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Physiological Influences on Wood-destroying Insects of Wood Compounds and Substances Produced by Microorganisms

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Summary

Wood-destroying insects react to and depend regarding their nutrition on compounds contained in wood or produced by microorganisms in wood. This relation is a complex matter in the biology of the insects and the chemistry of wood and of the metabolism of wood-inhabiting microorganisms. Results on the reaction of Coleoptera and Isoptera to attractive or repellent compounds in wood species or substances produced by fungi in wood are reviewed with emphasis to differences among various insect species. Nutrition of wood-destroying insects depends on nitrogen compounds of the wood; the content of nitrogen can be increased by the presence of fungi. Existing results on the relation between microorganisms and insects are also summarized including toxicity or parasitic influence of part of the microorganisms on insects. The survey may stimulate further investigations which are necessary for better knowledge of the complex interrelations.

Introduction

The deterioration of wood by xylophagous insects is of high economic importance and has therefore been studied long since. It is well known that some of these insect species are polyphagous while others are more specialized to certain wood species and may even be extremely stenophagous. Physiological and chemical reasons for the different behaviour have been disclosed so far in only a few cases. But the natural resistance of tropical wood species to wood-destroying insects has recently been the subject of an increasing number of investigations.

The influence of microorganisms on the wood-destroying insects is another subject that has long been neglected despite the fact that in most cases the insects come regularly into contact with fungi and bacteria. Entomologists have been attracted by the intracellular or intraintestinal symbiosis of xylophagous insects with microorganisms and the connection of special insects of freshly felled wood with the so-called "ambrosia"-fungi. Yet the significant and fascinating relations between other wood-insects and microorganisms always present in their external environment have been overlooked.

The aim of this paper is to give a survey of the present knowledge and recently gained results of orientation and reaction, as well as of nutrition and resistance to toxicants of wood-destroying insects with regard to the influence of wood components and substances produced by microorganisms in wood.

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Influences on Orientation and Reaction

Wood Compounds

It is known that *Lyctus* larvae depend on the starch content of hardwoods. The females seem to test the suitability of a wood for the larvae before egg-laying by tasting [CYMOREK 1966].

Hylotrupes bajulus (L.), the "Old house borer", widely distributed in Europe, develops in coniferous wood. The female beetle is attracted for egg-laying by hydrocarbons of the formula $C_{10}H_{16}$, mainly by α- and β-pinenes, by carene and less intensively by sabinene, but not by camphene. All O-containing compounds in coniferous wood, the respective alcohols, oxides, aldehydes and ketones are either of no influence or repellent to the beetles [BECKER 1942a, 1944a]. The reaction of the large Cerambycide *Ergates faber* L. is similar.

Recently it has been reported that turpentine attracts a number of wood borers and their predators in windthrown timber in Northern California [WICKMANN 1969].

From various observations and special chemical and bioassay investigations it became evident that the wood-inhabiting ambrosia beetles *Trypodendron lineatum* (Ol.) and *Xyleborus*, *Xylosandrus* and *Gnathotrichus* species are attracted by ethanol in low concentrations, while methanol and acetaldehyde had no influence and monoterpenes a repellent effect on *Trypodendron lineatum* [BUCHANAN 1941; BLETCHLY 1961; BINION 1962; MOECK 1970; CADE, HRUTFIORD, GARA 1970 and earlier investigators]. Ethanol as a fresh-wood component under anaerobic conditions seems to play an important role as the primary attractant for this group of wood-destroying beetles [MOECK 1970].

Reaction and orientation of insects are not only caused by attractive but also by repellent substances in wood. The repellent effect of many tropical wood species on termites may be the basis of their natural durability. It can even be combined with toxicity towards the insects. Some wood substances are toxic but not deterrent.

Since M. OSHIMA [1919] showed that special substances which can be extracted from wood are the reason for the natural durability of tropical wood species, many investigations were carried out with a large number of substances. Frequently cited are the results of R. N. WOLCOTT [1951, 1953, 1955, 1958] obtained with the dry-wood termite *Cryptotermes brevis* (Walker). W. SANDERMANN and H. H. DIETRICHS [1957] concluded from their intensive studies using *Reticulitermes flavipes* (Kollar) as a test species that most of the compounds found to be deterrent or toxic to this termite belong to the stilbenes, quinones and pyrane derivatives. In the class of quinones the principle for efficiency was the presence of a methyl or oxymethyl group in 2-position of the anthraquinone structure. For example, anthraquinone, 1,2-dihydroxyanthraquinone and 1,2,4-trihydroxyanthraquinone were not deterrent, while 2-methylanthraquinone, 4,5-dihydroxy-2-methylanthraquinone and 4,5-dihydroxy-2-hydroxymethylanthraquinone deterred the *Reticulitermes* species.

