Review

The biology of Australian weeds
55. *Salsola australis* R.Br.

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Name

Botanical name

Salsola (Family: Chenopodiaceae) is derived from the Latin *salsus* (salty), in reference to the salt tolerance commonly evident in species of this genus (eFloras 2009). The species name *australis* (Latin for south or southern) was assigned by Robert Brown, for the species he discovered on the southern coast of Australia on 3 February 1802 (Brown 1810, Flinders 1814).

The genus *Salsola* is most diverse in arid, semiarid or saline environments (Kuhn *et al.* 1993). Phylogeny within the genus is poorly understood, due to wide variation in species concepts. Some authors recognize a large number of species separated by minor morphological characteristics and others recognize broad 'metaspecies' (reviewed in Akhani *et al.* 2007). Common across the genus *Salsola* are the winged perianth on the fruiting structure (may be lost in a few species) and the utricle (small, one-seeded fruit with a tissue-like covering) with a spiral embryo (Akhani *et al.* 2007).

Australian populations of the *Salsola* genus were originally classified as *S. kali* L., a similar European species, by Joseph Banks in 1770 (Smith *et al.* 1980, Rilke 1999). However, the specimen collected by Banks did not contain fruiting bodies (Smith *et al.* 1980). Robert Brown (1810) described *S. australis* R.Br. and *S. macrophylla* R.Br. Brown's specimens, which contained fruiting bodies, were distinguished from *S. kali* by the five wings observed on the fruiting perianth (as *S. kali* has a perianth with three wings and two reduced wings). *S. macrophylla* was further distinguished by the thickness (succulence) of the leaves. Subsequently, all Australian taxa were placed under *S. kali* in the Flora of Australia (Wilson 1984), and an international review of the genus *Salsola* by Rilke (1999) reclassified all Australian populations to *S. tragus* L. Rilke (1999) determined that the common, weedy version of the genus *Salsola* found throughout Australia was the species Brown (1810) classified as *S. australis*. However, she did not consider that the lectotype of *S. australis* was sufficiently distinct from *S. tragus* to justify the classification by Brown. Akhani *et al.* (2007) suggested that *S. kali* and *S. tragus* (among other species) should be placed in the genus *Kali*, but this generic name is illegitimate and was merely adopted by some early botanists who objected to Linnaeus taking up the name *Salsola*. If these species are considered to be generically distinct, a new name will be required (Paul Wilson personal communication 2009). It should be noted that recent studies of the genus *Salsola* by Rilke (1999), Pyankov *et al.* (2001) and Kadereit (2005) assumed that *S. australis* is equivalent to *S. tragus*, but Rilke (1999) examined few Australian specimens in her review of the genus *Salsola*, and the other studies did not include any *Salsola* specimens from Australia. Akhani *et al.* (2007) recognized *S. tragus* as distinct from *S. australis*, but again, did not include Australian material in the study. Recent genetic, cytological and morphological analysis confirmed that *S. australis* is the common, weedy species found throughout south-western, and possibly all of Australia (Borger *et al.* 2008, Hrusa and Gaskin 2008). Research also confirmed that *S. australis* is found in North America (and South Africa), where it has been distinguished from *S. tragus* and *S. paulsenii* Litv. However, in North America, *S. australis* is occasionally classified as *S. kali* subsp. *austroafricana* Aellen, where authors are not aware that the *S. australis* lectotype predates the *S. kali* subsp. *austroafricana* lectotype (Gaskin *et al.* 2006, Hrusa and Gaskin 2008, Ayres *et al.* 2009). In Australia, the classification of *S. australis* is currently accepted by the Western Australian Herbarium (2009). However, Australian Plant Name Index (2008) indicates that most States retain the classification system proposed by Rilke (1999). For the purpose of this review, it is assumed that Australian literature discussing *S. kali* or *S. tragus* actually refers to *S. australis*.

Common names

Within Australia, *S. australis* is commonly referred to as roly poly, prickly saltwort or soft buckbush (Wilson 1984). Internationally, there is a very wide range of common names applied almost indiscriminately to *S. australis* and morphologically similar agricultural weed species of the *Salsola* genus. Tumbleweed is the most widely recognized common name, as the tumbleweeds formed by these species have become ingrained in film culture as one of few moving items in the wind-blown, dusty and deserted main street of westerns (O'Donnell 1981).

Description

The following description is based on Wilson (1984) (including Figure 1), Mitchell and Wilcox (1988) and Hrusa and Gaskin (2008).

Morphology

Erect (or occasionally prostrate) rounded annual herb to 0.6 m high (maximum diameter of 2 m). Plants densely (mainly horizontally) branched, succulent when fresh, often verrucose, sometimes woolly in axils. Stem vestiture usually glabrous or with trichomes <0.2 mm (rarely hispid with longer trichomes). Trichomes occasionally on stem ribs and absent from inter-rib areas. Leaves alternate, sessile, entire, linear-subulate, decurrent, 10–30 mm long, 2–3 mm wide, semiterete, broad and slightly clasping at base. Flowers axillary, subtended by prominent often rigid bracteoles, bisexual, solitary in leaf-axil, sessile, 2-bracteolate. Perianth glumaceous, hard and winged in fruit (five wings, or rarely four wings, and wingless fruit also observed on most plants). Winged perianth 4.8–7.9 mm wide, average 6.6 mm. Fruiting internode length generally longer than adjacent bract. Tepals 5, lanceolate, scarious, each usually developing a transverse scarious wing in fruit; 3–4 mm long, free, oblong, obtuse to acute, at first membranous (opaque to semi-translucent, white to light pink), but becoming cartilaginous, developing unequal obovate to reniform horizontal scarious wings 2–5 mm wide or these represented by pectinate protuberances. Tepal wing summit margin smooth to slightly irregular. Stamens 5; anthers sometimes bearing scarious or bladder-shaped appendages, 0.45–0.70 mm long (average 0.58 mm). Ovary superior, subglobular; stigmas 2, sessile or on a long style. Utricle dry, included in the scarious perianth, hemispherical, truncate above. Pericarp crustaceous above otherwise membranous. Seed orbicular, horizontal; testa membranous; embryo in a conical spiral; perisperm absent, filaments strap-shaped, attached to the outer surface of an annular or shallowly cup-shaped disc.

Chromosome number
The base chromosome number of the genus *Salsola* is nine. *S. australis* is diploid (2*n* = 18) (Borger *et al.* 2008).

Comparison with other species
Other morphologically and genetically distinct taxa of the genus *Salsola* are found in south-western Australia, but all specimens were diploid, and had a fruiting perianth structure similar to that of *S. australis* (Borger *et al.* 2008, Hrusa and Gaskin 2008). These other taxa of the genus *Salsola* have not been classified, and further work is required to correctly identify and describe them.

Both *S. kali* and *S. tragus* are tetraploid (2*n* = 36), unlike *S. australis* (Rilke 1999, Ryan and Ayres 2000, Borger *et al.* 2008). *S. australis* is most readily distinguished (visually) from *S. tragus* by the fruiting perianth. Both species have five papery wings on the perianth, two of which are minor. For *S. australis*, the minor wings are broadly obovate (Figure 1H, Figure 2A), whereas *S. tragus* has minor wings that are linear to blunt elliptic (Hrusa and Gaskin 2008, Figure 2B).

Further morphological differences are discussed by Hrusa and Gaskin (2008). Briefly, *S. australis* has winged fruit throughout the plant, anthers approximately 0.5 mm long, and seeds that readily abscise at maturity. *S. tragus* has winged fruit on the upper 4/5 to 1/5 section of the plant (fruit without wings throughout the rest of the plant), anthers approximately 1 mm long, and seeds that are persistent (seeds reach the soil due to branches fragmenting from the mature, senesced plant). One of the simplest measures evident in USA herbarium specimens to distinguish mature *S. australis* from *S. tragus* is to note if there is an accumulated pile of loose, separated fruits (Hrusa and Gaskin 2008).

