

Review

The biology of Australian weeds

49. *Conyza bonariensis* (L.) Cronquist

Hanwen Wu, E.H. Graham Centre for Agricultural Innovation, Wagga Wagga Agricultural Institute, Wagga Wagga, New South Wales 2650, Australia.

Name

Conyza bonariensis (L.) Cronquist is a species of the Asteraceae family. Synonyms include *C. albida* Willd. ex Spreng., *C. ambigua* DC., *C. bonariensis* var. *leiotheca* (S.F.Black) Cuatrec., *C. bonariensis* var. *microcephala* (Cabrera) Cabrera, *C. floribunda* Kunth, *Conyzella linifolia* Willd., *Conyza linifolia* Willd., *Erigeron albidus* (Willd. ex Spreng.) A.Gray, *Erigeron ambiguus* (DC.) Sch.Bip. *E. bonariensis* L., *Erigeron bonariensis* var. *leiotheca* S.F.Black, *E. bonariensis* var. *microcephalus* Cabrera, *E. crispus* Pourret, *E. floribundus* (Kunth) Sch.Bip., *E. linifolius* Willd., *Leptilon bonariensis* (L.) Small, *Leptilon linifolium* (Willd.) Small, *Marsea bonariensis* (L.) V.M.Babillo (Cronquist 1943, Danin 1976, Michael 1977, Wagner *et al.* 1999, Maia 2002, Randall 2002, Sida 2003, Pruski 2006).

Common names include hairy fleabane, flax-leaf fleabane, fleabane, wavy-leaved fleabane, asthma weed and Argentiinan-koiransilmä (Roy *et al.* 1998, Randall 2002). It is commonly known in Brazil as acatôia, arnicão, buva, capetiçoba, capiçoba, catiçoba, ervalanceta, lagarteira, margaridinha-do-campo, rabo-de-foguete, rabo-de-raposa, rabo-de-rojão, salpeixinho, and voadeira (Maia 2002, Barbosa *et al.* 2005).

Description (Taxonomy)

Annual or biennial herb to 1 m high, robust, erect, grey-hispid; stems usually unbranched below inflorescences, often branched near base, lateral branches regularly overtopping main axis, densely hirsute with spreading septate hairs. Leaves hispid with short antrorse hairs and with longer spreading septate hairs; leaves densely arranged, usually greyish-green, basal leaves linear, oblong, or narrow-oblong, 4–9 cm long, 5–15 mm wide, margins toothed, sometimes teeth obscure; leaves becoming progressively smaller, 3–6 cm long and 5–10 mm wide, oblong to linear, entire. Inflorescence a pyramidal or corymbiform panicle; head many, hemispherical, 5–6 mm long, 8–12

mm diam. Ray florets 50–200 or more per head; involucre urceolate, bracts in 3 or 4 series, linear, acute, hirsute, subequal or outer ones shorter, inner bracts 3–4 mm long, outer bracts ca. 2 mm long. Outer florets numerous, in 6–7 marginal rows, corolla white, filiform-tubular, 2–2.2 mm long, ligule minute, obscure; style ca. 2.5 mm long, slightly longer than pappus. Central disc florets 12–20, corolla 3–3.5 mm long; upper part narrowly cylindrical, longer than lower filiform part, 5-lobed, yellowish. Achenes oblong, pubescent, ca. 0.5–1 mm long, 0.2–0.3 mm thick, compressed, ribbed on both side, pale amber; pappus 1-seriate, united at base, barbelate, white to pink bristles c. 3 mm long. Flowers throughout year (Cunningham *et al.* 1981, Everett 1992, Peng *et al.* 1998, Wagner *et al.* 1999).

Conyza bonariensis is a hexaploid species (allopolyploid), with a chromosome number of $2n = 54$ (Razaq *et al.* 1994, Urdampilleta *et al.* 2005). In Australia, there are six other *Conyza* species, *C. leucantha*, *C. primulifolia* (previously named *C. chilensis*), *C. sumatrensis* (previously named *C. albida*), *C. canadensis* var. *canadensis*, *C. parva*, and *C. bilbaoana* (Everett 1992, Randall 2002). *C. bonariensis* is the most widespread introduced species in Australia, followed by *C. canadensis* and *C. sumatrensis* (Burry and Kloot 1982, Lazarides *et al.* 1997, Richardson *et al.* 2006).

There has been confusion amongst the three most widely distributed *Conyza* species. Both *C. canadensis* and *C. sumatrensis* are annuals. The former has a chromosome number of $2n = 18$, while the latter has $2n = 54$ (Thebaud and Abbott 1995). *Conyza bonariensis* has the narrowest leaves at the rosette stage when compared to other *Conyza* species (Thebaud and Abbott 1995). *Conyza bonariensis* has a more compact stature, with many short branches and bearing large capitula, while *C. canadensis* is essentially a single-stemmed taxon with few long branches and with small and elongated capitula (Thebaud and Abbott 1995).

Conyza sumatrensis can grow up to 2 m high. It is often confused with *C. bonariensis* because of the similar size of the flower head (Wilson *et al.* 1995). *Conyza sumatrensis* branches differently to *C. bonariensis*, with lateral branches near the top and not overtopping the central stem, forming a pyramidal inflorescence (Everett 1992, Wilson *et al.* 1995). It also differs from *C. bonariensis* in that there are no long hairs near the apex (Auld and Medd 1987). Leaves of *C. sumatrensis* are usually wider (5–20 mm) than those of *C. bonariensis* (6 mm) (Sida 2003).

History

Conyza bonariensis is generally believed to be native to South America (Michael 1977, Everett 1992, Wilson *et al.* 1995, Prieur-Richard *et al.* 2000). It was first described from Argentina (Michael 1977). *Conyza bonariensis* could have been introduced to eastern and southeast Asia and to Australia and New Zealand from both Europe and America. A number of specimens of *C. bonariensis* collected in Australia were dated back in the 1840s (Michael 1977). *Conyza bonariensis* may have been introduced accidentally to South Australia (Burry and Kloot 1982). It was widespread in the Adelaide area and around other settlements at the time of the first botanical collections in 1847.

Distribution

Conyza bonariensis is a cosmopolitan weed. It infests arable land, orchard, vineyard, forest, roadsides, abandoned fields, as well as industrial sites (Burry and Kloot 1982, Prieur-Richard *et al.* 2000, Heap 2007). It is naturalized in warm areas throughout the world, in Europe mainly in the Mediterranean Basin (Terzioğlu and Anşin 2001, Sida 2003). It is more thermophilous than its close relative *C. sumatrensis*. In temperate Europe, e.g. in the British Isles, it persists only in big cities and is absent from rural areas due to their colder climate (Wurzell 1994). *Conyza bonariensis* is rarely found in Central Europe, and occurs there only temporarily (Sida 2003).

It is widespread across all States in Australia (Michael 1977, Cunningham *et al.* 1981, Everett 1992). The current distribution of *C. bonariensis* in Australia is shown in Figure 1.

Conyza bonariensis is widely distributed in the northern grains region of Australia, infesting both winter and summer crops such as wheat, chickpea, cotton and sorghum (Wu and Walker 2004). It is one of the most difficult weeds to control in minimum tillage farming systems (Somerville and McLennan 2003). It is a common weed of horticulture in Perth and also common on disturbed sites, such as roadsides, from Perth to Esperance. It has also been found near Kununurra (Hussey *et al.* 1997).

Habitat

Climatic requirements

Conyza bonariensis is distributed widely throughout the warmer regions of the world (Terzioğlu and Anşin 2001, Sida 2003). The broad geographical distribution of *C. bonariensis* in Australia suggests that there is no specific climatic requirement. It is a pantropical weed, spreading into warm-temperate regions (GRIN 2007).

Substratum

Conyza bonariensis can occur in most soil types and plant communities, particularly in areas of disturbed soil and in and around gardens (Cunningham *et al.* 1981). It is more common on lighter soils, although it can sometimes be found on heavy textured soils (Wu *et al.* 2007). It is also commonly found in irrigation channels. Seed burial studies demonstrated no *C. bonariensis* emergence in pots containing a heavy textured soil (vertisol) under field conditions in south-eastern Queensland. In laboratory studies, *C. bonariensis* seeds readily germinated within two days at 20°C in continuous light, suggesting that in a field situation, *C. bonariensis* seeds would germinate after an adequate rainfall event in either autumn or spring. Similarly, Davies (1999) reported that seedling emergence occurred three days after sowing. However, seeds germinating on the heavy vertisol soil in south-eastern Queensland could encounter a disruption of moisture supply from deeper in the soil profile due to the self-mulching (surface cracking) characteristics of this soil type, resulting in a failure of further emergence (Wu *et al.* 2007). The impact of soil types on *C. bonariensis* emergence requires further investigation.

Plant associations

Conyza bonariensis occurs in most habitats throughout Australia and is common in urban areas (Auld and Medd 1987). It is a weed of disturbed areas and wasteland (Everett 1992). It is widespread and often a common component of pasture, particularly in areas which are neglected or where ground cover is poor (Cunningham *et al.* 1981). *Conyza bonariensis* is an opportunistic invader of subhumid, subtropical pastures of improved fertility status resulting from legume establishment (Tothill and Berry 1981). Prieur-Richard *et al.* (2000) reported that a high concentration of soil nitrate associated with legumes is a key factor for the increased vegetative growth and reproductive effort of *C. bonariensis*.

