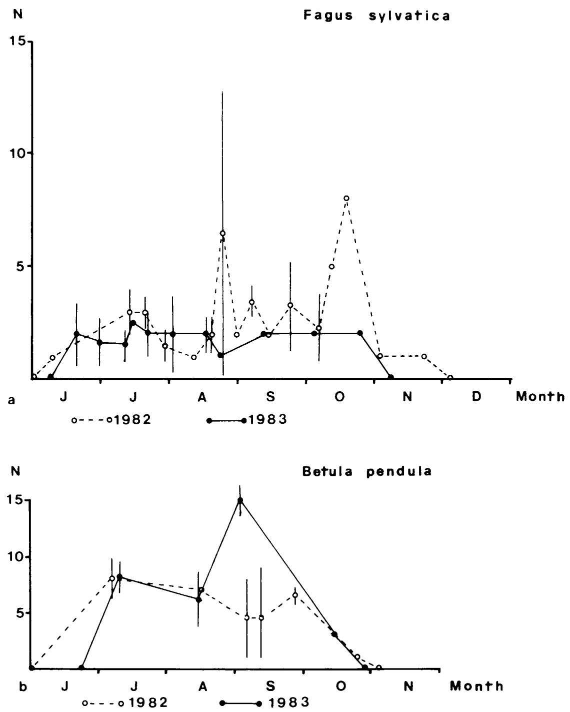

Fig. 7a, b. *Drapetisca socialis* (S.) on trunks of *Fagus sylvatica* and *Betula pendula* (hand collections, mean and standard deviation per trunk)

Some spider species living exclusively on richly structured bark use the microclimatic conditions to reproduce in early spring and in late autumn, and on fissured barks always more species and individuals were found.

2.3 Psocoptera

Many Psocoptera are known to live on bark of trees (Günther 1974). *Pseudopsocus rostocki* K. lives exclusively on bark, reproduces parthenogenetically, has wingless females, and the eggs pass the winter on the bark (Günther 1974). *P. rostocki* was mainly found on bark of *Quercus robur*. Larvae were collected with the vacuum cleaner from May–August, adults from June–December. The distribution on the trunks is uneven: positions facing west and south on the trunks were preferred (X^2 test, $P<0.01$). This uneven distribution around a trunk is not correlated with organic or inorganic masses of the epiphytic vegetation, but it follows the average temperature sums (difference bark-air) per day calculated for every day for three months (March–May 1982) of the same aspects on the bark of *Quercus robur* in a closed stand ($y=0.73+0.10\ x$, $r=0.99$, $P<0.001$).

Of all Psocoptera species living exclusively on bark 50% show size reduction in the wings of the females, while males have fully developed wings (e.g. *Reuterella helvimacula, Pseudopsocus meridionalis*). Another group is found in *Cerobasis guestfalicus, Elipsocus hyalinus, Pseudopsocus rostocki* and *P. subfasciatus:* they are micropterous or apterous and reproduce parthenogenetically. New trunks are settled by larvae while drifting with the wind (Hamilton 1978).

On fissured bark (*Quercus robur* and *Salix alba*) were always found more individuals of Psocoptera than on smooth or scaly bark (Table 4). Within the species communities on the different bark types, *Reuterella helvimacula* specializes on the smooth bark of *Fagus sylvatica* and is dominant there (Table 4). It is also present on fissured barks, but there other species are dominant (Table 4). The values of diversity and evenness (Shannon Weaver) on fissured barks are three times higher than on smooth bark.

Table 3. Araneae on trunks of different trees (mean number per collection)

	F.s.	Q.r.	B.p.	A.p.	S.a.	U.g.
Theridion vittatum C.L. Koch		0.01				
Theridion mystaceum L. Koch	0.01	0.05	0.02			
Theridion simulans Thorell		0.01				
Theridion varians Hahn.		0.01				
Theridion pallens Blackwall	0.01					0.03
Agyneta innotabilis (O.P.-Camb.)	0.01	0.24		0.55	0.05	0.06
Drapetisca socialis (Sundevall)	1.01	0.81	4.0	0.30	0.05	0.03
Entelecara penicillata (Westring)	0.04	3.32	0.04	0.70	0.11	
Kratochviliella bicapitata Miller						0.27
Micaria subopaca Westring	0.02	0.33				
Xysticus lanio C.L. Koch	0.01	0.01	0.01			
N	197	430	346	33	5	16
mean number per collection	1.1	4.7	4.1	1.6	0.3	0.5
total number of species	7	9	4	3	3	4
diversity (Shannon Weaver)	0.54	1.05	0.11	1.04	1.03	1.17
evenness (Shannon Weaver)	0.26	0.45	0.08	0.95	0.94	0.73