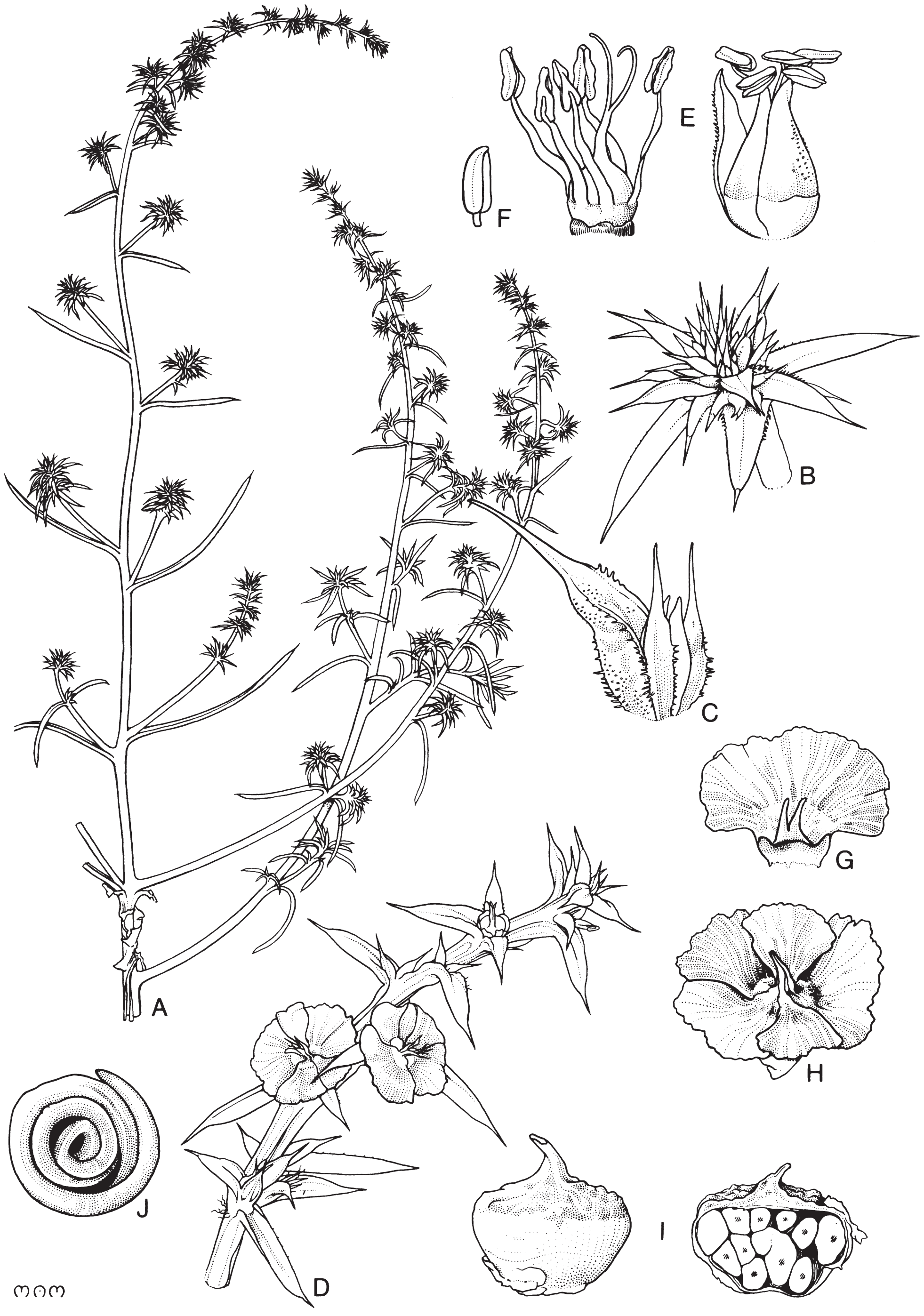

Figure 1. *Salsola kali* (authors' note: actually *S. australis*, as revealed by the five winged fruiting perianth, D and H). The number following the description of each object indicates the magnification. A, branch ×1; B, terminal glomerule ×5; C, bud in bract and bracteoles ×15; (A-C, Meekatharra, WA, A. Mitchell, Perth); D, branch ×2.5; E, flower, with and without tepals ×15; F, anther ×20; G, fruiting tepal ×7; H, fruiting perianth ×5; I, fruit, entire and from a longitudinal section ×15; J, seed ×15 (D-J, Meckering, WA, P. Wilson, Perth) (Wilson 1984). Artist: Margaret Menadue. Reproduced with permission from Flora of Australia, Volume 4.

History

The continental origins of the genus *Salsola* prior to immigration to Australia are unknown. Kadereit *et al.* (2005) estimated that Salsoleae is likely the Chenopodiaceae tribe of most recent origin in Australia. They concluded that it probably invaded via long distance dispersal from Asia, prior to European settlement. However, they also assumed that it was *S. tragus* and not *S. australis* that is found in Australia (Kadereit *et al.* 2005). Populations of the genus *Salsola* that are morphologically similar to *S. australis* have also been described in

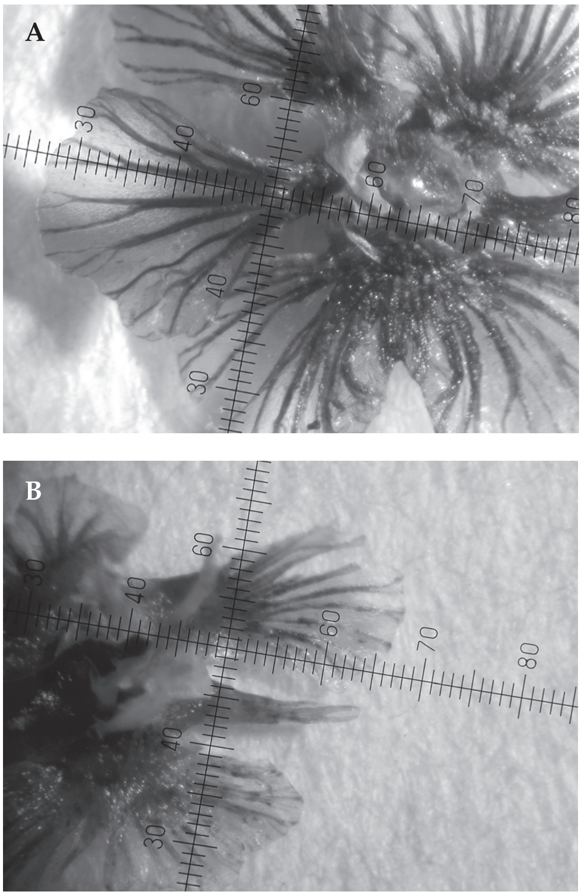

Figure 2. Section of the fruiting perianth of *Salsola australis* (A) showing the full sized wing structures, and *S. tragus* (B) showing one of the two reduced wing structures. Reproduced with permission of G.F. Hrusa, California Department of Food and Agriculture (2008).

South Africa, although the first specimen was not recorded until 1885 (Rilke 1999). So it is also possible that the genus originated from Africa, or conversely that Australian material migrated or was introduced to Africa through long distance seed dispersal.

Banks and Solander first recorded *S. kali* (now classified as *S. australis*) in Australia in the Endeavour River Valley in Queensland, in 1770 (Smith *et al.* 1980). Brown (1810) made a voucher specimen of *S. australis* R.Br. at Petrel Bay, Isle St. Francis, off the coast of South Australia. It is difficult to determine how widespread this species was prior to European settlement. Since *S. australis* is an early successional species that requires disturbed habitats, it is likely that its range expanded as a result of European agricultural and forestry practices. The genus *Salsola* was recorded (under various names) from Queensland, New South Wales, Victoria and Western Australia by 1870 (Bentham 1870), and in all mainland states by 1921 (Bentham 1870, Domin 1921, Rilke 1999). The first record of the genus *Salsola* in Western Australia was *S. macrophylla* (collection L. Preiss 2396), growing in sand among shrubs at the mouth of the Swan River, December 1836 (Lehmann 1844). *S. kali* was collected at Murchison River, Western Australia, by Oldfield (Bentham 1870). This may indicate that *S. australis* was native throughout Australia. Alternatively, it may be that this species was native to the eastern states of Australia, and the range increased with the expansion of agriculture.

A recent review of origin status for non-endemic plant species in Australia by Bean (2007) concluded that a species found in littoral habitats should be considered native if the historical evidence indicates that it predates European settlement, even if ecological and phytogeographical data for status are equivocal. Based on this evidence, *S. australis* should be classified as native.

