WOOD BREAK-DOWN IN MANGROVE ECOSYSTEMS: A REVIEW

S.M. Cragg[1,2]

ABSTRACT

This paper reviews information from a wide range of sources which relates to the process of wood break-down in mangrove ecosystems. A high proportion of the standing biomass in mangrove forests consists of wood with a life-span and residence-time as litter much greater than that for leaves. Mangroves are subject to attack by terrestrial and marine organisms, but are protected by chemical and physical mechanisms. The marine organisms which exploit mangrove wood include ascomycete fungi, teredinid molluscs, isopod crustaceans and possibly bacteria. The input of wood litter in a mature mangrove forest is constant though locally patchy. In a forest which is colonising a bare substrate, wood litter input slowly increases from zero. In a managed forest, pulses of wood litter input occur with each thinning but the bulk of wood biomass is removed from the ecosystem. Teredinids process wood on the forest floor, converting it into products which can be transported by currents. Nitrogen-fixing cellulolytic bacteria live symbiotically in teredinids. Some of the nutrients and energy derived from wood are carried offshore by currents and through food-webs.

Key words: biomass, forest, litter, teredinids, food-web.

INTRODUCTION

Significant flows of energy and matter occur between mangrove forests and adjacent ecosystems as a result of water movements, particularly tides, and of food-webs. The magnitude and direction of these flows is a matter of controversy and few efforts have been made to measure them directly. There is probably much variation among mangrove ecosystems with respect to the characteristics of these flows, a better understanding of which is a key to improved management practice in mangrove areas. Attempts to understand the dynamics of energy and matter flows in mangrove ecosystems have tended to focus on that proportion of net productivity channelled into "litter", namely the material readily gathered in collectors placed 1 - 2 metres above the substratum. In successional or managed forests, this is likely to be the main organic matter input to the ecosystem. In mature forests, however, the input of woody material is probably very important. This paper assesses the likely significance of such longer-lived and refractory tissues in the dynamics of mangrove ecosystems and considers the means by which they are broken down.

WOOD PRODUCTION

To assess the significance of wood in mangrove ecosystems, it is necessary to have estimates of the proportion of biomass represented by woody tissues, and an index of the rate at which matter passes through this biomass compartment. This rate is a function of the proportion of total production

---

[1] Officer in Charge, Forest Products Research Centre, Port Moresby, Papua New Guinea
[2] Present address: Buckinghamshire College, Queen Alexandra Road, High Wycombe, Bucks HP11 2JZ, U.K.

channelled into woody tissue, the life-span of tree organs formed of woody tissue (roots, branches, trunks) and the rate of turn-over of dead woody tissues.

Woody Biomass

Woody tissues form a high proportion of total biomass in mangrove forests. Suzuki and Tagawa (1983) found that in a low-canopied mixed stand of *Rhizophora mucronata* and *Bruguiera gymnorhiza* located near Okinawa, leaves formed only 6% of the total above-ground biomass. Woody tissues presumably formed the bulk of the remainder. Christensen (1978) estimated that in a taller 15-year-old stand of *Rhizophora apiculata* in Thailand, leaves constituted less than 5% of above-ground biomass and reproductive parts less than 0.2%, the remaining 95% being woody tissue (trunks 47%, branches 10%, prop roots 38%). Golley *et al.* (1975) found that leaves from a mature stand of *Rhizophora brevistyla* in Panama constituted less than 1.3% of the total above-ground biomass. Woody tissues were categorized into prop-roots (42%) and stems (57%). The indication from the above measurements is that the proportion of woody tissue within the total biomass increases with increasing tree size. This is supported by measurements of biomass partitioning in *Rhizophora mangle* in a forest in Puerto Rico given by Cintron and Schaeffer-Novelli (1984). They found that as trunk diameter increases from 1.1 cm to 15.4 cm the proportion of biomass consisting of leaves and that consisting of branches decrease (from about 16% to 4%, and from 23% to 13% respectively), but the proportions of biomass in trunks and prop-roots increase (from about 55% to 63%, and from about 7% to 20% respectively). Thus, in mature mangrove forests the proportion of biomass in woody tissue is likely to be even higher than it is in successional or managed forests.

Measures of partitioning of production into trunks and prop-roots have been obtained from an even-aged, managed mangrove forest (Gong *et al.* 1984), but it should be borne in mind that in such forests growth rates are probably much greater than in a "steady-state" mature mangrove forest. I know of no published data on growth rates in unmanaged mangrove forests, though records of permanent plots established at the time of the studies reported by Watson (1928) have been kept regularly up to the present day: the evaluation of this data remains to be undertaken (Ong, J.E., pers, comm.).

