

Tribulus terrestris L. (Zygophyllaceae) in Southern Africa: An outline of biology and potential biological control agents for Australia

John K. Scott*, CSIRO Biological Control Unit, Zoology Department, University of Cape Town, Rondebosch 7700, South Africa.

Summary

An outline is given of the biology of *Tribulus terrestris* L. (Zygophyllaceae) in southern Africa. The plant is native to the region and notable as a cause of poisoning in sheep. Potential biological control agents found in southern Africa are seed and stem feeding weevils, *Microlarinus* spp., a seed sucking bug, *Deroplax* sp., a noctuid defoliator, *Prodotis stolidus*, and a downy mildew, *Peronospora tribulina*. The organisms from southern Africa are compared with those found on *T. terrestris* in India and the Mediterranean region. Potential agents found in the latter regions include seed and stem feeding weevils, *Microlarinus* spp., leaf feeding moths, *Ephysteris subdiminutella* and *Tegostoma comparalis* and a leaf mite, *Eriophyes tribuli*. Most of the potential biological control agents include other *Tribulus* species as hosts. Biological control of *T. terrestris* will require a clarification of the taxonomy and origins of weedy forms of *Tribulus* in Australia. The use of a limited selection of highly specific agents such as Eriophyid mites and fungi may be necessary. Alternatively, attack on native *Tribulus* species by control agents may have to be accepted.

Introduction

Tribulus terrestris L. (Zygophyllaceae) has a cosmopolitan distribution. In Australia, the plant is found in a number of forms, including some considered to be native, and a weedy form, caltrop, which is thought to be introduced (Bourke 1987b, Squires 1969b). The origin of the weedy form in Australia is unknown, but may have included southern Africa. The plant is regarded as native to southern Africa (Wells *et al.* 1986) and has associated with it fauna and diseases (Kluge 1975) which could be used as biological control agents against *T. terrestris* in Australia.

Here I summarize the biology of *T. terrestris* in southern Africa and make comparisons with that in Australia. The fauna and fungi associated with *T. terrestris* in southern Africa are examined for potential use as biological control agents in Australia, and are compared with potential biological control agents which are known from other regions.

Tribulus terrestris in southern Africa

Five species of *Tribulus*, *T. cristatus* Presl, *T. excrucians* Wawra, *T. pterophorus* Presl, *T. terrestris* and *T. zeyheri* Sond., are known from southern Africa (Botswana, Lesotho, Namibia, South Africa, and Swaziland) (Gibbs Russell *et al.* 1987, Schweickerdt 1939). All are indigenous to this region.

A description and account of variation in *T. terrestris* in South Africa was given by Schweickerdt (1939) who was uncertain "whether *T. terrestris* ... is only one extremely variable species or whether at present several closely allied species are included under this name". Four ploidy levels (diploid to octoploid, $2n = 12, 24, 36$ and 48) are known for *T. terrestris* (Squires 1979, Hilu 1981), but chromosome counts for this species from southern Africa are unknown.

The first record of *T. terrestris* in southern Africa appeared in 1794 and early botanists suggested that it was an introduced species from southern Europe (references in Schweickerdt 1939). The plant is now considered indigenous to southern Africa (Kluge 1975, Wells *et al.* 1987).

Distribution and biology

Tribulus terrestris is found in ruderal and semiruderal areas throughout Africa including southern Africa (Kluge 1975, Schweickerdt 1939). It is one of the dominant plants of cattle pasture in semi-arid areas of southern Africa especially around boreholes (Tolsma *et al.* 1987). This is thought to be due to overgrazing which resulted in the disappearance of perennial palatable grasses (Tolsma *et al.* 1987).

In southern Africa, as elsewhere, *T. terrestris* is a summer growing annual. Ernst and Tolsma (1988) found that fresh, three and six year old seeds showed signs of dormancy and that germination was irregular. The highest level of germination of isolated seed was 66.9% with a mean of 37.3%. Few seeds (3.5%) within a coccus germinated at the same time. In the field, germination of not more than 1% of the seed pool occurred following rain of more than 10 mm. Maximum germination was 35% of the seed pool following heavy rainfall (Ernst and Tolsma 1988).

Fruits from Gaborone, Botswana, broke into three to seven cocci, each with between one and four potential seeds which mostly gave rise to one or two fertile seeds (Ernst and Tolsma 1988). Kluge (1975) observed that an average of 3.8 out of five possible

cocci developed and that fruits averaged 13.4 seeds.