Distribution

The distribution of *S. australis* in Western Australia is shown in Figure 3. This distribution is based on recent genetic analysis of Western Australian material and morphological examination of voucher specimens, and is correct according to currently available data on classification of the *Salsola* genus in Australia (Rilke 1999, Borger *et al.* 2008).

The genus *Salsola* is found throughout Australia, with the exception of Tasmania (Wilson 1984, Rilke 1999, Borger *et al.* 2008) (Figure 4). The majority of the points in Figure 4 likely refer to *S. australis* (although they are labelled *S. tragus* or *S. kali*), but it is impossible to determine the exact distribution of this species due to the

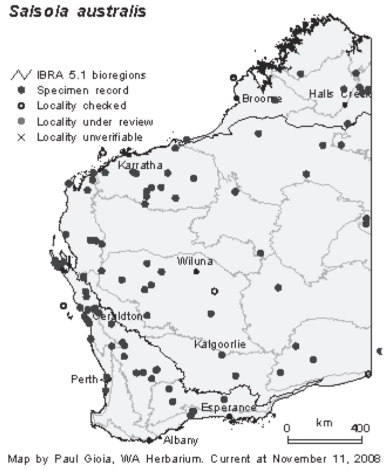

Figure 3. The distribution of *Salsola australis* in Western Australia (Western Australian Herbarium 2009). Mapping by Paul Gioia. Image used with the permission of the Western Australian Herbarium, Department of Environment and Conservation (http://florabase.calm.wa.gov.au/). Accessed on Tuesday, 10 February 2009.

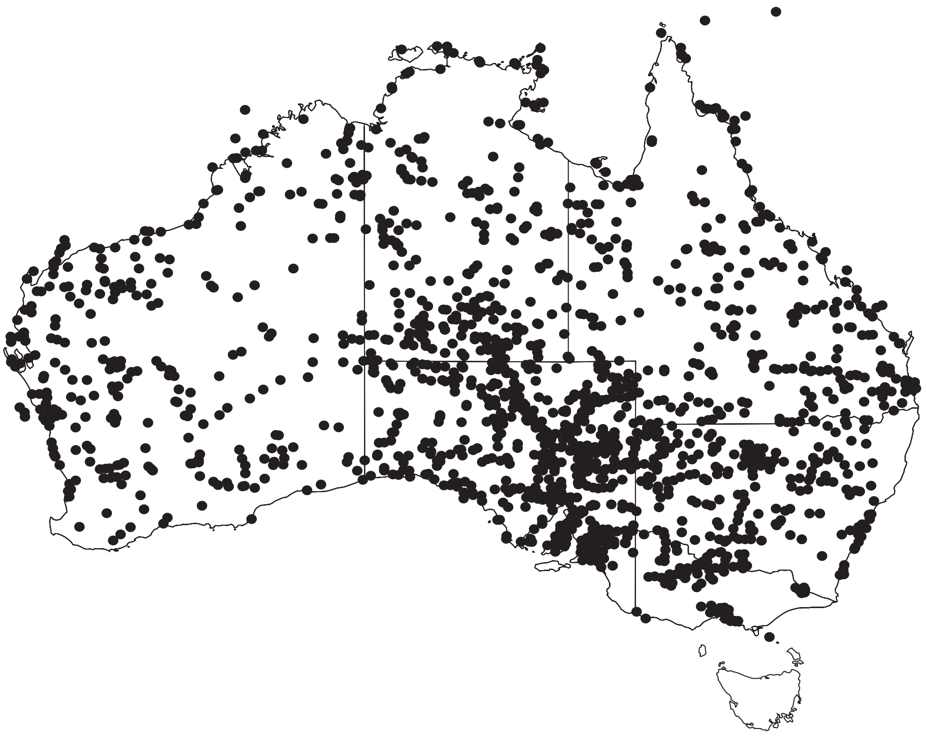

Figure 4. Herbarium records of the *Salsola* genus in Australia (Australia's Virtual Herbarium 2009).

classification issues mentioned earlier. It is probable that some points refer to other named or possibly new species of the *Salsola* genus (Rilke 1999, Borger *et al.* 2008). *S. australis* is found in North America and South Africa (Rilke 1999, Ryan and Ayres 2000, Hrusa and Gaskin 2008), but complete data on the international distribution are not available, again due to difficulties of accurate classification.

Habitat

Plant associations

The native plant associations in which *S. australis* (referred to as *S. kali*) is a prominent and persistent species are detailed in Beadle (1981), and summarized below. These native ecosystems have in common a canopy cover of 0% to 70% (often less than 30%) for at least part of the year. Further, the vegetation is usually sparse and short (i.e. open woodland communities with trees 10 to 15 m tall, grassland and shrubland less than 8 m tall), with areas open for colonization (Beadle 1981).

Within the arid interior of Australia, *S. australis* is commonly found over vast tracts of land. This region contains over 2600 native species, which have in common adaptations to arid conditions and temperature extremes. The most commonly represented families within the region include Myrtaceae, Papilionaceae, Proteaceae, Compositae, Gramineae and Mimosaceae. *S. australis* is likewise found in the arid to semi-arid regions surrounding the arid interior. In south-western Australia (around the 250 mm isohyet), *S. australis* dominates the sparse herbaceous layer of the *Eucalyptus loxophleba* Benth. (York gum) alliance, along with *Bassia diacantha* (Nees) F.Muell. and species of the *Atriplex* and *Zygophyllum* genera.

Throughout the southern half of the continent (mainly South Australia, but stretching into Western Australia, Victoria and New South Wales) are the halophytic shrublands, mainly consisting of species of the Chenopodiaceae family. *S. australis* is most common in the shrublands dominated by *Atriplex vesicaria* Heward ex Benth. (bladder saltbush) and species of the *Bassia* (copper burr) genus.

Salsola australis is also found in a range of natural grasslands and savannahs. Within the tropical northern regions of Australia, it is a common component of grasslands formed by the *Xerochloa* species alliance (on the landward side of *Sporobolus virginicus* (L.) Kunth grasslands or mangroves). The samphire, sedgeland and grassland communities dominated by *Arthrocnemum halocnemoides* Nees and *A. leiostachyum* (Benth.) Paulsen bushes, which likewise adjoin mangroves on the landward side, have *S. australis* colonizing the sandy deposits that form at the base of these bushes. Within the *Stipa variabilis* Hughes grasslands in western New South Wales, dense *S. australis* populations occur when the first significant rainfall of the season occurs in late summer or autumn rather than winter. *S. australis* is a common feature of the *Zygochloa paradoxa* (R.Br.) S.T.Blake (sandhill cane grass) alliance, occurring in the Simpson Desert and around salt lakes in central Australia.

Salsola australis thrives in a range of inland water course communities. It is found in the swampy areas dominated by the *Chenopodium auricomum* Lindl. (bluebush or golden goosefoot) alliance (i.e. Barkly Tableland). It colonizes the sandy (and frequently flooded) regions around playas (dry or ephemeral lakebeds), which are found throughout Australia.

Finally, *S. australis* is commonly found in littoral habitats. It grows alongside a wide range of other species on the frontal dune systems around Broome, Port Hedland, Shark Bay to Hill River and the tropics of Western Australia, and on the strandline (beach, above high tide level) in South Australia and Victoria.

Salsola australis is an early successional species, and aside from these native ecosystems where it is a dominant species, it has colonized many other disturbed habitats. It is a summer growing weed in ruderal systems such as rain-fed cropping and pastoral agricultural systems, waste areas, roadsides and mine sites throughout Australia (Beadle 1981, Mitchell and Wilcox 1988, Naidu and Harwood 1997, Borger *et al.* 2008). It invades more densely vegetated native ecosystems following disturbance such as flooding and burrowing animals (Westbrooke and Florentine 2005, Eldridge *et al.* 2006).

Substratum

The substratum of the native ecosystems and ruderal habitats that support dense and persistent populations of *S. australis* commonly consists of sandy soils or limestone banks, which are frequently saline or alkaline (Beadle 1981, Mitchell and Wilcox 1988, Naidu and Harwood 1997). The soils of the native ecosystems where *S. australis* is commonly found are detailed below, based on (Beadle 1981).