The abundance of *C. bonariensis* is increasing in no-till farming systems, possibly due to a better environment for germination and seedling survival as a result of stubble retention (Wu *et al.* 2007). Surface moisture conditions are likely to stay favourable for germination and emergence over an extended period under no-till

compared with the conventional tillage systems.

Growth and development

Morphology

The morphological development of *C. bonariensis* has been described in great detail by Finot *et al.* (1996). The expanded cotyledons are oblong to oval-elliptical, 7 mm in length and 4 mm in width. The first pair of expanded leaves is 1.4–1.5 cm long and 0.7–0.8 cm wide, whole margin, rounded in the apex and obtuse in the base. The second to fifth leaves are of oval/egg shape, 4.3–5 cm in length by 1–1.2 cm in width. *Conyza bonariensis* seedlings are shown in Figure 2.

Conyza bonariensis produces basal rosettes prior to bolting and flowering (Thebaud and Abbott 1995). Seedling emergence was observed three days after sowing. After 30 days, plants showed four true leaves in rosette disposition (Davies 1999). *Conyza bonariensis* seedling growth is very slow, and the rosette stage relatively prolonged, even under the optimal thermoperiods of 27/22°C (Zinzolker *et al.* 1985). Active growth commences in spring or early summer with plants producing, over a long period, a mass of light fluffy seeds which are readily dispersed by the wind (Cunningham *et al.* 1981).

It takes 11 weeks for *C. bonariensis* to reach the bolting stage. *Conyza bonariensis* spends about three weeks at the bolting stage before flowering (Thebaud and

Abbott 1995). At the flowering stage, *C. bonariensis* plants have an average dry weight of 90.3 g per plant. The ratio of leaf to stem dry weight at flowering is 1:1 (Davies 1999).

Conyza bonariensis has re-sprouting characteristics (Figure 3). There were about 4–6 buds at the top of the taproot (near the soil surface) of over-wintered

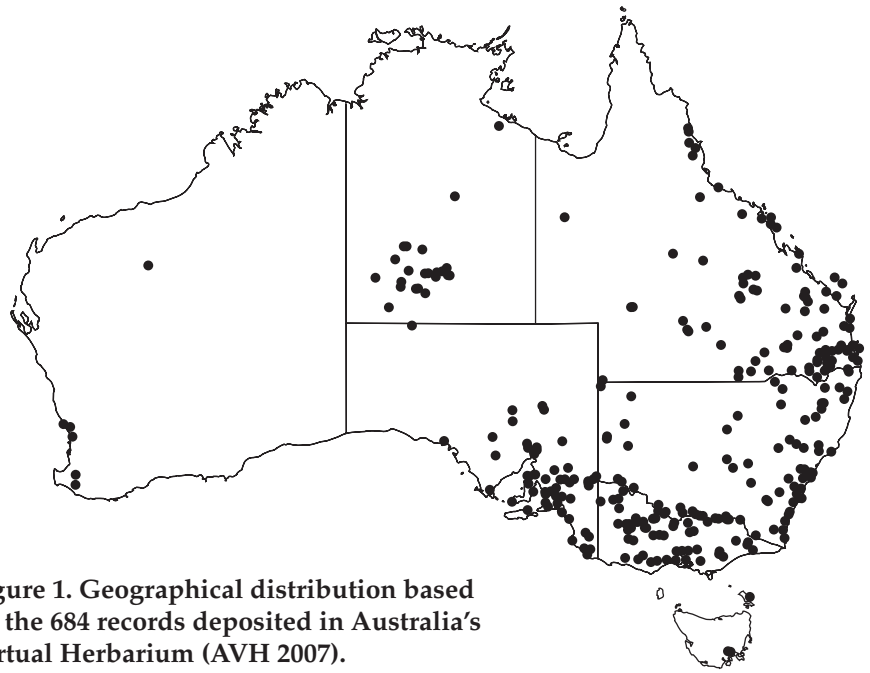


Figure 1. Geographical distribution based on the 684 records deposited in Australia's Virtual Herbarium (AVH 2007).

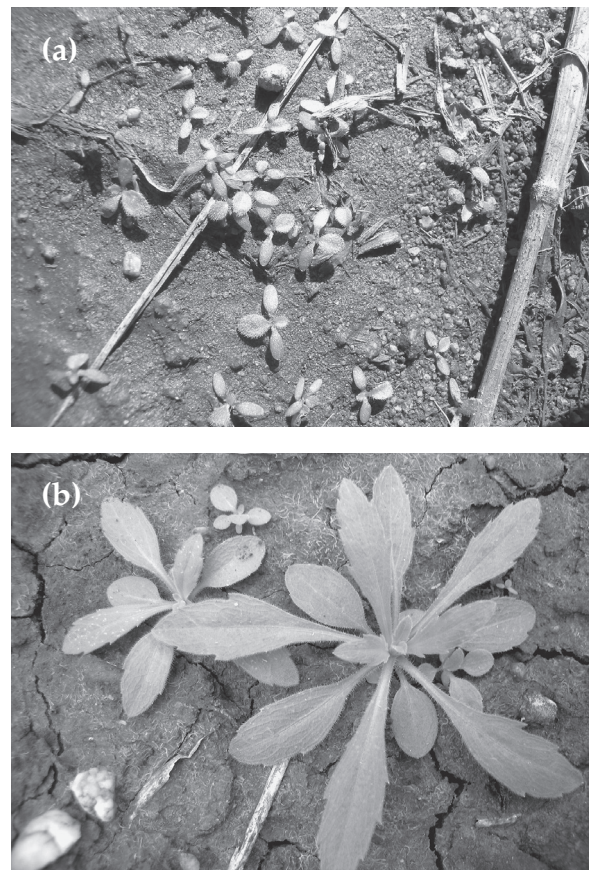


Figure 2. Young *Conyza bonariensis* seedlings at cotyledon (a) and rosette stages (b).

C. bonariensis plants (Wu *et al.* 2007). This feature enables the plant to regenerate from its basal buds after top removal. Davies (1999) reported that 45 days after top removal of *C. bonariensis* by cutting at the flowering stage, plants regrew and were able to produce an amount of dry matter of 67 g per plant, further confirming the regenerative ability of this weed.

Perennation

Conyza bonariensis is often reported as an annual and in some cases as a biennial (Cunningham *et al.* 1981, Lazarides *et al.* 1997, Peng *et al.* 1998, Wagner *et al.* 1999). The ability to regrow from its basal buds might contribute to its biennial nature.

Physiology

Conyza bonariensis is a quantitative long-day species. It bolts and flowers earlier under long-day (16 h) than under short-day (8 h) conditions (Zinzolker *et al.* 1985). However, plants grown under 10 h light period, 50 $\mu\text{E m}^{-2} \text{s}^{-1}$ at 25°C remain vegetative. Although bolting occurs, the stalk does not flower before senescence (Amsellem *et al.* 1993). *Conyza bonariensis* flowers considerably earlier than other *Conyza* species (Thebaud and Abbott 1995). Of the five species, *C. bonariensis* is the earliest to flower, followed by *C. sumatrensis*, *C. canadensis*, along with *C. parve* and probably *C. bilbaoana* (Michael 1977).

The light compensation point, light saturation point and the maximum net photosynthetic rate of *C. bonariensis* were estimated at 21.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 1606 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 22.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, respectively, compared to 13.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 2050 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 20.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ for *C. canadensis* (Guo *et al.* 2004), indicating that *C. bonariensis* is less tolerant to shading than *C. canadensis*.

Other physiological information has mainly derived from the investigation of mechanisms of herbicide resistance in *C. bonariensis*. Photosynthetic electron transport in the chloroplasts of triazine-resistant (R) biotypes of *C. bonariensis* is unaffected by atrazine and simazine, as shown by fluorescence induction measurements in whole leaves (Prado 1989). In Hill reaction assays, the R biotype shows high level of resistance to atrazine and simazine, with a resistance factor in the range of 350–550.

Extensive research has been conducted to understand the resistance of *C. bonariensis* to paraquat. As measured by chlorophyll fluorescence suppression, paraquat-resistant (R) *C. bonariensis* is about 100-fold resistant to paraquat compared to the susceptible (S) biotype (Vaughn *et al.* 1989). Shaaltiel *et al.* (1988) reported that one dominant gene pleiotropically controlled the paraquat resistance in *C. bonariensis*. *Conyza bonariensis* has two periods of resistance during vegetative (rosette) growth: a low level of resistance with an I_{50} value 10

times that of the S wild type during most of the vegetative growth phase and a high level of resistance at an age of 10 weeks, where it is 50–100 times more resistant to paraquat (Ye and Gressel 2000). Amsellem *et al.* (1993) also reported that resistance of *C. bonariensis* to paraquat increased when plants were induced to flower by long days.