F.s. = *Fagus sylvatica* L.; Q.r. = *Quercus robur* L.; B.p. = *Betula pendula* R.; A.p. = *Acer pseudo-platanus* L.; S.a. = *Salix alba* L.; U.g. = *Ulmus glabra* HUDS

Table 4. Psocoptera on trunks of different trees (mean number per collection)

	F.s.	Q.r.	B.p.	A.p.	S.a.
Cerobasis guestfalicus (Kolbe)					0.04
Elipsocus hyalinus (Stephens)	0.022				
Elipsocus mclachni Kimmins	0.003	0.007			
Pseudopsocus rostocki Kolbe		0.612		0.06	0.04
Pseudopsocus fuscipes (Reuter)				0.09	
Pseudopsocus meridionalis Bad.		0.014			
Reuterella helvimacula (Enderl.)	0.75	0.176		0.03	0.28
Peripsocus subfasciatus (Rambur)					0.09
Lachesilla quercus (Kolbe)					0.04
Amphigerontia contaminata (Steph.)	0.003				
Loensia fasciata (Fabr.)	0.026	0.302	0.511	0.06	
Loensia variegata (Latr.)	0.042	0.183	0.011		0.61
Trichadenotecnum sexpunctatum (L.)	0.003	0.021		0.03	0.09
Trichadenotecnum germanicum Roes.		0.035			
Trichadenotecnum incognitum Roes.		0.014			0.04
Hyalopsocus contarius (Reuter)					0.04
N	223	194	44	13	26
mean number per collection	0.8	1.3	0.52	0.27	1.3
total number of species	7	9	2	5	9
diversity (Shannon Weaver)	0.54	1.50	0.1	1.52	1.50
evenness (Shannon Weaver)	0.27	0.68	0.15	0.94	0.72

F.s. = *Fagus sylvatica* L.; Q.r. = *Quercus robur* L.; B.p. = *Betula pendula* R.; A.p. = *Acer pseudo-platanus* L.; S.a. = *Salix alba* L.

The microclimate of bark around a treetrunk influences the distribution of Psocoptera species living there. Psocoptera show certain adaptations in morphology and reproduction biology to the microhabitat and the bark structure of the different trees influences the species community.

2.4 Rhynchota

Empicoris vagabunda (L.) (Heteroptera, Reduviidae) is a species living exclusively on bark, mainly of *Quercus robur* and *Betula pendula*. It could be found only by hand collections (once in an arboreal photoeclector). Larvae were found from June to September and adults from July to October. Hatched exuvia on trunks demonstrated that hatching occurs on bark. *E. vagabunda* is not a kleptoparasite of spiders (Remane, unpublished data) but was found to be a predator of Collembola and of larvae of different insect taxa. Another species *Empicoris baerensprungi* (D.) lives only on the bark of *Quercus robur* and has previously been found very seldom (Zebe 1972).

Loricula elegantula (B.) (Heteroptera, Microphysidae) lives exclusively on bark: all stages of larvae and adults could be found by vacuum cleaner collections and by hand collections ($n = 297$), but very sledom in arboreal photoeclectors ($n = 6$). The species lives mainly on the bark of *Fagus sylvatica* during summer.

