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The ecological significances of trees' bark during ecosystem dynamics

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The thermal properties of different types of bark were investigated on central European, north American and south African tree species. Tree species with white barks avoid overheating by reflecting the solar radiation. Species with fissured and scaly bark types shade inner parts of their barks and some species show high insulation across their barks. Smooth and thin barks show little insulation and no reflection of global radiation. These tree species have to form closed stands and are not able to grow in open stands as tree species with more structured or with white bark types. In virgin forests, treefall gaps and other openings of the stands due to biotic or abiotic factors are typical components. Often a balance of mixed species composition with different bark types is found there. Species with white bark surfaces form the pioneer tree species in treefall gaps. During succession later, however, tree species with structured bark types and tree species with smooth bark types may follow. Tree species with thin barks are restricted to closed stands as they have no mechanism to tolerate strong global radiation on their trunks. The barks of trees have ecological functions for the trees themselves, for the tree species composition of natural forests, and for an arthropod community living exclusively in this microhabitat. The natural mosaic change within the tree species composition in the above mentioned forest ecosystems is discussed. The importance of such natural processes and possible utilization in the forest management are pointed out. The arthropod communities living exclusively on the barks of trees show adaptations to this changing tree species composition and also reflect this in their own species composition. Results from studies about the arthropod communities living on the barks of trees in the studied forest ecosystems are given. The effects by the forest managements to these arthropod communities are discussed.

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Introduction

Natural forests are heterogeneous and ever changing in space and time, thus natural disturbances of various kinds and degrees are the ecological forces. The dynamics of forest ecosystems have been studied for a long time (Drury and Nisbet 1973, Koike 1986, Mayer 1971, Mayer et al. 1979, Mayer & Neumann 1981, Schrempf 1986, Simak 1951) in nearly all parts of the world (Connell & Slatyer 1977, Forcier 1975, Jackson & Abrell 1977, Pickett & White 1985, Shugart & West 1980, Veblen et al. 1981, Veblen 1989). The theory of cyclic mosaically changing forest ecosystems is accepted widely (Lieberman & Lieberman 1987, Lieberman et al. 1989, Nicolai 1986, 1989, Pickett 1976, Schupp et al. 1989, Swaine & Hall 1988, Remmert 1987, Runkle 1989, Torquebian 1986). A cyclic mosaically changing forest ecosystem with its heterogenity in community structure, light conditions, young, mature, and dying species and individuals presents the habitats and resources for all its species in a large area. Tree trunks are one of the typical components in forest ecosystems. Different bark types have different physiological properties which are related to the ecology of the different tree species and provide different habitats for bark-living animals. The thermal properties of bark, which depend on its structure, have essential ecological functions enabling forests to survive disturbances. The species communities of bark-living arthropods reflect the dynamics of the ecosystem in their community structures. Structure and microclimate of the barks determine the distribution and phenology of arthropods living exclusively in this habitat.

Material and Methods

Study sites. The thermal properties on different types of barks were investigated on central European tree species near Marburg (50°48'N, 8°48'E), Federal Republic of Germany (Nicolai 1986); on south African tree species in a subtropical forest near George, Cape (33°57'S, 22°31'E) and in a savanna near Nylsvley, Transvaal (24°30'S, 28°45'E) (Nicolai 1989); on north American tree species in a mixed forest (Itasca State Park, Minnesota, U.S., 47°10'N, 95°15'W) (Nicolai 1993) and in an oak savanna at Cedar Creek Natural History Area, Minnesota (45°25'N, 39°10'W) (Nicolai 1991).

Microclimate. The temperatures on the barks of trees were measured using thermocouples (Cu/Konst., ∅: 0.1 mm) which were placed in and on the barks 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 using a pyranometer (300-3.000 nm) placed on the tree trunks. Due to the lack of tiny sensors no measurements of the relative humidity were conducted. Wind speed is reduced to 10 % of the surrounding air conditions in crevices of fissured barks. Absorption of radiation of barks of trees were measured in the laboratory using a Shimadzu multi-spectrophotometer. The methods are described in detail by Nicolai (1985).

The barks of trees may be roughly separated into four different types: smooth, white, fissured, and

Tab. 1. Insulation properties (°C/Joule · cm^{-2} · min^{-1}) of barks of south African trees.

