

coastal heaths to desert shrublands and alpine meadows (Kuijt 1969).

The adaptability and versatility of parasitic plants is manifested in their phenology (Watson 2001, 2004). As parasites, these plants can access nutrients and water when unavailable to autotrophic plants, enabling a broader range of phenological responses. Peak flowering in many taxa coincides with periods or seasons when few other species are able to flower, maximizing visitation rates by generalist pollinators. Fruiting is similarly coincident with periods of local scarcity, with seed vectors such as frugivorous birds further tempted by fruits high in available carbohydrates, amino acids, and (or) fats (Watson 2001). These competitive advantages are most evident in temperate and arid systems, where complementary phenologies have been mostly described (Davidar 1983; Polhill and Wiens 1998).

Given their parasitic habit, physiological resilience, and life-history plasticity, parasitic plants seem to have solved many of the resource-based challenges limiting autotrophic plants. Accordingly, they might be expected to be abundant and obvious components of many terrestrial habitats.

Yet, parasitic plants are characteristically uncommon-rare in undisturbed habitats. At community and population scales, they are a minor habitat component in terms of biomass, diversity, and abundance, wherever they occur (Kuijt 1969). They are easily overlooked in community-level studies, and frequently ignored in the botanical, ecological, and forestry literature (Pennings and Callaway 2002; Press and Phoenix 2005). Interestingly, however, they can become abundant at finer scales and often occur in nonrandom patterns within a habitat or stand (Overton 1996; Aukema and Martinez del Rio 2002a). Hence, parasitic plant distributions are clearly constrained even though variously unaffected by most of the factors limiting the distributions of autotrophic plants. The identity and role of these constraints, however, have proven elusive, motivating this contribution.

I begin by summarizing previous work on the spatial ecology of parasitic plants, highlighting progress at broad and fine scales. I then propose the host-quality hypothesis to account for unexplained distribution patterns at the mesoscale, using an ongoing study of mistletoe and sandalwood distribution in an arid shrubland as a worked example. Using previously published case studies from other systems, I apply the host-quality hypothesis and evaluate whether it helps understand distribution patterns of parasitic plants. Finally, I highlight priorities for further research on spatial ecology of parasitic plants, making explicit predictions and indicating the data required to test the host-quality hypothesis. Although root-parasitism is the more widespread habit, most knowledge on the distribution and spatial ecology of parasitic plants has come from the aerially hemiparasitic mistletoes (primarily Viscaceae and Loranthaceae; Restrepo 1987; Dean et al. 1994; Watson 2001; Aukema and Martinez del Rio 2002a, 2002b; Restrepo et al. 2002; Watson 2004). Accordingly, even though this contribution relates to parasitic flowering plants generally, most of the examples I use involve mistletoes.

Previous research: progress at two scales

Distribution and occurrence patterns of parasitic plants

have previously been studied at broad and fine scales. We have an emerging appreciation of the suite of factors that limits the larger-scale distribution of parasitic plants, with minimum temperature isotherms, host occurrence, and fire history considered critical (Hawksworth and Wiens 1996; Polhill and Wiens 1998; Shaw et al. 2004; Mathiasen et al. 2008). In terms of hosts, there are a suite of well-supported traits considered to make potential host species more prone to parasitism (see Pennings and Callaway 2002). For example, nitrogen-fixing species are consistently favoured as hosts (Dean et al. 1994; Tennakoon et al. 1997), as are species without persistent bark or periderm on roots (Hoffmann et al. 1986; Woodall and Robinson 2003).

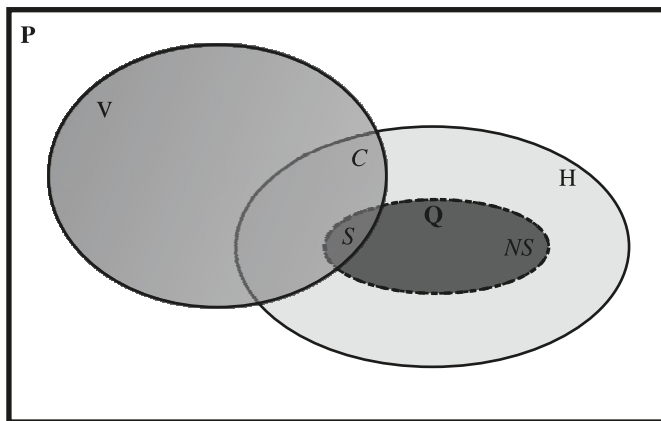
At finer scales, research has focused on the role of seed vectors. For animal-dispersed parasitic plants, it has been assumed that occurrence patterns of plants mirror habitat usage, microhabitat selection, and substrate use by vectors (primarily frugivorous birds). For mistletoes, twig size consistently emerges as a significant factor in terms of both disperser efficacy (i.e., selection of perches and defecation sites; Aukema and Martinez del Rio, 2002b) and parasite establishment (Restrepo 1987; Sargent 1995).