Life-spans of Biomass Partitions

The partitions of mangrove biomass (i.e. the proportions of biomass represented by leaves, branches, trunks, prop roots and subterranean roots) have strikingly different life-spans and rates of break-down after death. The life-span is the period during which the biomass is available to herbivores. Christensen (1978) reports a mean leaf life-span of 0.7 years in a managed mangrove forest in Thailand. No direct measurements of branch life-spans have been made, but since few twigs grow into large branches, twigs probably have a relatively short life-span, perhaps one to two years and, like leaves, are shed throughout the life of the tree. Branch-shedding must also be a regular occurrence during the life of the tree, particularly in the case of species such as members of the Rhizophoraceae, which are self-pruning (i.e. lower branches naturally drop off in approximately the order in which they appeared). Branch life-spans would depend on species. However, it is likely that most branches fall within fifteen years of first appearing. As the tree becomes senescent, branch-fall may increase in a sporadic fashion up to and after death.

The life-span of the trunk is generally that of the tree; unfortunately reliable data on life-spans of mangrove trees are not available. In Papua New Guinea, specimens of *Rhizophora* or *Bruguiera* exceeding 30 m in height and 50 cm in diameter are quite common in sites where conditions favour mangrove growth (Percival and Womersley 1975; Floyd 1977). Such trees frequently show signs of senescence. In comparison with the size of mangroves in managed forests which have grown under conditions conducive to rapid growth for up to 30 years, it is likely that these mature or over-mature mangrove trees are over seventy and may even exceed one hundred years in age (Ong, J.E., pers, comm.).

Root life-spans are also likely to be at least partially a function of diameter. It is unlikely that fine hair-roots are long-lived. Thus, as they appear to represent a substantial but difficult-to-quantify proportion of biomass (Golley *et al.* 1975) it is likely that they represent a significant proportion of primary production. Prop-roots like branches, though longer-lived, are probably shed throughout the life of a mangrove tree. Observations at Bootless Inlet near Motupore Island, Papua New Guinea Island, Papua New Guinea indicated that a proportion of prop-roots in a healthy forest get damaged or infected so that they eventually become detached form the tree (Cragg and Swift unpub.).

There are extensive data available on litter-fall rates which give a good indication of the rate of turnover of leaves, twigs and reproductive parts (see for example Duke *et al.* 1981; Gong 1984). However, litter-traps do not collect longer branches efficiently and they are unable to catch falling trunks. Furthermore they are situated above the height of prop-roots so they do not measure turnover of this very significant biomass partition.

Litter Break-Down Rates

Studies of leaf-litter decomposition are reviewed by Polunin (1986). Root-litter break-down has been investigated by Van der Valk and Attiwill (1984), but the break-down of woody tissues has received little attention until the study of Robertson and Daniel (1989). Certain mangrove management practices rely on the biodegradation of branches and roots left behind after harvesting. Casual observation suggests that the break-down rate for main stems may be quite slow. For example, in late 1974 a road was built to the Kaut timber concession in New Ireland, Papua New Guinea which traversed an area of mature mangrove forest. The trees felled during road construction were left in an area subjected to daily tides unimpeded by the road. Observations in late 1985 showed that though the tree stems were extensively decayed by basidiomycetes, they were still intact. By measuring standing stocks of dead wood and rates of break-down of logs of known ages of up to 15 years old, Robertson and Daniel (1989) estimated that the rate of flux for wood detritus was 4 g C.m^{-2}.y^{-1} in a young mangrove forest and 44g C.m^{-2}.y^{-1} in a mature mangrove forest in tropical Australia. More such systematic measurements of wood break-down rates in a range of mangrove environments are required before the significance of energy flow through the biomass compartments represented by woody tissues can be properly understood.

