Background document for the National Recovery Plan for *Olearia macdonnellensis*, *Minuria tridens* (Minnie Daisy) and *Actinotus schwarzii* (Desert Flannel-flower)

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Rationale for the multispecies approach to the recovery plan

The species covered in this plan are all confined to arid Australia. All have a restricted distribution and are characterised by small and highly fragmented subpopulations that are limited in area and surrounded by apparently suitable habitat. They face a similar suite of threatening processes; and are each poorly understood in terms of their general biology and critical life history processes.

Species' names and Conservation Status

This Recovery Plan covers three threatened plant species with small and highly fragmented sub-populations in arid Australia. Included are two daisies (Asteraceae), *Olearia macdonnellensis* (D.A.Cooke) and *Minuria tridens* (D.A.Cooke) Lander, and the desert flannel flower *(*Apiaceae), *Actinotus schwarzii* F.Muell. All species are endemic to Australia and have a global and national conservation status of Vulnerable under the EPBC Act 1999. They are listed as Vulnerable under section 29 of the *Territory Parks and Wildlife Conservation Act 2000*.

International Obligations

None of the three plant species covered in this Recovery Plan is listed in the Appendices of the *Convention on International Trade in Endangered Species of Wild Fauna and Flora* (CITES) or other international treaties. As a consequence, implementation of Australia's responsibilities under various international treaties is not affected by this plan.

Distribution and Climate

The species covered in this plan are all confined to arid Australia. All have a restricted distribution and are characterised by widely-spaced subpopulations that are limited in area and surrounded by apparently suitable habitat.

Olearia macdonnellensis is restricted to the MacDonnell Ranges Bioregion (MAC) where it occurs as several fragmented populations, mainly in the western portion of the MacDonnell Ranges (Cooke 1986, Kerrigan *et al*. 2006). *Minuria tridens* occurs in the MacDonnell Ranges Bioregion and the Simpson-Strzelecki Dunefields Bioregion (SSD) of the NT, and in the Murchison Bioregion (MUR) of WA. In the NT, it is largely confined to south-facing slopes of dolomite, limestone and calcrete-impregnated sandstone hills and ranges (Kerrigan & Albrecht 2006a). *Actinotus schwarzii* is endemic to the Chewings and Heavitree Ranges in the West MacDonnell Ranges. It is known from less than 20 small and widely spaced populations. There are unconfirmed reports of this species in the Petermann Ranges (Central Ranges Bioregion) (Kerrigan & Albrecht 2006b).

The central Australian climate is characterised by low and unpredictable rainfall, high-ranging temperatures, and high evaporation rates. Maximum daily temperature during summer regularly exceeds 40°C and winter nights are cold with frosts often occurring between late May and early September. Rainfall in the region is extremely variable in terms of spatial and temporal distribution and intensity (Bureau of meteorology www.bom.gov.au/). This variability is of fundamental ecological importance to the growth and reproductive success of many arid zone plants (Whitford 2002). The Murchison Bioregion forms part of the Eremaean Botanical Province of WA. This area is also arid, receiving c. 200 mm per annum (Cowan 2001).

Known and potential threatening processes

In general terms Asteraceae is extremely successful in desert regions (Gutterman 1993; van Rheede van Oudtshoorn & van Rooyen 1999). An understanding of the reasons for the rarity and the heightened extinction risk of these arid daisies therefore requires careful consideration of how their critical life history attributes and their habitat requirements differ from those of their more common congeners. This likewise applies to the flannel flower that *prima facie* is functionally similar to the daisy species. In each case, apparent correlates of rarity include: small geographic range; high habitat specificity; poor competitive ability, hindered dispersal, and low seed output. Any of these traits may in turn result in a heightened vulnerability to threatening processes. Identified actual and potential threats common to the species covered in this plan are: disrupted gene flow, inappropriate fire regimes, exotic perennial grass invasion; climate change and natural enemies (predators and pathogens). These are detailed below.

Disrupted gene flow

It is widely acknowledged that small subpopulations are more susceptible to declines than are larger ones (Soulé 1986). It is also now understood that population dynamics and plant-animal interactions within a habitat can be greatly influenced by the degree of population connectivity (Tscharntke & Brandl 2007). Population theory predicts that declines may be caused by small-population effects like inbreeding depression and genetic drift through disrupted gene flow (Neel & Ellstrand 2003). There is no information on the population genetics of any of the species in this plan. It is possible, however, that in each case there is little genetic exchange among populations and a high level of inbreeding within.