Salsola australis is found in both saline and non-saline regions, on sand sheets, subsaline clays, limestone based alkaline soils and solonized brown soils within the arid and semi-arid zones. The areas of the *Eucalyptus loxophleba* alliance colonized by *S. australis* are found on solodized, slightly acidic, grey to grey-brown sandy loams over clay subsoils (often slightly alkaline). In addition, *S. australis* is found in the halophytic shrublands formed on soils with a high clay content, which are usually saline or subsaline, and sometimes highly calcareous. Further, these regions also contain Gilgai clay soils that support *S. australis* growth. Of the grassland and savannahs that support *S. australis*, the *Xerochloa* species alliance is formed on saline or subsaline Solonetz mudflats, the *Stipa* grasslands on soils with a sandy surface horizon, and the *Zygochloa paradoxa* alliance on sand dunes and sandy alluviums. Within the samphire, sedgeland and grassland communities in the tropics, *S. australis* grows on small patches of sand that collect over the mudflats. These areas are occasionally inundated with a shallow layer of seawater, and the high evaporation rate ensures that this region is extremely saline. Of the inland watercourse communities containing *S. australis*, the *Chenopodium auricomum* alliance forms on grey, cracking clays, and the playa communities develop on saline or subsaline sandy soils. The soils of the littoral zones are all sandy and often saline.

Climatic requirements

From the distribution maps (Figures 3 and 4), it is clear that *S. australis* is found within all the major climatic regions of Australia, except the very cool, temperate regions, such as Tasmania, and mountainous regions. It is most common in environments that are arid for parts of the year and experience temperature extremes (Beadle 1981, Mitchell and Wilcox 1988, Australia's Virtual Herbarium 2009). Within the arid interior, *S. australis* is found in regions with winter or summer dominant rainfall of less than 250 mm. The semi-arid grassland and shrubland regions that support *S. australis*, as well as the *Eucalyptus loxophleba* alliance, which surround the interior, likewise occur around the 250 mm isohyet. These desert or near desert regions experience temperature extremes and high rates of evaporation. The natural grasslands and savannahs containing *S. australis* usually form in regions receiving 150–250 mm of rainfall (Beadle 1981, Australia's Virtual Herbarium 2009).

Salsola australis is common in littoral zones in southern and northern Australia, which may have high seasonal rainfall. These areas are arid for parts of the year, evaporation is high and excess water drains rapidly due to the extremely porous nature of the sandy soils. Likewise, the sandy regions around playas that are colonized by *S. australis* are occasionally flooded, but the climate for much of the year is arid, with rapid drainage and high evaporation.

While *S. australis* is most abundant in arid regions, it is not restricted to these habitats (Beadle 1981, Australia's Virtual Herbarium 2009). The *Chenopodium auricomum* alliance supports prolific *S. australis* populations, and this ecosystem develops in regions with 250–400 mm of rainfall (mainly in summer). Further, the run-off from neighbouring regions ensures that these regions are a flooded swamp for parts of the year. The communities bordering mangroves that support *S. australis* are inundated with seawater throughout the year, and rainfall is also seasonally high in these tropical regions. However, *S. australis* is less common in the monsoonal, tropical regions of Queensland, the Northern Territory and Western Australia, and the high rainfall, mediterranean or temperate regions of south-western and south-eastern Australia (Australia's Virtual Herbarium 2009).

Growth and development

Morphology

Seedlings emerge from the soil within a few days of exposure of non-dormant seeds to sufficient moisture (generally less than a week, depending on burial depth). The cotyledons are approximately 10 mm long, and round in section (Figure 5A). Less than a week after emergence, the seedlings enter the juvenile stage of vegetative growth, with leaves that are round, succulent and range in length from less than 5 mm to over 50 mm (Figure 5B). Plants may remain in this stage for several weeks or months, or progress to the stage of adult vegetative growth in less than a month. Adult vegetative growth is characterized by leaves that are short (usually less than 10 mm), flat and taper to a spine (1–5 mm long, Figure 5C). Mature plants are highly branched from the main stem, and grow in a spherical or hemispherical shape (Figure 5E) (Borger *et al.* 2009b). However, some plants, especially in saline environments, develop a prostrate growth form (Mitchell and Wilcox 1988). Flowering/reproduction is indeterminate, commencing immediately upon entering the adult vegetative stage or up to six months later. Flowers and fruits are partially protected from stock grazing by the spiny adult leaves. Adult vegetative growth continues during the reproductive stage. Some plants produce juvenile growth from axillary buds near the stem base during the adult vegetative growth or reproductive stage (Figure 5D). The new branches in the juvenile vegetative stage then progress through subsequent growth stages to reproduction and senescence (Borger *et al.* 2009b).

Once the entire plant has senesced, including any new branches that have sprouted, the above ground section of the plant is released from the root system to become mobile (Figure 5F,G). The degradation of the abscission layer at the base of the stem of *S. australis* plants (and subsequent release of the plant) may be related to moisture stress, as has been found for the abscission of other plant organs (Taylor and Whitelaw 2001, Roberts *et al.* 2002, Borger *et al.* 2009b). The seed is dispersed when the fruit reaches maturity, which occurs before, during and after plant senescence. Most plants that reach the reproductive stage, and subsequently senesce, become mobile. Plants that die prior to seed production usually degrade without being released from their root system (Borger *et al.* 2009b). The characteristics of the root system of *S. australis* have not been examined, although morphologically similar species of the *Salsola* genus develop a root system extending over 1 m both laterally and vertically (Crompton and Bassett 1985, Creager 1988, Young 1988, Pan *et al.* 2001).

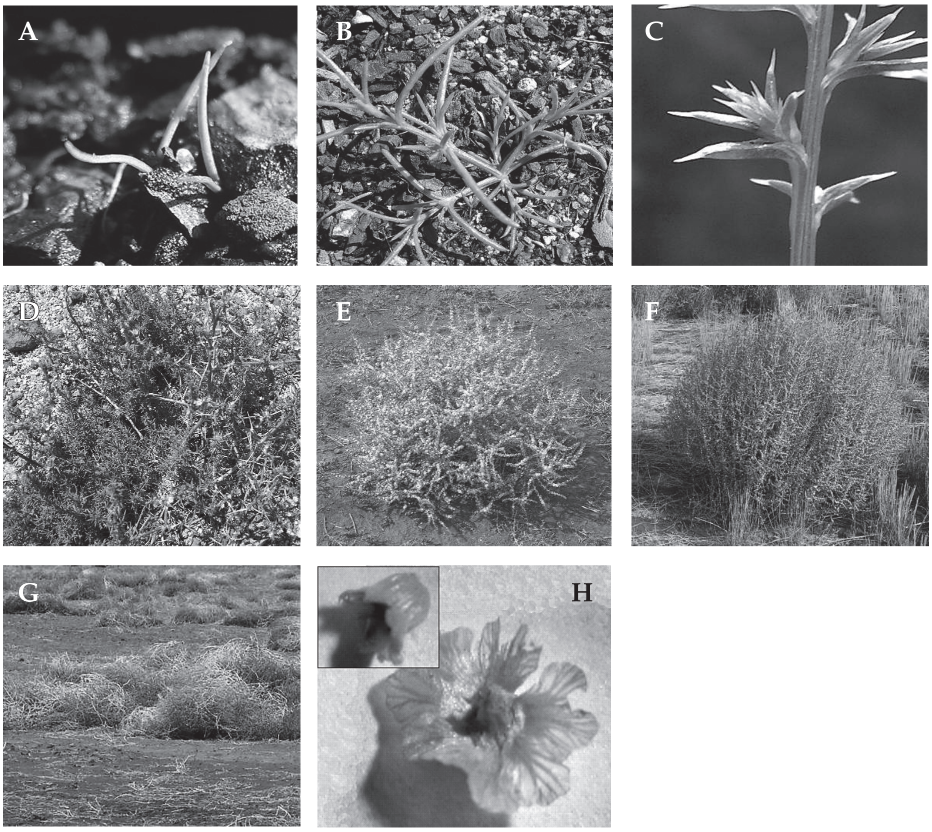

Figure 5. *Salsola australis* at various stages of the life cycle. Photos were taken from plants in the Lake Grace district in 2004 and 2005. Stages of the life cycle pictured above include: seedlings (A), juvenile vegetative growth stage (B), adult vegetative growth stage (C), combined juvenile and adult vegetative growth stage (D), reproductive stage (E), senesced plant with viable seed (F), mobile plants with viable seed (G) and fruiting perianth with or without wings, containing seed (H) (Borger *et al.* 2009b).