P. RUDMAN and F. J. GAY [1961a,b, 1963, 1964, 1967a] and P. RUDMAN [1963a, 1965, 1966], who carried out many investigations on wood extractives with *Nasutitermes exitiosus* (Hill) and *Coptotermes lacteus* (Frogg.), found that a number of anthracenes, anthrones, anthraquinones and xanthones prevent the attack of timber by the *Nasutitermes* species. A carbon-containing substituent in the 2- or 3-position in the anthrone-system is thought to be the fundamental unit for termite deterrency in substances of this type. Increasing length of simple alkyl and alkoxy side chains in the β-position of anthrones and anthraquinones did not produce marked change in antitermitic activity, but an increase in the number of nuclear hydroxyl substituents did tend to lower the efficiency.

In another paper, R. RUDMAN and F. J. GAY [1967 b] studied the antitermitic activity of free and combined saturated fatty acids, unsaturated fatty acids and saturated fatty alcohols between C_{12} and C_{20}. Maximum acitivity to deter *Coptotermes lacteus* was found for the C_{18} and C_{19} saturated fatty acids and the C_{12} and C_{20} fatty alcohols. In detail the glyceryl and cycloeucalenyl esters of palmitic acid were as effective as the free acid, whereas the ethyl ester was not as effective.

W. SANDERMANN and M. H. SIMATUPANG [1966] pointed to the toxic efficacy of anthraquinone compounds with aldehyde and carboxylic acid groups in 2-position. Further tests with anthraquinones were carried out by U. ARNDT [1968].

The chemical principles of deterrency and toxicity of wood substances to insects are not yet fully understood. Many compounds are deterrent but not toxic to termites and probably also not to other insects. Being based on volatile substances, the deterrent or toxic efficacy decreases during ageing of the wood.

The natural resistance of Zapote wood to termites still lasting after many centuries in Central America proved to be produced by the sapogenins dihydroxy oleanic acid and hydroxy oleanolic acid [SANDERMANN, FUNKE 1970].

Most investigations on the repellency and the toxicity of wood extracts and compounds have been carried out with one termite species only. Therefore an important question is whether the results gained with one species would be true of other species too. To answer this, comparative tests have been conducted with 4 species of Kalotermitidae, 2 species of Termopsidae, 5 species of Rhinotermitidae and 3 species of Termitidae from various parts of the world. Lapachonone, lapachol, tectoquinone and pinosylvin-monomethylether were chosen as test substances and a solution containing 1 mg of the respective substances was given on small disks of filter paper (diameter 2 cm). Repellency and toxicity of the four compounds were remarkably different with the various termite species. Especially the Kalotermitidae reacted differently from the Rhinotermitidae [BECKER, LENZ, DIETZ 1971]. Details cannot be described in this brief survey. But as a result it can be concluded that the terms efficacy, deterrency or toxicity "against termites" should be used with much more care and restriction, and general statements should always be based on investigations with a number of different termite species.

Finally, the recently disclosed chemical reason can be given for an example of the deterrent effect of a non-tropical wood species. Pine sapwood (*Pinus sylvestris* L.), which is eaten by many termites, shows when freshly cut blocks are given as food initially, especially when wet, a surprising repellent effect towards these insects. Spruce and fir have no such repelling influence. The repellent substance can be extracted by water and alcohol and transferred to attractive wood species making them repellent [BECKER 1966]. Investigation of the alcohol extract by means of thin-layer chromatography indicated that three water-soluble substances, the ketones 2,5-hexandione and camphor and the aldehyde furfural were contained in pine in small quantities, but—with the exception of camphor—not in spruce wood [PETROWITZ 1971]. In tests with termites, 2,5-hexandione and camphor attracted termites, whereas furfural repelled them. This compound may provoke a short attraction, but it then has a strong repellent effect, for a few days, if wood is treated with the compound. The reaction of termites to furfural differs with the species. The investigations, which cannot be described in detail here, led to the conclusion that furfural is most probably the volatile substance causing the repellency of pine wood to many termite species [BECKER, PETROWITZ, LENZ 1971].