Thus, previous research has focused on which regions, which species, and which particular parts of a plant are most likely to receive and support parasitic plants. To date, however, it is unclear what leads to the highly nonrandom occurrence patterns of parasitic plants within an area — patterns widely reported from a variety of landscapes (Hoffmann et al. 1986; Hobbs and Atkins 1991; Overton 1996; Norton and Stafford-Smith 1999; Aukema and Martinez del Rio 2002a; Watson 2002, 2004; Mathiasen et al. 2008). Vector occurrence and behaviour may dictate the outer bounds of a population, but previous findings indicate that the seed shadows are often extensive and far more regular than occurrence patterns of established parasites (Aukema and Martinez del Rio 2002b). Why are some individual plants more susceptible to parasitic plants than others? Why do trees growing on roadsides or remnant edges have higher parasite loads? What explains highly nonrandom distributions of parasitic plants in apparently continuous, homogeneous habitat? While many previous workers have encountered such patterns and, occasionally offered inductive explanations to account for them, I suggest that these three situations (and many others) can be explained, at least in part, by variation in host quality at the mesoscale.

The host-quality hypothesis

While vector behaviour and host occurrence ultimately limit the potential distribution of parasitic plants, I propose that host quality is one of the critical proximate factors determining which potential host plants are susceptible to infection (Fig. 1). Rather than being a random subset of the population, I suggest that there are measurable differences in potential host plants that define a group of individuals physiologically capable of supporting a parasite (i.e., truly susceptible to infection). Rather than relating to safe sites, germination requirements, perching preferences, or other mechanisms associated with seed dispersal, host quality is a secondary factor that determines which dispersed seeds go

Fig. 1. This generalized model depicts the importance of host quality on susceptibility to parasitism, and can be considered at a range of scales, from the entire distribution of a species down to a particular site being studied. P, occurrence of the parasite; H, occurrence of host plant(s); Q, subset of hosts of sufficient quality to support parasites; V, occurrence of seed vector(s). Where the vector overlaps with the distribution of hosts; parasite, vector and host all co-occur (C) and, over time, the likelihood of parasite seeds being deposited on co-occurring hosts increases. Only when hosts are of sufficient quality, can it be considered susceptible (S), while hosts of sufficient quality beyond the range of seed vectors are not susceptible (NS).



on to establish and yield mature parasitic plants. Note that, while the distributional ranges of hosts and vector are absolute (they are either present or absent), susceptibility may not be as clear-cut and likely represents a continuum rather than a dichotomy.

The subset of susceptible hosts within a stand or population is not static, but would comprise a dynamic assemblage changing over space and time. Hence, moving from one area to the next along an environmental gradient, frequency of infection would change. Similarly, as conditions change between seasons or years, individual plants would move along the continuum from being susceptible to nonsusceptible. This may entail no longer being receptive to new infections, or may even result in the death of any existing parasitic plants already dependent on the host (Reid and Lange 1988).

Worked example: mistletoe and sandalwood occurrence in an arid shrubland

The highly nonrandom occurrence of parasitic plants is clearly illustrated in Fig. 2, depicting distribution patterns of hosts (*Acacia tetragonophylla* F.Muell., a long-lived, nitrogen fixing shrub), and two parasites (shoot-parasitic mistletoes, *Amyema* spp. (Loranthaceae) and root-parasitic sandalwood *Santalum lanceolatum*, (Santalaceae)). These maps were developed as part of ongoing research into parasitic plant ecology in an arid shrubland in central Australia (see Watson et al. 2008 for more details). As with most mistletoes, both species of mistletoe in this system are bird dispersed, primarily by mistletoe specialists (Watson 2004). This dispersal syndrome would explain within-host clumping patterns of mistletoe occurrence, presumably reflecting nonrandom habitat use, perch selection, and defecation sites

by the seed-dispersing birds (Sargent 1995; Aukema and Martinez del Rio 2002a).