ECOLOGICAL CONSEQUENCES OF WOODY TISSUE CHARACTERISTICS

Owing to the limitations on the distribution of wood-consuming organisms imposed by tidal inundation, the spatial distribution of woody tissues is of ecological significance (Rimmer *et al.* 1983). This is particularly so in the genus *Rhizophora* with its elaborate root architecture, which has been analysed by Sato (1978). The tree consists of a range of aerial, intertidal and subterranean niches for wood-dependent organisms. Furthermore the spatial distribution of tissues within a given limb may also affect susceptibility to bio-degradation. Young *Rhizophora* prop-roots consist of spongy tissues within which is embedded a cylinder of woody tissue (Gill and Tomlinson 1971). Teredinid borers are restricted to the woody tissue while the crustacean *Sphaeroma* frequently occurs in the spongy tissue (unpub. obs.). *Rhizophora* responds to animal or fungal damage to its prop-roots by branching in the damaged area (Kohlmeyer 1969; Ribi 1981, 1982). The differentation of woody tissues into bark, sapwood and heartwood is also of ecological significance. The bark of certain mangroves contains high levels of polyphenolics: up to 40% of the dry weight in *Rhizophora mucronata* bark consists of polyphenolics (Hills 1985). Tannin levels can be sufficient for commercial exploitation (Percival and Womersley 1975). The sapwood of many trees contains starch, which can be exploited by certain beetle larvae. The sapwoods of the mangrove genera *Avicennia, Exceocaria* and *Sonneratia* are rated as susceptible to the starch-dependent beetles of the family Lyctidae, while those of *Bruguiera, Rhizophora* and *Xylocarpus* are rated non-susceptible (Eddowes 1978).

Wood consists principally of three classes of organic chemicals:- celluloses, hemicelluloses and lignins. Few organisms apart from white rot basidiomycete fungi are capable of breaking down the lignins, whereas the celluloses and hemicelluloses can be broken down to simple sugars by organisms possessing the requisite combination of enzymes. Though energy-rich, these molecules are relatively refractory and only certain groups of organisms are capable of utilising them.

Some organisms can attack live trees. These organisms include a range of marine animals and basidiomycete fungi, and beetles and termites which occur also in dry land forests. The isopod crustacean *Sphaeroma* (Rehm and Humm 1973; Simberloff *et al.* 1978; Ribi 1981, 1982), the pholad bivalve *Martesia* (Dharmaraj and Nair 1981) and the teredinid bivalve *Bactronophorus* (Roonwal 1954) have all been reported to be capable of burrowing into live trees. *Sphaeroma* and *Bactronophorus* also occur in live mangroves in Papua New Guinea (unpub. obs.). Attack by marine animals may be sufficiently severe to affect the survival of the trees attacked (Roonwal 1954; Rehm and Humm 1973). However, if attack on live mangroves were as severe as that on dead mangrove wood in the intertidal zone, the mangrove forest could not exist, because most trees would be felled by borer activity before they reached maturity.

Whereas animals respond to disease and injury by healing, trees compartmentalise damaged portions, isolating them from sound wood (Shigo 1985). Apparently mangrove trees have some form of defence against marine borers, which is lost after death. The water soluble polyphenolics found in high concentrations in the bark may provide this defence. It is likely that they continue to be secreted and leached into the water while the tree is alive, but secretion ceases at death. Mangroves such as *Xylocarpus, Rhizophora, Sonneratia* and *Bruguiera* have heartwood rated as durable or moderately durable, that is to say they have some natural resistance to basidiomycete and termite degradation owing to extractives in the heartwood. *Excoecaria* and *Avicennia* have non-durable heartwood (Eddowes 1978). No clear data are available regarding the ecological influence of these variations in natural durability. The degree of durability may affect not only the ability of the tree to withstand disease and insect attack, but also the rate of breakdown and decay once the tree falls to the forest floor. Ritchie (1968) found that the heartwood of *Rhizophora mangle* is naturally resistant to marine fungi.

WOOD-DEPENDENT BIOTA

The wood-dependent biota of mangrove forests can be categorized into terrestrial and marine groups. The domains of activity of these groups have a boundary at about the high-tide mark, with some overlap. The terrestrial biota closely resembles that of adjacent non-tidal forests, with basidiomycete fungi, adult and larval beetles, subterranean and drywood termites predominating. The ecology of these organisms and their importance in wood breakdown is well documented (see Swift *et al.* 1979) but no detailed studies specifically relating to their role in mangrove ecosystems have been carried out. It is noteworthy that subterranean termites are active in areas subjected to regular tidal inundation. They build their earth runways extending from the forest floor up into the tree in the usual fashion (Cragg 1983) despite the tides.

Kohlmeyer (1969) reviewed the limited records of distribution of fungi in mangrove forests. Above the high-tide line, wood is colonised by basidiomycetes whereas in the intertidal zone, ascomycetes and deuteromycetes occur. This distribution pattern has also been observed in Papua New Guinea (Cragg and Swift, unpub.). Further information regarding the distribution of fungi in mangrove forests is provided by Hughes (1975). Leightley (1980) investigated the wood-decaying capacity of marine fungi occurring in mangrove forests.