Substances Produced by Microorganisms

Under natural conditions, wood-destroying insects are regularly confronted with wood-inhabiting microorganisms. After early investigations on the consumption of fungus mycelium as food [BECKER 1948], the author could observe in choice tests with termites carried out in 1955/56 that *Reticulitermes lucifugus* (Rossi) and *Kalotermes flavicollis* (Fabr.) preferred wood decayed by several brown rot fungi to undecayed wood. *Lenzites trabea* Pers. ex Fries showed the strongest attraction, but other brown rot fungi were also attractive [BECKER 1955; 1965]. Both termite species reacted differently regarding species of fungi. The results on the attraction of termites by *Lenzites trabea*-decayed wood published by G. R. ESENTHER [1961] and G. R. ESENTHER, T. C. ALLEN, J. E. CASIDA and R. D. SHENEFELD [1961] found wide interest. They demonstrated that the active substance in the attacked wood can be extracted by hot water and is efficient in extremely low concentrations. *Lenzites trabea* attracts *Reticulitermes flavipes* also when cultivated on synthetic media, as A. E. LUND [1962] observed. The response of *Reticulitermes* and *Zootermopsis* species to extracts from wood invaded by *Lenzites trabea* and other fungi was studied in detail by R. V. SMYTHE, T. C. ALLEN and H. C. COPPEL [1965] and R. V. SMYTHE, H. C. COPPEL and T. C. ALLEN [1967].

The attractive substances produced by *Lenzites trabea* are steam-volatile, neutral, unsaturated compounds. Furthermore, the testing of compounds of known structure by T. WATANABE and J. E. CASIDA [1963] showed that the propenyl and styryl radicals were essential for activity; cinnamyl alcohol, acetate and cinnamate, trans-isosafrole, 6 ionones and certain camphor analogs are attractants.

In comparative investigations of T. C. ALLEN, R. V. SMYTHE and H. C. COPPEL [1964], *Reticulitermes, Coptotermes* and *Heterotermes* species from various parts of America and Eastern Asia responded positively to *Lenzites trabea*-infested wood, with differences in the case of *Reticulitermes*; various Kalotermitidae and few Termitidae species, however, showed no appreciable attraction.

G. BECKER [1964] found that some acids and aldehydes produced by Basidiomycetes in wood attract several termite species and lead to preferred wood consumption. Vanillic acid, p-hydroxybenzoic acid, p-coumaric acid and protocatechuic acid had an attractive effect, in some cases even in a quantity of only 0.01 mg of the substance, on all termite species used that belonged to the genera

Kalotermes, Zootermopsis, Heterotermes, Reticulitermes and *Nasutitermes*. Ferulic acid and the aldehydes vanillin, protocatechualdehyde and p-hydroxybenzaldehyde attracted only part of the termite species and in small concentrations, in the other cases the aldehydes deterred the termites.

Also other vanillic compounds proved to be active in investigations of A. E. LUND [1966, 1969] with *Reticulitermes* species.

R. V. SMYTHE, H. C. COPPEL, S. H. LIPTON and F. M. STRONG [1967] detected that the extract from *Lenzites trabea*-decayed wood produces also trail-following of *Reticulitermes flavipes* and *Reticulitermes virginicus*. When gas-chromatographed, the active region corresponds to that found for the respective termite gland substance. According to F. MATSUMURA, H. C. COPPEL and A. TAI [1968] the active substance in *Lenzites trabea*-infested aspen wood and in the abdominal gland of *Reticulitermes virginicus* (Banks) appears to be cis, cis, trans-dodecatriene(3, 6, 8)-ol(1). C. M. A. COENEN-SARABER and F. J. RITTER [1969], however, using *Pinus sylvestris* as substrate and *Reticulitermes santonensis* Feytaud, identified two well separated fractions in the decayed wood highly active as attractants and trail-producing substances, but only one in the termites. One of the fungus-wood fractions may contain the compound identified by MATSUMURA et al. The food attraction is based on more than one highly active trail-producing substance.

Attraction of termites is not limited to Basidiomycetes and wood infested by this group of fungi. Tests with blocks of *Pinus sylvestris* and *Fagus sylvatica* exposed to several species of Ascomycetes and Fungi imperfecti resulted in attractancy of part of the soft rot fungi. After more serious wood deterioration, some species may become deterrent to termites [BECKER, LENZ, unpublished].