Given that vectors move throughout the study area and potential hosts are relatively widespread, what explains the highly restricted distribution of mistletoe at the stand scale? I suggest host quality is involved. The acacias supporting mistletoes were growing at the low points in the drainage line and, as such, would have greater access to water over longer periods (Slatyer 1961). Hence, rather than resulting from vector behaviour or seed shadow, the restriction of mistletoe to hosts growing adjacent to the creek-line may reflect variation in host quality, whereby dispersed seeds only establish and grow on hosts of sufficient quality.

The root-parasitic sandalwood is a small tree, originally widespread in central Australia. Owing to commercial harvesting and the local extinction of presumed seed dispersers (including *Bettongia penicillata* (Gray 1837), a scatter-hoarding marsupial recently confirmed to disperse *Santalum acuminatum* A. DC. seeds; Murphy et al. 2005) it is now highly restricted, and several populations are known to be clonal (Warburton et al. 2000). The spatial arrangement of sandalwoods was found to be highly clumped at several scales (Fig. 2B), with large sandalwoods having a halo of smaller plants around them, and sandalwoods clustered around acacias. This may reflect facilitation, seed rain in the absence of dispersers, or clonal suckering, and has been discussed in detail elsewhere (Watson et al. 2008). None of these mechanisms, however, explains the clustering of sandalwoods at greater distances, i.e., their restriction to areas immediately adjacent to the creek-line. The host-quality hypothesis, invoked to explain mistletoe occurrence, may also apply to sandalwood. Thus, regardless of dispersal mechanism, a sandalwood can only establish and grow if it is parasitizing a host of sufficient quality; in this case, a host that experiences less water stress owing to its proximity to the creek-line.

Applying the host-quality hypothesis to previous findings

In addition to being a novel concept to stimulate further research, the host-quality hypothesis also provides new perspective for reconsidering previous research findings and comparing results previously deemed idiosyncratic. Thus, roadside acacias supporting more mistletoes (Norton and Stafford Smith 1999), higher dwarf mistletoe infection on spruce in mesic sites (Singh 1982), the propensity for sandalwood to grow beside tracks and reserve boundaries (Hobbs and Atkins 1991), and the close association between sandalwood and granite outcrops (Fox 1997) may all relate to the same underlying mechanism: in areas where water is limiting, parasites are more likely to establish on hosts with greater access to water.

This contention is supported by several studies, reinforcing the thesis that parasitic plants are more likely to establish and survive on host trees with greater access to water. Direct evidence comes from a recent study of eucalypts in southern Australia (Miller et al. 2003), in which stands of trees with higher pre-dawn water potentials had the highest proportion of trees infected with mistletoe. Similarly, foliar water content was found to be consistently higher in trees growing along roadsides than those growing 100 m away from the road (Norton and Stafford Smith 1999), mirroring

mistletoe infection rates of 43% and 25%, respectively. In addition to spatial variation, temporal variation in host quality also affects parasite establishment. Long-term monitoring of acacias in central Australia (Reid and Stafford Smith 2000) revealed higher rates of mistletoe establishment in above-average rainfall years, with no observed detrimental effects of infection in either study.

Rather than soil water, host quality may relate to other characteristics (edaphic and otherwise), including availability of nutrients. Hence, Vermeulen (unpublished data, reported in Polhill and Wiens 1998) studied host ranges and distribution patterns of three mistletoe species in Zimbabwe. All species parasitized leguminous hosts, with *Erianthemum virescens* known from “at least 35 different host species, especially those associated with old termite mounds” (pp. 9–10; Polhill and Wiens 1998). Similar patterns were exhibited by *Viscum menyharthii* Engl. & Schinz, found primarily on *Ficus* trees growing atop old termite mounds. These mounds are relatively high in available nutrients compared with surrounding lateritic soils (Takeshita and Tohru 2004), and are preferentially used by elephants for foraging (Holdo and McDowell 2004). Hence, rather than invoking vector behaviour to account for this pattern, the host-quality hypothesis would suggest that leguminous hosts are higher quality, and individual trees growing in nutrient-rich patches are more able to support parasites.

van Ommeren and Whitham (2002) studied a three-way interaction between mistletoe, juniper hosts, and a frugivorous bird (*Myadestes townsendi*) that dispersed seeds of both. They examined stands of differing mistletoe density, monitored fruit availability of both species, and estimated solitaire abundance. They found that stands of junipers infected with mistletoe supported higher bird abundances, leading to greater probability of host fruits being consumed and dispersed. They interpreted this three-way interaction as an example of parasitism leading to mutualism, mediated via a shared vector. This was supported by the occurrence of juniper seedlings, growing in twice the density in stands with high mistletoe density than in stands with little or few mistletoes.