Tree species	Insulation per mm bark (°C/Joule · cm^{-2} · min^{-1})	Insulation per whole bark (°C/Joule · cm^{-2} · min^{-1})
Forest		
Podocarpus latifolius	9.6	57.6
Ekebergia capensis	7.6	30.4
Olinia ventosa	8.0	20.0
Podocarpus falcatus	7.8	19.5
Apodytes dimidiata	4.2	16.8
Gonioma kamassi	1.8	15.3
Nuxia floribunda	0.9	9.9
Ilex mitis	0.9	9.0
Pittosporum viridiflorum	2.3	5.7
Cassine peragua	0.07	0.6
Scolopia mundii	0.01	0.1
Ochna arborea	0.01	0.03
Savanna		
Strychnos cocculoides	2.6	56.4
Strychnos pungens	4.5	40.4
Ochna pulchra (1.0 m)	4.2	37.8
O.pulchra (1.7 m)	2.8	16.8
Combretum apiculatum	1.6	19.2
Faurea saligna	1.3	13.0
Sclerocarya birrea	0.6	12.6
Albizia tanganyicensis	1.4	11.9
Peltophorum africanum	1.8	11.7
Securidaca longipedunculata	2.3	11.5
Burkea africana	1.9	4.0
Terminalia sericea	0.6	3.6
Acacia karroo	0.3	3.3

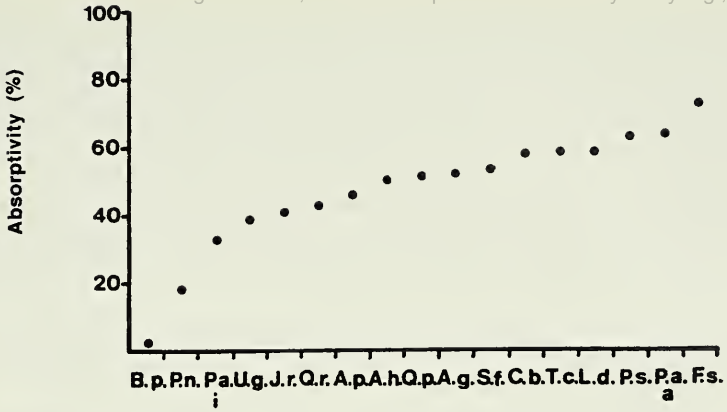

Fig. 1. Infrared absorptivity (%) of barks of different central European trees (mean 700-1.600 nm). Bp: *Betula pendula*, Pn: *Populus nigra*, Paj: *Picea abies* (girth > 50 cm), Ug: *Ulmus glabra*, Jr: *Juglans regia*, Qr: *Quercus robur*, Ap: *Acer pseudoplatanus*, Qp: *Quercus petraea*, Ag: *Alnus glutinosa*, Sf: *Salix fragilis*, Cb: *Carpinus betulus*, Ld: *Larix decidua*, Ps: *Pinus sylvestris*, Paa: *Picea abies* (girth > 50 cm), Fs: *Fagus sylvatica*.

scaly barks. In central Europe I investigated the thermal properties on smooth barks of 8 tree species; on white barks of one tree species; on fissured barks of 9 tree species; on scaly barks of 6 tree species (in total 24 tree species). In southern Africa I investigated the thermal properties on smooth barks of 11 tree species; on white barks of two tree species; on fissured barks of 10 tree species; on scaly barks of 3 tree species (in total 26 tree species). In northern America I investigated the thermal properties on smooth barks of one tree species; on white barks of two tree species; on fissured barks of 11 tree species; on scaly barks of 6 tree species (in total 20 tree species).

Fauna. The fauna living on the outer surface on the bark of healthy trees was only investigated on

Tab. 2. Insulation properties (°C/Joule · cm^{-2} · min^{-1}) of barks of north American trees.

Tree species	Insulation per mm bark (°C/Joule · cm^{-2} · min^{-1})	Insulation per whole bark (°C/Joule · cm^{-2} · min^{-1})
Pinus banksiana	0.76	61.43
Pinus strobus	0.51	61.27
Pinus resinosa	0.54	43.54
Quercus ellipsoidalis	0.25	15.60
Fraxinus nigra	0.61	15.32
Quercus macrocarpa	0.22	13.24
Populus grandidentata (0.5 m)	0.54	10.86
Thuja occidentalis	0.56	8.53
Acer rubrum	0.33	8.32
Ulmus rubra	0.37	5.55
Ulmus americana	0.24	4.87
Prunus serotina	0.32	4.83
Quercus rubra	0.56	4.81
Quercus alba	0.30	4.58
Tilia americana	0.52	3.70
Fraxinus pennsylvanica	0.21	2.61
Acer saccharinum	0.19	1.94
Betula papyrifera	0.22	1.59
Populus grandidentata (1.5 m)	0.14	1.02
Populus tremuloides	0.09	0.64
Picea mariana	0.08	0.62

adult trees, since the typical bark surfaces are only formed by older individuals. Animals were mainly collected by hand. Starting from 20 cm above the ground up to 2.5 m, all animals around the trunk of the entire tree were collected in pooters and preserved in 70 % ethanol. Additional collections were made by using a vacuum cleaner on previously marked areas on the barks. Tree species, time of day, weather conditions, girth and position of the tree, and behaviour of the bark fauna was noted. Animals were sorted, identified, and counted. Statistics follow Sachs (1969) and Mühlenberg (1993). Methods are described in detail by Nicolai (1985). The fauna on the barks was investigated on the same bark types as the microclimatic studies were done. This was carried out in central Europe on smooth bark of *Fagus sylvatica*, on white bark of *Betual pendula*, on fissured barks of *Quercus robur*, *Ulmus glabra*, and *Salix alba*, on scaly bark of *Acer pseudoplatanus*. It was also completed in southern Africa on smooth barks of

