TERMITES IN MULGA LANDS

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ABSTRACT

The various termites of mulga lands exploit their environment in different ways, and many species show great plasticity in feeding and nesting behaviour. The biomass of harvester termites may be comparable with that of stock, but only when plant productivity falls to very low levels, as during drought, do stock and termites compete for food. During drought, the combined grazing pressure, and the nesting habits of the termites, can lead to lasting denudation, but such denudation is only known in areas where the mulga cover has been lost.

INTRODUCTION

The insects that affect mulga lands are virtually all native species, and their relationships with the intact mulga communities are as stable as the pressures that selected for the establishment of the mulga systems allow them to be. The effects that we observe contain an element of this natural relationship, and in most cases it appears to predominate—the intermittent defoliation of mulga or associated plants by grasshoppers, caterpillars, or beetles, the formation of leaf galls by thrips, the destruction of seeds by seed weevils or wasps, the sucking of sap by bugs, the attack on roots and trunks by termites and other wood borers, or the possibility, as yet undocumented, of insect involvement in pollination. On the other hand, there is another element in the relationships between insects and mulga, an instability introduced by man's disturbance of the mulga environment. In some situations the disturbance can lead to long-term changes in insect populations, and may involve increases in populations to levels that we call pest proportions. But whatever form the change might take, or whatever its level, it will always originate from the disruption of patterns long established in the undisturbed community.

It is this disruption with which we must be concerned. We know at least something of man's alterations to the mulga communities, but we know very little about the reactions of invertebrates to the changes, or the role of these reactions in later events. The only insects for which we have useful data are the termites, and in terms of the relationships between the changes in plant and termite communities, our data are restricted to the harvester termites.

TERMITES OF MULGA LANDS

The termites of mulga lands all utilise the same source of energy, cellulose. For the present analysis, three principal sources of cellulose can be recognised—wood; dry grass and forbs; and debris, including leaf litter and cow dung. "Wood" includes both standing and fallen timber, weathered or sound, and roots. As an illustration, the main termites from mulga lands in the Alice Springs area, and their main diets, are shown in Table 1. The data are taken from our field observations, and from the accession records for termites in the Australian National Insect Collection, which cover all material accumulated by the CSIRO Division of Entomology during the last 40 years.

The main point that follows from the table is that different species utilise different sources of cellulose, but that the sources overlap widely. Not only do they overlap, but the preferences may change from one area to another, apparently in relation to the availability of food.

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TABLE 1

Feeding preferences of termites from mulga lands near Alice Springs, N.T.

Species	Wood	Main diet Grass	Debris
MASTOTERMITIDAE			
Mastotermes darwiniensis Froggatt	*		
RHINOTERMITIDAE			
Schedorhinotermes actuosus (Hill)	*	*	*
TERMITIDAE			
Amitermes perarmatus (Silvestri)	*		
Amitermes abruptus Gay, *A. capito* Hill	*		*
Amitermes obtusidens Mjöberg		*	*
Amitermes agrilus Gay, *A. dentosus* Hill, *A. vitiosus* Hill	*	*	*
Drepanotermes (five species)		*	*
Microcerotermes distinctus Silvestri, *M. serratus* (Froggatt)	*		*
Nasutitermes sp. near *N. magnus* (Froggatt)		*	
Tumulitermes (three species)		*	*

Thus *Schedorhinotermes actuosus*, a member of a family that is almost entirely xylophagous, feeds mainly on wood in timbered areas, but harvests grasses when wood is absent (*cf.* Watson, 1969). *Amitermes obtusidens* and *A. dentosus* apparently depended largely on weathered wood or debris before man introduced stock, but many series are now taken from dry cow- or horse dung (*cf.* Ferrar and Watson, 1970); in the Alice Springs area these two *Amitermes* are the dominant termites in such situations, where both species are abundant.