Perennation

Salsola australis can grow as an annual or biennial. Within the annual life cycle, plants can survive for two to 12 months, as development is highly plastic. As mentioned previously, adult plants can resprout branches from the base of the stem in the juvenile vegetative growth stage and continue growth through a second season. These plants rarely reach full size, and often have a prostrate growth form, as opposed to the standard spherical or hemispherical shape of the mature plant (Hrusa and Gaskin 2008, Borger *et al.* 2009b). The ability of *S. australis* to resprout and extend its life span beyond a single year is unique among species of *Salsola* sect. *Kali* (Hrusa and Gaskin 2008).

Physiology

There is no information available on the physiology of *S. australis*, although other weed species of the genus *Salsola* have the C_4 system of photosynthesis (Fowler and Hageman 1978, Allen 1982, Young 1986, 1988, Kadereit *et al.* 2003).

Phenology

Emergence and seed production of *S. australis* within agricultural systems were investigated in the Lake Grace region, Western Australia during 2004–2005 (Borger *et al.* 2009b). Cohorts of seedlings established throughout the year, resulting in overlapping generations of plants in various life cycle stages. Further, within each cohort, plants experienced uneven progression through life cycle stages due to highly plastic growth. Each cohort declined as plants died prior to reproduction or through senescence following the reproductive stage. In contrast, crop sowing and the associated soil disturbance removed all cohorts in May and further establishment was prevented until August.

Approximately 29% of all seedlings established during summer (December to February). The resulting plant survivorship was related to infrequent summer rainfall, with cohorts declining very rapidly if they established prior to a sequence of dry months. The largest cohorts (40% of seedlings) established in autumn, followed by smaller cohorts in winter (18%) and spring (13%). Plant density in the largest cohorts ranged from 26 to 36 plants m^{-2}. Plants that completed their life cycle (seedling establishment to mobility) during the 12 month study period had estimated seed production of between 95 and 19 596 seeds per plant. However, there was no correlation between life span (two to 12 months) and plant size (or life span and seed production per plant estimated from plant width). Average life span for plants that were not disturbed was 6.25 months, although this fell to 4.6 months in cropping areas where crop sowing killed all plants present at the end of autumn. Reproduction (flowering and seed production) occurred throughout the year, but was greater in summer and autumn. Fruit was produced as individual flowers matured, and so occurred for several weeks or months throughout the reproductive period. Fruit abscised at maturity, i.e. throughout the reproductive stage, during and after senescence. Plants most commonly reached senescence and became mobile in summer and autumn (Borger *et al.* 2009b).

Mycorrhiza

There is no research to indicate whether mycorrhizal fungi form a symbiotic or detrimental relationship with *S. australis*. Research on the morphologically similar *S. kali* indicated that mycorrhizal fungi can colonize plants, extract nutrients and successfully reproduce. The fungi did not assist with nutrient uptake by the plant, and fungal infestation led to 25–30% mortality within the *S. kali* population (Allen and Allen 1988, Allen 1989, Allen *et al.* 1989, O'Conner *et al.* 2001). *S. australis* is an early successional species, and mycorrhizal fungi are at relatively low levels in soil following a disturbance event, as the removal of vegetation retards their growth (Smith and Read 1997). Within the disturbed regions that *S. australis* colonizes, the gradual increase in fungal populations may contribute to the concomitant decline of *S. australis* populations.

Reproduction

Floral biology and seed production

No research has been conducted on the pollination strategy of *S. australis*. Morphologically similar species of the *Salsola* genus (*S. kali*, *S. pestifer* A.Nels.) are wind pollinated and viable seed is produced autogamously or allogamously (Crompton and Bassett 1985, Young 1991).

In *S. australis*, seed production ranges from less than 100 seeds to approximately 20 000 seeds in agricultural conditions, and is directly related to plant size (plant width or biomass) (Borger *et al.* 2007, Borger *et al.* 2009b). Plants collected in Morawa and Lake Grace, Western Australia in 2006, ranged in size from 3 to 110 g dry biomass and produced 139 to 7734 seeds (Figure 6) (Borger *et al.* 2007).

Salsola australis, like other agricultural weed species of the *Salsola* genus, produces a mobile seed bank. Following senescence, the spherical, mature plants break free of their root system and the wind driven plants move considerable distances (1.6–1247.2 m) (Borger *et al.* 2007). Approximately 50% of plants move less than 100 m as they became entangled with other *S. australis* plants within the stand (Figure 7). Seed shedding commences before the plants become mobile and increases with movement, but is also related to the aging and weathering processes experienced by stationary or mobile plants. The oldest seeds, lower on the branches, shed readily. Younger seeds on the tips of branches take the longest time to shed, and may remain

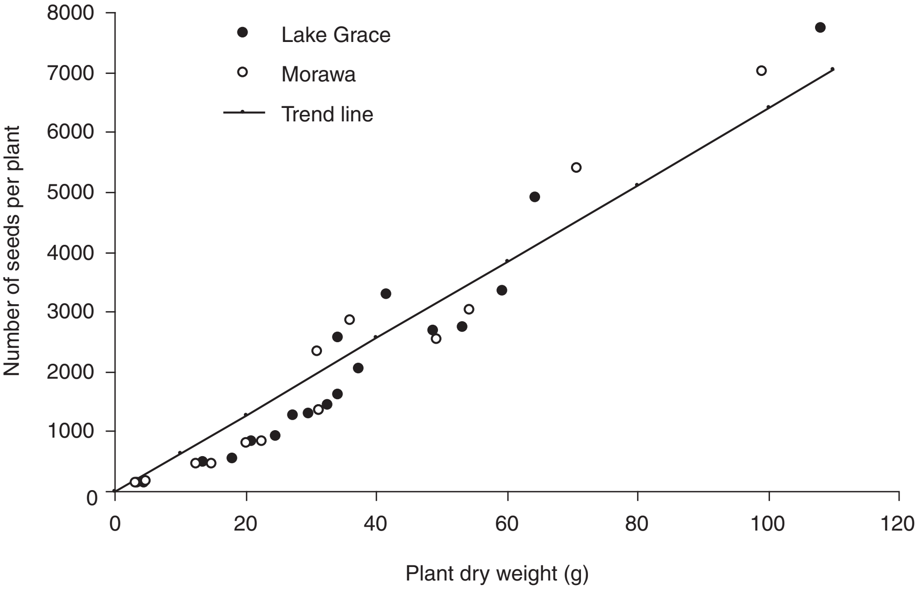

Figure 6. Total seed production and dry weight of *Salsola australis* plants collected from the regions of Morawa and Lake Grace. The legend indicates the plant collection region and the trend line, which represents the relationship $y = -560 + 74.6x$ ($r^2 = 94.8\%$, $P < 0.001$) (Borger *et al.* 2007).