Two mechanisms of paraquat resistance in *C. bonariensis* have been proposed: sequestration at plasmalemma, and detoxification of toxic oxygen species generated by paraquat (Norman and Fuerst 1997). Norman *et al.* (1994) reported that the lateral movement of ^{14}C paraquat from the point of application on the adaxial surface of intact leaves incubated in darkness was significantly restricted in the R biotype relative to the S biotype, indicating that paraquat resistance in *Conyza* is correlated with restricted movement (sequestration) of the herbicide in the R biotype. On the other hand, *C. bonariensis* contains a complex of enzymes capable of detoxifying the reactive oxygen species generated by the photosystem I blocker paraquat, keeping the plant alive until the paraquat is dissipated (Ye *et al.* 2000, Ye and Gressel 2000). The levels of plastid superoxide dismutase and glutathione reductase are generally higher in resistant compared with susceptible plants during periods of high-level paraquat resistance, but they were similar during periods of low-level resistance (Amsellem *et al.* 1993).

These two mechanisms act in a synchronized manner. Shaaltiel and Gressel (1987) reported that paraquat is not immediately sequestered. It rapidly inhibits the chloroplast function of both S and R plants. However, the inhibition is transient (2 h) in the R biotype and irreversible in the S biotype. The R biotype has the capability to mobilize the high constitutive levels of the enzymes in the active oxygen detoxification pathway to temporarily protect the plant from paraquat damage while the paraquat is being actively sequestered. In fact, it has been suggested that only small increases in enzyme levels would be needed for 20-fold resistance, based on the moderate enzyme increases correlated with 300-fold resistance (Amsellem *et al.* 1993).

Phenology

Conyza bonariensis often follows a winter or summer annual life cycle. It predominantly emerges in autumn and early



Figure 3. Re-sprouting of *Conyza bonariensis* after the removal of aboveground part.

winter, forms a basal rosette stage over winter and produces seeds in the following spring or summer. A small fraction of *C. bonariensis* also germinates in spring and bolts without an over-wintering growth stage. On-farm monitoring of field emergence over time in a light sandy loam soil showed that 99% emergence occurred in late autumn, early and late winter, and 1% emerged in mid spring (Wu *et al.* 2007). *Conyza bonariensis* flowers all year round, although flowering is promoted by a long photoperiod, such as a 14 h light period (Zinzolker *et al.* 1985, Amsellem *et al.* 1993).

Little information is available on the importance of emergence cohorts (autumn or spring) to the population dynamics of *C. bonariensis*. Over-wintering *C. bonariensis* plants of the autumn cohort seem to have certain ecological advantages. Although very limited emergence occurs in mid-winter, young autumn or early winter seedlings actively grow during winter despite cold and dry conditions. Surprisingly, while there does not appear to be much growth above ground, root growth progresses extremely well. The tap roots of *C. bonariensis* can grow more than 35 cm deep into the soil to absorb available water, thereby surviving the severe drought conditions frequently experienced in the winter in south-eastern Queensland. Regehr and Bazzaz (1976) also found that over-wintering plants of *C. canadensis* at the rosette stage were capable of substantial carbon fixation and energy storage at low temperatures. The establishment of a strong root system over winter months provides sufficient food reserves for rapid growth during the following spring. It is difficult to control these over-wintered *C. bonariensis* plants, although they are small in appearance (Figure 4). In fact these plants are well developed, thereby requiring higher management inputs to control them (Wu and Walker 2004).

Mycorrhiza

Little information is available. One report

shows that there is no vesicular-arbuscular mycorrhizal association with *C. bonariensis* plants collected from Heron Island, Australia (Peterson *et al.* 1985).

Reproduction

Floral biology

Conyza bonariensis is self-compatible, and apparently not actively pollinated by insects, suggesting either autogamy or wind-pollination (Thebaud *et al.* 1996, Zelaya *et al.* 2007). *Conyza bonariensis* produced large and rounded capitula, with capitulum total length of 5.1 mm and base width of 3.6 mm, while *C. canadensis* produced small and elongated capitula, with capitulum total length of 4.0 mm and base width of 2.2 mm. The number of florets per capitulum was estimated at 211, which is about three times greater than *C. canadensis*, and two times greater than *C. sumatrensis* (Thebaud and Abbott 1995).

Seed production and dispersal

Reproductive capacity of *C. bonariensis* is high relative to total plant biomass (Figure 5). *Conyza bonariensis* plants are capable of producing up to 357 561 wind-dispersed seeds per plant (Kempen and Graf 1981). Average seed production was estimated at 290 per head and 266 753 per plant from Kern County, California (Kempen and Graf 1981), and at 400 per head and 119 100 per plant from south-eastern Queensland (Wu *et al.* 2007). Among the mature seeds produced, 80% are viable. The prolific seed production of *C. bonariensis* suggests a capacity of the weed to build up seed banks in a short time.

Seed settling velocity is a useful indirect measure of dispersal ability, with low settling velocity corresponding to high dispersal ability (Andersen 1992). The seeds of *C. bonariensis* plants are enclosed singly in small hard achenes. The achenes are equipped with a tuft of bristles known as the pappus (Figure 6). The pappus enhances the seed dispersal distance by reducing the rate of gravitational settling. *Conyza bonariensis* seeds have an average settling velocity of 0.291 m sec^{-1} (SD = 0.0728) (Andersen 1992), which is lower than 0.323 m sec^{-1} (SD = 0.0687) reported for a similar *Conyza* species, *C. canadensis* (Dauer *et al.* 2006). There were significant variations in seed settling velocity among plants within *C. bonariensis* and among inflorescences and seeds within plants. The variability in seed settling velocities within *C. bonariensis* could be due to differences in the ratio of pappus area to seed mass, or to variations in pappus geometry (Andersen 1992). These differences may arise through differences in the amount of pappus produced by an individual achene, in the mass of the enclosed seed or both (Augspurger 1986).

The small, light seed of *C. bonariensis* is prone to long distance dissemination by

the frequent high intensity summer storms experienced in the northern grain region, through a combination of strong wind and surface run-off, and through the water movement in irrigation channels and waterways. Prolific seed production, in combination with dispersal by wind and water, suggests that the spread of *C. bonariensis* across an agricultural landscape could be very rapid.

Physiology of seeds and germination

Conyza bonariensis is photoblastic and germination is greatly stimulated under light

(Michael 1977, Zinzolker *et al.* 1985, Wu *et al.* 2007). A 10 minute exposure to light induced full germination after the seeds were soaked in darkness for 1–2 days. However, after 4–6 days of dark incubation, soaked seeds became unresponsive to the short period of light treatment. Exposure to continuous white light stimulated germination of the unresponsive soaked seeds. Pre-chilling also exerted a positive effect on germination (Davies 1999). However, it was found that pre-chilling of soaked seeds at 5°C did not replace the light requirement for germination (Zinzolker *et*



Figure 4. Over-wintered small seedlings of *Conyza bonariensis*.



Figure 5. Fecundity of *Conyza bonariensis*.

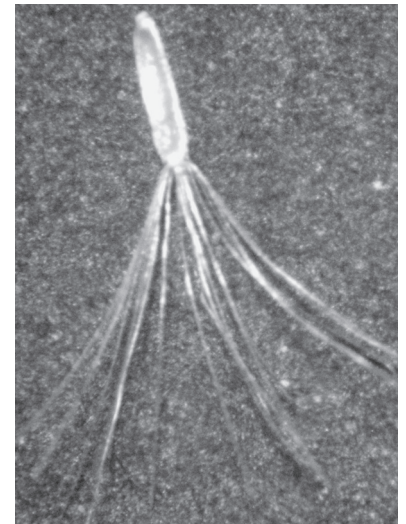


Figure 6. *Conyza bonariensis* seeds.

al. 1985). The cardinal (base, optimum and maximum) temperatures for germination of *C. bonariensis* are estimated at 4.2, 20 and 35°C (Wu *et al.* 2007).

Conyza bonariensis seed is readily germinable when it matures and germinates as long as conditions favour germination. Due to the fact that the weed flowers all year round, it has potential to complete multiple life cycles in a year. The potential for population growth will be very high if the weed is not controlled.

Conyza bonariensis emergence is very sensitive to soil burial. Seedlings emerge only from the soil surface or from a depth of 0.5 cm. No emergence occurred below 2 cm of burial depth (Wu *et al.* 2007).

Soil burial depths have significant effects on seed persistence. The persistence pattern shows an initial rapid drop followed by a slow but steady decline over time. Wu *et al.* (2007) reported that after three years of burial, there were about 7.5%, 9.7% and 1.3% viable seeds at 10, 5, and 0–2 cm soil depths, respectively. Although 1.3% viability after three year burial at 0–2 cm soil depth is a relatively small fraction, its significance should not be underestimated due to the massive seed production of the weed. Weed management plans would need to be in place for more than three years in order to control populations of this weed.

Seed persistence is also affected by soil type. *Conyza bonariensis* seeds buried in a light sodosol soil had significantly higher percentage viability than those buried in the heavy textured vertosol soil. When exhumed after 24 months of burial, 8% viable seeds were detected in the light soil, and 2% in the heavy soil (Wu *et al.* 2007).

Vegetative reproduction

Conyza bonariensis reproduces only by seeds.