They (van Ommeren and Whitham 2002) did not consider what led to the initial nonrandom pattern of mistletoe occurrence in their stands, and this may be related to host quality. Sites with mistletoe were, on average 78 m higher in elevation than sites without mistletoe ($n = 10$), and even though not significantly different, this may have affected soil water availability or other edaphic factors. Although van Ommeren and Whitham (2002) noted this difference, they did not consider the influence of stand location further. Higher elevation sites may be more suitable for junipers, producing trees of higher quality that were better able to support parasites, more attractive to seed dispersers, and more conducive to seedling establishment. This parsimonious inference may explain not only the proximate pattern of seedling establishment, but also the underlying nonrandom distribution of the parasite across stands.

Priorities and predictions

The host-quality hypothesis was developed through detailed examination of parasitic plants in areas of high abun-

dance, i.e., situations in which constraints appear to have less influence. By comparing these sites with more typical sites of low parasitic-plant abundance, potential constraints can be distinguished. Once particular traits or factors have been identified, host quality can then be measured directly. While water may be a key component of host quality in arid and semi-arid systems, a range of other factors could be involved, either directly (nutrient content, bark thickness, root depth) or indirectly (age, position in landscape, proximity to nutrient sources). Importantly, aspects of host variation must all be defined relative to the parasite and so rely on a complete understanding of parasite life history, particularly establishment requirements.

To reveal these requirements and evaluate particular traits directly, germination trials are advocated. By inoculating hosts representing a range of presumed qualities, parasite establishment and growth can be measured and related directly to a range of host traits. While initially a binary response (i.e., established vs. did not establish), following established parasitic plants and measuring aspects of vigour (e.g., growth, longevity, number of seeds produced) can reveal the overall influence of host variation on parasite ecology.

To guide this research, I offer the following two testable predictions:

- (1) Host quality is a critical factor constraining parasitic plant occurrence, with temporal and spatial variation in host quality explaining occurrence patterns of both aerial and root-parasitic plants.
- (2) Shoot parasites are more sensitive to variation in host quality than root parasites (which can simultaneously parasitize multiple hosts).