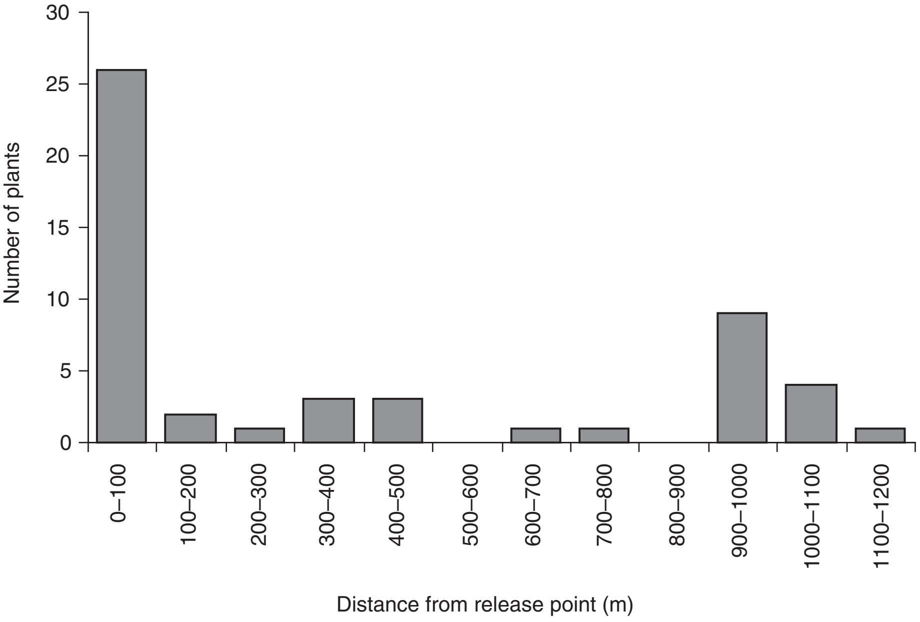

Figure 7. The number of *Salsola australis* plants found within a set radius (0–1200 m) from the release point in a field of wheat stubble, 27 days after they were released in the field (Borger *et al.* 2007).

on the senesced plant skeleton for over a year. All plants retain a proportion of their seed in spite of movement, weathering and aging of the dead plant. However, the germinability of retained seed drops to less than 2% after two months. There are no data available on the fate of seeds after shedding, but the seeds are small and light, so it is likely that further dispersal occurs following seed shedding (Borger *et al.* 2007). *S. australis* plants do not disperse as effectively as *S. tragus*, possibly due to their less compact shape (Hrusa and Gaskin 2008).

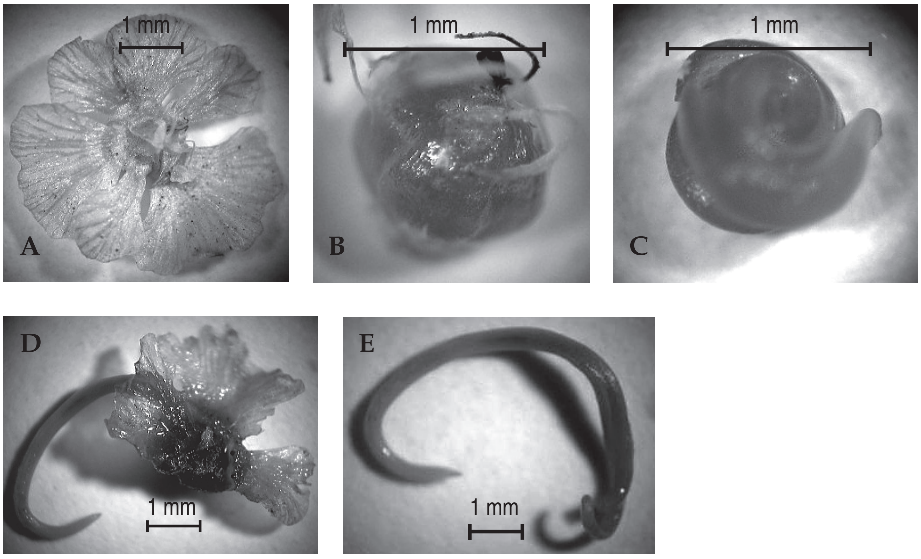

Figure 8. The fruiting perianth (A), seed (B), coiled embryo within the seed (C), embryo emerging from a seed still contained within the fruiting perianth (D), and fully emerged seedling (E), from a Lake Grace *Salsola australis* plant (Borger 2007).

Physiology of seeds and germination

Salsola australis plants produce seeds with no stored energy reserves or complex coverings to offer protection. As described previously, seeds consist of coiled embryos (Figure 8C) contained within a very thin seed coat (Figure 8B) within the fruiting perianth (Figure 8A). Germination occurs when the seed is exposed to water. Once the seed imbibes, the cells swell and elongate and the embryo uncoils to escape from the fruiting perianth (Figure 8D,E). The uncoiling motion of the embryo forces the radicle into the soil (Borger 2007). This process occurs less than 24 hours following exposure to moisture. Similar germination occurs in morphologically similar species of the *Salsola* genus (*S. kali*, *S. vermiculata* L. and *S. pestifer*). For these species, rapid germination occurs because the coiled embryo is actually a fully differentiated plant. The active chloroplasts in the cotyledons allow photosynthesis to start within the seedling immediately following exposure to light (Wallace *et al.* 1968, Dwyer and Wolde-Yohannis 1972, Evans and Young 1972, Crompton and Bassett 1985, Creager 1988, Young 1991).

Seed viability varies considerably due to ecotype and environment, ranging from less than 10% to over 90%. The low fertility of populations with less than 10% viable seed may have a genetic origin, as environmental causes of low fertility (pathogens, herbicides, resources) were not apparent and low fertility was consistent when plants were grown in controlled conditions (Borger 2007). Viability was uniform between the seeds that shed easily following senescence and the seeds that were retained on the plant (Borger 2007, Borger *et al.* 2009b).

Salsola australis seed harvested directly following plant senescence was able to germinate over a wide temperature range (5–37°C), with 11–20°C being the optimum range. However, there is some ecotypic variation evident in germination of seeds collected from different climatic regions (Borger 2007, Borger *et al.* 2009b).

Cumulative germination of viable seed during the year following seed production (of seed from ecotypes collected at Lake Grace, Morawa and Merredin, Western Australia, buried at 10 mm depth) varied from less than 10% to approximately 100% of the viable seed, indicating considerable difference in proportion of dormant seeds (Borger 2007, Borger *et al.* 2009b). The amount of dormant seed produced by a population varies between ecotype, but is also heavily influenced by the environment of the maternal parent. Seed from plants with access to adequate resources are more likely to germinate in the year following seed production, whereas seed from plants in resource poor environments are more likely to be dormant (Borger 2007, Borger *et al.* 2009b). The result of altered seed dormancy levels is that populations of *S. australis* in stressful, resource limited locations establish a dormant seed bank to insure the population against years of low seed production. In locations where resources are not limited, dormancy is minimized to maximize the population growth rate, a trait observed in other weed species (Steadman *et al.* 2004, Fenner and Thompson 2005, Luzuriaga *et al.* 2006).

Dormancy of seed on a single plant is related to seed age and shedding ability. While most seed is shed from the plant as it reaches maturity, some seeds are retained on the senesced plant skeleton. Cumulative germination of the easily shed seed is greater than that of retained seed. The retained seeds were predominately the youngest seeds on the plant and so their germination may be inhibited by immaturity of the embryo. Dormancy in the second year after seed production has not been investigated, but seed viability drops to less than 2% over the first year, and so it is unlikely that any seed remains viable for more than two years (Borger *et al.* 2007).

Hybrids

Four genetically and morphologically distinct taxa of the *Salsola* genus are found in south-western Australia. Even though the taxa in the southwest have similar life cycles (i.e. time of reproduction), live in close proximity, and have the same diploid chromosome number, there was no evidence of hybridization (Borger *et al.* 2008). This is unusual, as morphologically similar species of the *Salsola* genus in other countries frequently hybridize (Rilke 1999, Hrusa and Gaskin 2008). However, hybridization of *S. australis* with other species has not been investigated outside south-western Australia.

Population dynamics

The demography of *S. australis* was examined at Lake Grace, Western Australia, at various sites (i.e. in fields cropped with barley, left fallow, or periodically grazed by sheep; Table 1) (Borger *et al.* 2009b). While *S. australis* seedlings established throughout the year, there were generally two or three large cohorts each year (in summer and in autumn or winter). Initial seedling density within each cohort varied from fewer than five to more than 40 plants m^{-2}, and so the number of vegetative plants m^{-2} (averaged over an entire year) varied between sites. However, density dependent mortality ensured that there was less difference between the average numbers of plants m^{-2} y^{-1} reaching the reproductive stage. The number of plants that subsequently senesced following seed production, and the annual seed production m^{-2} y^{-1} (estimated from plant size) did not vary between sites.

As seedlings can germinate throughout the year, and growth and reproduction are

Table 1. Average annual *Salsola australis* plant density (m^{-2}) in each life stage (vegetative, reproductive and senescence), and estimated average annual seed production (m^{-2}) for each site (with standard error), from December 2004 to November 2005, at sites under various agricultural land uses (Borger *et al.* 2009b).