Hybrids

Hybridization has been suspected between *C. bonariensis*, *C. canadensis* and

C. sumatrensis because they frequently occur in sympatry, along with the presence of morphologically intermediate forms in Europe (Thebaud and Abbott 1995). However, detailed morphological studies and isozyme analyses have confirmed that hybridization does not occur between these species. The isozyme banding patterns within each taxon are neither a combination of those observed in any pair of the other taxa nor a subset of that of any other taxon. Thebaud and Abbott (1995) concluded that these three *Conyza* species have diverged genetically prior to their introduction to Europe and maintained their genetic integrity despite the potential for hybridization due to their broad sympatry. They suggest that hybridization or gene introgression is rare among these species because of pre- or postzygotic isolation, including the possibility of strong selection against hybrids in the introduced range. Zelaya *et al.* (2007) also claimed that the scarcity of natural hybridization in *Conyza* is probably due to the enclosed involucre arrangement in *Conyza* and the autogamous nature of the genus.

However, hybrids with unknown fecundity, namely *Conyza* × *flahaultiana* (Thell.) Sennen and *Conyza* × *daveauiana* Sennen have been reported to have derived from crosses between *C. bonariensis* and *C. sumatrensis* in Spain and France (McClintock and Marshall 1988, Zelaya *et al.* 2007). Hybrids, *Conyza* × *mixta* Fouc. & Neyr are reportedly derived from crosses between *C. bonariensis* and *C. canadensis* in Belgium, France, Britain and Portugal (Zelaya *et al.* 2007). Sida (2003) also reported a putative hybrid between *C. bonariensis* and *C. triloba* Decne. in the Czech Republic.

The European *Conyza* hybrids are commonly poor in vigour. It has been speculated that ploidy differences may be a key barrier limiting hybridization between *Conyza* species. More compatible and vigorous hybrids would be expected from crosses between the allopolyploids ($2n = 54$) *C. bonariensis* and *C. sumatrensis*,

compared to crosses with the diploid ($2n = 18$) *C. canadensis* (Zelaya *et al.* 2007).

Population dynamics

Conyza bonariensis is often reported as a weed of no-till farming systems (Somerville and McLennan 2003). Compared to spring emergence, over-wintering *C. bonariensis* plants that emerge in autumn have greater implications for the population dynamics of this weed (Wu *et al.* 2007).

Prieur-Richard *et al.* (2000) studied the invasiveness of *C. bonariensis* in pre-established plant communities consisting of three functional groups (legumes, grasses and Asteraceae) and a range of plant species within each group. Increasing species richness of the resident communities impacted the demographic dynamics of *C. bonariensis* through both a loss in biomass and a decreased allocation to reproduction. The establishment, vegetative growth (final biomass) and net fecundity of *C. bonariensis* reduced significantly with the increased number of species per functional group. Species richness had no effects on *C. bonariensis* survival.

Functional richness (the number of functional groups) had no effect on the vegetative, reproductive and establishment parameters of *C. bonariensis*. However, the functional identity (species composition) played an important role in regulating the growth and net fecundity of *C. bonariensis* (Prieur-Richard *et al.* 2000). The introduction of any legume species into the species mix increased the biomass and consequently the net fecundity of *C. bonariensis*, resulting in an increased number of seeds per seedhead. However, the presence of grass species tended to decrease vegetative growth and reproductive effort. Communities with fewer Asteraceae and grasses were associated with increases in the reproductive effort of *C. bonariensis*, while its establishment was inhibited by the presence of grasses. Soil nitrates affected *C. bonariensis* net fecundity both indirectly via its biomass and directly through its

allocation to reproduction (Prieur-Richard *et al.* 2002a). Soil nitrate concentration was negatively correlated with grass biomass and positively correlated with legume biomass (Prieur-Richard *et al.* 2000).

Conyza bonariensis seedling establishment and survival increased with an increase in Asteraceae species richness (Prieur-Richard *et al.* 2000). The increased seedling establishment of *C. bonariensis* in the absence of Poaceae or Fabaceae was not due to light competition but to light quality. Abundant grass and legume foliage can modify far red light radiation. The increased survival of *C. bonariensis* in communities dominated by Asteraceae species was a result of reduced herbivory on *C. bonariensis* seedlings when compared to communities dominated by grasses (Prieur-Richard *et al.* 2002b).

Importance

Detrimental

Conyza bonariensis is innocuous to stock (Andrade and Holzhaecker 1959). However, it imparts taint to the milk and depreciates milk quality (Molfino 1947, Whittet 1968). It is rarely eaten by stock unless other forage is not available (Molfino 1947). The sap of *C. bonariensis* plants can cause skin irritation (Cunningham *et al.* 1981). *Conyza bonariensis* has also been reported to cause contact dermatitis in South Australia (Burry and Kloot 1982).

Conyza bonariensis is a wild host to a range of pests and diseases. It is a host to *Nyctelia graminicola* Kolenati and *N. cymoides* Spinola, which cause serious damage to a range of summer vegetable and fruit crops, particularly sorghum, grape, tomato and peach (Blando and Mineo 2005). It is an alternate host for *Basidiophora entospora* Roze & Cornu, causing downy mildew on ornamental crops (asters) (Francis 1998). Reniform nematode (*Rotylenchulus reniformis* Linford & Oliveira) is also found on the roots of *C. bonariensis* in Brazil (Ferraz 1985).

Conyza bonariensis is identified as a host of the formicid *Dorylus orientalis* Westwood, a pest infesting a variety of horticultural crops in Hunan, China (Xie and Yao 1989). *Dorylus orientalis* eggs are laid 3–5 cm underground on the roots of *C. bonariensis* plants. Wingless adults feed on the epidermis of the host's root system and on the stem up to 3 cm from the ground. In addition, *C. bonariensis* serves as a wild host to *Uroleucon bereticum* (E.E. Blanchard) (Hemiptera: Aphididae) in Argentina (Delfino and Stary 2004).

Conyza bonariensis has been reported as an alternative host of a number of viruses, such as witches' broom virus and tomato spotted wilt virus. Witches' broom virus causes severe infection of tomatoes. New leaves develop chlorotic margins, axillary buds and flower calyces show hypertrophy; eventually the plants die (Costa

1955). Tomato spotted wilt virus causes spotted wilt of groundnut in Queensland (Helms *et al.* 1961). More recently, the presence of lettuce mosaic virus (LMV) on *C. bonariensis* plants in Brazil has been confirmed by a range of techniques, including electron microscopy, biological, serological and molecular analysis (Chaves *et al.* 2003). The occurrence of pests, diseases and viruses in *C. bonariensis* is significant since this weed may act as a reservoir for potential infestation in agricultural crops.

Research on allelopathy has shown that shoot residues of *C. bonariensis* increase parasite infestation of branched broomrape (*Orobancha ramosa* L.) on tomato plants (Qasem 2002).

Conyza bonariensis is listed as an agricultural and environmental weed by Randall (2002). It is rated 4 on a scale of 0–5 as a weed affecting natural ecosystems and a highest rating of 5 in agricultural ecosystems (Groves *et al.* 2003). *Conyza bonariensis* is a weed of pastures and many field crops, such as maize, soybean, sorghum, cotton, chickpea, wheat, and lucerne (Milne 1991, Chaudhry *et al.* 2001, Wu and Walker 2004, Heap 2007). It competes significantly for water and nutrients, especially stored soil moisture in wheat and dryland sorghum crops. Walker and Wu (2006) reported that *C. bonariensis* causes significant yield reduction in sorghum. Compared to the weed-free treatment achieved by early pre-plant application of atrazine at 2000 g a.i. ha⁻¹, *C. bonariensis* caused sorghum yield loss of 30–31% even in the low-rate atrazine treated plots at 1000 g a.i. ha⁻¹.

Conyza bonariensis has doubled fallow weed control costs (Thorn 2004). The cost is likely to increase substantially due to the weed's rapid development of resistance to herbicides. Biotypes of *C. bonariensis* have evolved resistance to a range of herbicides with different modes of action in seven countries (Heap 2007). Populations resistant to paraquat have been identified in orchards, vineyards and roadsides in Egypt, Japan and South Africa (Fuerst *et al.* 1985, Heap 2007). Triazine resistant populations have been reported in Israel and Spain (Prado *et al.* 1989, Heap 2007). Biotypes of *C. bonariensis* have also been confirmed to have evolved resistance to chlorsulfuron, an acetolactate synthase (ALS) inhibitor, in industrial sites and forests in Israel. Since the first report of a *C. bonariensis* population resistant to glyphosate in South Africa in 2003, glyphosate-resistant populations of *C. bonariensis* have been identified in Brazil, Colombia and Spain (Urbano *et al.* 2005, Moreira *et al.* 2007, Heap 2007).

Differential responses to glyphosate have also been found among *C. bonariensis* populations in Australia. Populations collected from cropping paddocks are more tolerant than those collected from non-agricultural situations (Walker and Robinson 2007). Application of glyphosate at 675 a.e.

g ha⁻¹ caused 60 to 82% biomass reduction of *C. bonariensis* populations collected from 21 cropping paddocks, compared to the untreated controls, while the biomass reduction was 73 to 99% on populations from non-cropping areas with little or no suspected previous exposure to glyphosate.