Tab. 3. Oribatei living on the barks of central European trees (mean number per collection). Fs: *Fagus sylvatica*, Qr: *Quercus robur*, Bp: *Betual pendula*, Ap: *Acer pseudoplatanus*, Sa: *Salix alba*, Ug: *Ulmus glabra*. w: white bark type, s: scaly bark type, f: fissured bark type, sm: smooth bark type.

Tree species bark type	Fs sm	Qr f	Bp w	Ap s	Sa f	Ug f
Phthiracarus sp. 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 sp.	0.005			0.75		
Belba gracilipes Kulcz.	0.06	0.01	0.02	0.28	0.12	0.07
Belba sp.	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 (Oud.)		0.01		0.08		
Chamobates lapidarius (Lucas)		0.14				
Chamobates schützi (Oud.)					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		
Number of species (N)	12	23	9	16	14	9
Mean number of specimens per m^2 (n/m^2)	45.6	13.0	10.9	41.5	48.9	1.1
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

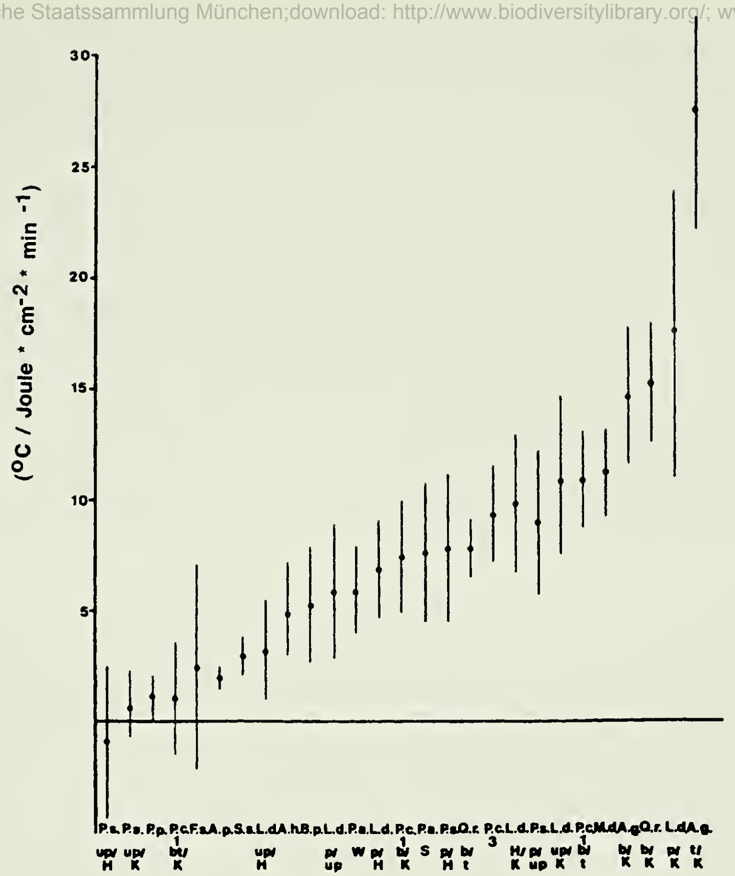

Fig. 2. Insulation properties (°C/Joule · cm^{-2} · min^{-1}) of barks of central European trees (averages and standard deviation of all values > 0.2 Joule · cm^{-2} · min^{-1}). Trees on forest edges facing south. Ps: *Pinus sylvestris*, Pp: *Prunus persica*, Pc: *Populus canadensis*, Fs: *Fagus sylvatica*, Ap: *Acer platanoides*, Sa: *Salix alba*, Ld: *Larix decidua*, Ah: *Aesculus hippocastaneum*, Bp: *Betual pendula*, Pa: *Prunus avium* (w: winter, s: summer), Qr: *Quercus robur*, Pc3: *Prunus domestica x cerasifer*, Md: *Malus domestica*, Ag: *Alnus glutinos*. Thermocouples are measuring temperature differences between: up/w: under bark plate/wood, up/c: under bark plate/cambium, bv/c: barkvalley/cambium, p/up: plate/under plate, p/w: plate/wood, h/c: barkhill/cambium, h/v: barkhill/barkvalley, c/w: cambium/wood, p/c: plate/cambium.