The significance of bacteria in wood break-down should not be overlooked. Buckley and Triska (1978) found that nitrogen-fixing bacteria participate in wood decomposition in freshwater streams in the United States of America. No comparable study has been conducted on mangrove wood, but bacteria have been found forming tunnels in wood from marine pilings in Papua New Guinea. This bacterial activity may prepare the wood for colonisation by marine wood-borers (Cragg and Nilsson, unpub. obs).

Rather more is known about the ecology of marine wood-borers than of other wood-degrading organisms found in mangroves. This is perhaps a reflection of the economic significance of the damage caused by these organisms to man-made structures. The isopod *Limnoria* is a major pest in maritime pilings, but is not particularly important in mangrove areas. In addition to occuring at port sites around Papua New Guinea, it has been observed colonising *Sonneratia* pneumatophores in a small stand of mangroves at Motupore Island near Port Moresby, Papua New Guinea. However, extensive collection in major mangrove areas in the country have failed to locate any *Limnoria*. It appears that in Papua New Guinea *Limnoria* favours sites with marine salinities (Cragg and Aruga 1987). A variety of other isopods are found inhabiting burrows in mangrove wood. Whether these animals simply excavate their burrows, or consume the wood excavated remains to be established (Bowman 1977; Jones *et al.* 1983).

The most significant wood inhabiting isopod in mangrove forests is *Sphaeroma.* This animal is mainly found in prop roots of *Rhizophora*, but it also burrows into detached dead wood and can tolerate extremely low salinities (Cragg and Aruga 1987). It burrows at right angles to the surface of the wood and there is still doubt as to whether it digests the wood removed (John 1968). The most detailed account of the ecology of this animal is provided by Estavez and Simon (1975). There has been considerable unresolved debate as to whether the burrowing activity of this animal is beneficial for (encouraging extra branching, increasing stability) or detrimental to (causing structural weakening), the mangrove trees in Florida (Rehm and Humm 1973; Simberloff *et al.* 1978; Ribi 1981, 1982).

Little is known about the feeding of the species of *Sphaeroma* which inhabit mangroves. Rotramel (1975) described how a non-mangrove species, *Sphaeroma quoyanum*, uses feather-like hairs on its walking legs as a filtering net. Cragg and Icely (1982) found that *S. terebrans* has similar hairs, but that *S. triste* does not. Both these species occur in mangroves in the vicinity of Port Moresby. These authors were unable to identify gut contents, but found that most animals examined had empty guts suggesting that feeding is intermittent. John (1968) reports that an extract from the hepatopancreas of *S. terebrans* is capable of converting chemically-prepared cellulose into glucose, but cellulose in wood is less liable to enzyme conversion than artificial cellulose substrates (Dean 1976).

In terms of their importance in breaking down dead wood, teredinids are by far the most significant marine wood-borers in mangrove swamps. These highly modified bivalves with worm-like bodies excavate cylindrical burrows which may extend into the centre of large tree stems, but generally run parallel to the axis of the branch stem or root. There are nearly forty species of teredinids in Papua New Guinea (Rayner 1983). These vary considerably in their salinity-tolerance range. Some species are commonly associated with mangrove ecosystems and two species *(Bactronophorus thoracites* and *Dicyathifer manni)* are virtually restricted to mangrove wood (Rayner 1983). Cragg and Aruga (1987) found that the teredinid fauna of the mangroves of the Gulf of Papua is very distinct from that in wood washed offshore from this mangrove ecosystem.

Teredinids consume the wood they excavate and digest it. The mechanism of digestion has been studied in detail (Dean 1978; Morton 1978). Recent studies have shown that nitrogen fixing symbiotic bacteria are implicated in the digestion process (Waterbury *et al.* 1983). Teredinids are also able to filter-feed on phytoplankton (Pechenik *et al.* 1979). Differences in gut structure appear to reflect the relative importance of phytoplankton and wood in the diet of different shipworm species. The "mangrove specialist" *Bactronophorus* apparently emphasies filter-feeding (Turner 1966). It is generally assumed that teredinids filter phytoplankton. However, other particulate food sources may be available to teredinids in mangrove ecosystems including bacteria inhabiting clay particle flocs which tend to form in tropical estuarine areas (Paerl and Kellar 1980) or particulate organic matter.