Arboreal photoeclectors collect other speices: they are caught while in transit between different forest strata (soil/crown), where most of their life-cycle is spent. Larvae of *Tachycixius pilosus* (O.) live in the ground and the adults climb up the trunks and live in the crowns of *Quercus robur*. The eggs of *Jassus lanio* (L.) are found in the soil, larvae climb up the trunks, and larvae and adults live in the crowns of *Quercus robur* (Fig. 8). The abundances of these two species differ greatly from year to year (X^2 test, $P < 0.01$)

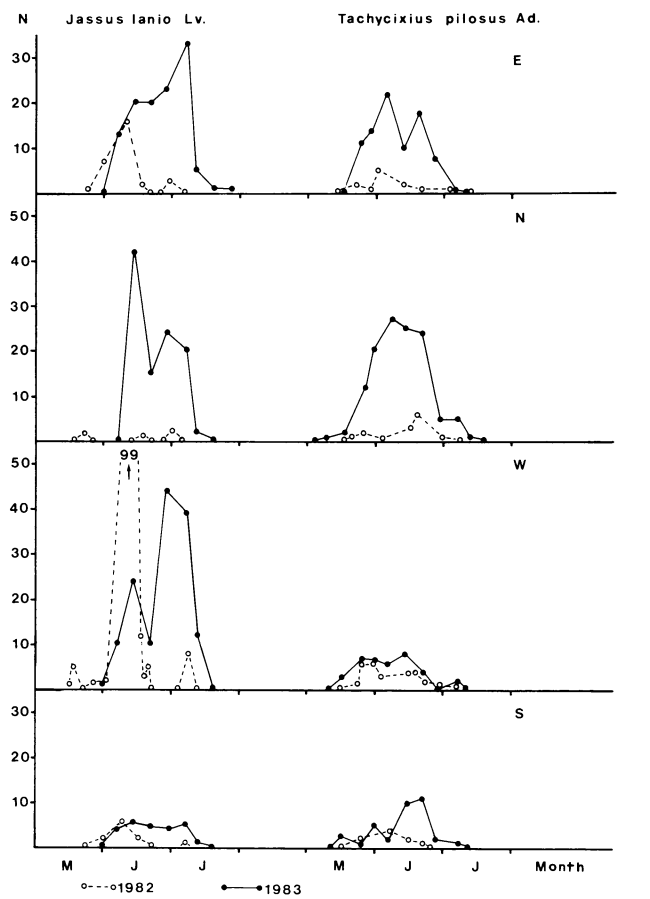

Fig. 8. ***Jassus lanio*** **larvae (*Lv*) and** ***Tachycixius pilosus*** **adults (*Ad*) on trunks of** ***Quercus robur*****. Arboreal photoeclector collections facing east (*E*), north (*N*), west (*W*) and south (*S*)**

Table 5. Brachycera on trunks of different trees (mean number per collection)

	F.s.	Q.r.	B.p.	A.p.	S.a.	U.g.
Tachypeza nubila Meigen	5.52	1.47	0.48	0.80	0.05	
Tachypeza fuscipennis Fall.	0.02					
Neurogona quadrifasciata Fabr.	0.71	0.07	0.07	0.10		
Medetera cuspidata Collin	0.02					
Medetera jacula Fall.	0.06	0.06	0.03		0.29	0.25
Medetera dendrobaena Kowarz	1.31	0.20				
Medetera ambigua Zett.	0.01					
Medetera truncorum Meigen				0.05	0.11	0.10
Medetera insignis Girschner						0.05
Medetera excellens Frey		0.44			0.11	0.50
Medetera perfida Parent	0.005					
Lycia rorida Fall.	0.03	2.07	0.09	1.30	0.70	1.45
Tricholauxania praeusta Fall.	0.01	0.12				
Peplomyza discoidea Meigen		0.73				
Peplomyza litura Meigen				0.05	0.05	
Rhagio scolopaceus L.	0.10					
Rhagio lineola F.		0.04				
Rhagio latipennis Loew	0.26	0.07	0.01	0.25		
Rhagio maculatus Deg.	0.005					
N	1406	479	59	51	23	47
mean number per collection	8.06	5.27	0.68	2.55	1.31	2.35
total number of species	13	10	5	6	6	5
diversity (Shannon Weaver)	1.13	1.65	1.28	1.28	1.07	1.23
evenness (Shannon Weaver)	0.42	0.69	0.71	0.66	0.67	0.63

F.s. = *Fagus sylvatica* L.; Q.r. = *Quercus robur* L.; B.p. = *Betula pendula* R.; A.p. = *Acer pseudo-platanus* L.; S.a. = *Salix alba* L.; U.g. = *Ulmus glabra* HUDS

(Fig. 8). Climbing up the trunks, larvae of *J. lanio* avoid positions facing south (X^2 test, $P<0.01$) while adults of *T. pilosus* avoid positions facing south and west (X^2 test, $P<0.01$). The preferred aspects for climbing up a trunk differs within the phytophagous species, e.g. larvae of *Fagocyba douglasi* (E.) prefer positions facing south and west to climb up on trunks of *Fagus sylvatica* and do not correlate with the main wind direction (in central Europe north west). The larvae emerge from the soil and climb up the trunks without being previously drifted by the wind.