A third case involves the mulga lands of Western Australia. At least nine species of *Drepanotermes* are known from these lands, and all harvesters, *i.e.* they gather grass and forbs and store them in their nests. Up to five species have been found together, as, for example, on Mileura Station, in the Wiluna-Meekatharra area (Mabbutt *et al.* 1963), and near Kumarina, in the Upper Gascoyne (Watson and D. H. Perry, unpublished). In such situations each species tends to occupy a different part of the environment, involving differences in soil, in the siting of nests in relation to trees and grasses, and in the type of nest. There are parallel differences in food preference, some species harvesting a predominance of grass, others mulga leaves, some taking a wide variety of grass and debris, others taking only a few species of grasses. These preferences—if that is the right term—vary from one area to another, so that a species confined to sandy levees on Mileura Station occurs in heavy soils farther north, and around Alice Springs; two species that feed mainly on mulga phyllodes on Mileura Station extend south through the mulga-eucalypt line in Western Australia, with a change to a mixed diet with a predominance of grass; and *Drepanotermes rubriceps*, commonly associated with *Triodia* and *Plectrachne* in the mulga lands of western and central Australia, feeds selectively on other grasses in the absence of spinifex in northern Queensland (Watson and D. H. Perry, unpublished).

In other words, the dietary requirements of termites are not necessarily restrictive, and the preferences reflected in the food that they take can vary according to the supply. Thus the termites are well adapted for the changed and changeable conditions that man has brought to the mulga lands.

A further relevant point is the nesting habits of termites. These can vary widely, even among mulga termites. *Amitermes vitiosus*, *Drepanotermes rubriceps*, and *Tumulitermes tumuli* build mounds, or compact nests at ground level. Other species are subterranean and do not build mounds, including *Mastotermes*, *Schedorhinotermes*, and most *Amitermes*, *Drepanotermes*, *Microcerotermes*, and *Tumulitermes*. The mounds vary greatly in structure from species to species, and in *Drepanotermes* *perniger*, there is great intraspecific variability—some populations build tall mounds, others low mounds, some construct compact nests near the soil surface, while others apparently have diffuse, subterranean nests (Watson and D. H. Perry, unpublished). This variability has important repercussions in disturbed situations (see below).

THE NUMBERS AND DEMANDS OF TERMITES

Two further points must be documented here, the numbers (and biomass) of termites in mulga lands, and the amount of material required to support these termites.

Data on the numbers of termites are few, and most estimates are based on the abundance and populations of mounds. We know virtually nothing of the numbers of subterranean termites, including *Mastotermes*, *Schedorhinotermes*, the subterranean *Amitermes* and *Drepanotermes*, *Microcerotermes*, or *Tumulitermes dalbiensis*, major termites in the Alice Springs region (Table 1).

Estimates of up to 350 mounds per hectare have been made for *Drepanotermes* (Watson and Gay, 1970), and rates of 50-100 mounds per hectare are not uncommon (Watson, unpublished). The few measurements that we have for the area occupied by presumed single colonies of subterranean *Drepanotermes* suggest figures of up to 10-15 m^2, much less than the common figures for mound builders, assuming no substantial overlap of foraging areas, of approximately 100-200 m^2. The potential maximum density of subterranean *Drepanotermes* colonies could therefore approach 1,000/ha.

The populations of subterranean colonies are unknown, so that we cannot yet estimate their biomass. Preliminary counts of colonies from moderately sized mounds of *Drepanotermes perniger* indicate that the populations are relatively low, averaging a minimum of approximately 20,000; such a colony would weigh approximately 200-250 g. The biomass of mound-building *Drepanotermes* at the "common" rates of infestation would therefore amount to approximately 20-25 kg/ha.

The demand imposed by these numbers of *Drepanotermes* has been estimated in several ways. The two best documented estimates are based on foraging activity, and on the stores of forage; they agree closely.

1 Moderately sized nests of *Drepanotermes perniger* in the Murrumbidgee Irrigation Area of New South Wales can open 1,000 or more foraging holes during the summer, and large, active nests 4,000-5,000 holes (Watson, unpublished). Foraging holes are usually open for at least an hour, and commonly for 2-3 hours. At 26-27°C, foraging parties of 100-200 termites, a common number, carry approximately 30-40 pieces of forage underground per minute. Pieces of forage stored in these nests weigh, on the average, approximately 0.6 mg (Watson, unpublished). Thus small nests could readily account for at least a kilogram of forage per year, or 50-100 kg/ha for the "common" rates of infestation; and larger colonies could remove several times these estimates.

2. Moderately sized, active nests of *Drepanotermes perniger* in northern New South Wales contain 200-500 g of dry grass and leaf litter when foraging ceases in early winter, and large nests may contain more than a kilogram. Much of this grass can be consumed by the time that foraging resumes in the spring, and the rate of consumption is presumably higher in the higher temperatures of summer, when foraging, reproduction, and development are most active (Watson, unpublished). The annual consumption in moderately sized nests could therefore exceed a kilogram, and in large nests, several kilograms.