Wood-boring members of the Pholadidae also burrow into woody litter in mangrove forests. They have been observed in this niche in, for example, the mangrove forests of eastern India (Turner and Santhakumaran 1989), of the Gulf of Papua (Cragg and Aruga 1987) and of Singapore (Cragg and Murphy, unpub.). These bivalves are rarely as important as teredinids in the breakdown of mangrove wood.

LIFE, DEATH AND BREAK-DOWN OF MANGROVE TREES

The Fate of the Individual Tree

During its life, a tree is subject to herbivory which includes not only the consumption of live leaves, but also other plant tissues including live wood. Live tree tissue is also catabolized by certain fungi. It is likely that only a small proportion of the woody biomass is utilised in this fashion, the majority entering decomposer-dominated food-webs. Regular twig and branch-fall will enter the pool of material available to the decomposer community on the forest floor. With senescence and death, fungal and borer activity increases sharply, tree limbs are shed at an accelerated rate, and eventually the main stem falls. Further break-down occurs on the forest floor.

Teredinids are the principal agents of wood breakdown on the forest floor. They riddle fallen wood until over 50% of the original volume (Cragg and Swift unpub.) has been consumed and metabolised. This vastly increases the surface area available for fungal and bacterial degradation and mechanically weakens the wood, eventually leading to its fragmentation into smaller pieces.

The end result of the activities of the marine decomposer community is the conversion of a large and (particularly in the case of a main stem) relatively immobile structure into a range of products which can be readily transported by water currents. These products include particulate and dissolved organic matter, the planktonic larvae of teredinids, and teredinid faeces.

Wood Break-down in Different Forest Types

In a mature mangrove forest unaffected by human activity, if a sufficiently large areas is taken into consideration, a steady state with respect to wood input and breakdown is likely to exist. The distribution of wood detritus is very patchy, with high concentrations where a large tree has recently fallen. In a recently established forest there is initially no wood litter input at all. As the colonising trees grow older, wood litter builds up due to branch-fall and eventually stem-fall. The situation in a managed forest is that there are pulses of branch and root wood input after thinning and final felling, but main stems are removed from the ecosystem.

Sources and Output of Wood

The mangrove ecosystem receives a variety of inputs of wood. In Papua New Guinea, substantial quantities of wood are transported by rivers into mangrove swamps from the forests inland (Cragg 1983). This input will be particularly high in times of flood. The input of wood from the mangrove forest itself may be dramatically increased by natural disasters of the type detailed by Johns (1986) such as cyclones, lightning, tidal waves or erosion. A small input of drift-wood may occur in mangrove areas subject to strong tidal currents.

The wood input to mangrove ecosystems is either consumed by the decomposer community and converted into transportable products as already described, or is physically removed. Some wood may become buried due to the very dynamic deposition/erosion regime found in many mangrove areas. Any wood of a size, shape and density suitable for water transport may be exported due to the residual seaward component of the current regime.

NUTRIENT AND ENERGY FLUXES

Because of the paucity of experimental data it is only possible to discuss fluxes of nutrients and energy associated with wood break-down in very general terms.

The initial energy resource, the wood partition of the tree biomass, has been measured in a range of mangrove ecosystems (see for example Golley *et al.* 1975; Christensen 1978; Suzuki and Tagawa 1983; Cintron and Schaeffer-Novelli 1984). No estimates of the proportion of this biomass which is consumed before the tree dies are available. The standing stock of wood litter has been estimated from one site in Papua New Guinea (Cragg and Swift unpub.) and from sites in Australia (Robertson & Daniel 1989), but casual observations show that the stock varies considerably between different mangrove sites.

The flow of wood-derived energy through the mangrove related food-webs has not yet been mapped. Observations in a *Rhizophora*-dominated forest in Papua New Guinea suggest that at least 50% of wood litter biomass is converted by teredinids (Cragg & Swift unpub.). The products of this conversion would be teredinid tissue, planktonic larvae, excretory products and perhaps dissolved organic matter. Owing to the protection afforded by their burrows it is unlikely that teredinids are subject to severe predation. Thus, teredinid tissue will be mainly converted by the decomposer community *in situ.* Their larvae, on the other hand will be broadcast by water currents, as will excretory products and dissolved organic matter.