Arboreal photoeclectors are inefficient in collecting species living exclusively on bark; they collect mainly (phytophagous) species in the act of changing strata. Species living exclusively on bark have little tendency for migration and are not caught by arboreal photoeclectors but by hand collections.

2.5 Coleoptera: Curculionidae

The phenology of the Curculionidae is described by Nielson (1974). When the leaves of the trees are not fully developed, e.g. 1983 on 27 April (Table 1), the wingless adults of *Strophosoma melanogrammum* (F.), *S. capitatum var. rufipes* S. and *Otiorhynchus singularis* (L.) climb up the trunks mainly of *Fagus sylvatica*. At this time a mean of 87 individuals of *S. melanogrammum*, 6.6 individuals of *S. capitatum var. rufipes* and 10.8 individuals of *O. singularis* climb up one trunk of *Fagus sylvatica* within 1 h during night (full darkness). Of the total hand collections of *S. melanogrammum* 80% were made by night. One week later all weevils are in the crown of the trees and can only seldom be found on trunks. They climb up within a short period of time during night and settle in the crown very quickly.

2.6 Diptera: Brachycera

Empididae are the most important Diptera in forest ecosystems (Funke 1973). *Tachypeza nubila* M. (Empididae) is present on the bark of all tree species except *Ulmus glabra* (Table 5). The larvae live in the soil (Altmüller 1976). From the middle of May until mid-November the adults could be collected by hand (Fig. 9). They were rarely recorded in the arboreal photoeclectors. This species lives exclusively on bark and is a predator of all insect taxa occurring there up to their own body size. It occurrs in spring on the trunks with great regularity (1981: 19 May, 1982: 17 May, 1983: 17 May, 1984: 22 May, 1985: 17 May). There are two generations per year (Fig. 9), and copulations were observed during May/June and in September. The prey is caught with the first pair of legs (thorns). Males and females are quick hunters while running on the smooth bark of *Fagus sylvatica*. During hunting they establish a hunting area of about 20 cm^2 which is defended against other individuals of the same species. If there is no prey observed for about 15 min, the animal leaves this area and establishes a new hunting area on the same or another trunk. There is a continuous turnover in the individuals of *T. nubila* on the trunks in forests of *Fagus sylvatica*.

Neurogona quadrifasciata F. (Dolichopodidae) was found in hand collections mainly on trunks of *Fagus sylvatica*, and only a few appeared in arboreal photoeclectors. The biology of the species was previously unknown. Females and males occurred from mid-May to June; they sit on the trunks always head up, and the surface of the trunks are the mating grounds. Courthship behaviour is described elsewhere (Nicolai 1985).

Nearly all Lauxaniidae were collected by hand on fissured bark of *Quercus robur*, *Ulmus glabra* and *Salix alba* (91.6%). The most abundant species was *Lycia rorida* F. ($n=183$). By day and night the adults could be seen in bark valleys during summer while air temperature is more than 26° C. *Peplomyza discoidea* M. could be collected by hand only on the bark of *Quercus robur*. As the species has wings striped black it is camouflaged well on bark. Some Lauxaniidae lay their eggs on bark, and the larvae and pupae live under bark (Czerny 1949). *Peplomyza discoidea* lay their eggs singly on bark; for this species fissured bark is where egg, larvae and adult hatching take place. They harden their wings and copulate on the bark.