Importance and control methods

Tribulus terrestris is included on the southern African list of problem plants (Wells *et al.* 1986) and as a weed of gardens and cultivated lands (Henderson and Anderson 1966) including vineyards (Fourie and Van Huyssteen 1987). The spiny fruits cause damage to the feet of stock (Henderson and Anderson 1966). In the context of its importance in farming and disturbed lands, Kluge (1975) mentioned "it is difficult to estimate the financial loss attributable to this weed".

The primary importance in southern Africa of *T. terrestris* is as a cause of the hepatogenous photosensitivity disease "geeldikkop" (Kellerman and Coetzer 1984). This disease causes extensive stock losses (mainly sheep) in southern Africa, but despite considerable research (see reviews by Kellerman and Coetzer 1984 and Watt and Breyer-Brandwijk 1962), the causal toxin and the conditions for its production remain unknown.

Tribulus terrestris is a subject of herbicide registration (Wells *et al.* 1986). In vineyards the pre-emergence herbicides, trifluralin, simazine and fluorochloridone are recommended for *T. terrestris* control, along with other summer annuals (Fourie and Huyssteen 1987).

Control methods aside from herbicides are hand pulling or cutting the tap root (Henderson and Anderson 1966). In vineyards, mechanical weed control is not recommended since it promotes further germination of *T. terrestris* (Fourie and Huyssteen 1987).

In southern Africa, *T. terrestris* has associated fauna and diseases which appear to exert little influence on the plant's population, possibly due to their own biotic controls (e.g. parasites) as suggested by Kluge (1974). Kluge (1975) discussed the possibility of manipulating the parasites of the naturally occurring biological control organisms by using insecticides. This has not been attempted.

Comparison with Australia

The biology of *T. terrestris* in Australia was reviewed by Parsons (1973) and Squires (1969a, 1979). As in southern Africa, there is a similar lack of understanding of the taxonomy and origins of the forms of *T. terrestris* in Australia (Squires 1969b, Bourke 1987b). *Tribulus terrestris* is the only member of the southern African Zygophyllaceae known in Australia. However, in Australia there are possibly 15 native *Tribulus* species in contrast to five in southern Africa.

A major difference between southern Africa and Australia is the much less severe historical incidence of the disease "geeldikkop". This disease and other toxic responses to *T. terrestris* ingestion are possibly on the increase in Australia as witnessed by recent reports (Bourke 1983, 1984, 1987a, 1987b, Glastonbury and Boal 1985, Glastonbury *et*

*Present Address: CSIRO Division of Entomology, Private Bag, P.O. Wembley 6014, Western Australia.

al. 1984, Jacob and Peet 1987).

A similarity between Australia and southern Africa is the weed's importance in vineyards. In Australia, *T. terrestris* is a problem on drying greens associated with vineyards (Parsons 1973), but this problem does not seem to arise in South Africa possibly due to the use of manual weed control.

Thus it seems that *T. terrestris* is a weed of similar importance in Australia as in southern Africa. However, the fauna and diseases associated with *T. terrestris* in southern Africa are absent from Australia and may be suitable for use as biological control agents.

Potential biological control agents from southern Africa

Kluge (1975) undertook a survey of the insect fauna associated with *T. terrestris* at four widely separated sites: Stellenbosch (S.W. Cape Province), Jan Kempdorp (N.W. Cape Province), Messina (N.E. Transvaal) and Pretoria (Transvaal) in South Africa. In Namibia, a more extensive survey, during one month, examined 17 sites of *T. terrestris*. The survey in South Africa found 24 species and the survey in Namibia found 11 species feeding on the plant. Two species had larvae which fed inside the plant, the remainder being either foliage feeders (all Lepidoptera) or sucking insects on stems or fruits (Hemiptera). Most damage was caused to the fruits, defoliation was occasionally caused by mainly polyphagous insects, but at the other extreme, there was no damage to the roots. Kluge (1975) found that 30% of seeds showed damage due to sucking insects. The following potential biological control agents were considered in more detail by Kluge (1975).

Microlarinus hypriformis Woll. (Curculionidae)

This weevil is widely distributed in southern Africa and has larvae which tunnel in the stems and crown. It is also found in India and the Mediterranean regions from where it was imported into mainland USA and Hawaii (Andres and Angalet 1963). It was rated a successful biological control agent (Julien 1987) following studies that showed that it and the related seed feeding species, *M. lareynii* (Jacquelin du Val), have significantly contributed to a decline in plant density (Huffaker *et al.* 1983). The adults are not host specific and will feed on a number of plant families, although egg development occurred only after feeding on plants of the family Zygophyllaceae (Andres and Angalet 1963). In the field, *M. hypriformis* was found feeding on other *Tribulus* species (Kluge 1975) and in the laboratory larvae developed to maturity on *Kallstroemia grandiflora* (Zygophyllaceae) (Andres and Angalet 1963).