Wood which is carried out to sea becomes water logged and eventually sinks. Even if it sinks in deep water, it will become colonised by marine borers. Turner (1977) has described how wood "islands" in the deep-sea can support communities of animals in areas otherwise virtually devoid of animal life. Cragg and Aruga (1987) investigated wood collected by prawn trawlers operating some kilometres off-shore of the mangroves of the Gulf of Papua and found that this wood (some of which originated inland of the mangrove forest) supported a number of species of teredinids.

As a nutrient resource, wood litter tends to be less rich than leaf litter. Aksornkoae and Khemnark (1984) found that in the main stems of a number of mangrove species, the concentration of nitrogen was generally one half to one quarter of that of leaves, and that of phosphorus approximately half that of leaves. During the wood break-down process, the nutrient status of the wood may change. Nitrogen fixation occurs due to the symbiotic bacteria of teredinids (Waterbury *et al.* 1983). Calcium is extracted from the seawater and deposited to line the burrows, or form the shells of the teredinids. Additional nitrogen and other nutrients are taken by filter-feeding teredinids from the seawater in the form of phytoplankton or other particulate food. Nitrogen is lost as a result of excretion. Nutrient translocation is also likely to occur as a result of the microbial break-down of wood.

AREAS FOR FUTURE INVESTIGATION

The role of wood break-down in mangrove ecosystems is important, but is very poorly understood. It is not yet possible to determine the relative importance of leaf and wood litter in mangrove ecosystems. Further estimates of wood litter standing stocks, wood export rates, wood break-down rates, and associated nutrient fluxes are needed. Foodwebs associated with wood break-down also require detailed investigation. Attention should be given to the wide range of animals including fish, crabs, polychaetes and nemertines which utilize burrowed wood as shelter. The importance of wood is not just of academic interest. It is also of concern to those who manage mangrove forests, who need to be able to forecast the impact of the removal of the bulk of woody biomass on the rest of the ecosystem.

ACKNOWLEDGEMENTS

This manuscript has benefitted from discussions with many colleagues and in particular a debt of gratitude is owed to Professor M.J. Swift. During field investigations I was assisted by staff of the Forest Products Research Centre, especially Ben Pul, Kelly Matoli, Monica Rau and John Aruga whose efforts are gratefully acknowledged.

REFERENCES

AKSORNKOAE, S. and KHEMNARK, C. (1984). Nutrient cycling in mangrove forest of Thailand. p. 545-557. In: *Proceedings of the Asian Symposium on Mangrove Environment: Research and Management, Kuala Lumpur 1980* Ed. E. Soepadmo, A.N. Rao and D.J. MacIntosh, University of Malaya.

BOWMAN, T.E. (1977). *Ceratolana papuae,* a new genus and species of mangrove boring cirolanid isopod from Papua New Guinea. *Proceedings of the Biological Society of Washington, 90:* 819-825.

BOYLE, P.J. and MITCHELL, R. (1978). Absence of microorganisms in crustacean digestive tracts. *Science* 200: 1157-1159.

BUCKLEY, B.M. and TRISKA, F.J. (1978). Presence and ecological role of nitrogen-fixing bacteria associated with wood decay in streams. *Verhandlungen der International Verein von Limnologie,* 20: 1333-1339.

CHRISTENSEN, B. (1978). Biomass and primary production of *Rhizophora apiculata* B1 in a mangrove in southern Thailand. *Aquatic Botany,* 4: 43-52.

CINTRON, G. and SCHAEFFER-NOVELLI, Y. (1984) Methods of studying mangrove structure. p. 91-113. In: *The Mangrove Ecosystem: Research Methods* Eds. S.C. Snedaker and J.G. Snedaker, UNESCO.

CRAGG, S.M. (1983). The mangrove ecosystem of the Purari Delta. p. 295-324. In: *The Purari: Tropical Environment of a High Rainfall River Basin* Ed. T. Petr. Junk, The Hague.

CRAGG, S.M. and ARUGA, J.A. (1978). Intertidal and sub-tidal wood boring faunas from the Gulf of Papua, Papua New Guinea. p. 263-274. In: *Advances in Aquatic Biology.* Prof. N.B. Nair Felicitation Volume, U. of Kerala, India.

CRAGG, S.M. and ICELY, J.D. (1982). An interim report on studies of the tolerance by *Sphaeroma* (Crustacea: Isopoda) of CCA-treated timber. *International Research Group on Wood Preservation Document* No: IRG/WP/491, 26 pp.

DEAN, R.C. (1976). Cellulose and wood digestion in the marine mollusk *Bankia gouldi* Bartsch. p. 955-965. In: *Proceedings of the Third International Biodegradation Symposium,* Applied Science, London.