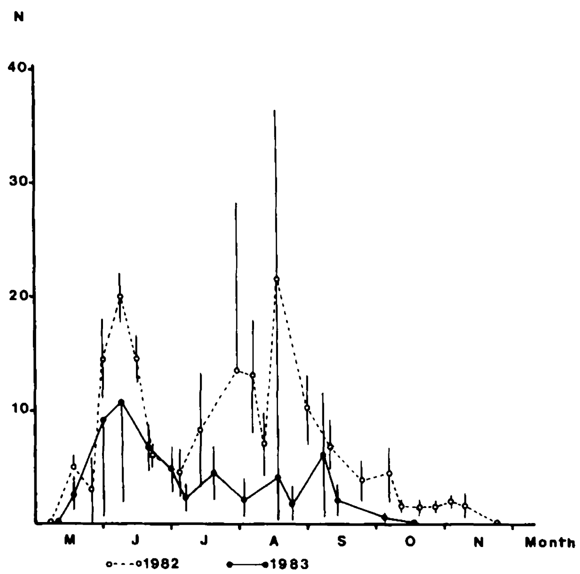

Fig. 9. *Tachypeza nubila* M. on trunks of *Fagus sylvatica* (hand collections, mean and standard deviation per trunk)

Table 6. Main Brachycera families (% of all collected species) on trunks of different trees

	F.s.	Q.r.	B.p.	A.p.	S.a.	U.g.
Rhagionidae	3.6	2.0	0.8	1.6		
Empididae	64.5	25.8	59.6	27.4	2.7	3.7
Dolichopodidae	28.1	14.3	8.8	8.0	27.0	26.5
Lauxaniidae	0.7	49.9	6.4	43.5	35.1	36.7
Chloropidae			14.5			
Sum (%)	96.9	92.0	75.6	80.5	64.8	66.9

F.s. = *Fagus sylvatica* L.; Q.r. = *Quercus robur* L.; B.p. = *Betula pendula* R.; A.p. = *Acer pseudo-platanus* L.; S.a. = *Salix alba* L.; U.g. = *Ulmus glabra* HUDS

Among Brachycera, Rhagionidae, Empididae, Dolichopodidae and Lauxaniidae play the most important roles on trunks of different trees (Table 6). Lauxaniidae are the most numerous on fissured and scaly barks (Table 6) whereas Empididae dominate on bark of *Betula pendula* (white bark), and Empididae plus Dolichopodidae on smooth bark of *Fagus sylvatica*. The other Brachycera are distributed among 17 other families.

A closer look at species level (hand collections) shows that *Tachypeza nubila* is the most dominant species on smoth bark of *Fagus sylvatica*. Scaly and fissured barks give more opportunities to hide, for pairing and egg-laying than the smooth bark of *F. sylvatica*. This is represented in the indices of diversity and evenness (Shannon Weaver) (Table 5).

Some species are vicariant on different tree species: *Peplomyza discoidea* on *Quercus robur* versus *P. litura* on *Acer pseudoplatanus* and *Salix alba* (Table 5).

2.7 Dominant species community on bark

On the smooth bark of *Fagus sylvatica* five species of different arthropod groups *Carabodes labyrinthicus* (Oribatei), *Drapetisca socialis* (Araneae), *Loricula elegantula* (Heteroptera), *Tachypeza nubila* (Diptera, Empididae) and *Medetera dendrobaena* (Diptera, Dolichopodidae) make up 96.7% of the dominant fauna (Table 7). They can be found with great regularity on the trunks, e.g. *C. labyrinthicus* during the whole year, *T. nubila* from mid-May until mid-November, and the other species according to their phenology. This prediction in the field is possible for the bark fauna of other tree species as well (Table 7).

On bark of different trees with different bark types the dominant arthropods species living their are often the same (Table 7) but the species communities including all species differ within the different types of bark. Specialists on richly structured bark are not found on smooth bark.

2.8 Preying birds on bark

In central Europe *Certhia brachydactyla* (Tree creeper), *Certhia familiaris* (Short-toed tree creeper) and *Sitta euro-*

Table 7. Fauna of the dominant arthropod species on trunks of different trees (relative dominance of frequent species)