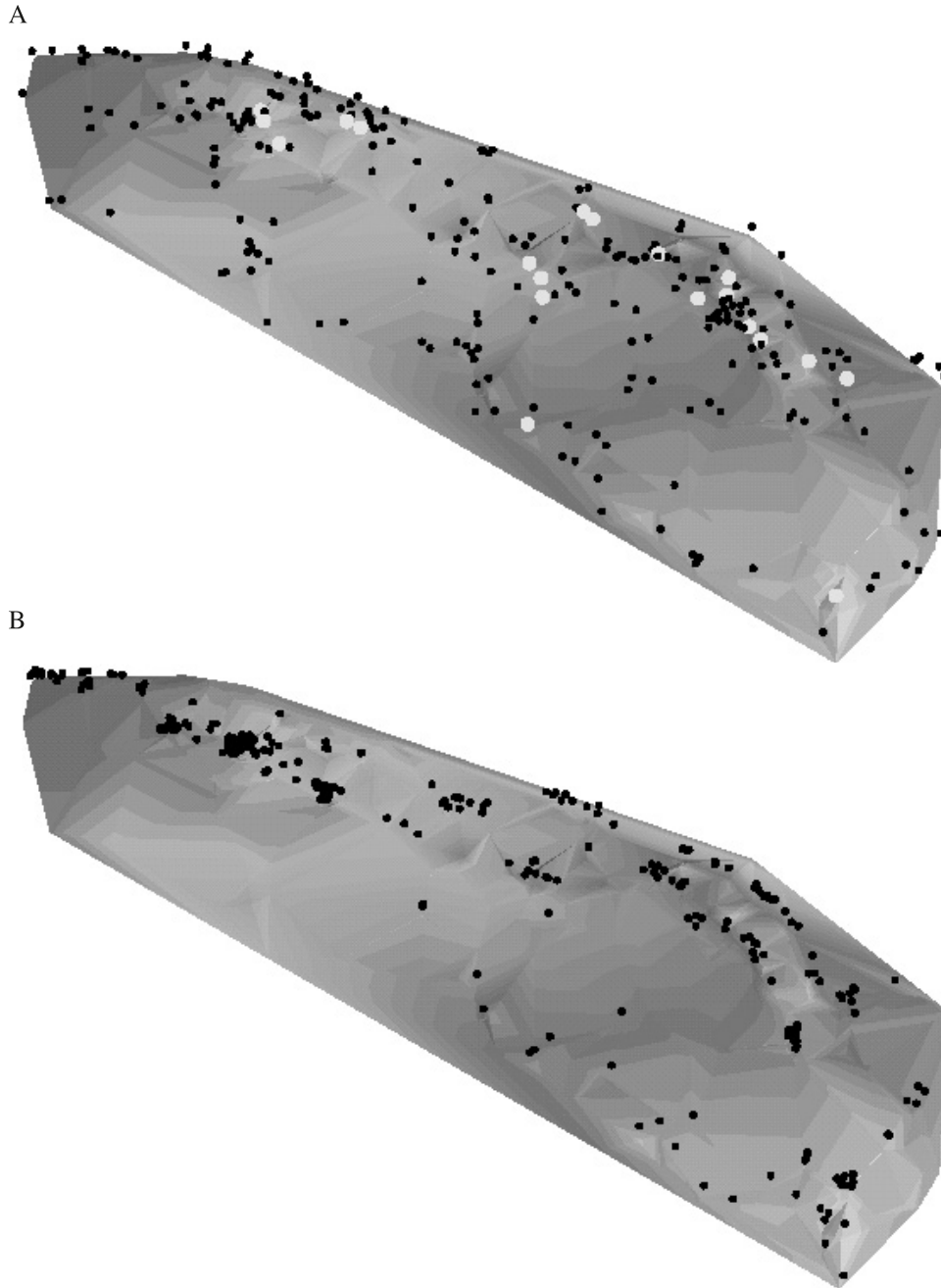
The host-quality hypothesis has been considered in terms of individual plants at the stand scale, but it may also extend to entire populations and even species of hosts. Broad-scale changes in host quality may underlie geographic patterns of host switching, the apparent immunity of some host populations to infection, and other large-scale trends in abundance and geographic range of parasites (Hawksworth and Wiens 1996; Press and Phoenix 2005).

While addressing many hitherto unexplained phenomena, the host-quality hypothesis also raises a number of unanswered questions. Is host quality another form of inducible defence, such that hosts can moderate their own quality and in some way regulate their susceptibility to parasitism? Does parasite infection change host quality, and therefore affect the likelihood of secondary infection (either by conspecifics or another parasite)? Do parasites on higher-quality hosts exhibit greater control over phenology, leading to more accentuated patterns of complementarity? Clearly, the distribution and spatial ecology of parasitic plants is an area ripe for further research, and by integrating measures of host quality with vector behaviour at the landscape scale, we can attain a more holistic understanding of their spatial and temporal dynamics.

Acknowledgements

Several of the ideas expressed here arose from ongoing collaborative research with David Roshier, to whom I am indebted. Ian Lunt and Val Smith contributed useful perspective, highlighting the broader relevance of variation in host

Fig. 2. Map of an area corresponding to the extent of vegetation occurring along a creek-line. Vegetation continued beyond the mapped area both up and downstream, but there were no plants (of any species) growing further out. In 2A, *Acacia tetragonophylla* is depicted; those with mistletoes (*Amyema* spp.) are denoted as pale dots, while 2B depicts every sandalwood (*Santalum lanceolatum*). While acacias are scattered throughout the site, most are concentrated in the low-lying areas associated with the stream channel and only those acacias occurring within or adjacent to the channel support parasites (Watson et al. 2008). Overlaying that pattern is pronounced clustering in both parasite populations. Figure prepared by D. Roshier.



susceptibility, and Maggie Watson helped refine an earlier draft. This research was supported by grants from the ARC DP0342549 and DP0449417. Figure 2 was prepared by David Roshier.