DEAN, R.C. (1978). Mechanisms of wood digestion in the shipworm *Bankia gouldi* Bartsch: enzyme degradation of celluloses, hemicelluloses and wood cell walls. *Biological Bulletin,* 155: 297-316.

DHARMARAJ, K. and NAIR N.B. (1981). Timber boring animals of Talapady mangroves and adjoining areas with a record of *Martesia* sp. boring into live trees. *Mahasagar,* 14 (2): 159-162.

DUKE, N.C., BUNT, J.S. and WILLIAMS, W.T. (1981). Mangrove litter fall in north-eastern Australia. I. Annual totals by component in selected species. *Australian Journal of Botany,* 29: 547-553.

EDDOWES, P.J. (1978). Commercial Timbers of Papua New Guinea. Office of Forests, Port Moresby. 195 pp.

ESTAVEZ, E.D. and SIMON, J.L. (1975) Systematics and ecology of *Sphaeroma* (Crustacea: Isopoda) in the mangrove habitats of Florida. p. 286-304. In: *Proceedings of the International Symposium of Biology and Management of Mangroves* Eds. G.E. Walsh, S.C. Snedaker and H.J. Teas.

FLOYD, A.G. (1977). Ecology of the tidal forests in the Kikori-Romilly sound area, Gulf of Papua. *Papua New Guinea Office of Forests, Division of Botany, Ecology Report* No. 4, 52 pp.

GILL, A.M. and TOMLINSON, P.B. (1971). Studies on the growth of red mangrove (*Rhizophora mangle* L.). 2. Growth and differentation of aerial roots. *Biotropica,* 3: 63-77.

GOLLEY, F.B., McGINNIS, J.T., CLEMENTS, R.G., CHILD, G.I. and DUEVER, M.J. (1975). *Mineral Cycling in a Tropical Moist Forest.* University of Georgia Press, U.S.A., 248 pp.

GONG, W.K. (1984). Mangrove primary productivity. p. 10-19. In: *Productivity of the Mangrove Ecosystems Management Implications.* Ed. J.E. Ong and W.K. Gong. UNESCO/Universiti Sains, Malaysia.

GONG, W.K., ONG, J.E., WONG, C.H. and DHANARAJAN, G. (1984). Productivity of mangrove trees and its significance in a managed mangrove ecosystem in Malaysia. p. 216-225. In: *Proceedings of the Asian Symposium on Mangrove Environment: Research and Management.* Eds. E. Soepadmo, A.N. Rao and D.J. MacIntosh. University of Malaya, Kuala Lumpur.

HILLS, W.E. (1985). Biosynthesis of tannins, In: *Biosynthesis and Biodegradation of Wood Components.* Ed. T. Higuchi, Academic Press.

HUGHES, G.C. (1975). Studies of fungi in oceans and estuaries since 1961. 1. Lingnicolous, caulicolous and foliicolous species. *Oceanography and Marine Biology Annual Review*,13: 69-180.

JOHN, P.A. (1968). Habits, Structure and Development of *Sphaeroma terebrans* (a Wood-Boring Isopod). University of Kerala, India, 82 pp.

JOHNS, R. (1986). Natural disturbance in mangrove ecosystems. p. 37-44. In: *Workshop on Mangrove Ecosystem Dynamics.* Eds. S.M. Cragg and N.V.C. Polunin. UNESCO, New Delhi.

JONES, D.A., ICELY, J.D. and CRAGG, S.M. (1983). Some corallanid isopods associated with wood from Papua New Guinea including three new species (Isopoda: Corallanidae). *Journal of Natural History,* 17: 837-847.

KOHLMEYER, J. (1969). Ecological notes on fungi in mangrove forests. *Transactions of the British Mycological Society*, 53: 237-250.

LEIGHTLEY, L.E. (1980). Wood decay activities of marine fungi. *Botanica Marina,* 23: 387-395.

MORTON, B. (1978). Feeding and digestion in shipworms. *Oceanography and Marine Biology Review.* 16: 107-145.

PAERL, H.W. and KELLAR, P.E. (1980). Some aspects of the microbial ecology of the Purari River, Papua New Guinea. p. 25-32. In: *Purari River (Wabo) Hydroelectric Scheme Environmental Studies,* Vol. 11, Ed. T. Petr, Office of Environment and Conservation, Papua New Guinea.