Pollen limitation is one reason for reduced gene flow among small fragmented plant populations (Knight *et al*. 2005). As individuals become more isolated, insect pollinator behaviour becomes altered and their abundance diminished. This can lead to a reduced number of pollination events and ultimately, lower seed set (Vamosi & Vamosi 2005). Each of the three species in this recovery plan only reproduce sexually and therefore have no alternative modes of reproduction in times of scarce pollinators. Limited reproduction therefore represents a common potential threat.

The seed dispersal pattern of a species also has important consequences for shaping the genetic structure of populations: restricted dispersal will lead to reduced gene flow and a higher level of inbreeding (van Rheede van Oudtshoorn & van Rooyen 1999; Wilson &

Traveset 2000). Further, the ‘escape hypothesis’ (Janzen 1970) predicts disproportionate success for seeds that escape the vicinity of the parent plant. Known advantages include reduced parent/offspring and sibling competition and reduced predation and pathogen attack (van Rheede van Oudtshoorn & van Rooyen 1999). The seeds of the two daisy species in this plan have a persistent pappus. This should theoretically aid long-distance wind dispersal, especially given the low air humidity of the central Australian desert environment (Guttermann 1993). It is somewhat surprising therefore, that each exhibits a clumped distribution pattern, implying localised seed dispersal. Similar patterning has been recorded in other threatened *Olearia* species (Ogle 2004; Department of Environment & Conservation (NSW) 2004).

The breeding system of *O. macdonnellensis* has not been investigated and both self-compatibility and incompatibility are known to occur in the genus. Threats associated with each system have been identified in regard to various fragmented *Olearia* species (Heine 1938; Haase 1986; NSW NPWS 2000; Department of Sustainability and Environment 2004). Plants that are self-incompatible have a reliance on insect vectors for cross pollination and are thus at risk from pollen limitation, and hence low seed set if there is a diminished abundance of pollinators in isolated populations. By contrast, an absence of pollinators from small and isolated self-compatible populations can lead to an alteration of mating structure and increased levels of inbreeding depression (Neel & Ellstand 2003). While it is not currently possible to determine the likelihood of either mechanism, pollinator absence from small isolated *O. macdonellensis* subpopulations should be treated as a potential threat to this species.

The highly clumped distribution of subpopulations of *O. macdonellensis* implies poor seed dispersal. Other species within the genus (e.g. *O. pannosa*, see Department of Sustainability and Environment 2004) are likewise thought to be threatened because of their small dispersal range. Alternatively, seeds may be widely dispersed but successful recruitment is limited because conditions that are favourable for growth are restricted to a few small and isolated microhabitats. This type of limitation on germination safe sites is well documented for arid environments (see van Rheede van Oudtshoorn & van Rooyen 1999). Either way, the distribution of this species remains highly fragmented, and it thus has a heightened risk of extinction through reduced gene flow.

Preliminary assessment indicates that sexual reproduction in *M. tridens* is poor and highly variable (Kerrigan & Albrecht 2006a). This species is patchily distributed and the movement of pollinators among populations may constrain viable seed production (see above discussions). The clumped distribution of this species additionally implies restricted dispersal.

The pollination biology of *A. schwarzii* is unknown but is unlikely to involve a specialised insect relationship: the closely related *A. helianthi* is pollinated by a range of insects such as beetles, flies, wasps and possibly moths (Anon. 2006). A reliance on a range of vectors does not, however, guarantee an avoidance of pollen limitation in the context of habitat fragmentation given that pollinators may simply not attend small plant populations. The clumped distribution of this species additionally implies restricted dispersal. Given that populations are small and widely space, it is possible that *A. schwarzii* is threatened because of reduced gene flow & low seed set.

Fire

Fire has for some time been recognised as a potential hazard to local population persistence in a wide range of central Australian shrub species (Bowman *et al*. 1994). Our understanding of the level of fire-threat and of the actual mechanisms of decline is, however, currently constrained by the lack of life-history information about most species. Importantly too, we are far from understanding the extent to which fire patterns have been altered since European occupation of central Australia.