F.s.		Q.r.		B.p.		A.p.		S.a.		U.g.	
C.l.	88.1	C.l.	63.6	C.l.	62.8	C.l.	70.1	T.v.	34.8	L.r.	36.9
T.n.	5.3	E.p.	8.3	D.s.	24.2	E.r.	13.4	C.l.	32.9	C.l.	15.8
M.d.	1.2	L.r.	5.2	L.f.	3.1	C.c.	5.8	E.r.	12.5	M.e.	12.7
L.e.	1.2	T.n.	3.7	T.n.	2.9	C.h.	2.0	E.h.	10.0	K.b.	6.8
D.s.	0.9	C.c.	2.6	C.s.	2.3	L.r.	1.2	Ch.s.	3.0	M.j.	6.3
Sum	96.7		83.5		95.3		91.3		93.2		78.5

F.s. = *Fagus sylvatica*; Q.r. = *Quercus robur*; B.p. = *Betula pendula*; A.p. = *Acer pseudo-platanus*; S.a. = *Salix alba*; U.g. = *Ulmus glabra*; C.l. = *Carabodes labyrinthicus*; T.v. = *Tectocepheus velatus*; L.r. = *Lycia rorida*; T.n. = *Tachypeza nubila*; E.p. = *Entelecara penicillata*; D.s. = *Drapetisca socialis*; E.r. = *Eporibatula rauschenensis*; M.d. = *Medetera dendrobaena*; L.f. = *Loensia fasciata*; C.c. = *Cymberemaeus cymba*; M.e. = *Medetera excellens*; L.e. = *Loricula elegantula*; C.h. = *Camisia horrida*; E.h. = *Eremaeus hepaticus*; K.b. = *Kratochviliella bicapitata*; C.s. = *Camisia segnis*; Ch.s. = *Chamobates schützi*; M.j. = *Medetera jacula* *paea* (Nuthatch) are known to prey on the arthropod fauna on barks (Berndt 1977). Stomach contents of these birds showed that they feed mainly on Coleoptera, especially Curculionidae, and on Diptera. Curculionidae do not live exclusively on bark (Table 7) but were found while changing the strata. In the stomachs no pieces of plants were found. One trend becomes obvious: inside one stomach there is always one taxon dominant, the birds are very selective feeders but not by all means on arthropods living exclusively on bark of trees. This confirms the results of Duderstadt (1964) on songbirds. On the other hand it was found that when searching for food the birds spend only half the time on the bark of *Fagus sylvatica* (Schöck, unpublished data). In mixed stand of *F. sylvatica* and *Quercus robur* they clearly preferred *Q. robur*. More arthropod individuals per trunk were found on trees with fissured bark (Tables 3, 4).

Discussion

It is well documented for American forest ecosystems (Drury and Nisbet 1973; Abrell and Jackson 1977; Christensen 1977; Connell and Slatyer 1977; Jackson and Abrell 1977; Marquis 1981), for South American forests (Veblen et al. 1981), and for forests in Switzerland (Simak 1951) that there exists no climax vegetation, but it is new to central Europe (compare Ellenberg 1982; Remmert 1985). Forcier (1975) showed autonomous cycles in natural forests of America in relation to minor and catastrophic disturbances. Up to now the functional aspects of different types of bark has been little studied. In this study, I showed that trees in central Europe have different bark adaptations to avoid overheating of their cambium. Beadle (1940) and Peace (1962) showed the heat protecting function of thick and fissured bark during fire. This ecological factor was eliminated by man a long time ago in central Europe, but is a normal factor and essential for diversity in forest ecosystems (Zackrisson 1977). In natural forests treeless areas are produced by fires (Zackrisson 1977), through the influence of wind (Brewer and Merritt 1978), of animals (e.g. *Castor fiber*), phytophagous species (Whitney 1984), or diseases (Bosch et al. 1983; Menges and Loucks 1984).

In central Europe *Betula pendula* is a pioneer species of open areas. There are normally high values of global radiation on the trunk. As nearly all of the radiation is reflected by the white bark, there is little overheating of the bark surface and cambium temperatures do not reach values of more than 30° C. From this point of view the species seems well adapted to their habitat.

Many central European tree species form thick fissured or scaly bark types. They avoid overheating for their cambium by shading the inner parts of the bark: the duration of radiation inside a bark valley or under a bark plate is significantly reduced (75%–100%) and there were found strong gradients in the temperatures between bark hills and bark valleys (plates/under plates), which are located side by side (beneath the other).