Beneficial

Conyza bonariensis has been used in popular medicine as an anti-inflammatory, diuretic, vermifuge, and for the treatment of haemorrhoids and diarrhoea (Maia *et al.* 2002). It is commonly used to treat dermatological disorders (Pereira *et al.* 2005). Ground seed is highly aromatic and can be used as an insect repellent (Cunningham *et al.* 1981). Internally, a 1% infusion of the whole plant is used as a liver protector and against stomach ulcers (Lombardo 1970, Alonso *et al.* 1992). Infusions at 3–4% are used as a diuretic in problems of the genital-urinary system. Decoctions of the whole plant (10%) are used for the elimination of uric acid, a depurative and as an antirheumatic (Arrillage 1969, Lombardo 1970). *Conyza bonariensis* is also used externally as antiseptic in wounds (Alonso 1992, Lombardo 1970). Cataplasms made with fresh leaves are very popular for their healing properties (Davies 1999). It is possible to cultivate *C. bonariensis* for a potential biomass production of 17 444 kg dry weight ha⁻¹ (Davies 1999).

Conyza bonariensis is rich in essential oils, with 0.1–0.5% oil content found for the whole plant (Maia *et al.* 2002, Barbosa *et al.* 2005). Concerted efforts have been made to identify the volatile constituents of the essential oils from *C. bonariensis* (Kong *et al.* 2001, Maia *et al.* 2002, Barbosa *et al.* 2005, Tzakou *et al.* 2005). The oils of *C. bonariensis* were rich in limonene, (E)- β -ocimene, (E)- β -farnesene, β -caryophyllene, *cis*-lachenophyllum ester, matricaria ester, and germacrene D (Maia *et al.* 2002, Tzakou *et al.* 2005, Barbosa *et al.* 2005). Tzakou *et al.* (2005) detected a total of 56 compounds and identified 26 from the essential oils. The essential oil profiles of *C. bonariensis* differ between collections (Maia *et al.* 2002), growth stages (Tzakou *et al.* 2005), and plant parts (Barbosa *et al.* 2005).

The essential oils from *C. bonariensis* have been screened for anti-inflammatory activity in the mouse model of pleurisy induced by zymosan and lipopolysaccharide (LPS) (Souza *et al.* 2003). Oral administration of the main monoterpene constituent of the essential oil, limonene, was able to inhibit LPS-induced inflammation, including cell migration, which helped to control the inflammatory process during some bacterial infections. Kuate *et al.* (2005) reported that the essential oils of *E. floribundus* (a synonym to *C. bonariensis*) showed broad antifungal activities against *Trichophyton rubrum* (Castelani) Semon,

Trichophyton mentagrophytes (Robin) Blanchard, *Candida albicans* (Robin) Berkhout and *Cryptococcus neoformans* (Sanfelice) Vuillemin. The flower oil was more active than the leaf oil.

The fungicidal activity of *C. bonariensis* against *Macrophomina phaseolina* (Tassi) Goid has been assessed (Gautam *et al.* 2003). A methanol extract of *C. bonariensis* at 1000 µg mL⁻¹ caused 17% inhibition against *M. phaseolina*, a soilborne fungus causing charcoal rot. In addition, Charu and Kaushik (2003) claimed that a dry methanolic extract of *C. bonariensis* significantly inhibited three soyabean fungal pathogens: *Colletotrichum truncatum* (Schw.) Angdrus and Moore, *Fusarium oxysporum* (Schlet) emend Snyder & Hans, and *M. phaseolina*, which cause pod blight, wilt/root rot, and charcoal rot diseases of soyabean, respectively. Methanol extracts from the leaves of *C. bonariensis* are inhibitory to mushroom fungal pathogens, *Mycogone perniciosa* Magn. and *Verticillium fungicola* (Preuss) Hassebrauk (Charu *et al.* 2003). The essential oil from *C. bonariensis* at 1000 ppm inhibited mycelial growth of *Aspergillus flavus* Link ex Gray and at 3000 ppm was fungitoxic (Singh *et al.* 1984). *Aspergillus flavus* is a fungus that produces aflatoxins (Mahmoud 1999).

Alcoholic extracts of *C. bonariensis* showed a broad spectrum of antimicrobial activity (Gautier *et al.* 1959, Olano *et al.* 1996). Chaudhry *et al.* (2001) reported that petroleum ether extracts of the aerial parts of *C. bonariensis* were toxic to brine shrimp, and the methanol extract of *C. bonariensis* displayed significant antifungal activity against *Cladosporium cucumerinum* Ellis & Arth. A methanol extract of *C. bonariensis* was found to be inhibitory against xanthine oxidase (Kong *et al.* 2001), an enzyme closely related to hyperuricemia and gout (Tsutomu *et al.* 1991, Cos *et al.* 1998). Further study also found that the crude extracts of *C. bonariensis* contain inhibitors against butyrylcholinesterase (Khan *et al.* 2006).

Conyza bonariensis is a potential oilseed source of epoxy, crepenynic, erucic and other fatty acids, as well as of seed gum, steroids and pulp (White *et al.* 1971).

Legislation

Conyza bonariensis is not currently classified as a noxious weed in Australia. No regulatory legislation is applied.

Weed management

Herbicides

Currently only Spray.Seed® and Tordon 75-D are registered for *C. bonariensis* control in Australia. However, in the past decade, a range of pre- and post-emergence herbicides have been evaluated in both fallow and in-crop situations.

Conyza bonariensis plants, especially at a mature growth stage, seem to naturally

tolerate high levels of glyphosate application, due to leaf structures that protect against herbicide penetration, such as high trichome density, high cuticle thickness and low stomatal density in the adaxial side of the leaf (Procopio *et al.* 2003). The natural leaf barriers to herbicide penetration determine the limited success of any single herbicide application. A successful herbicide control program depends highly on the timing of application, the use of herbicide mixtures, sequential application as well as the strategic use of residual herbicides (Kempen 1988, Wu *et al.* 2007)

Timeliness of herbicide application has a significant effect upon control efficacy. It is critical to apply herbicides when the plant is small and actively growing. Herbicide efficacy decreases as the plant matures. Young seedlings at the rosette stage (<10 cm across) are easy to control. However, applying herbicide to very young seedlings (from the cotyledon to two-leaf stage) is not successful due to limited leaf area for herbicide uptake (Taylor 2007). Control programs should target winter fallow, rather than summer fallow, due to the predominant emergence in autumn. In addition, control efficacy in the summer declines rapidly due to the fact that weeds are often under severe moisture stress, as well as unfavourable spraying conditions (high temperature and low relative humidity) at the time of application.

Effective control of *C. bonariensis* in fallow cannot be achieved with any single herbicide alone (Wu *et al.* 2006). Contact herbicides alone, such as Spray.Seed® (paraquat + diquat at 324 and 276 g a.i. ha⁻¹), or paraquat at 325 g a.i. ha⁻¹, are ineffective, even when they are applied early. Re-growth after 2–3 weeks is common after these treatments (Wu *et al.* 2006).

Use of appropriate herbicide mixtures is a key to success. The addition of a suitable mixing partner to glyphosate, such as Ally (metsulfuron methyl), Amitrole T (amitrole + ammonium thiocyanate), 2,4-D ester, 2,4-D amine, Tordon 75D (2,4-D amine and picloram), Grazon DS (triflopyr and picloram), dicamba and Garlon 600 (triclopyr), improves control efficacy to over 90%. Three non-glyphosate mixes, 2,4-D ester + Amitrole T, 2,4-D amine + Amitrole T, and 2,4-D amine + Ally, also achieved over 90% control. These mixes provide alternative solutions to rotate with glyphosate, thereby minimising the risk of evolving glyphosate resistance (Wu *et al.* 2006).

The re-sprouting characteristics of *C. bonariensis*, and prolonged emergence patterns between autumn and spring suggest that sequential application techniques are important tactics for effective *C. bonariensis* control. *Conyza bonariensis* plants of different growth stages often co-exist in the field (Figure 7). A double-knock technique, i.e. glyphosate followed several days later by

Spray.Seed®, achieved the most effective and consistent control of *C. bonariensis* at various growth stages in fallows (Wu *et al.* 2006).

The use of residual herbicides through root uptake is another control strategy which overcomes the difficulty of foliar uptake arising from the protective leaf barriers of *C. bonariensis* (Wu *et al.* 2006, Wu *et al.* 2007). Residual herbicides are often used in mixture with glyphosate to perform dual actions through both foliar and root uptake. Higher rates of atrazine (2000 g a.i. ha⁻¹) or Primextra (atrazine + metolachlor at 1184 and 928 g a.i. ha⁻¹) provide good control of subsequent flushes in winter fallows. The efficacy of pre-emergence herbicide often depends on the timing and amount of rainfall.

For in-crop weed control, it is imperative to control emerged weeds prior to sowing. Application of glyphosate ± 2,4-D amine followed by Spray.Seed® or paraquat effectively controls *C. bonariensis* at various growth stages (Wu and Walker 2004).