Slow growing species that are incapable of surviving repeated fire exposure – and are therefore dependent on post-fire recruitment for site persistence – are regarded as being most at risk from fire. It is expected that these ‘obligate-seeder’ species face an ‘immaturity risk’ (*sensu* Keeley & Fotheringham 2000) if fire frequency is too high i.e. it reoccurs before sufficient seed banks have established. It is also recognised though, that many supposedly fire-resistant species (i.e. those that can consistently resprout) can also be disadvantaged by too frequent, too hot or badly-timed fire events (Bond & van Wilgen 1996). *Minuria tridens* falls into this category. A third group of species also exists for which even less is known in terms of their risk of fire extinction. These species have little, or possibly no, ability to resprout after fire exposure. Importantly though, they are not obligate seeders in the true sense in that recruitment is not cued to fire events i.e. their life histories are not closely tied to fire cycles. The remaining two species covered in this plan are likely to be characterised by this latter combination of traits. In each case, the loss of established adults will not be compensated for by the initiation of a mass post-fire recruitment event. Novel heightened levels of fire exposure in response to exotic perennial grass invasions and an increased wildfire occurrence will therefore potentially exacerbate the extinction risk associated with each of these species.

Olearia macdonnellensis is threatened by wildfire (Kerrigan *et al*. 2006). Various mechanisms of fire-related decline may be in operation in the case of this species. While its seed bank dynamics are presently unknown, research on other desert Asteraceae (Schutz & Milberg 1997) indicates that site persistence in *O. macdonnellensis* likely relates more to drought tolerance in its long-lived adults than to the formation of persistent seed banks. For species with this type of life history, population dynamics can be severely disrupted by external factors such as fire that reduce the survival-rate of adults. Fire also clearly has the potential to interrupt other life history events in this species. It is highly likely, for example, that fire will kill seedlings (e.g. see Department of Environment & Conservation (NSW) 2004); thus the timing of a fire event can be critical, especially if recruitment is rare. This species would also face an immaturity risk if fires occur before individuals have reached reproductive maturity and set seed.

Fire management is an identified priority action for numerous threatened *Olearia* species, including certain with fire-tolerant adults (NSW NPWS 2000; Carter & Walsh 2006). In this particular case however, an absence of detailed biological and fire-response information precludes accurate assessment of the overall fire-extinction risk. It also constrains the formulation of effective management practice. Specifically, it is not clear whether or not a policy of complete fire exclusion should be adopted. It is possible for example, that this species has some ability to survive fire exposure under certain conditions. Fire-resistance in other *Olearia* species is known to relate to a range of factors including the age of individual plants, fire season and intensity, as well as drought stress (NSW NPWS 2000; Department of Environment & Conservation (NSW) 2004; Carter & Walsh 2006). Further, it may be possible that fire plays some role in *O. macdonnellensis’* ecology by opening up habitat to allow seedling recruitment. Many species of *Olearia* are regarded as classic disturbance specialists (Nelson 1993), reflecting their propensity to rapidly colonise newly-created canopy gaps and their light-requirement for the germination of buried seed. It may be necessary therefore, for management practice to take account of a possible requirement for periodic controlled fire disturbance at some sites (e.g. those with a high perennial grass cover) to facilitate germination. Again, though, details are lacking and research and monitoring are urgently required.

While *Minuria tridens* is known to have some resprouting capacity, its overall fire response is poorly understood. The fire response of *Actinotus schwarzii* is likewise unknown. Research has shown that for certain *Actinotus* species, fire plays an important role in the germination of non-dormant buried seed (Baker *et al*. 2005). *A. schwarzii* may therefore exhibit a similar response but information is lacking. Stochastic fire events are a potential threat to *A. schwarzii* because of its small population size. The fire threat level for this species is, however, expected to be relatively low given the predicted low grass fuel loads in its habitat.

Predators and pathogens

Little is known about the effect of plant pathogens in deserts, but the enormous impact of seed predation by desert granivores is well documented (Morton 1985; Guttermann 1993). For desert regions (including arid regions of Australia) it has been estimated that more than 70% of seed production is consumed by granivores (Guttermann 1993). This level of attrition must represent a major constraint on population persistence in rare and highly fragmented species that have little ability to satiate predator demand through mass seed production. Seed predation thereby represents a potential threat to each species in this plan, given that they are each probably already constrained by low seed output.