Microlarinus pilosus Gyll. (Curculionidae)

The larvae of this weevil develop in the young fruits. The species is widely distributed in southern Africa and also feeds on *T. pterophorus* and *T. zeyheri*, but otherwise the host specificity is unknown. Between 5.5 and 14.7% of burrs of *T. terrestris* were damaged and within each burr about 20% of seeds were destroyed. Kluge (1975) found considerable parasitism (estimated at 60%) and predation, particularly of eggs of the weevil. The closely related species, *M. lareynii*, which also feeds on developing fruits of *T. terrestris*, but is not known from southern Africa, has been imported from Italy into Hawaii and continental USA where it contributes to successful control of the weed (Julien 1987). This species lays its eggs in developing fruits, whereas *M. pilosus* oviposits in flower buds (Kluge 1975).

Prodotis stolidi (F.) (Noctuidae)

The larvae of this moth are foliage feeders on *Tribulus* spp. and are found throughout southern Africa (Kluge 1975). This insect is reported to be polyphagous elsewhere in its distribution (Africa, southern Europe and Asia) (Pinhey 1975) and a minor pest of flax (*Linum usitatissimum* L. (Linaceae)). Kluge (1975) was unable to rear first instar larvae of *P. stolidi* on flax, *Sesbania punicea* L. (Leguminosae), *Quercus* sp. (Fagaceae) and *Lactuca sativa* L. (Asteraceae). Fourth instars did not feed on flax. Kluge (1975) noted that *P. stolidi* from southern Africa differed from the description of the moth in India and it is possible that the southern African insect represents a different species.

Deroplax sp. (Scutelleridae)

The nymphs and adults of the shield bug, *Deroplax* sp., were found associated with *T. terrestris* and *T. zeyheri* during the survey by Kluge (1975). He was able to rear adult insects from second instar nymphs which were fed dry burrs of *T. terrestris*, *T. pterophorus* and *T. cristatus*.

Development of second instar nymphs failed on *Datura ferox* L., *Helianthus annuus* L. (Asteraceae), *Gossypium hirsutum* L. (Malvaceae), but two adults developed from 33 second instar nymphs fed seeds of *Curcubita pepo* L. (Cucurbitaceae). This latter result was possibly due to a broken seed coat allowing access to seed. Kluge (1975) suggests that food selection could be based on the physical attributes of the seed coat. Although *Deroplax* sp. was commonly found associated with *T. terrestris* in many cultivated fields, it has never been reported as a crop pest in southern Africa (Kluge 1975).

Fungi

No systematic surveys have been made of the fungi associated with *T. terrestris* in southern Africa. Kluge (1975) noted that plants were destroyed by a fungus, identified

as "a hitherto unknown fungus similar to *Alternaria zinniae* Hbl.". Jooste (1975) described *Drechslera multififormis* Jooste (Hyphomycetes) based on an isolation from *T. terrestris* hay which was collected during a study of toxigenic fungi in sheep pasture. Another saprophyte, *Pithomyces chartarum* (Berk & Curt.) M.B. Ellis (Hyphomycetes), associated with *T. terrestris* in South Africa is a known cause of hepatogenous photosensitivity in livestock (Kellerman and Coetzer 1984) and is found as a disease-causing agent in Australia (Jacob and Peet 1987). Gorter (1981) recorded the downy mildew, *Peronospora tribulina* Pass. (Peronosporales) on *T. terrestris*. This fungus has also been recorded from *T. terrestris* in Italy (Saccardo 1888).

Discussion

Surveys for biological control agents

Kluge (1975) showed that there are insects from southern Africa which could be considered as biological control agents. The species found were the seed feeding weevil, *M. pilosus*, the seed sucking bug, *Deroplax* sp., and the foliage feeding noctuid, *P. stolidi*. In addition a fungus, *P. tribulina*, is found in the region and may have potential for use as a biological control agent and further surveys may identify other fungi such as the *Alternaria*-like species mentioned in Kluge (1975).

Surveys and collections of other organisms have also been made on *T. terrestris* in the Mediterranean region, India and Australia. In the Mediterranean region, Andres and Angalet (1963) found two *Microlarinus* species and further surveys in this area may find additional biological control agents (Wapshere 1989).