Apodytes dimidiata and *Cassine peragua*, on white barks of *Albizia tanganyicensis*, on fissured barks of *Olinia ventosa*, *Ocotea bullata*, *Peltophorum africanum*, and *Acacia karroo*, on scaly barks of *Podocarpus falcatus*, *Sclerocarya birrea*, and *Burkea africana*; and in north America on smooth bark of *Abies balsamea*, on white bark of *Betula papyrifera* and *Populus tremuloides*, on fissured barks of *Pinus strobus*, *Acer saccharum*, *Fraxinus pennsylvanica*, *Tilia americana*, *Quercus macrocarpa*, and *Quercus ellipsoidalis*, on scaly barks of *Pinus resinosa*, *P. banksiana*, and *Picea mariana*.

Results

1. Microclimate

Both the temperature of the air surrounding the trunk and the bark temperature were taken at the same time. To compare bark temperatures of different trees, an "absolute bark temperature" (bark temperature minus air temperature) was calculated for every value. If the surface temperature of the bark, the cambial temperature, and global radiation on the same spot are measured at the same time, the variation of absolute bark temperature per unit solar radiation, and per mm bark or across the whole bark can be calculated and compared within the different tree species. Although there are other definitions these values may be called insulation of the bark (°C/Joule · cm^{-2} min^{-1}). The calculations were made for all tree species and for all values of global radiation > 0.2 Joule · cm^{-2} min^{-1}.

Tree species with white barks avoid overheating of their surface by reflecting the strong solar radiation which reaches the trunk (Fig. 1). Species with fissured and scaly bark types shade inner parts of their barks, and some species show high insulation across their barks (Fig. 2, Tab. 1, Tab. 2). Smooth and thin barks show little insulation and may have high values of absorptivity (700-1.600 nm), e.g. *Fagus sylvatica* (Fig. 1). When this strong overheating occurs on the surface and even in the cambium, the bark cracks off leading to irreparable damages, and in the long run the trees die. In central Europe, species that suffer from this so-called "sun-burn" are especially beeches (*Fagus sylvatica*). In southern Africa shade tolerant tree species which naturally occur inside dense forests (e.g. *Apodytes dimidiata*) are known to suffer similar damage and also have a smooth bark type. In my study area in north America, no tree species with a smooth bark type appears. East of that area *Fagus grandifolia* occurs in large well-known dense stands showing a smooth bark.

In the open savanna ecoysystems of South Africa and of North America, all tree species show high insulating properties of their mostly fissured or scaly bark types (Nicolai 1989, 1991) or they have white bark types owing high values of reflection.

2. Fauna

Europe. The arthropod communities living exclusively on the barks of trees consist of about 100 different species belonging mainly to the Oribatei (Acari), Araneae, Psocoptera and Brachycera. Results of these studies are given in detail by Nicolai (1985, 1986). Other taxonomical groups, e.g. Coleoptera, were found to be migrants on trunks of healthy trees and are therefore no exclusive inhabitants in this sense. One example for a taxonomical group may be presented. Within the oribatid mites on barks of central European trees (Tab. 3), the dominant species are quite similar on the barks of *Fagus sylvatica, Quercus robur*, and *Betual pendula*. On barks of *F. sylvatica* live only few species of Oribatei, which coexist with *Carabodes labyrinthicus* (Tab. 3). More species were found on more structured bark types (Tab. 3). The values of diversity and evenness (Shannon-Weaver) calculated for Oribatei living on the trunks with richly structured barks (fissured and scaly) differ markedly from the values on smooth and white bark types (Tab. 3). Thus the structure of the bark determines the species communities of Oribatei on tree trunks. Similar results were found for other arthropod groups (Araneae, Psocoptera, Brachycera) (Nicolai 1986). The different epiphytic plant communities on the barks had no significant influence on the distribution of the bark living fauna (Nicolai 1986).

America. A comparison between the bark-living arthropods on deciduous and on coniferous tree species is only feasible in an area where both types of trees grow together in similar proportions under the same natural conditions of soil and climate. This cannot be found in central Europe but in North America, e.g. in the Itasca State Park, MN, USA. This park with an area of 3.200 ha was founded in 1891 and since then little or no managements or man-made disturbances are known.