There is currently no information on the levels of leaf and stem predation on any of the species. Caterpillars have been recorded feeding on the foliage of other species of *Olearia* (Haase 1986) implying an absence of defence mechanisms. Others species of *Olearia* and *Minuria* are known to be highly palatable to kangaroos and wallabies (Urban, 1990; Department of Sustainability and Environment 2004) and may be threatened by severe grazing by these animals. Stochastic events such as disease and predator attack are potential threats to *A. schwarzii* due to its small population size. However, information on the likelihood of these events is currently unavailable.

Exotic perennial grass invasion

The two daisy species in this plan – *O. macdonellensis* and *M. tridens* – are potentially threatened by the highly-invasive C_4 (summer growing) perennial grass *Cenchrus ciliaris* (buffel grass). The habitat of *A. schwarzii* is, by contrast, likely to be more resilient to invasion given its somewhat extreme edaphic parameters.

Buffel grass is becoming increasingly widespread throughout central Australia and the threats associated with this species are intensifying with time. It is likely that this species will be further advantaged in the future by processes such as altered fire regimes and climate change. Buffel grass is recognised as a severe threat to biodiversity in arid and semi arid world regions (Arriaga *et al*. 2004). This species changes the ecology and disturbance regime of the natural systems in which it grows. It produces large amounts of plant biomass which, when dried, represents a significant increase in site fuel load. This shift increases the frequency and intensity of fire regimes which in some cases lead to local plant and animal extinction. The combination of fire tolerance, vigorous growth, prolific seed production, persistent seed banks, and effective seed dispersal enables this species to form dense monocultures and displace native vegetation (Arriaga *et al*. 2004).

The degree of buffel-grass invasion in *O. macdonnellensis* habitat has not yet been properly assessed. This species is highly abundant in run on areas throughout the MacDonnell Ranges and is therefore likely to occupy creek lines where *O. macdonnellensis* occurs. Once established, buffel-grass has the ability to directly negatively affect *O. macdonnellensis* through resource competition at early life stages. Buried seed of *O. macdonnellensis* likely has a light requirement for germination meaning that its regeneration requirements could not be met in severely affected sites. Further, theory predicts that *Olearia* seedlings would be poor competitors due to a trade off in competitive and colonising ability (see Kitajima & Fenner 2000). This means that *O. macdonnellensis* would likely experience heightened recruitment failure if its habitat becomes severely infested with buffel grass. There is documented evidence of the negative effects of established grasses on early recruitment of other species of *Olearia* (Department of Environment & Conservation (NSW) 2004; Ogle 2004).

Buffel-grass occurs throughout the range of *M. tridens* and thereby represents a uniform threat to this species. This grass possibly has its greatest density in the Alice Springs Municipality sites which may require some restorative work in future years. Records indicate that the Palm Valley sites have a similarly high density of buffel grass and may therefore likewise require intensive conservation effort. The mechanisms of decline are poorly known but light and resource competition as well as increased fire occurrence are obvious concerns. For certain plant species, there is a known negative relationship between rarity and competitive ability. Poor competitors may occupy specialised habitat that acts as a refuge from competition (Lloyd *et al.* 2002). It is possible that the distribution of *M. tridens* reflects an avoidance of native perennial grasses, meaning that the novel invasion of buffel grass could result in its localised extirpation through resource competition.

Human-induced climate change

Climate change in central Australia is expected to cause higher temperatures and more sporadic and heavier rainfall events. These changes are likely to affect the timing of flowering and seed set in plants. Weeds such as *C. ciliaris* that reproduce several times in a year may reproduce more frequently (Hughes, 2003). The specific threats posed by climate change for these three threatened species are currently poorly understood. The process represents a future threat given its potential to disrupt reproductive output and germination and to decrease adult vigour and survival. It is also possible that species such as these with limited dispersal capacity may be unable to adapt to shifting climate zones.

Species descriptions

Olearia macdonnellensis (D.A.Cooke)

Viscid erect, divaricately-branched aromatic shrub to 1.2 m. Leaves are green varnished and appearing glabrous, to 2.5 cm long. Ray florets are female, uniseriate and with white ligules. Disc florets are numerous, bisexual and yellow. Seeds to 3mm long, silky villous. Pappus uniseriate to 8 mm long. Flowering February and July-October; fruiting July, August and October (Cooke 1986).