Conyza bonariensis control in wheat requires residual herbicides to manage a number of flushes in-crop. Pre-plant application of Glean (chlorsulfuron at 15 g a.i. ha⁻¹) provides effective seasonal control of *C. bonariensis* in wheat, which can be followed up by Tordon 242 (MCPA + picloram), or 2,4-D amine to target survivors. Post-emergent application of Ally (metsulfuron methyl at 4.2 g a.i. ha⁻¹) achieved variable results between years. Consistent results were obtained with Ally either mixed with Tordon 242 (MCPA + picloram), or followed by 2,4-D amine (Wu *et al.* 2006).

In sorghum, control efforts should be focused on the existing *C. bonariensis* populations before sowing. In-crop emergence is expected to be very limited due to temperatures unfavourable for germination during summer (Wu *et al.* 2007). A pre-plant application of atrazine at 2000 g a.i. ha⁻¹ is very effective in providing residual control in sorghum. A sequential application of glyphosate at 900 g a.e. ha⁻¹



Figure 7. Co-existence of *Conyza bonariensis* plants at different growth stages.

mixed with 2,4-D amine at 900 g a.e. ha⁻¹ or dicamba at 500 g a.e. ha⁻¹, followed by at-planting atrazine at 1000 or 2000 g a.i. ha⁻¹ also provides effective control.

In lucerne, Milne (1991) reported that hexazinone at 750 or 1000 g a.i. ha⁻¹ + Caltex Summer Oil (1%) achieved 94–99% control of *C. bonariensis*. Metribuzin at 0.48 kg ha⁻¹ gave excellent control of *C. bonariensis* in an established ley system of lucerne/white clover/*Dactylis glomerata* L./*Bromus inermis* Leyss, producing the highest fodder dry matter yield (Perez and Duarte 1991).

Fallow treatment with Flame (imazapic) and in-crop treatment with Balance (isoxaflutole) + simazine are thought to be reasonable options for *C. bonariensis* control in chickpea. In cotton, combinations of diuron, fluometuron and prometryn followed by inter-row cultivation or chipping have been suggested (Wu and Walker 2004).

Other treatments

Conyza bonariensis is a poor competitor. Its growth (biomass) significantly decreased with increasing species richness in a diverse plant community (Prieur-Richard *et al.* 2000). Ward and Hamilton (2004) found that *C. bonariensis* grew well in wide-row crops such as chickpea and sorghum and in areas of poor crop establishment irrespective of the time of year and crop type. Growing more competitive winter cereals and avoiding wide row spacing should achieve better control (Wu and Walker 2004).

There is also potential for the strategic use of tillage to control this weed. Wu *et al.* (2007) reported that *C. bonariensis* is very sensitive to seed burial, with no emergence occurred below 2 cm soil depth. *Conyza bonariensis* is highly responsive to cultivation. Werth and Walker (2007) showed that chisel and disc plough were effective in suppressing *C. bonariensis* emergence. Limited emergence with cultivation is probably due to the burial effect and changing soil surface dynamics. Similarly, Brown and Whitwell (1988) found that even minimum tillage (discing) in spring or autumn effectively controlled *C. canadensis*. Inter-row cultivation and chipping are available options to control mature and stressed weeds in wide-row crops such as cotton and sorghum (Wu and Walker 2004).

Mowing is not an effective control option. It encourages lateral branching from the base of the plants, hardening them off. Mowing has also resulted in reducing the leaf area for herbicide coverage (Milne 1991), making control with post-emergent herbicides ineffective. *Conyza bonariensis* is not controlled by solarization under plastic sheets (Silveira *et al.* 1988).

Natural enemies

There is no information available on the natural enemies of this weed.

Acknowledgments

Mr Andrew Storr of NSW Department of Primary Industries and Dr Rex Stanton of E.H. Graham Centre are kindly acknowledged for their constructive and critical comments on this manuscript.

References

- Alonso, E., Bassagoda, M.J. and Ferreira, F. (1992). Yuyos; Uso Racional de las Plantas Medicinales. Editorial Fin de Digno, Montevideo, pp. 156.
- Amsellem, Z., Jansen, M., Driesenaar, A. and Gressel, J. (1993). Developmental variability of photooxidative stress tolerance in paraquat-resistant *Conyza*. *Plant Physiology* 103, 1097-106.
- Andersen, M. (1992). An analysis of variability in seed settling velocities of several wind-dispersed Asteraceae. *American Journal of Botany* 79, 1087-91.
- Andrade, S.O. and Holzhaecker, E.L. (1959). Investigations on toxic plants in Sao Paulo State. *Arquivos do Instituto biológico de São Paulo* 26, 55-88.
- Arrillaga, B. (1969). Plantas Medicinales. Editorial Nuestra Tierra, Montevideo. Nuestra Tierra No 31, pp. 60.
- Augspurger, C.K. (1986). Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 70, 1031-7.
- Auld, B.A. and Medd, R.W. (1987). 'Weeds – an illustrated botanical guide to the weeds of Australia', p. 96. (Inkata Press, Melbourne).
- AVH. (2007). Australia's Virtual Herbarium. Distribution map of *Conyza bonariensis*. <http://www.rbq.vic.gov.au/cgi-bin/avhpublic/avh.cgi>. Accessed on the 26 June, 2007.
- Barbosa, L.C.A., Paula, V.F., Azevedo, A.S., Silva, E.A.M. and Nascimento, E.A. (2005). Essential oil composition from some plant parts of *Conyza bonariensis* (L.) Cronquist. *Flavour and Fragrance Journal* 20, 39-41.
- Blando, S. and Mineo, G. (2005). Tritrophic interrelations of two economically interesting ligaeid pests (*Heteroptera*). *Bollettino di Zoologia Agraria e di Bachicoltura* 37, 211-23.
- Brown, S.M. and Whitwell, T. (1988). Influence of tillage on horseweed, *Conyza canadensis*. *Weed Technology* 2, 269-70.
- Burry, J.N. and Kloot, P.M. (1982). The spread of Composite (Compositae) weeds in Australia. *Contact Dermatitis* 8, 410-3.
- Charu, A. and Kaushik, R.D. (2003). Fungicidal activity of plants extracts from Uttaranchal hills against soybean fungal pathogens. *Allelopathy Journal* 11, 217-28.
- Charu, A., Kaushik, R.D., Kumar, A. and Garg, G.K. (2003). Fungicidal potential of Kumaon and Tarai region plants against mushroom fungal pathogens. *Allelopathy Journal* 11, 63-70.
- Chaudhry, B.A., Janbaz, K.H., Uzair, M. and Ejaz, A.S. (2001). Biological studies of *Conyza* and *Euphorbia* species. *Journal of Research (Science)* 12, 85-8.
- Chaves, A.L.R., Braun, M.R., Eiras, M., Colariccio, A. and Galletti, S.R. (2003). *Erigeron bonariensis*, an alternative host of lettuce mosaic virus in Brazil. *Fitopatologia Brasileira* 28, 307-11.
- Cos, P., Ying, L., Calomme, M., Hu, J.P., Cimanga, K., Van Poel, B., Pieters, L., Vlietinck, A.J. and Berghe, V.D. (1998). Structure activity relationship and classification of flavonoids as inhibitors of xanthine oxidase and superoxide scavengers. *Journal of Natural Products* 61, 71-6.
- Costa, A.S. (1955). Witches' broom of *Erigeron bonariensis*. *Bragantia* 14, iii-v.
- Cronquist, A. (1943). The separation of *Erigeron* from *Conyza*. *Bulletin of the Torrey Botanical Club* 70, 629-32.
- Cunningham, G.H., Mulham, W.E., Milthorpe, P.L. and Leigh, J.H. (1981). 'Plants of western New South Wales'. p. 662. (N.S.W. Government Printing Office, Soil Conservation Service of NSW, Sydney).
- Danin, A. (1976). On three adventive species of *Conyza* (Compositae) in Greece. *Candollea* 31, 107-9.
- Dauer, J.T., Mortensen D.A. and Humston, R. (2006). Controlled experiments to predict horseweed (*Conyza canadensis*) dispersal distance. *Weed Science* 54, 484-9.
- Davies, P. (1999). Propagation of "Yerba carniceira" (*Conyza bonariensis* (L.) Cronq. var. *bonariensis*, Compositae). *Acta Horticulturae* 502, 121-4.
- Delfino, M.A. and Sary, P. (2004). *Uroleucon bereticum* (E.E. Blanchard) (Hemiptera, Aphididae) and its new endemic parasitoid species (Hymenoptera, Braconidae, Aphidiinae) in Argentina. *Neotropical Entomology. Sociedade Entomologica do Brasil (SEB)* 33, 577-81.
- Everett, J. (1992). *Conyza*. In 'Flora of New South Wales', ed. G.J. Harden, Volume 3, pp 197-200. (New South Wales University Press, Sydney).
- Ferraz, L.C.C.B. (1985). Susceptibility of various common weeds in Sao Paulo State to *Rotylenchulus reniformis*. *Nematologia Brasileira* 9, 143-52.
- Finot, S.V.L., Urbina, P.A., Minoletti, O.M.L., Wilckens, E.R., Figueroa, R.M. and Riquelme, C.M. (1996). Achene and seedling morphology of Asteraceae weed species from south-central Chile. *I. Agro-Ciencia* 12, 15-29.
- Fuerst, E.P., Nakatani, H.Y., Dodge, A.D., Penner, D. and Arntzen, C.J. (1985). Paraquat resistance in *Conyza*. *Plant Physiology* 77, 984-9.