A survey for biological control agents for *T. terrestris* was made in Bangalore and nearby areas in South India by Sankaran and Ramaseshiah (1981). They concluded after a one year survey that a leaf-feeding mite, *Eriophyes tribuli* Keifer, a leaf-mining gelechiid, *Ephysteris subdiminutella* Stn., a leaf-feeding pyralid, *Tegostoma comparalis* Hb. and the weevils, *Microlarinus angustulus* Hb. and *M. rhinocylloides* Hch. whose larvae fed in the seeds, warranted further evaluation as biological control agents. In an earlier study in India, Pathak (1968) refers to the biological control of *T. terrestris* by a pentatomid, *Poecilocoris* sp. It is not clear in Pathak (1968) if this insect was the cause of the damage to plants and it is possible that the author was observing the effect of eriophyiids.

Insects which appear to specialize on *T. terrestris* are also known from Australia. The gelechiid moth, *Aristotelia turbiba* Turn., has larvae which feed on the immature fruits of *T. terrestris*, often destroying large numbers of seed (Squires 1965). This insect has even been suggested as a possible biological control agent for *T. terrestris* in South Africa (Kluge 1974).

Potential biological control agents

The above surveys show that there are four groups of potential biological control agent for *T. terrestris*: the *Microlarinus* weevils, leaf-feeding lepidoptera, seed sucking bugs and highly specialized organisms such as mites and fungi.

Two *Microlarinus* species have been used successfully as biological control agents against *T. terrestris* (Julien 1987). Andres (1978) described in detail the polyphagous habits of adult *Microlarinus* spp. after they were released as biological control agents in North America. Damage to citrus was noted once, but ascribed to an unusual set of circumstances and the insect has been found on a number of crops, but not feeding (Andres 1978). The degree of specificity indicates that some feeding on crops during epidemic levels shortly after introduction (Andres 1978) would have to be accepted if this insect was to be released in Australia (Wapshere 1989). The surveys in southern Africa and India show that there are another three species of *Microlarinus* which could be studied, but these may have similar host ranges to the species already used in North America. The *Microlarinus* species found in India included *M. angustulus* which was described from South Africa (Marshall 1921), but was not found in survey by Kluge (1975), and it is possible that a taxonomic study may show that some of these species are identical.

The two moths, *E. subdiminutella* and *T. comparalis* which are found in India on *T. terrestris*, are known from southern Africa (Vari and Kroon 1986). However, Kluge (1975) only found the related species, *T. subditalis* Zell. on *T. terrestris*. These Lepidoptera and *P. stolidus* are all species which defoliate the plant and include other *Tribulus* species as hosts. In contrast to adult *Microlarinus*, the adult moths are unlikely to have problems with host specificity.

The remaining insect, the seed sucking bug, *Deroplax* sp., also includes other *Tribulus* species as hosts. Since this species can survive on dry burrs of *T. terrestris* it is not dependent on the presence of live plants (Kluge 1975). This could prove to be an important attribute for a biological control agent given the ephemeral nature of the host plant.

The insects mentioned so far feed on other *Tribulus* species besides *T. terrestris* which implies that the approximately 15 native Australian species will also be accepted as hosts. Mites are often highly host specific (Comroy 1978) and it is likely that the eriophyid, *E. tribuli*, will not present a threat to native *Tribulus* species in Australia. It was first described from *T. terrestris* from Sudan (Keifer 1974) and is reported to be damaging to *T. terrestris* in India (Sankaran and Ramaseshiah 1981) and is unknown from other species. It has not been reported from South Africa, although *T. terrestris* does not appear to have been examined for eriophyids. Like-

wise, the obligately pathogenic fungus, *P. tribulina*, may prove to be host specific, although species of this genus have yet to be used as biological control agents. Biological control agents such as mites and fungi can be highly host specific and will damage only some forms of a weed. For this reason it is desirable to have a good understanding of the weed's taxonomy and origins.

Sources for agents

It is unknown whether the various forms of *T. terrestris* in Australia are the same as those from southern Africa and other origins for the Australian forms are possible, such as India or the Mediterranean region. The presence of insects with a close association with *T. terrestris* in southern Africa, in particular the seed feeding species, *M. pilosus*, which is not found elsewhere, shows that the plant is probably native to this region. The well developed fauna on *T. terrestris* in India is evidence contrary to the view that the plant and associated species spread to the region in recent times (Sankaran and Ramaseshiah 1981, Squires 1979), and thus India may also be a suitable source for biological control agents. Correct identification of the target plant and origin is critical for a biological control project and this aspect would demand priority in any future research.