Deterring activity may also be found with Basidiomycetes. While *Lentinus lepideus* is deterrent and toxic to *Reticulitermes flavipes* [LUND 1960] and other *Reticulitermes* species [BECKER 1955, 1965], it is attractive and non-toxic to other termite species [BECKER 1965]. Methyl-p-methoxycinnamate and p-methoxycinnamic acid produced by this fungus, and probably the reason for the deterrency to *Reticulitermes* [LUND 1960], are not deterring *Nasutitermes exitiosus* [RUDMAN 1963]. *Lentinus pallidus* Berk. and Curt is beneficial to *Coptotermes niger* Snyder, making the heartwood of *Pinus caribaea* suitable for termites and improving their diet [WILLIAMS 1965]. White rot fungi in wood which may be toxic to some termites [KOVOOR 1964] but not to other species [FOUGEROUSSE, personal information] may prevent the decayed wood from termite attack [BECKER 1969].

A remarkable result is that wood-destroying fungi in wood not only attract the termites but also increase their food consumption [BECKER, LENZ, unpublished].

Nutritional and Toxic Influences

Wood Compounds

A second group of complex problems exists in nutritional physiology. The influences of wood components and products of fungal metabolism differ from indispensable and beneficial nutritional value to noxiousness and toxicity for wood-destroying insects.

The decisive role of nitrogen in wood on xylophagous insects has been emphasized and investigated long since [Becker 1942b, 1942c, 1949, 1963a]. The results will not be repeated here. It has recently been shown that even a change in the composition of the aminoacids during normal ageing of the wood may lead to natural resistance of the wood against *Hylotrupes* larvae which need a special composition of aminoacids [Becker 1963a]. Addition of suitable nitrogen renders the old timber suitable for the larval development again. More investigations on the influence of nitrogen quantity and distribution as given by J. D. Bletchly [1969a] and J. M. Baker, R. A. Laidlaw and G. A. Smith [1970] as well as on the special composition of amino-acids and of vitamins and trace elements on the development of various wood-destroying insects are still necessary. The carbohydrate-physiology of xylophagous insects shall not be discussed here.

The natural resistance of heartwood, especially of tropical species, against wood-destroying insects has been dealt with already in connection with repellent reactions of the insects. Many toxic substances which were identified and tested as to their efficiency to termite species are also deterrent. But numerous investigations are necessary until the toxicity of wood components can be more completely understood and the variation between insect species is better known.

Examples for the different reaction of various insects are the coniferous heartwood substances pinosylvin and β-thujaplicin. Pinosylvin is known to be active against the dry-wood termite *Cryptotermes brevis* [Wolcott 1951, 1956], but of low efficacy against *Hylotrupes bajulus* larvae [Becker 1963]; β-thujaplicin, however, is toxic to the larvae of this longhorn beetle [Becker 1963], but not against *Reticulitermes flavipes* [Arndt 1968].

While termites are polyphagous—with the exception of toxic or repellent heartwood—many Coleoptera species are stenophagous. Larvae of *Hylotrupes bajulus* die in hardwood species. Treatment with low-concentrated sodium alkaline solutions followed by leaching in water removes the toxic substances from the wood, which are perhaps lignin compounds of low molecular structure, and renders the wood suitable for the larvae [Becker 1944b]. The respective compounds are not kown so far. In some fir trunks (*Abies pectinata* DC.) inner parts of the cross section may contain an unknown substance, also toxic to larvae of *Hylotrupes bajulus*, which is soluble in water [Becker 1970].

Substances Produced by Microorganisms

Wood-destroying fungi of the brown rot type increasing the nitrogen content of wood accelerate the development of beetle larvae of *Hylotrupes bajulus* and *Anobium punctatum* if the fungi species are free from toxic substances and if the carbohydrate content of the decayed wood is still high enough [Becker 1942b, c 1963a; Bletchly 1953, 1969a], and also soft rot fungi may be favourable for *Anobium punctatum*-larvae [Bletchly 1959b] while for many Coleoptera species fungi are an additional non-compulsory factor. The incipient larval stages of the Anobiid species *Xestobium rufovillosum* (De Geer) depend on fungal infestation of the wood [Campbell, Bryant 1940], or in the case of the Cerambycid *Ergates faber* the older larvae need and prefer decayed wood [Becker 1943]. Coleoptera larvae depending on high wood moisture are always associated with brown rot, white rot or soft rot fungi. Non-toxic species contribute to their nitrogen source which is decisive for their growth.