On the barks of deciduous trees in this park, similar results to that of central Europe were found. A more diverse arthropod fauna lives on richly structured bark types of e.g. *Tilia americana* or *Acer saccharum* compared to poorly structured bark types of e.g. *Populus tremuloides* or *Betula papyrifera* (Nicolai 1993). Surprisingly, in this area the opposite was found on the barks of coniferous tree species. On the smooth bark of *Abies balsamea* nearly the same amount of species but more individuals per m^2 were found then on the richly structured (fissured and scaly) barks of *Picea mariana, Pinus resinosa*, and *Pinus strobus* (Tab. 4).

On the whole, more arthropod species live on bark of deciduous tree species then were found on the bark of coniferous tree species. Only a few arthropod species live on the barks of both types of trees species (Nicolai 1993). The arthropod communities on the bark of deciduous and coniferous tree species are well separated from each other.

To investigate the reactions of the bark living arthropod fauna to the intensities and frequencies of a naturally occurring disturbance factor I visited the Cedar Creek Natural History Area (Nicolai 1991).

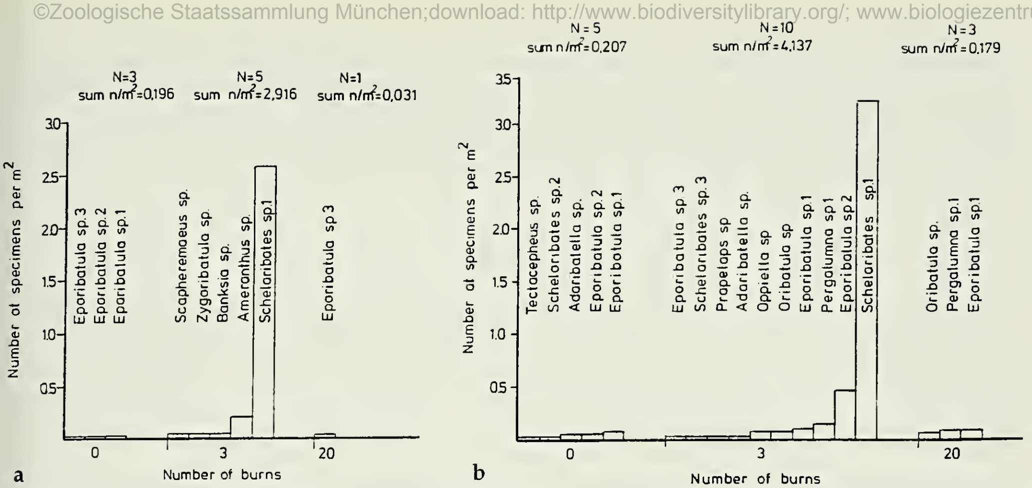

Fig. 3. Oribatei on trunks of *Quercus macrocarpa* (a) and *Quercus ellipsoidalis* (b). Number of specimens (n) per m² of bark of the given species (N) in relation to the number of burns in areas of the Cedar Creek Natural History Area.

Here oaks *(Quercus ellipsoidalis* and *Q. macrocarpa)* with their fissured bark type are the dominant tree species and a program of prescribed burning has been conducted since 1964. Initially, this program was started to restore the oak savanna (Irving 1985). The effects of the different fire frequencies on the vegetation and soils are summarized by Tester (1989). The highest numbers of species and individuals of bark living arthropods on the fissured barks of the oaks were found in areas with a moderate frequency of fires (Fig. 3). Fewer bark living species and individuals live in areas with a very high frequency of disturbances or in areas with no disturbances at all since 1964 (Nicolai 1991). The bark-living arthropods could be divided into three main groups: "Undisturbed-adapted" species occur on trunks of trees in the area not disturbed by fires at least since 1964. "Disturbed-adapted" species occur on trunks of trees in moderate disturbed areas, and "true-fire-adapted" species were found in correlation to the frequencies of fires on trunks of trees (Nicolai 1991).

Africa. In the indigenous forest at southern Africa, both the number of species and the number of individuals found on a trunk differ according to the bark type. The most diverse fauna is found on the scaly bark of *Podocarpus falcatus*, followed by that on the fissured bark of *Olinia ventosa* and *Ocotea bullata*. The bark fauna of *Cassine peragua* has medium values of diversity, and the bark fauna of *Apodytes dimidiata* (smooth bark type) has the lowest value. Only two species of oribatid mites make up 87 % of all specimens found on the bark of *Apodytes dimidiata* per m².

The dominant species composition of the arthropod fauna (>5 % of all collected animals on the barks of one tree species) on trunks with richly structured barks (scaly and fissured bark types) are closely related. This may be calculated by the similarity of the dominant species. Of the dominant species on the bark of *Podocarpus falcatus* (scaly bark) 54.2 % are also found to be dominant on the bark of *Olinia ventosa* (fissured bark type). On the other hand, the diverse fauna on richly structured bark types differs from that found on the smooth bark of *Apodytes dimidiata*; only 13.8 % of the dominant species are the same. If the bark types are ordered by the complexity of their structure (smooth - white - fissured - scaly), the values of similarity in the dominant species composition as well as species richness increases from poorly to richly structured bark types (Fig. 4).