Thus mound-building harvester termites alone may often account for 100 kg/ha dry weight of plant productivity each year, and presumably the subterranean harvesters, and the wood- and debris feeders, add to the total. Of the material removed, some at least reverts directly to the nutrient pool, even if only after a delay through being locked up in the structural materials or rejected matter in a termite nest. The question then arises: What is the significance of the weight of material removed? The significance apparently varies from one area to another. We can take as examples the situation in the cattle country near Alice Springs, and that in the sheep country of south-western Queensland.

HARVESTER TERMITES IN THE ALICE SPRINGS REGION

Observations in the Alice Springs region are based on the Kunoth Paddock of Hamilton Downs Station, centred at approximately 23.32S 133.35E, with an area of 15,300 ha. Frequent observations over a period of two years have shown that the main herbivores are cattle, kangaroos, and termites, although other primary consumers—caterpillars, grasshoppers, and graminivorous birds—irrupt periodically.

Seven major range types occur on Kunoth (Low 1972)—mulga-perennial grass, mulga-short grass, savannah woodland, calcareous shrubby woodland, floodplain, gilgaied plain, and the foothills. The foothills are floristically similar to the savannah woodland. Mulga dominates two of these range types, mulga-perennial grass, and mulga-short grass, which are important communities, as they occupy 8,600 ha, or 53% of the paddock; Ross and Lendon (1973) describe mulga-perennial grass in more detail elsewhere in this Symposium.

It is most convenient to treat the distribution and grazing behaviour of the three herbivores, cattle, kangaroos, and termites, in turn.

Between 500 and 700 cattle graze at will over Kunoth, the number varying with the season; they constitute a biomass of approximately 10-15 kg live weight/ha. Although the distribution of watering points gives the cattle access to all the mulga areas, the mulga-perennial grass was the least preferred of the range types following both summer and winter rains; mulga-short grass ranked fifth of the seven major types in both seasons (Low 1972). In the mulga-perennial, cattle will graze on green plants, particularly in depressions at the run-on of the mulga groves. The mulga-short grass includes an understorey of annual grasses and forbs palatable to cattle, particularly in the green state.

Kangaroos, unlike the other two herbivores, can move into and out of the paddock at will, and their populations vary widely with seasonal conditions; but the estimated biomass over two years has been much lower than those of cattle and termites, ranging from zero to, rarely, about 1.5 kg live weight/ha, with an average of roughly 0.16 kg/ha. The kangaroos consistently prefer the savannah woodland and mulga-short grass, and graze little in the mulga-perennial. Even more than cattle, kangaroos seek out green feed.

Nine species of termites behave as harvesters on Kunoth Paddock—*Amitermes vitiosus*, five species of *Drepanotermes*, a species of *Nasutitermes* near *N. magnus*, *Tumulitermes dalbiensis*, and an undescribed species of *Tumulitermes*. *Drepanotermes* is the most important of these genera. The biomass of termites has not yet been measured, but probably approximates that in the "common" rates of infestation with *Drepanotermes*, a biomass comparable to that of cattle. The harvester termites are concentrated in the two mulga communities, most so in the mulga-perennial grass (Table 2); their distribution differs strikingly from that of cattle or kangaroos. The termites generally take material in a dry state, and at least *Drepanotermes* does not harvest in winter. Thus plants are only marginally liable to termite attack when they are green, and palatable to the vertebrates, while plants that respond to winter rains, like the forbs, are probably not liable to attack.

The evidence therefore suggests that the consumption of grass and forbs by termites does not interfere directly with the raising of cattle on Kunoth. In periods of protracted drought, however, the perennial grasses of the mulga-perennial community form the most persistent and long-standing "hay crop", and must act as a drought reserve for termites and cattle alike. Yet in the severe 9-year drought, broken in 1966, the combined grazing pressures did not result in widespread disappearance of either the main forage plants, or of the primary consumers, indicating that the Kunoth mulga-perennial community is an ecosystem of considerable stability.

TABLE 2

Occurrence of harvester termites in the range types on Kunoth Paddock, N.T.