Site	Average annual number of plants (m^{-2})			Seed production (m^{-2})
	Vegetative	Reproductive	Senescence	
1 – Cropped field	13.8 (2.28)a	4.4 (0.91)ab	0.8 (0.23)a	2698 (326.9)a
2 – Fallow field	14.2 (1.30)a	5.1 (0.72)b	1.2 (0.30)a	8303 (429.2)a
3 – Grazed pasture	8.1 (1.10)b	3.1 (0.62)a	0.8 (0.25)a	4951 (838.6)a
4 – Grazed pasture	25.8 (2.56)c	3.2 (0.49)a	1.3 (0.24)a	6680 (411.6)a

^{abc}Indicates similarity between values for each site (1–4), for each life stage (P <0.001).

indeterminate, plants at all growth stages were present at all times of the year (Figure 9). However, within a cropping field, all plants were killed during autumn by the application of herbicides and the crop sowing operation. Plants did not re-establish until late winter (Borger *et al.* 2009b). Where plants had not been artificially removed, plant density ranged from 9 to 61 plants m^{-2}. Density was generally greater in winter, due to greater seedling establishment. In summer, there were more mature plants and fewer seedlings, resulting in lower plant density (Borger *et al.* 2009b).

Modelling of the population ecology data from Lake Grace (Figure 10) indicated that population growth rate was 1.5 (i.e. the population was increasing by approximately half every year). Population growth rate was most strongly affected by seed dispersal between populations. Population growth rate increased to 8.2 if it was assumed that a constant number of seed immigrated into the area from neighbouring populations of *S. australis*, through broad scale seed dispersal. Population growth was virtually unaffected by the dormant seed bank, even when assuming that the proportion of seed entering the seed bank is much higher than the 1% of seed that actually remains dormant (Borger *et al.* 2009a).

Persistence

Persistent populations of *S. australis* are usually found in habitats that are too degraded or environmentally harsh (due to aridity, salinity, temperature extremes etc.) to support dense vegetation, and are discussed in detail in the Habitat section (Beadle 1981, Mitchell and Wilcox 1988). Non-persistent populations occur in disturbed sites where *S. australis* acts as an early successional species. Examples include mining rehabilitation sites and agricultural areas, or sites of native vegetation that have been temporarily disturbed (Naidu and Harwood 1997, Westbrooke and Florentine 2005, Eldridge *et al.* 2006, Borger *et al.* 2009b).

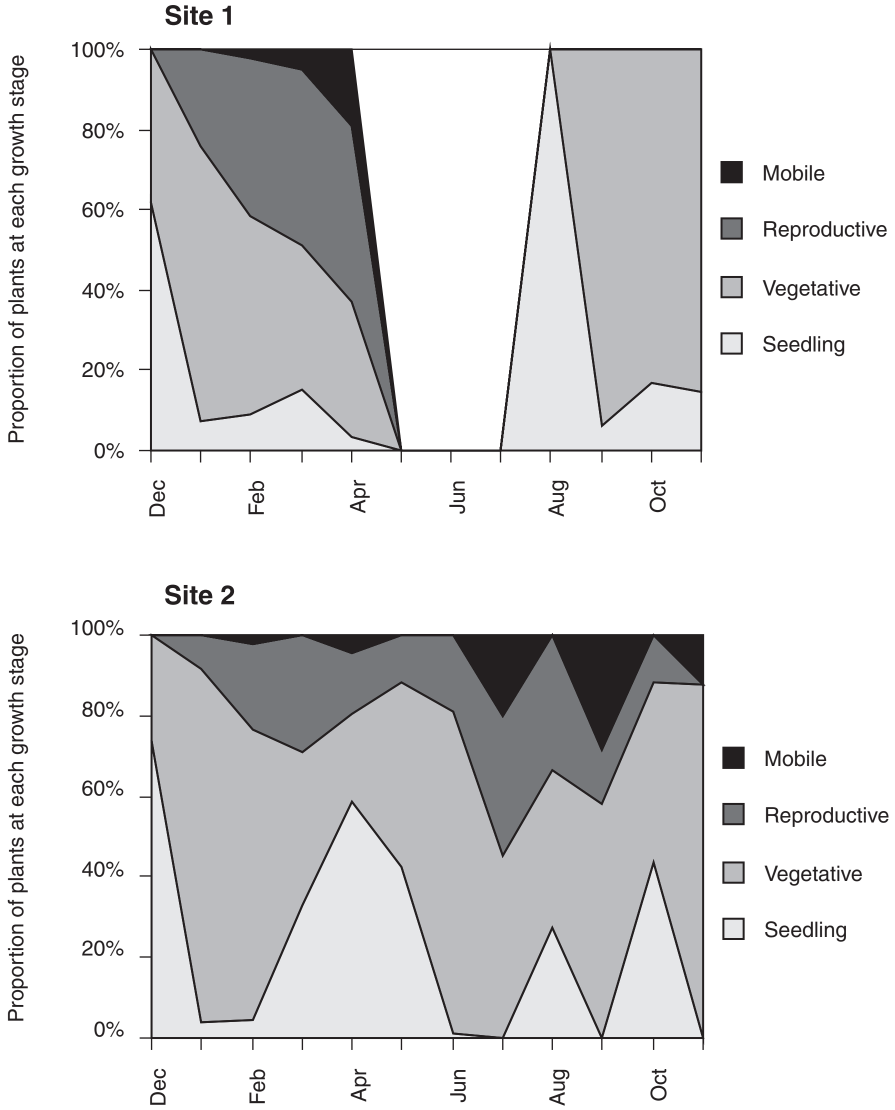

Figure 9. Proportion of *Salsola australis* plants within each stage of the life cycle throughout the year at Lake Grace. Site 1: cropped field where all plants were removed by crop sowing in May. Site 2: fallow field where plants were not disturbed throughout the year. Figure produced from data in Borger (2007) and Borger *et al.* (2009b).

Importance

Detrimental

Salsola australis is economically important as a summer annual weed in Australian agricultural systems, and is abundant in the Western Australian broad scale farming region (Borger *et al.* 2007, Borger *et al.* 2009b, Western Australian Herbarium 2009). The effect of *S. australis* on the yield of the following crop has not been investigated, although summer weeds remove nitrogen and stored soil moisture over the summer fallow, reducing the yield potential of subsequent winter crops (Tennant 2000, Osten *et al.* 2006). *S. australis* may cause a delay to crop sowing, as it can take time to clear the mature plants at the end of the summer/autumn growing period. Clearing plants can be very difficult if they are not fully senesced at time of crop sowing, and any delay to crop sowing also results in loss of moisture and reduced crop yield in Western Australia. Within agricultural environments *S. australis* is a fire hazard and senesced, mobile plants damage infrastructure such as fencing (Figure 11) (Smith 2005, Borger *et al.* 2007).

Salsola australis is likewise a weed of pasture systems in Western Australia. Stock do not graze on the prickly, mature plants, and may be injured attempting to move through them. *S. australis* has previously been claimed to cause oxalate poisoning (Royce 1963, Petheram and Kok 2003). Most tests indicate that the oxalate concentrations in this species are not sufficient to poison sheep (Jacob and Peet 1989, Jacob *et al.* 1992). However, oxalate levels are influenced by nitrogen availability and fluctuate from non-poisonous to poisonous levels in other species of the genus *Salsola*, in the presence of sufficient nitrogen (Crompton and Bassett 1985).

Beneficial

Salsola australis is a native species, and therefore has intrinsic value in the wide range of ecotypes to which it belongs (detailed in Habitat section). Another positive attribute of the species is the ability to colonize highly degraded soils, as it is an extremely hardy and versatile early successional species. Colonization by *S. australis* results in the prevention of erosion, addition of humus, encouragement of soil microbes and improvement of soil aggregate formation and water infiltration (Naidu and Harwood 1997). As such, it may play a valuable role in rehabilitation of ecosystems that have been disturbed, including both native habitats and mine sites or other areas of artificially degraded land (Mitchell and Wilcox 1988, Naidu and Harwood 1997, Westbrooke and Florentine 2005, Eldridge *et al.* 2006).

Salsola australis is not commonly used as a forage plant in Western Australia, although stock graze the young plants (Mitchell and Wilcox 1988, Borger *et al.* 2009b). Further, dominance of a pasture by *S. australis* in Australia generally indicates poor soil/pasture condition and management (Mitchell and Wilcox 1988). Internationally, several morphologically similar species of the *Salsola* genus have been considered as useful forage species, especially in arid, saline, degraded agricultural regions (Hageman *et al.* 1978, Fowler and Hageman 1979, Crompton and Bassett 1985, Toderich *et al.* 2002, Osman *et al.* 2006).