- Francis, S.M. (1998). *Basidiophora entospora*. IMI Descriptions of Fungi and Bacteria. CAB International, Wallingford, UK, 69, Sheet 681.
- Gautam, K., Rao, P.B. and Chauhan, S.V.S. (2003). Antifungal potency of some species of family Asteraceae (Compositae) against *Macrophomina phaseolina* (Tassi) Goid. *Journal of Mycology and Plant Pathology* 33, 294-95.
- Gautier, E. and Gerber, F. (1959). Investigación de la actividad antibacteriana de plantas de Córdoba. *Boletín de la Sociedad Argentina de Botánica* 8, 1-8.
- GRIN (Germplasm Resources Information Network) (2007). <http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?104170#dist>. GRIN Taxonomy for Plants, USDA-ARS. Accessed on 25 June 2007.
- Groves, R.H. (Convenor), Hosking, J.R., Batianoff, G.N., Cooke, D.A., Cowie, I.D., Johnson, R.W., Keighery, G.J., Lepshi, B.J., Mitchell, A.A., Moerkerk, M., Randall, R.P., Rozefelds, A.C., Walsh N.G. and Waterhouse, B.M. (2003). Weed categories for natural and agricultural ecosystem management. (Bureau of Rural Sciences, Canberra).
- Guo, S.L., Fang, F., Huang, H. and Qiang, S. (2004). Studies on the reproduction and photosynthetic ecophysiology of the exotic invasive plant, *Plantago virginica*. *Acta Phytocologica Sinica* 28, 787-93.
- Heap, I. (2007). The International Survey of Herbicide Resistant Weeds. Online. July 05, 2007. Available www.weed-science.com.
- Helms, K., Grylls, N.E. and Purss, G.S. (1961). Peanut plants in Queensland infected with tomato spotted wilt virus. *Australian Journal of Agricultural Research* 12, 239-46.
- Hussey, B.M.J., Keighery, G.J., Cousens, R.D., Dodd, J. and Lloyd, S.G. (1997). 'Western weeds', p. 94. (Plant Protection Society of Western Australia, Western Australia).
- Kempen, H.M. (1988). Horseweed (mare-stail) and flax-leaf fleabane, their identification and control. Proceedings of the California weed conference. 1988. (40), p. 179-81. Paper presented at a conference on 'Education and communication—the keys to the future', January 18-21, 1988, Sacramento, California.
- Kempen, H.M. and Graf, J. (1981). Weed seed production. *Proceedings of the Western Society of Weed Science* 34, 78-81.
- Khan, R.A., Bukhari, I.A., Nawaz, S.A. and Choudhary, M.I. (2006). Acetylcholinesterase and butyrylcholinesterase inhibitory potential of some Pakistani medicinal plants. *Journal of Basic and Applied Sciences* 2, 7-10.
- Kong, L.D., Abliz, Z., Zhou, C.X., Li, L.J., Cheng, C.H.K. and Tan, R.X. (2001). Glycosides and xanthine oxidase inhibitors from *Conyza bonariensis*. *Phytochemistry* 58, 645-51.
- Kuiate, J.R., Tsona, A.A., Foko, J., Bessiere, J.M., Menut, C. and Amvam-Zollo, P.H. (2005). Chemical composition and in vitro antifungal properties of essential oils from leaves and flowers of *Erigeron floribundus* (H.B. et K.) Sch.Bip. from Cameroon. *Journal of Essential Oil Research* 17, 261-4.
- Lazarides, M., Cowley, K. and Hohnen, P. (1997). 'CSIRO handbook of Australian weeds', pp. 47-48. (CSIRO Publishing, Melbourne).
- Lombardo, A. (1970). 'Planta Medicinales de la Flora Indígena', pp. 99-109. (Almanaque del Banco de Seguros del Estado, Montevideo).
- Mahmoud, A.L.E. (1999). Inhibition of growth and aflatoxin biosynthesis of *Aspergillus flavus* by extracts of some Egyptian plants. *Letters in Applied Microbiology* 29, 334-6.
- Maia, J.G.S., da Silva, M.H.L., Zoghbi, M.G.B. and Andrade, E.H.A. (2002). Composition of the essential oil of *Conyza bonariensis* (L.) Cronquist. *Journal of Essential Oil Research* 14, 325-6.
- McClintock, D. and Marshall, J.B. (1988). On *Conyza sumatrensis* (Retz) E.Walker and certain hybrids in the genus. *Watsonia* 17, 172-3.
- Michael, P.W. (1977). Some weedy species of *Amaranthus* (amaranths) and *Conyza/Erigeron* (fleabanes) naturalised in the Asian-Pacific region. Proceedings of the 6th Asian-Pacific Weed Science Society Conference, (Jakarta, Indonesia, 11-17 July 1977). Asian-Pacific Weed Science Society, Jakarta, Indonesia, 1, 87-95.
- Milne, B.R. (1991). Flax-leaf fleabane (*Conyza bonariensis*) control in lucerne. In 'Result 1991', pp. 51-2. (Weed Research and Demonstration Unit, Agricultural Research and Veterinary Centre, Orange, Australia).
- Molfino, R.H. (1947). Argentine plants which produce changes in the characters and properties of milk and its derivatives. *Comunicacion del Instituto Agrario Argentino* (Argentinian Agrarian Institute Report) 7, 23-34.
- Moreira, M.S., Nicolai, M., Carvalho, S.J.P. and Christoffoleti, P.J. (2007). Glyphosate-resistance in *Conyza canadensis* and *C. bonariensis*. *Planta Daninha* 25, 157-64.
- Norman, M.A. and Fuerst, E.P. (1997). Interactions of cations with paraquat in leaf sections of resistant and sensitive biotypes of *Conyza bonariensis*. *Pesticide Biochemistry and Physiology* 57, 181-91.
- Norman, M.A., Smeda, R.J., Vaughn, K.C. and Fuerst, E.P. (1994). Differential movement of paraquat in resistant and sensitive biotypes of *Conyza*. *Pesticide Biochemistry and Physiology* 50, 31-42.
- Olano, I., Alonso Paz, E., Cerdeiras, M.P., Fernandez, J., Ferreira, F., Moyna, P., Soubes, M., Vazquez, A., Vero, S. and Bassagoda, M.J. (1996). Screening of Uruguayan medicinal plants for antimicrobial activity. Part II. *Journal of Ethnopharmacology* 53, 111-5.
- Peng, C.I., Chung, K.F. and Li, H.L. (1998). Compositae. In 'Flora of Taiwan', eds. D.E. Boufford, C.F. Hsieh, P.P. Lowry, H. Ohashi and C.I. Peng, 2nd edition, Vol. 4, pp. 807-1101. (National Taiwan University, Taipei).
- Pereira, C.O., Lima, E.O., Oliveira, R.A.G., Toledo, M.S., Azevedo, A.K.A., Guerra, M.F. and Pereira, R.C. (2005). Ethnobotanic study of medicinal plants used in dermatological disorders in Joao Pessoa-Paraiba, Brazil. *Revista Brasileira de Plantas Mediciniais* 7, 9-17.
- Perez, M. and Duarte, G. (1991). Weed control in leys. *Revista de los CREA* 146, 58-64.
- Peterson, R.L., Ashford, A.E. and Allaway, W.G. (1985). Vesicular-arbuscular mycorrhizal associations of vascular plants on Heron Island, a Great Barrier Reef Coral Cay. *Australian Journal of Botany* 33, 669-76.
- Prado, R. de, Dominguez, C. and Tena, M. (1989). Characterization of triazine-resistant biotypes of common lambsquarters (*Chenopodium album*), hairy fleabane (*Conyza bonariensis*), and yellow foxtail (*Setaria glauca*) found in Spain. *Weed Science* 37, 1-4.
- Prieur-Richard, A.H., Lavorel, S., Grigulis, K. and Dos Santos, A. (2000). Plant community diversity and invasibility by exotics, invasion of Mediterranean old fields by *Conyza bonariensis* and *Conyza canadensis*. *Ecology Letters* 3, 412-22.
- Prieur-Richard, A.H., Lavorel, S., Dos Santos, A. and Grigulis, K. (2002a). Mechanisms of resistance of Mediterranean annual communities to invasion by *Conyza bonariensis*, effects of native functional composition. *Oikos* 99, 338-46.
- Prieur-Richard, A.H., Lavorel, S., Linhart, Y.B. and Dos Santos, A. (2002b). Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. *Oecologia* 130, 96-104.
- Procopio, S.O., Ferreira, E.A., Silva, E.A.M., Silva, A.A., Rufino, R.J.N. and Santos, J.B. (2003). Leaf anatomical studies in weed species widely common in Brazil. III – *Galinsoga parviflora*, *Crotalaria incana*, *Conyza bonariensis* and *Ipomoea cairica*. *Planta Daninha* 21, 1-9.
- Pruski, J.F. (2006). *Conyza sumatrensis* var. *leiotheca* (Compositae: Asteraceae), a new combination for a common neotropical weed. *NOVON* 16, 96-101.
- Qasem, J.R. (2002). Plants as sources of natural herbicides against branched broomrape (*Orobanche ramosa* L.). In 'Allelopathy, from molecules to ecosystems'. pp. 153-82. (Science Publishers, Inc., Enfield, USA).