Siricidae doubtless depend on the fungi which they transfer to the infested wood [Francke-Grosmann 1957]. The ectosymbiosis of Scolytidae and Platypodidae with the so-called ambrosia fungi has long been known. In the latter case the manifold mechanism of transport of the fungi by the adult insects for infestation of the freshly attacked wood, in which the larvae develop, has attracted the interest of entomologists [Francke-Grosmann 1967; Schedl 1962]. Various species of fungi may be involved [Baker, Norris 1968]. Recently biochemical investigations on the ambrosia fungi and their nutritional value were started.

Contradictory results reported in literature on the influence of blue stain fungi on *Hylotrupes* larvae could be explained by the result that part of the blue stain fungi concerned is highly beneficial, part strongly toxic to the beetle larvae [Becker 1968]. Also soft rot and mould fungi may be for *Hylotrupes* larvae either of nutritional value, or indifferent, or noxious because of their toxicity [Becker, unpublished]. Similar conditions may be expected for other wood-inhabiting Coleoptera species. Different reaction to various fungi was found with *Lyctus brunneus*-larvae [Cymorek 1966, 1970]; larvae of *Anobium punctatum* De Geer are favoured in their development by staining fungi [Bletchly 1969]. Basidiomycetes of the brown rot type in wood, which cause the already described attraction of termites, accelerate the development of the latter [Becker 1955, 1965]. A mass loss of the decayed wood of as little as a few per cent leads to a significant increase in the number of termites in incipient colonies, or in weight or number of individuals of larger termite groups, and mortality is reduced. The most favourable range of fungus attack was found between 5% and 15% mass loss. Fungus attack of wood is advantageous for the development of the imago caste and neotenic forms. Termite species reacted differently to fungi species. Very suitable fungi for *Kalotermes flavicollis* are *Merulius lacrimans*, *Lentinus lepideus*, *Paxillus panuoides*, *Coniophora cerebella* and *Merulius sylvester*; *Lenzites abietina* is indifferent, *Lenzites trabea* noxious. *Heterotermes indicola* is favoured by *Coniophora cerebella*, *Poria monticola*, *Merulius lacrimans* and less by *Lenzites abietina*, whereas *Lenzites trabea* and *Lentinus lepideus* seem to be toxic. *Reticulitermes santonensis*, however, was not affected by *Lenzites trabea* and *Lentinus lepideus*.

The termites consume more fungus-infested wood than non-infested. The degree of dissimilation of the wood is equal. Thus the increase of food consumption may influence the termites proportionally. Probably the production of nitrogen and vitamins by the fungal mycelium is an additional a reason for the accelerated development of the termites in slightly decayed wood. It seems that a special influence on the relation of castes may be possible.

Ganoderma applanatum [Kovoor 1964] and other white rot fungi [Becker 1969] are toxic to at least a number of termite species.

The mycelium of different species of Ascomycetes and Fungi imperfecti may be of some nutritional value for the termites, or indifferent, or toxic [Becker, Kerner-Gang 1964]. A number of species of these mould fungi contain strains that are highly toxic and others with low or no toxicity at all. In the case of *Aspergillus flavus*, which can be very dangerous to termites [Beal, Kais 1962;

BECKER, KERNER-GANG 1964] a correlation between the content of Aflatoxin-compounds and toxic efficacy against termites could be stated [BECKER, FRANK, LENZ 1969]. Several toxins have been chemically identified from other fungi. Toxicity was found also with *Aspergillus fuliginosus*, *Trichoderma viride* and other *Trichoderma* species. G. BECKER and W. KERNER-GANG [1964], R. V. SMYTHE and H. C. COPPEL [1966], M. LENZ [1969] and W. A. SANDS [1969] gave or compiled a number of other reports on fungi found to be toxic to or parasitic of termites. The chemical reason for the beneficial role of fungi to termites, however, has not yet been explained. It might be a specific nutritional effect of aminoacids or an influence of other substances on physiological processes.

Final Remarks

Better knowledge of natural toxic or repellent substances may become a basis for the development of new preservatives. Since certain of the synthetic contact insecticides with their outstanding efficacy also against wood-destroying insects have been banned in some countries the search for new types of preservatives has gained new importance. Natural resistance of wood species, or toxicity, repellency and attractancy of microorganisms may lead to new ways for the old problem of wood protection.

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