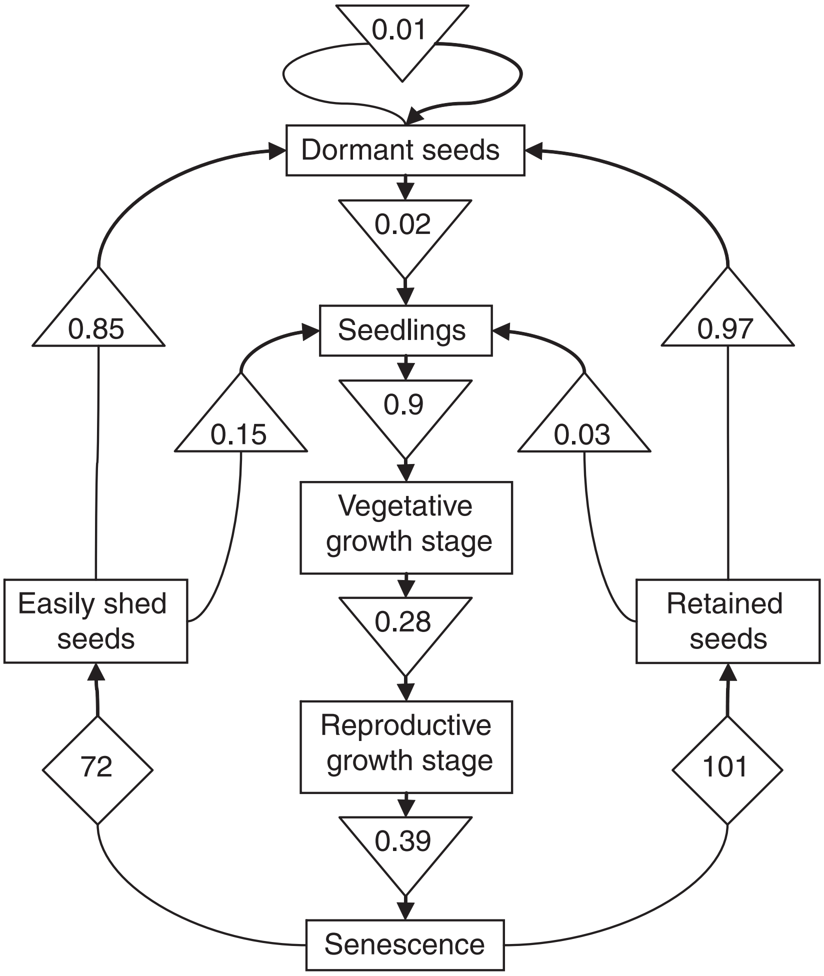

Figure 10. Diagrammatic life table of *Salsola australis* in a cropping field at Lake Grace. Rectangles represent stages of the life-cycle; triangles represent the probabilities of transition between each life cycle stage; diamonds represent fecundity (Borger *et al.* 2009a).

Figure 11. Senesced, mobile *Salsola australis* 'tumbleweeds' in the district of Morawa, Western Australia.

Weed management

Legislative status

Salsola australis is not included on the Noxious Weed List of any Australian State or Territory, and so there is no legislation in place to regulate the control of this species (Weeds Australia 2007). As a native species, it is highly unlikely that *S. australis* will be included on the Noxious Weed List in future.

Herbicides

Chemical control is the most common management strategy applied to *S. australis* in agricultural systems. A broad range of herbicides can kill young plants, although only 2,4-D amine based products and Spray.Seed® (paraquat and diquat) are registered in Western Australia (Young and Whitesides 1987, Young and Thorne 2004, Moore and Moore 2007). Herbicides are not highly effective against mature plants (Moore and Moore 2007), possibly because most plants are exposed to stressful environments (i.e. hot, arid summer climate), which makes many weed species difficult to control with herbicides (Lanini and Radosevich 1982, Harvey and Crothers 1988).

Residual herbicides from the sulfonylurea chemical group are commonly applied after crop harvest to control spring to autumn germination in the regions where *S. australis* is the predominant summer weed. However, these chemicals cannot be used if legumes, canola or barley crops are planned for the following winter cropping season, due to crop compatibility issues with herbicide residue (Hollaway *et al.* 2006, Moore and Moore 2007). These residual herbicides do not normally affect barley crops, except in regions with low summer rainfall and alkaline soils favoured by *S. australis*, where decay of residual herbicides is severely delayed (Hollaway *et al.* 2006). Unfortunately, barley is commonly the crop of choice in these saline or alkaline areas. Other chemicals used when sulfonylureas are not available include paraquat and diquat combined with 2,4-D and triclopyr (Moore and Moore 2007), but plants can rejuvenate from the stem base if they are not treated with either a systemic or residual herbicide.

Modelling work indicated that if it was assumed that there were no neighbouring plants, herbicides reducing seed production by 40% or more resulted in a population growth rate of less than 1 (population declining towards extinction), and a 22.8% chance of the population becoming extinct over 25 years (Borger *et al.* 2009a). When it was assumed that seeds could disperse into the region from neighbouring populations, use of herbicides to reduce seed production made virtually no difference to population growth rate.

Herbicide resistance is not evident in Australian populations of *S. australis*, but resistance to sulfonylurea herbicides is widespread for similar species of the *Salsola* genus in North America and Canada (Guttieri *et al.* 1992, Mallory-Smith *et al.* 1993, Morrison and Devine 1994).

Physical control

Physical control of *S. australis* is practised in both cropping and pasture systems in Western Australia. Within a cropping system, cultivation may be used to kill plants before sowing the crop (Borger *et al.* 2009b). In a pasture phase *S. australis* can be controlled through heavy grazing while the plants are young (Borger *et al.* 2009b). Mature plants can also be windrowed and then burnt, but this may result in shedding and dispersal of seed. There are no data available on the effectiveness of physical control in pastures.

Biological control

Biological control has not been attempted in Australia. Further, it is unlikely that exotic biological control agents will be released against *S. australis*, given the likely native origin of this species (Bean 2007, Borger *et al.* 2008). A rust fungus (*Uromyces salsolae* Reich.), which is a potential biological control agent, has already been found on *Salsola* populations in Australia (Hasan *et al.* 2001, Figure 5). It was noted in Western Australia at East Yuna in April 1963 (MacNish 1964). Preliminary investigations into the effectiveness of this biological control agent (in controlled conditions and using rust sourced from Turkey) indicated that mortality of infected *S. kali* (possibly *S. australis*) plants increased by 54.5%, and seed production was prevented (Hasan *et al.* 2001).

Salsola australis seed may be highly susceptible to ant predation, as has been found for the seeds of other annual weed species in Western Australia (Spafford Jacob *et al.* 2006). Experimental removal of ants in Western Australia pastures resulted in a significant increase in *S. australis* density and seed production. This effect was further enhanced by removal of ants through cultivation (Theo Evans personal communication 2009).

Figure 12. *Salsola australis* infected by the rust fungus, *Uromyces salsolae*, where the fungus is indicated by arrows (image from M. Jourdan, CSIRO Australia).

Other treatments

Prevention may be the best option for control of *S. australis*. Only 25% or less of the mobile *S. australis* plant skeletons produced in one field will migrate into neighbouring fields (as most fields in Australian cropping/pasture systems are fenced). Further, most seed shedding occurs before the plants become mobile and during the initial 500–1000 m of movement. Therefore, once the senesced plant skeletons arrive in a new field, they shed little additional seed (Borger *et al.* 2007). Unfortunately, these plants are often crushed prior to and during the crop sowing process, ensuring that unshed seed is incorporated into the soil seed bank. Removal of these mobile plants, as opposed to crushing them, would probably prevent or delay the establishment of new populations in fields that do not already contain *S. australis* (Borger *et al.* 2007). For those fields that do have well established populations of *S. australis*, it has already been indicated that seed production from a population is less important to population growth than seed dispersal from neighbouring populations, making removal of mobile plants (i.e. through burning) the key to effective weed control (Borger *et al.* 2009a).

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