References

- Aukema, J.E., and Martinez del Rio, C. 2002a. Mistletoes as parasites and seed-dispersing birds as disease vectors: current understanding, challenges and opportunities. *In* Seed dispersal and frugivory; ecology, evolution and conservation. *Edited by* D.J. Levey, W.R. Silva, and M. Galetti. CAB International, Wallingford, Oxfordshire, UK. pp. 99–110.
- Aukema, J.E., and Martinez del Rio, C. 2002b. Variation in mistletoe seed deposition: effects of intra- and interspecific host characteristics. *Ecography*, **25**: 139–144. doi:10.1034/j.1600-0587.2002.250202.x.
- Brand, J.E., and Jones, P.J. 2002. The influence of landforms on

- sandalwood (*Santalum spicatum* (R.Br.) A. DC.) size structure and density in the north-eastern goldfields, Western Australia. *Rangeland J.* **24**: 219–226. doi:10.1071/RJ02012.
- Calder, M. 1983. Mistletoes in focus. *In* The biology of mistletoes. Edited by M. Calder and P. Bernhardt. Academic Press, Sydney, Australia. pp. 1–18.
- Davidar, P. 1983. Similarity between flowers and fruits in some flowerpecker pollinated mistletoes. *Biotropica*, **15**: 32–37. doi:10.2307/2387995.
- Dean, W.R.J., Midgley, J.J., and Stock, W.D. 1994. The distribution of mistletoes in South Africa: patterns of species richness and host choice. *J. Biogeogr.* **21**: 503–510. doi:10.2307/2845654.
- Ehleringer, J.R., and Marshall, J.D. 1995. Water relations. *In* Parasitic plants. Edited by M.C. Press and J.D. Graves. Chapman and Hall, London, UK. pp 125–140.
- Fox, J.E.D. 1997. Why is *Santalum spicatum* common near granite rocks? *J. R. Soc. West. Aust.* **80**: 209–220.
- Hawksworth, F.G., and Wiens, D. 1996. Dwarf mistletoes: biology, pathology, and systematics. Agriculture handbook 709. 2nd ed. United States Department of Agriculture Forest Service, Washington, D.C.
- Hobbs, R.J., and Atkins, L. 1991. Interactions between annuals and woody perennials in a Western Australian nature reserve. *J. Veg. Sci.* **2**: 643–654. doi:10.2307/3236175.
- Hoffmann, A.J., Fuentes, E.R., Cortés, I., Leberonna, F., and Costa, V. 1986. *Tristerix tetrandus* (Loranthaceae) and its host-plants in the Chilean matorral: patterns and mechanisms. *Oecologia* (Berl.), **69**: 202–206. doi:10.1007/BF00377622.
- Holdo, R.M., and McDowell, L.R. 2004. Termite mounds as nutrient-rich food patches for elephants. *Biotropica*, **36**: 231–239.
- Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley, Calif.
- Mathiasen, R.L., Nickrent, D.L., Shaw, D.C., and Watson, D.M. 2008. Mistletoes: pathology, systematics, ecology and management. *Plant Dis.* **92**: 988–1006. doi:10.1094/PDIS-92-7-0988.
- Miller, A.C., Watling, J.R., Overton, I.C., and Sinclair, R. 2003. Does water status of *Eucalyptus largiflorens* (Myrtaceae) affect infection by the mistletoe *Amyema miquelii* (Loranthaceae)? *Funct. Plant Biol.* **30**: 1239–1247. doi:10.1071/FP03117.
- Murphy, M.T., Garkaklis, M.J., and Hardy, G.E.St.J. 2005. Caching by woylies *Bettongia penicillata* can increase sandalwood *Santalum spicatum* regeneration in Western Australia. *Austral Ecol.* **30**: 747–755. doi:10.1111/j.1442-9993.2005.01515.x.
- Norton, D.A., and Stafford Smith, M. 1999. Why might roadside mulgas be better mistletoe hosts? *Aust. J. Ecol.* **24**: 193–198. doi:10.1046/j.1442-9993.1999.00962.x.
- Overton, J.M. 1996. Spatial autocorrelation and dispersal in mistletoes: field and simulation results. *Vegetatio*, **125**: 83–98. doi:10.1007/BF00045207.
- Pennings, S.C., and Callaway, R.M. 2002. Parasitic plants: parallels and contrasts with herbivores. *Oecologia* (Berl.), **131**: 479–489. doi:10.1007/s00442-002-0923-7.
- Polhill, R., and Wiens, D. 1998. Mistletoes of Africa. Royal Botanic Gardens, Kew, Surrey, UK.