Species	Range Type: Mulga-perennial	Mulga-short grass	Savannah woodland	Calcareous woodland	Flood-plain	Gilgai
Amitermes vitiosus Hill	*	*			* (margin)	
Drepanotermes sp. nov. "B"**	*	*				
Drepanotermes sp. nov. "C"**	*	*	*			?
Drepanotermes sp. nov. "D"**	*	*	*			?
Drepanotermes perniger (Froggatt)	*	*				
Drepanotermes rubriceps (Froggatt)	*					
Nasutitermes sp. near *N. magnus* (Froggatt)				*		* (margin)
Tumulitermes dalbiensis (Hill)	*	*	*			
Tumulitermes sp. nov.	*					
Estimate of abundance	abundant	moderate	low-moderate	low	low	low

** To be described elsewhere (Watson and D. H. Perry, in preparation).

HARVESTER TERMITES IN SOUTH-WESTERN QUEENSLAND

Unlike the situation near Alice Springs, the relationships among stock, *Drepanotermes* and mulga in south-western Queensland have been unstable. Some of the interrelationships were examined by Watson and Gay (1970) on Wittenburra Station, near Eulo; the important conclusions were as follows.

1. The loss of mulga under pastoral management, apparently through fire and the inhibitory effect of sheep on regeneration of mulga, opened up the tree cover, increasing the potential for the growth of grass under favourable climatic conditions.

2. Such favourable phases, possibly two or three in number since pastoral activity commenced in the area a century ago, led to rapid increases in the populations of both sheep and harvester termites.

3. With the inevitable return to low rainfall, grass growth slowed or ceased, and the termites, sheep, and possibly other vertebrates denuded the grassed areas. In addition, *Drepanotermes* attacked, and in severe cases destroyed, the bases of the grass tussocks, so that the grassed areas were rendered incapable of rapid regeneration. Erosion was severe. The denudation, and its durability, were also attributable in part to the depletion of the mulga itself, for had more mulga remained, the termites would have gathered the relatively abundant mulga debris during drought, easing the grazing pressure on the tussocks.

4. The deleterious effects of the denudation were heightened by the nesting habits of the termites. In the Warrego region of south-western Queensland, *Drepanotermes perniger* builds compact nests at or just below soil level, and each nest has a hard cap commonly 2-3 m in diameter. The nests can occupy up to 20% of the soil surface in dense infestations. In situations where denudation and erosion have occurred, the hard tops of the nests impede water penetration and seed lodgement, and hence, impede the recovery of the system. Data suggest that the inhibitory effects of such termite infestations can persist for 70 years or more (Watson and Gay, 1970).

Thus the differences in stability between south-western Queensland and Kunoth under grazing by stock apparently involve differences in land management—most critically, the loss of mulga—and the difference in nesting habits of the termites.

DISCUSSION

The material presented points to the nature of the action and reaction between the disturbance of the mulga environment by stocking and the activities of termites.

First, we can envisage the termites in a natural situation. They have sufficient adaptability in their food preferences to cover the range of grassy and non-grassy materials normally available to them within a wide range of climatic conditions. At least one species, *Drepanotermes perniger*, can commonly remove up to 100 kg/ha of material annually, most of it dry, and this must be regarded as normal recycling, the material reverting to the nutrient pool of the soil. Other termites will similarly recycle plant material.

Second, we can envisage the introduction of further herbivores, depending in the long run on green forage. At least under favourable climatic conditions, the introduced herbivores will scarcely interact with the termites; sufficient dry material will survive for the harvesters, there will be little if any effect on the supplies of wood, and the dung will provide additional food for some of the termites.

However, in regions of irregular rainfall—and this applies to all of the mulga regions—it is inevitable that during the drier seasons the harvester termites will take material that might otherwise be eaten by stock. Dry material will be the only food available, and supplies of grass may dwindle to very low levels. Under such conditions it is likely that the harvesters would switch to leaf litter or other debris, on which we know they can survive. This likely switch of diet raises two related points—it assumes that the original mulga cover is substantially intact, and can provide an adequate supply of litter, and that in consequence, the termites do not graze the bases of the tussocks.

Third, we have the instability induced by the alteration of plant communities, and the grazing pressure that they will withstand, the periodic excesses of total grazing pressure over the modified plant productivity, and a decrease in the availability of alternative food for the termites. This is the situation where termites can affect the structure of the mulga community, and the economics of pastoral industries based on it.

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