Minuria tridens (D.A.Cooke) Lander

Dwarf erect and repeatedly-branched perennial sub-shrub to 35 cm. Stems and flower are stalks covered with short, soft hairs. Leaves to 18 mm, may be hairless, or covered with short, soft, hairs. Leaf margins incurved, apices distinctly 3-toothed. Ray florets with pale blue ligules, producing fertile achenes. Disc florets yellow, mainly producing sterile achenes. Pappus uniseriate to 3 mm long (Lander 1987). Flowering February-March, May-October and December; fruiting most months (Kerrigan & Albrecht 2006a).

Actinotus schwarzii F.Muell. *(*Apiaceae)

Erect perennial shrub to 60cm, covered with a soft dense tomentum. Leaves to c. 4.5 x 4 cm, dark grey-green above and paler below, divided into many deep, narrow segments. Involucre of 10 softly tomentose whitish bracts to 7 cm diameter surrounding a dense many-flowered head, the whole resembling a daisy inflorescence. Outer flowers often male. Fruit 1-seeded, to c 3.5 x 1mm, covered with silky hairs to 3mm (Jessop 1981). Flowering has been recorded in July and from October through to January. Fruit are produced in December. It is most closely allied to *A. periculosus* and *A. helianthi* (Henwood, 2000).

References

Anon. (2006). Care and maintenance notes - Flannel flowers, Greengold garden concepts. Accessed at http://www.greengold.com.au/carenotes/crenotes/flannel.html>.

Arriaga, L., Castellanos, A., Moreno, E. & Alarcon, J. (2004) Potential ecological distribution of alien invasive species and risk assessment: a case study of buffel grass in arid regions of Mexico. *Conservation biology*, **18**: 1504-1514.

Baker, K., Steadman, K., Plummer, J., Merritt, D. & Dixon, K. (2005). The changing window of conditions that promotes germination of two fire ephemerals, *Actinotus leucocephalus* (Apiaceae) and *Tersonia cyathiflora* (Gyrostemonaceae). *Annals of botany* **96**: 1225-1236.

Bond, W. & van Wilgen B. (1996) *Fire and plants*. Chapman & Hall, London, UK.

Bowman, D.M.J.S., Latz, P.K. & Panton, W.J. (1994) Pattern and change in an *Acacia-aneura* shrubland and *Triodia* hummock grassland mosaic on rolling hills in central Australia. *Australian Journal of Botany*, **43**, 25-37.

Carter, O. & Walsh N. (2006) *National recovery plan for the marble daisy-bush* Olearia astroloba. Department of Sustainability and Environment, Victoria.

Cooke, D. (1986) Two new species of *Olearia* Moench (Compositae: Asterae) from central Australia. *Muelleria* **6(3)**: 181-184.

Cowan, M. (2001) A biodiversity audit of Western Australia's 53 biogeographical subregions in 2002 Murchison 1 (MUR1 - East Murchison subregion). The Department of Conservation and Land Management. At: http://www.naturebase.net/pdf/science/bio_audit/murchison01_p466-479.pdf.

Department of Environment & Conservation (NSW) (2004) Draft Recovery for *Olearia floctoniae* (Dorrigo Daisy Bush), Department of Environment & Conservation (NSW), Hurstville.

Department of Sustainability and Environment (2004) Velvet Daisy-bush *Olearia pannosa* subsp. *cardiophylla*. Action Statement accessed at <http://www.dse.vic.gov.au/CA256F310024B628/0/27F9B3B158F85ADECA2570ED001C7CF7/$File/189+Velvet+Daisy+Bush+2003.pdf>.

Gutterman, Y. (1993) *Seed germination in desert plants*. Springer-Verlag.Berlin, Germany.

Haase, P. (1986) Phenology and productivity of *Olearia ilicifolia* (Compositae) at Arthur's Pass, South Island, New Zealand. *New Zealand Journal of Botany* **24**: 369-379.

Heine, E. (1938) Observations on the pollination of New Zealand flowering plants. *Transactions and proceedings of the Royal Society of New Zealand*, **67**, 133-148.

Henwood, M. (2000) *Actintous periculosus* (Apiaceae): a new perennial species from eastern Australia. *Telopea* **8(4)**: 455-459.