Conclusions

Tribulus terrestris in southern Africa has associated with it organisms suitable for consideration as biological control agents. Other potential biological control agents are known from India and surveys are needed elsewhere in the distribution of *T. terrestris* to establish the full range of potential agents. Among the known organisms which should be considered first for further assessment and host specificity testing are the mite, *E. tribuli*, and the pathogen, *P. tribulina*. Next in priority should be the moths, *E. subdiminutella*, *T. comparalis* and *T. solida*, followed by *Deroplax* sp. and the *Microlarinus* spp. Most of the known potential biological control agents may prove to be specific to the level of the genus *Tribulus* and consequently may present a threat to the native Australian *Tribulus* species. An elucidation of the taxonomy of Australian *Tribulus* would determine which species may be at risk as well as providing a better understanding of the origins of *T. terrestris*.

Acknowledgements

I thank K. Harmer, R.L. Kluge, C. Kleinjan, S. Naser and R.G. Shivas for comments on aspects of the manuscript.

References

Andres, L.A. (1978). Biological control of puncturevine, *Tribulus terrestris* (Zygophyllaceae): post introduction collection records of *Microlarinus* spp. (Coleoptera: Curculionidae). Proceedings of the IV In-

ternational Symposium on Biological control of Weeds, Gainesville, Florida 1976, pp. 132-136.

Andres, L.A. and Angalet, G.W. (1963). Notes on the ecology and host specificity of *Microlarinus lareynii* and *M. lypriformis* (Coleoptera: Curculionidae) and the biological control of puncture vine, *Tribulus terrestris*. *Journal of Economic Entomology* 56, 333-340.

Bourke, C.A. (1983). Hepatopathy in sheep associated with *Tribulus terrestris*. *Australian Veterinary Journal* 60, 189.

Bourke, C.A. (1984). Staggers in sheep associated with the ingestion of *Tribulus terrestris*. *Australian Veterinary Journal* 61, 360-363.

Bourke, C.A. (1987a). A novel nigrostriatal dopaminergic disorder in sheep affected by *Tribulus terrestris* staggers. *Res. Vet. Sci.* 43, 347-350.

Bourke, C.A. (1987b). Some taxonomic, agronomic and animal health aspects of *Tribulus*. Proceedings of the 8th Australian Weeds Conference. pp. 182-185.

Comroy, H.L. (1978). The potential use of eriophyid mites for control of weeds. Proceedings of the IV International Symposium on Biological Control of Weeds, Gainesville, Florida 1976, pp. 294-296.

Ernst, W.H.O. and Tolsma, D.J. (1988). Dormancy and germination of semi-arid plant species, *Tragus berteronianus* and *Tribulus terrestris*. *Flora* 181, 243-251.

Fourie, J.C. and Van Huyssteen, L. (1987). Practical hints for the control of weeds in vineyards. *Deciduous Fruit Grower* 37, 347-356.

Gibbs Russell, G.E., Welman, W.G., Retief, E., Immelman, K.L., Germishuizen, G., Pienaar, B.J., Van Wyk, M. and Nicholas, A. (1987). List of species of southern African plants. Edition 2, Part 2. *Mem. Bot. Surv. S. Afr. No.* 56: 1-270.

Glastonbury, J.R.W. and Boal, G.K. (1985). Geeldikkop in goats. *Australian Veterinary Journal* 62, 62-63.

Glastonbury, J.R.W., Doughty, F.R., Whitaker, S.J. and Sergeant, E. (1984). A syndrome of hepatogenous photosensitization, resembling geeldikkop, in sheep grazing *Tribulus terrestris*. *Australian Veterinary Journal* 61, 314-316.

Gorter, G.J.M.A. (1981). Index of plant pathogens, II and the diseases they cause in wild growing plants in South Africa. *Rep. S. Afr. Dept. Agric. Fish. Sci. Bull.* 398, 1-84.

Henderson, M. and Anderson, J.G. (1966). Common weeds in South Africa. *Bot. Surv. S. Afr. Mem.* 37, 1-440.

Hilu, K.W. (1981). Cytotaxonomical studies in *Tribulus terrestris* and *T. alatus* (Zygophyllaceae). *Nord. J. Bot.* 1, 531-534.