In savanna ecosystems, richly structured bark types (fissured and scaly) are more often found then smooth bark types. All types in the savanna provide suitable microhabitats for many species. The arthropod fauna on all investigated tree species was as diverse as that on richly structured bark types in the subtropical forest. One indicator of the structure of bark may be its thickness. Smooth bark types are always thin, while fissured and scaly bark types are thicker. In the subtropical forest the diversity of the bark living arthropod fauna is related to the structure of the bark. The bark thickeness of the tree species from which the fauna was collected were all significantly different from each other, whereas bark thickeness of the savanna tree species were similar to each other and sometimes identical.

Therefore, the correlation bark thickeness : diversity of the arthropod fauna was not significant in the savanna ecosystem (Fig. 4). The arthropod fauna on the bark of trees may be separated into herbivorous, fungivorous species and carnivorous species. In the subtropical forest the ratio of herbivorous and fungivorous species to carnivorous species was much higher (2.2:1) than in the dry savanna (1.1:1). The frequency of carnivorous species per m^2 of bark on trunks of trees is higher in the savanna ecosystem then in subtropical forests.

Discussion

The process of the natural mosaic change in the tree species composition was found to be similar in the investigated three different forest ecosystems. Treefall gaps and other openings are typical and important components of forest ecosystems (Connell 1989, Frehlich et al. 1993, Lang & Knight 1983, Nicolai 1986, 1989, 1993, Palik & Pregnitzer 1993, Remmert 1985, 1987, 1991 a,b, 1993, Schrempf 1986) and all the tree species have to be adapted to this factor. Pioneer tree species with white barks (*Betula pendula* in central Europe; *Betula papyrifera* and *Populus tremuloides* in north America; *Albizia tanganyicensis* in south Africa) colonize these open areas. There are other characteristics of these pioneer tree species such as wind dispersed seeds (Whitemore 1989), limited life span (about 100 years), and fast growth. This is the reason that the timber of those tree species is often of low quality for man's use. Tree species with white bark types avoid overheating of their trunks by reflection of solar radiation and are able to form open stands. They even occur on natural and man-made forest edges. Tree species with more structured bark types may follow these pioneer tree species during succession. Some of them are even able to form open stands as they show high insulating properties across their bark. Most of them have fissured, although some have scaly bark types; they often have animal dispersed seeds, and a longer life span than the pioneer tree species. They are slower growing and their timber is of more value to man. Species with high insulating properties may even survive wild fires and thus are able to exist inside a pioneer tree species stand after a fire (or other disturbances). In both types of stands tree species having structured bark types and even tree species with a smooth and thin bark type which have low values of insulation across their bark may grow; but they have to form closed stands. These tree species save energy not producing a thick structured bark (Pavlov 1973), but they do not survive to exist on edges of treefall gaps. If the trunks are exposed to solar radiation strong overheating occurs, the bark cracks off, and in the long run the trees die. From the evolutionary point of view, smooth and thin bark of adult trees may be seen as neoteny. In the forest ecosystem the risk of an opening, which cannot be stopped by tree species with thin and smooth bark types, is reduced by the presence of trees with richly structured bark types and better insulating properties, which can survive on natural forest edges. Light regime in gaps in relation to geographical factors describe Poulson & Platt (1989).

Diversity of forest ecosystems is related to the degree of disturbance (Bradshaw 1993, Connell &

Tab. 4. Number of species (N) and sum of the number of individuals per m^2 (n/m^2) of main arthropod groups (> 5 % of all) living exclusively on barks of north American trees. Pt: *Populus tremuloides*, Bp: *Betual papyrifera*, As: *Acer saccharum*, Ta: *Tilia americana*, Fp: *Fraxinus pennsylvanica*, Ab: *Abies balsamea*, Pm: *Picea mariana*, Pb: *Pinus banksiana*, Pr: *Pinus resinosa*, Ps: *Pinus strobus*. w: white bark type, s: scaly bark type, f: fissured bark type, sm: smooth bark type.