Additionally to this, some trees with (thick) fissured bark types, e.g. *Quercus robur*, show a reduction in temperature between bark valleys and cambium, what may be called insulation of the bark. The formation of thick fissured or scaly bark costs energy: Nihlgard (1972) and Pavlov (1973) showed that e.g. *Picea abies* (scaly bark) invested 22 t/ha of its total biomass in bark formation whereas *Fagus sylvatica* with its thin and smooth bark invested only 9 t/ha. Saving of energy in bark formation is one adaptation of *Fagus sylvatica* in competition with other tree species. On the other hand this makes it impossible for *F. sylvatica* to form open stands, and in natural forests of central Europe *F. sylvatica* forms closed stands, where the values of solar radiation reaching the trunks are very low (e.g. Lauscher and Schwabl 1934; Trapp 1938; Mitscherlich et al. 1967).

In the thin and smooth bark of *F. sylvatica* no mechanism to avoid overheating of the cambium was found. The values of absorptivity of the bark were the highest of all species studied, there is no shading by the structure of the bark and no insulation. Individuals which stand singly for any reason (e.g. cutting of the stand, wind throw, fire) die in the long run. *F. sylvatica* is not able to shade the tree trunks with branches as *Quercus robur*. On bright days with strong radiation there occurs strong overheating and the bark cracks off. The splits cannot be repaired (Seeholzer 1935). The phenomenon has been known for a long time (Münch 1914; Gerlach 1929; Krenn 1933; Koljo 1950; Peace 1962), but the central European forest industry has taken no account of it: so at every man-made border of *F. sylvatica* (highways as well as inside forests) this type of damage can be seen. Economic assessment of this damage has never been attempted.

Under natural conditions *F. sylvatica* with its smooth bark may occur as one piece of in time and space mosaiccally changing forest ecosystem. Over longer periods of time there will be changes in the tree species composition inside the forest, a switching to treeless areas and combinations of both. The species composition depends on abiotic factors, soil, and biogeographical factors. The ecosystem forest remains stable but the tree species forming the forest may change.

Do the arthropods living exclusively on bark react to such a mosaiccally changing forest?

Southwood et al. (1982a, b) showed with the exception of phytophagous species that there are no significant differences in arthropods living on natural occurring and on introduced tree species. Phytophygous on trees are mainly influenced by the C/N ratio, contents of lignin and polyphenols in their food (Karban and Ricklefs 1984).

None of the arthropods living exclusively on bark feed on leaves. It was demonstrated that the dominant communities living on bark are similar to each other (Table 7), and could be found even on different types of bark. A change of the tree species in central European forest ecosystems will give rise to changes in the species communities and the numbers of individuals of arthropods, but the dominant arthropods on bark will not die out. Specialists which were exclusively found on fissured bark will die out in forests of *Fagus sylvatica* or emigrate.

Compared with the smooth bark of *F. sylvatica* the surface on fissured barks were enlarged 20% for *Quercus robur* and 25% for *Salix alba* and *Ulmus glabra*. Even if one takes this into consideration for fissured barks the values of diversity and evenness indices (Shannon Weaver), calculated for all arthropods living exclusively on bark, are twice as high as on the smooth bark of *F. sylvatica*. For the coexistence of species on bark the enlargement due to fissured bark plays a minor role. More important is the microstructure forming microareas with favourable microclimatic conditions. These are responsible for clumped distributions of *Carabodes labyrinthicus* (Oribatei) around a trunk, and for the frequency per cm^2 of some species (*C. labyrinthicus*, Oribatei, *Pseudopsocus rostocki*, Psocoptera) on different aspects of a trunk. On fissured bark the microclimate was found to differ (positively) during winter from air temperatures over longer periods of time. Two spider species living on fissured bark of *Quercus robur* are adult throughout the year, what may be seen as exceptions within central European species of Araneae.

Other groups of arthropods show some more adaptations to the habitat bark: it was demonstrated that Psocoptera and Rhynchota species living exclusively on bark tend to microptery or aptery and to parthenogenesis. Small wings are of advantage on the habitat bark to reduce the surface of an individual. A micropterous population which reproduces parthenogenetically once settled on a trunk does not have to leave it. Hamilton (1978) showed that in such a case new trunks are settled by larvae having a high mortality rate while drifting with the wind.

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