Huffaker, C.B., Hamai, J. and Nowierski, R.M. (1983). Biological control of puncturevine, *Tribulus terrestris* in California after twenty years of activity of intro-

- duced weevils. *Entomophaga* 28, 387-400.
- Jacob, R.H. and Peet, R.L. (1987). Poisoning of sheep and goats by *Tribulus terrestris* (caltrop). *Australian Veterinary Journal* 64, 288-289.
- Jooste, W.J. (1975). A new species of *Drechslera* on *Tribulus terrestris*. *Bothalia* 11, 511-513.
- Julien, M.H. (1987). 'Biological control of weeds: a world catalogue of agents and their target plants'. 2nd ed. CAB International, Wallingford, 144 pp.
- Keifer, H.H. (1974). Eriophyid studies. Ser. C. No. 9. 1-24. Sacramento, California. (Taken from: *Biol. Abst.* 60, 61527).
- Kellerman, T.S. and Coetzer, J.A.W. (1984). Hepatogenous photosensitivity diseases in South Africa. *Dept. Agric. Rep. S. Afr. Tech. Communication No.* 193, 1-23.
- Kluge, R.L. (1974). *Tribulus terrestris* L. - an indigenous weed. First National Weeds Conference of South Africa, 13-14 August 1974, pp. 196-203.
- Kluge, R.L. (1975). Observations on insects associated with *Tribulus terrestris* L. in southern Africa. Unpublished M Sc (Agric.) Thesis, University of Pretoria, 128 pp.
- Marshall, G.A.K. (1921). On twelve new species of Curculionidae from South Africa. *Ann. Mag. nat. Hist.* 8, 145-160.
- Parsons, W.T. (1973). 'Noxious weeds of Victoria'. Inkata Press, Melbourne, 300 pp.
- Pathak, P.S. (1968). Biological control of *Tribulus terrestris* by an insect of Hemiptera. Proceedings of the Symposium on Recent Advance in Tropical Ecology. Part II. (Ed. R. Misra and B. Gopal). pp. 697-701.
- Pinhey, E.C.G. (1975). 'Moths of southern Africa'. Tafelberg, Cape Town, 273 pp.
- Saccardo, P.A. (1888). *Sylloge Fungorum*. Vol 7. 882 pp.
- Sankaran, T. and Ramaseshiah, G. (1981). Studies on some natural enemies of puncturevine *Tribulus terrestris* occurring in Karnataka State, India. Proceedings of the V International Symposium on Biological Control of Weeds, Brisbane 1980. pp. 153-160.
- Schweickerdt, H.G. (1939). An account of the South Africa species of *Tribulus* Tourn. ex Linn. *Bothalia* 3: 157-178.
- Squires, V.R. (1965). A note on *Aristotelia* sp. (Lep., Gelechiidae) attacking *Tribulus terrestris* L. *Journal of the Entomological Society of Australia (N.S.W.)* 2, 43-44.
- Squires, V.R. (1969a). Ecological factors contributing to the success of *Tribulus terrestris* L. as a weed in a winter rainfall environment in southern Australia. Proceedings of the Ecological Society of Australia 4, 55-66.
- Squires, V.R. (1969b). Distribution and polymorphism of *Tribulus terrestris* sens. lat. in Australia. *Victorian Naturalist* 86, 328-334.
- Squires, V.R. (1979). The biology of Australian weeds 1. *Tribulus terrestris* L. *Journal of the Australian Institute of Agricultural Science* 45, 75-82.
- Tolsma, D.J., Ernst, W.H.O. and Verwey, R.A. (1987). Nutrients in soil and vegetation around two artificial waterpoints in eastern Botswana. *Journal of Applied Biology* 24, 991-1000.
- Vari, L. and Kroon, D. (1986). 'Southern African Lepidoptera'. Transvaal Museum, Pretoria. 198 pp.
- Wapshere, A.J. (1989). Biological control of weeds. In 'Mediterranean landscapes in Australia. Mallee ecosystems and their management'. pp. 443-463. (Eds J.C. Noble & R.A. Bradstock).
- Watt, J.M. and Breyer-Brandwijk, M.G. (1962). 'The medicinal and poisonous plants of southern and eastern Africa'. E. & S. Livingstone Ltd, Edinburgh, 1457 pp.
- Wells, M.J., Balsinhas, A.A., Joffe, H., Engelbrecht, V.M., Harding, G., and Stirton, C.H. (1986). A catalogue of problem plants in southern Africa. *Mem. Bot. Surv. S. Afr.* 53, 1-658.