Tree species	Pt	Bp	As	Ta	Fp	Ab	Pm	Pb	Pr	Ps	sum
	deciduous					coniferous					
bark type	w	w	s	f	f	sm	s	s	s	f	
Oribatei	1	3	6	6	3	6	1	3	4	1	19
Araneae	1	5	2	3	3	3	4	1	2	2	11
Psocoptera	2	5	2	2	3	2	3	3	3	3	8
Diptera	6	4	8	6	4	1	3	3	3	5	14
Lepidoptera	2	1	1	5	1	1	1	–	2	–	8
sum(N)	12	18	19	22	14	13	12	10	14	11	60
sum (n/m^2) all	1.4	5.9	7.9	7.2	2.3	13.1	1.9	2.8	1.5	0.7	

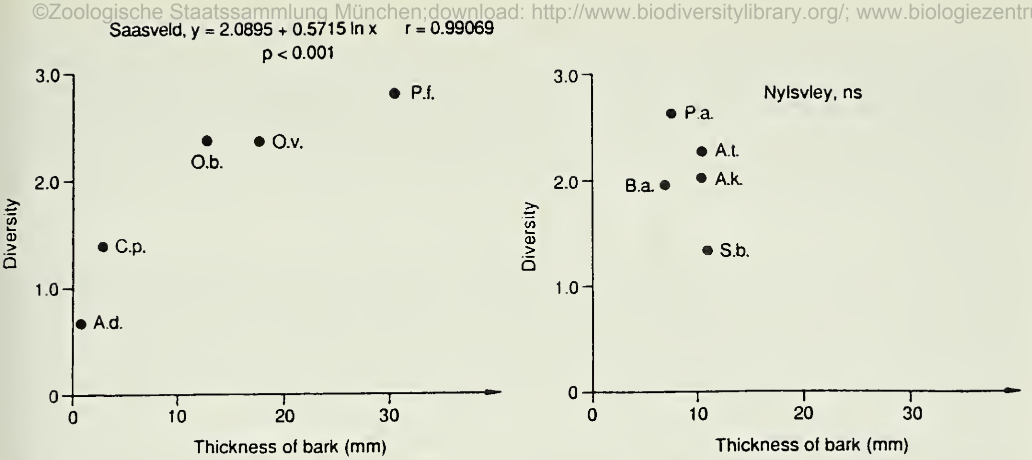

Fig. 4. Diversity (Shannon-Weaver) of arthropods living on the bark of trees in relation to the thickness of the bark in a subtropical forest (Saasveld) and a savanna (Nylsvley). Pf: *Podocarpus falcatus*, Ov: *Olinia ventosa*, Ob: *Ocotea bullata*, Ad: *Apodytes dimidiata*, Cp: *Cassine peragua*, Pa: *Peltophorum africanum*, Sb: *Sclerocarya birrea*, Ba: *Burkea africana*, Ak: *Acacia karroo*, At: *Albizia tanganyicensis*.

Slatyer 1977, Connell 1978, Drake & Mueller-Dombois 1993, Jacobs 1989, Maarel 1993, Whitemore 1989). In virgin forests of Europe, a mosaic representing the different successional stages of a forest in time and space was found by Mayer & Neumann (1981) in a large area at the same time.

Gaps in forests are necessary for successful regeneration of certain tree species (Bongers et al. 1988). Besides natural death disturbances in forest ecosystems may be caused by abiotic factors like fire (Foster & Zebryk 1993, Granström 1993, Lamont et al. 1993, Steward 1986), wind (Brewer & Merritt 1978, Matlack et al. 1993), drought (Clinton et al. 1993), or even volcanic eruptions (Spies & Franklin 1989). Disturbance may also be caused by biotic factors: animals (Basey et al. 1988, Doucet & Fryxel 1993, Gerken et al. 1992, Naiman 1988, Pastor et al. 1993, Prins & Jeugd 1993), phytophagy (Baltensweiler 1993, Molvar et al. 1993, Whitney 1984), diseases (Menges & Loucks 1984). Shure & Wilson (1993) describe the effect of patch size to plant phenolics. Wayne & Bazzaz (1993) give results for seed germination of birches on west and east sides of gaps. Davidson (1993) summarizes the worldwide effects of herbivory and granivory on terrestrial plant succession. Langvatn and Hanley (1993) show that deers feed mainly in gaps.

Many of these disturbance factors are extinguished in central Europe and tree species composition has been influenced by man for a long time [compare Motzkin et al. (1993) for the situation in north America]. Only few native species (mainly *Fagus sylvatica*, *Quercus robur*, *Q. petraea*, and *Picea abies*, *Pinus* spp.) form most of the production area for the forest industry in central Europe. *F. sylvatica* (smooth and thin bark type) does not survive openings exposed to south. Sun burn of the bark occurs, the bark cracks off and in the long run one line after the other of a stand dies back. At every man-made border of stands of *F. sylvatica* this type of damage can be seen (especially on edges facing south). In southern Africa, the same holds for *Apodytes dimidiata* on north facing edges of forest openings. Economic assessment of these damages has not been attempted. Oaks and many other tree species but not beeches are able to produce branches on the trunks which shade them if suddenly exposed to the sun.