- Randall, R.P. (2002). 'A global compendium of weeds'. p. 187. (RG and FJ Richardson, Melbourne).
- Razaq, Z.A., Vahidy, A.A. and Ali, S.I. (1994). Chromosome numbers in Compositae from Pakistan. *Annals of the Missouri Botanical Garden* 81, 800-8.
- Regehr, D.L. and Bazzaz F.A. (1976). Low temperature photosynthesis in successional winter annuals. *Ecology* 57, 1297-303.
- Richardson, F.J., Richardson, R.G. and Shepherd, R.C.H. (2006). 'Weeds of the south-east, an identification guide for Australia'. (R.G. and F.J. Richardson, Melbourne).
- Roy, B., Popay, I., Champion, P., James, T. and Rahman, A. (1998). 'An illustrated guide to common weeds of New Zealand', p. 62. (New Zealand Plant Protection Society, Canterbury, NZ).
- Shaaltiel, Y., Chua, N.H., Gepstein, S. and Gressel, J. (1988). Dominant pleiotropy controls enzymes co-segregating with paraquat resistance in *Conyza bonariensis*. *Theoretical and Applied Genetics* 75, 850-56.
- Shaaltiel, Y. and Gressel, J. (1987). Kinetic analysis of resistance to paraquat in *Conyza* – evidence that paraquat transiently inhibits leaf chloroplast reactions in resistant plants. *Plant Physiology* 85, 869-71.
- Sida, O. (2003). *Conyza triloba*, new to Europe, and *Conyza bonariensis*, new to the Czech Republic. *Preslia* 75, 249-54.
- Silveira, H.L., Caixinhas, M.L., Leitao, A. and Gomes, R. (1988). Evolution of actual and potential weed flora after soil solarisation. *VIII Colloque International sur la Biologie, l'Ecologie et la Systematique des Mauvaises Herbes* 1, 59-69.
- Singh, S., Dube, N.K., Tripathi, S.C. and Singh, S.K. (1984). Fungitoxicity of some essential oils against *Aspergillus flavus*. *Indian Perfumer* 28, 164-6.
- Souza, M.C., Siani, A.C., Ramos, M.F.S., Menezes-de-Lima Junior, O. and Henriques, M.G.M.O. (2003). Evaluation of anti-inflammatory activity of essential oils from two Asteraceae species. *Pharmazie* 58, 582-6.
- Somerville A. and McLennan B. (2003). 'The 2nd fallow weed management guide'. (Conservation Farmers Inc., Toowoomba).
- Taylor, F. (2007). Nufarm research with fleabane control options. Proceedings of a fleabane workshop held at DPI&F in Toowoomba, 7 February 2007, p. 47.
- Terzioğlu, S. and Anşın, R. (2001). A chorological study on the taxa naturalized in the eastern black sea region. *Turkish Journal of Agriculture and Forestry* 25, 305-9.
- Thebaud, C. and Abbott, R. (1995). Characterization of invasive *Conyza* species (Asteraceae) in Europe, quantitative trait and isozyme analysis. *American Journal of Botany* 82, 360-8.
- Thebaud, C., Finzi, A., Affre, L., Debussche, M. and Escarre, J. (1996). Assessing why two introduced *Conyza* differ in their ability to invade Mediterranean old fields. *Ecology* 77, 791-804.
- Thorn, S. (2004). Fleabane – implications for current farming systems in Goondiwindi region. Proceedings of a national workshop on fleabane. 25th February 2004, DPI&F, Toowoomba, Queensland. pp. 25-26.
- Tothill, J.C. and Berry, J. (1981). Cool season weed invasion of improved subtropical pastures. Proceedings of the Sixth Australian Weeds Conference, Volume 1, eds. B.J. Wilson and J.T Swarbrick, pp. 29-33. (Queensland Weed Society, Toowoomba, Australia).
- Tsutomu, H., Taeko, Y., Rieko, Y., Yukihiko, I., Muneto, M., Kazufumi, Y., Isao, A., Sansei, N., Tadaka, N., Masao, Y. and Takuo, O. (1991). Inhibitory effects of galloylated flavonoids on xanthine oxidase. *Planta Medica* 57, 83-4.
- Tzakou, O., Vagias, C., Gani, A. and Yannisaros, A. (2005). Volatile constituents of essential oils isolated at different growth stages from three *Conyza* species growing in Greece. *Flavour and Fragrance Journal* 20, 425-8.
- Urbano, J.M., Borrego, A., Torres, V., Jimenez, C., Leon, J.M. and Barnes, J. (2005). Glyphosate-resistant hairy fleabane (*Conyza bonariensis*) in Spain. *Proceedings of Weed Science Society of America* 45, 394.
- Urdampilleta, J.D., Amat, A.G. and Bidau, C.J. (2005). Karyotypic studies and morphological analysis of some reproductive features in five species of *Conyza* (Asteraceae, Asteraceae) from northeastern Argentina. *Contenido del Volumen* 40, 91-9.
- Vaughn, K.C., Vaughan, M.A. and Camilleri, P. (1989). Lack of cross-resistance of paraquat-resistant hairy fleabane (*Conyza bonariensis*) to other toxic oxygen generators indicates enzymatic protection is not the resistance mechanism. *Weed Science* 37, 5-11.
- Wagner, W.L., Herbst, D.R. and Sohmer, S.H. (1999). Manual of the flowering plants of Hawaii. Revised edition, (two volumes). Bernice P. Bishop Museum special publication. p. 288. (University of Hawaii Press/Bishop Museum Press, Honolulu)
- Walker, S. and Robinson, R. (2007). National screening for glyphosate resistance in fleabane. Proceedings of a fleabane workshop held at Queensland Department of Primary Industries and Fisheries in Toowoomba on 7th February 2007, pp. 32-33.
- Walker, S. and Wu, H. (2006). Knocking out flaxleaf fleabane. *Australian grain*, northern focus i-iii. (July-August 2006).
- Ward, L. and Hamilton, R. (2004). Fleabane – a declining problem on 'Callitris' in the Roma region. Proceedings of a national workshop on fleabane held at Queensland Department of Primary Industries and Fisheries in Toowoomba on 25th February 2004, p. 27.
- Werth, J. and Walker, S. (2007). Tillage effects on fleabane emergence Proceedings of a fleabane workshop held at Queensland Department of Primary Industries and Fisheries in Toowoomba on 7th February 2007, pp. 22-23.
- White, G.A., Willingham, B.C., Skrdla, W.H., Massey, J.H., Higgins, J.J., Calhoun, W., Davis, A.M., Dolan, D.D. and Earle, F.R. (1971). Agronomic evaluation of prospective new crop species. *Economic Botany* 25, 22-43.
- Whittet, J.N. (1968). 'Weeds', 2nd edition. (Government Printing, Sydney).
- Wilson, B.J., Hawton, D. and Duff, A.A. (1995). 'Crop weeds of northern Australia'. p. 61. (Department of Primary Industries, Queensland).
- Wu, H. and Walker, S. (2004). Flaxleaf fleabane, a difficult-to-control weed in dryland cropping systems associated with zero-tillage. *Australian Grain*, northern focus iii-v, November-December 2004.
- Wu, H., Walker, S., Rollin, M.J., Tan, D.K.Y. and Werth, J. (2007). Germination, persistence and emergence of flaxleaf fleabane (*Conyza bonariensis* (L.) Cronq.). *Weed Biology and Management* 7, 192-9.
- Wu, H., Walker, S.S., Taylor, I.N. and Robinson, G. (2006). Biology and management of flaxleaf fleabane (*Conyza bonariensis* L. Cronq.). Proceeding of the 15th Australian Weeds Conference, eds C. Preston, J.H. Watts and N.D. Crossman, pp. 137-40. (Weed Management Society of South Australia, Adelaide).
- Wurzell, B. (1994). A history of *Conyza* in London. *BSBI News*, London, 65, 34-8.
- Xie, F.Y. and Yao, L.X. (1989). A study on *Dorylus orientalis* Westwood. *Insect Knowledge* 26, 291-3.
- Ye, B., Faltin, Z., Ben-Hayyim, G., Eshdat, Y. and Gressel, J. (2000). Correlation of glutathione peroxidase to paraquat/oxidative stress resistance in *Conyza* determined by direct fluorometric assay. *Pesticide Biochemistry and Physiology* 66, 182-94.
- Ye, B. and Gressel, J. (2000). Transient, oxidant-induced antioxidant transcript and enzyme levels correlate with greater oxidant-resistance in paraquat-resistant *Conyza bonariensis*. *Planta* 211, 50-61.
- Zelaya, I.A., Owen, M.D.K. and Van Gesel, M.J. (2007). Transfer of glyphosate resistance: evidence of hybridisation in *Conyza* (Asteraceae). *American Journal of Botany* 94, 660-73.
- Zinzolker, A., Kigel, J. and Rubin, B. (1985). Effects of environmental factors on the germination and flowering of *Conyza albida*, *C. bonariensis* and *C. canadensis*. *Phytoparasitica* 13, 229-30.