PECHENIK, J.A., PERRON, F.E. and TURNER, R.D. (1979). The role of phytoplankton in the diets of adult and larval shipworms, *Lyrodus pedicellatus* (Bivalvia: Teredinidae). *Estuaries,* 2 (1): 58-96.

PERCIVAL, M and WOMERSLEY, J.S. (1975). Floristics and ecology of the mangrove vegetation of Papua New Guinea. *P.N.G. Department of Forests, Division of Botany, Botany Bulletin,* No. 8, 96 pp.

POLUNIN, N.V.C. (1986). Decomposition processes in the mangrove ecosystem. p. 95-104. In: *Workshop on Mangrove Ecosystem Dynamics* Eds. S.M. Gragg and N.V.C. Polumin, UNESCO, New Delhi.

RAYNER, S.M. (1983). Distribution of teredinids (Mollusca: Teredinidae) in Papua New Guinea. *Records of the Australian Museum* 35: 61-76.

REHM, A and HUMM, H.J. (1973). *Sphaeroma terebrans:* a threat to the mangrove of South-western Florida. *Science* 182: 173-174.

RIBI, G. (1981). Does the wood boring isopod *Sphaeroma terebrans* benefit red mangrove (*Rhizophora mangle*)? *Bulletin of Marine Science,* 31: 925-925.

RIBI, G. (1982). Differential colonization of roots of *Rhizophora mangle* by the wood-boring isopod *Sphaeroma terebrans* as a mechanism to increase root density. *Marine Ecology,* 3: 13-19.

RIMMER, M.A., BATTAGLENE, S.L. and DOSTINE, P.L. (1983). Observations on the distribution of *Bankia australis* Calman (Mollusca: Teredinidae) in Patonga Creek mangrove swamp, New South Wales. *Australian Journal of Marine and Freshwater Research,* 34: 355-357.

RITCHIE, D. (1986). Invasion of some tropical timbers by fungi in brackish waters. *Journal of the Elisha Mitchell Scientific Society,* 84 (1): 221-226.

ROBERTSON, A.I. and DANIEL, P.A. (1989). Decomposition and the annual flux of detritus from fallen timber: tropical mangrove forests. *Limnology and Oceanography,* 34: 640-646.

ROONWALL, M.L. (1954). The marine borer *Bactronophorus thoracites* (Gould) (Mollusca; Eulamellibranchia, Teredinidae) as a pest of living trees in the mangrove forest of the Sundarbans, Bengal, India. *Proceedings of the Zoological Society of Bengal,* 7: 91-102.

ROTRAMEL, G. (1975). Filter-feeding by the marine boring isopod, *Sphaeroma quoyanum* H. Milne Edwards, 1840 (Isopoda, Sphaeromatidae). *Crustaceana,* 28: 7-10.

SATO, K. (1978). Studies on the protective functions of the mangrove forest against erosion and destruction: (I) the morphological characteristics of the root system of yaeyamahirugi (*Rhizophora mucronata* Lamk). *Scientific Bulletin of the College of Agriculture, University of the Ryukyus,* 25: 615-630.

SHIGO, A.L. (1985). Compartmentalisation of decay in trees. *Scientific American,* 252: 76-83.

SIMBERLOFF, D., BROWN, B.J. and LOWRIE, S. (1978). Isopod and insect root borers may benefit Florida mangroves. *Science,* 201: 630-632.

SUZUKI, E. and TAGAWA, H. (1983). Biomass of a mangrove and a sedge marsh on Ishagaki Island, South Japan. *Japanese Journal of Ecology,* 33: 231-234.

SWIFT, M.J., HEAL, O.W. and ANDERSON, J.M. (1979). *Decomposition in Terrestrial Ecosystems.* Blackwell, Oxford.

TURNER, R.D. (1966). *A Survey and Illustrated Catalogue of the Teredinidae.* Museum of Comparative Zoology, Harvard, U.S.A. 265 pp.

TURNER, R.D. (1977). Wood, mollusks and deep-sea food chains. *Bulletin of the American Malacological Union Incorporated,* 1977: 13-19.

TURNER, R.D. and SANTHAKUMARAN, L.N. (1989). The genera *Martesia and Lignopholas* in the Indo-Pacific (Mollusca: Bivalvia: Pholadidae). *Ophelia,* 30: 155-186.

VAN DER VALK, A.G. and ATTIWILL, P.M. (1984). Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia. *Aquatic Botany,* 18: 208-221.

* * *