These results support well-known consequences for forest managements which were recently summarized by Sturm (1993): large clearcuttings in forests formed mainly by *F. sylvatica* or other tree species with smooth and thin bark types should be avoided. Newly constructed roads and highways through closed forests should be avoided. However, if there is a strong demand to do so, there should be a plan to establish pioneer tree species with white bark types along the opened sides prior to construction.

In natural forests many trees species coexist beneath each other and they show the different bark types. The arthropod fauna living on the outer surface of healthy tree trunks is highly specialized to this microhabitat and cannot be found in other habitats of forest ecosystems (e.g. litter, soil) (Nicolai

1985, 1986, 1991, 1993, Weigmann & Jung 1992). The diversity of the arthropod communities living exclusively on the bark of trees is related to the structure of the bark. Smooth and thin bark types own a fauna dominated by one or two species (within the different arthropod groups), which may live there in high numbers per m^2. On richly structured bark types (fissured and scaly) a richer fauna can be found consisting of more species (within the different arthropod groups) in equal numbers per m^2 of bark. Even considering that the surface area of fissured bark is larger, the values of diversity are at least twice as high as on smooth bark types. Another key factor in forest ecosystems is the life time of the different tree species.

The life time of many tree species forming a fissured bark type (in central Europe and America e.g. oak species, in southern Africa *Podocarpus* species, *Olinia ventosa*) lasts considerably longer than that of tree species forming a smooth bark type (in central Europe *Fagus sylvatica*, in north America *F. grandifolia*, in southern Africa *Apodytes dimidiata*). The arthropod fauna shows an interesting correspondence to the habitat bark of trees in the investigated study areas. Many of the species found are very small in body size, many of the insects are wingless, some of them reproduce parthenogenetically while their offsprings colonize the new habitats. Some spider species were found to reproduce even during winter, but these are restricted to live on fissured bark types. In the crevices on fissured barks during winter there exist higher temperatures compared to the surrounding air temperature (Nicolai 1986). These adaptations are summarized by Nicolai (1987). For instance, a group of a wingless Psocopteran species reproducing twice a year on the fissured bark of oaks may produce 1,000 generations in this habitat with its physical conditions producing juveniles which may colonize the same area on the trunk again, different areas on the same trunk, or on other trunks (assuming a life span of about 500 years of the tree species which is no overestimation). Only about 200 generations are possible on the bark of a tree species showing a smooth bark type (assuming a life span of about 100 years for the tree species).

The bark fauna responds to the natural changing tree species composition in the forest. A change of the natural tree species composition will give rise to changes in the bark arthropod species composition and the number of individuals of the bark arthropods, but the dominant bark arthropods will not die out.

Arthropod species that were found only on fissured bark types will die out in forests formed by a tree species with a smooth bark type. Uniform stands dominated by one tree species should be avoided by the forest management. There should be given attention to the natural processes of regeneration in forest ecosystems and these may be used to avoid risks in forest stands.

In savanna ecosystems, high insulation properties of trees' bark help to avoid damages due to strong solar radiation reaching the trunks and help to survive fires. In a long term study program at the Cedar Creek Natural History Area, the arthropod fauna reacts to the different fire regimes. High numbers of arthropod species and arthropod specimens were found on areas with a moderate frequency of fires, low numbers were found at areas which are burned annually or are protected from fires at least since 1964. The suppression of fires for only 25 years in this ecosystem lead to a reduction of the typical savanna species inhabiting the barks of *Quercus macrocarpa* and *Q. ellipsoidalis*. This shows that a change of the natural disturbance regime has strong consequences on species adapted to the disturbance factors and changes the typical species composition e.g. living on the barks of trees. This corresponds well with other studies which showed that a change of the natural disturbance regime give rise to a decrease of several native species (Bergeron & Danserau 1993, Negi et al. 1993) and increases the probability of invasions of foreign species (Drake & Mooney 1989). Hobbs & Huenneke (1992) summarized this "intermediate disturbance hypotheseis". In this study Jack pine (*Pinus banksiana*) was found to have the highest values of insulation properties per mm of bark (Table 2). This corresponds well with other studies which showed that Jack pines are only able to colonize areas where fire occurs as the typical disturbance factor in a high frequency (Desponts & Payette 1993, Frissell 1973). On the other hand this may be one reason that on smooth bark of coniferous trees a richer arthropod fauna was found then on the barks of coniferous trees with more structured bark types (Nicolai 1993).

Due to the low latitude in the African savannas, the sun reaches the trunks only for short periods of time during sunrise and sunset per day. Most of the day the trunks are shaded by their own crown and sun burn could not be observed. Almost all of the tree species had high insulating properties across their barks which may help them again to survive fires which are frequent events in the savanna ecosystem (Gandar 1982).

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