Hughes, L. (2003) Climate change impacts on biodiversity in Australia Chapter 4: Indicators of climate change, Department of the Environment and Heritage. At http://www.environment.gov.au/biodiversity/publications/greenhouse/chapter4.html.

Janzen, D. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**: 501-528.

Jessop, J. (1981) *Flora of central Australia*. Reed Books PtyLtd, Sydney, NSW.

Keeley, J. & Fotheringham C. (2000) Role of fire in regeneration from seed. *Seeds: the ecology of regeneration in plant communities* (ed. M. Fenner), pp. 311-330. CABI Publishing, Wallingford, UK.

Kerrigan, R. & Albrecht, D. (2006a) *Minuria tridens*. Threatened species profile at www.nt.gov.au/nreta/wildlife/threatened/pdf/plants/Minuria_tridens_VU.pdf.

Kerrigan, R. & Albrecht, D. (2006b) *Actinotus schwarzii*. Threatened species profile at www.nt.gov.au/nreta/wildlife/threatened/pdf/plants/Actinotus_schwarzii_VU.pdf.

Kerrigan, R., Albrecht, D., Duguid, A., & Schubert, A. (2006) *Olearia macdonnellensis*. Threatened species profile at www.nt.gov.au/nreta/wildlife/threatened/pdf/plants/Olearia_macdonnellensis_VU.pdf.

Kitajima, K. & Fenner, M. (2000) Ecology of Seed Regeneration. *Seeds: the ecology of regeneration in plant communities* (ed. M. Fenner), pp. 331-360. CABI Publishing, Wallingford, UK.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J. & Ashman, T. (2005) Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution and Systematics* **36**: 467-497.

Lander, N. (1987) New combinations in *Minuria* DC. (Asteraceae: Astereae). *Nuytsia* **6(1)**: 63-66.

Lloyd, K., Lee, K.& Bastow Wilson, J. (2002) Competitive abilities of rare and common plants: comparisons using *Acaena* (Rosaceae) and *Chionochloa* (Poaceae) from New Zealand. *Conservation Biology* **16(4)**: 975-985.

Morton, S. (1985) Granivory in Arid Regions: Comparison of Australia with North and South America. *Ecology* **66(6)**: 1859-1866.

Neel, M. C. and N. C. Ellstrand. 2003. Conservation of Genetic Diversity in the Endangered Plant *Eriogonum ovalifolium* var. *vineum*. *Conservation Genetics* 4:337-352.

Nelson, N. (1993) The subalpine and alpine vegetation on the central sedimentary belt of Palaeozoic rocks in north-western Nelson, New Zealand. *New Zealand Journal of Botany* **31**: 65-90.

NSW NPWS (2000) *Olearia cordata*. Threatened Species Information Sheet accessed at<http://www.nationalparks.nsw.gov.au/PDFs/TSprofile_*Olearia_cordata*.pdf>.

Ogle, C. (2004) Conservation of *Olearia gardneri*. Report for the rare, small-leaved tree daisy recovery group. Wellington, New Zealand, Department of Conservation.

Schutz, W. and P. Milberg (1997) Seed germination in *Launaea arborescens*: a continuously flowering semi-desert shrub. Journal of Arid Environments **36**: 113-122.

Soulé, M.E. (1986) (ed.) Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Tscharntke, T. & Brandl R. (2004) Plant-insect interactions in fragmented landscapes. *Annual review of Entomology* **49**: 405 - 430.

Urban, A. (1990) Wildflowers and plants of central Australia. Southbank Communications Group, Melbourne.

Vamosi, C. and Vamosi, S.M. 2005. Present day risk of extinction may exacerbate the lower species richness of dioecious clades. *Diversity and Distributions* **11**: 25-32.

van Rheede van Oudtshoorn, K. & van Rooyen, M. (1999) *Dispersal biology of desert plants*. Springer-Verlag, Berlin, Germany.

Whitford, W. (2002) *Ecology of desert systems*. Elsevier Science Ltd, London, UK.

Wilson, M.F. and Traveset, A. 2000. The Ecology of Seed dispersal. pp. 85-110 in Fenner, M. ed. *Seeds. The Ecology of Regeneration in Plant Communities* (2nd Edition), CABI publishing, Wallingford, UK.