- Press, M.C., and Graves, J.D. (Editors). 1995. Parasitic plants. Chapman and Hall, London, UK.
- Press, M.C., and Phoenix, G.K. 2005. Impacts of parasitic plants on natural communities. *New Phytol.* **166**: 737–751. doi:10.1111/j.1469-8137.2005.01358.x. PMID:15869638.
- Reid, N., and Lange, R.T. 1988. Host specificity, dispersion and persistence through drought of two arid zone mistletoes. *Aust. J. Bot.* **36**: 299–313. doi:10.1071/BT9880299.
- Reid, N., and Stafford Smith, M. 2000. Population dynamics of an arid zone mistletoe *Amyema preissii* (Loranthaceae) and its host *Acacia victoriae* (Mimosaceae). *Aust. J. Bot.* **48**: 45–58. doi:10.1071/BT97076.
- Restrepo, C. 1987. Aspectos ecológicos de la diseminación de cinco especies de muérdagos por aves. *Humboldtia*, **1**: 65–116.
- Restrepo, C., Sargent, S., Levey, D., and Watson, D.M. 2002. The role of vertebrates in the diversification of New World mistletoes. *In* Seed dispersal and frugivory: ecology, evolution and conservation. Edited by D.J. Levey, W.R. Silva, and M. Galetti. CABI Publishing, Wallingford, Oxfordshire, UK. pp. 83–98.
- Sargent, S. 1995. Seed fate in a tropical mistletoe: the importance of host twig size. *Funct. Ecol.* **9**: 197–204. doi:10.2307/2390565.
- Shaw, D.C., Watson, D.M., and Mathiasen, R.L. 2004. Comparison of dwarf mistletoes (*Arceuthobium* spp., Viscaceae) in the western United States with mistletoes (*Amyema* spp., Loranthaceae) in Australia — ecological analogs and reciprocal models for ecosystem management. *Aust. J. Bot.* **52**: 481–498. doi:10.1071/BT03074.
- Singh, P. 1982. Eastern dwarf mistletoe: distribution and severity in black spruce in Newfoundland. *Plant Dis.* **66**: 312–316.
- Slatyer, R.O. 1961. Internal water balance of *Acacia aneura* F. Muell. in relation to environmental conditions. *Arid Zone Res.* **16**: 137–146.
- Takeshita, M., and Tohru, A. 2004. Soil nutrient loss caused by intensive land use and the retention of nutrients inside termite mounds in Niger, Africa. *Jpn. J. Ecol. (Otsu)*, **54**: 117–124.
- Tennakoon, K.U., Pate, J.S., and Stewart, G.R. 1997. Haustorium-related uptake and metabolism of host xylem solutes by the root hemiparasitic shrub *Santalum acuminatum* (R. Br.) A. DC. (Santalaceae). *Ann. Bot. (Lond.)*, **80**: 257–264. doi:10.1006/anbo.1997.0433.
- van Ommere, R.J., and Whitham, T.G. 2002. Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. *Oecologia* (Berl.), **130**: 281–288.
- Warburton, C.L., James, E.A., Fripp, Y.J., Trueman, S.J., and Wallace, H.M. 2000. Clonality and sexual reproductive failure in remnant populations of *Santalum lanceolatum* (Santalaceae). *Biol. Conserv.* **96**: 45–54. doi:10.1016/S0006-3207(00)00049-5.
- Watson, D.M. 2001. Mistletoe — a keystone resource in forests and woodlands worldwide. *Annu. Rev. Ecol. Syst.* **32**: 219–249. doi:10.1146/annurev.ecolsys.32.081501.114024.
- Watson, D.M. 2002. Effects of mistletoe on diversity: a case-study from southern New South Wales. *Emu*, **102**: 275–281. doi:10.1071/MU01042.
- Watson, D.M. 2004. Mistletoe — a unique constituent of canopies worldwide. *In* Forest canopies. 2nd ed. (fully revised). Edited by M. Loman and B. Rinker. Academic Press, New York. pp. 212–223.
- Watson, D.M., Roshier, D.A., and Weigand, T. 2007. Spatial ecology of a parasitic shrub: from pattern to process. *Austral Ecol.* **32**: 359–369. [In review.] doi:10.1111/j.1442-9993.2007.01701.x.
- Woodall, G.S., and Robinson, C.J. 2003. Natural diversity of *Santalum spicatum* host species in south-coast river systems and their incorporation into profitable and biodiverse revegetation. *Aust. J. Bot.* **51**: 741–753. doi:10.1071/BT02118.