

Research Reports

The Biology of Australian Weeds

19. *Bromus diandrus* Roth and *B. rigidus* Roth.

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Introduction

There are about 130 species of annual, biennial and perennial herbs in the genus *Bromus* L. (Smith 1970). They are widely distributed in the temperate regions of the world and are known as brome grasses. Two perennial species, *B. inermis* Leyss. and *B. catharticus* Vahl., are cultivated pasture species but all the annual species are ruderals and weeds (Smith 1980). *B. diandrus* Roth and *B. rigidus* Roth are widely distributed across southern Australia. They have increased in importance as weeds and are difficult to manage (Kon and Blacklow 1988). However, there is confusion over their identification and naming, and details of their biology aimed at assisting with their management is limited to recent publications. This paper summarises information on the identification, distribution, ecology and management of the species in Australia.

Taxonomy

Classification and nomenclature

Bromus diandrus Roth and *Bromus rigidus* Roth are classified in Table 1 after Smith (1970; 1980; 1985). Additional *Bromus* species in the section *Genea* that are of some importance in Australia are *B. madritensis* L., *B. rubens* L., *B. sterilis* L. and *B. tectorum* L..

Table 1. Taxonomy of *B. diandrus* Roth^A and *B. rigidus* Roth^B (After Smith 1970; 1980; 1985).

Family	<i>Poaceae</i> Barnh. (<i>Gramineae</i> Juss.)
Subfamily	<i>Pooideae</i> A. Br.
Tribe	<i>Bromeae</i> Dumort.
Genus	<i>Bromus</i> L.
Subgenus	<i>Stenobromus</i> (Griseb.) Hackel
Section	<i>Genea</i> Dumort.
Species (common names ^C)	<i>B. diandrus</i> Roth (great brome) <i>B. rigidus</i> Roth (rigid brome)

^A Roth, A. W. 1787. *Bot. Abh. Beobacht.* 44-45; synonyms: *B. gussonii* Parl., *Anisantha gussonii* (Parl.) Nevski and *A. diandra* (Roth) Tutin.

^B Roth, A. W. 1790. *Bot. Mag.* 4(10), 21; synonyms: *B. villosus* Forsskål, *B. maximus* Desf. and *A. rigida* (Roth) Hylander.

^C After Hartley (1979) and Williams (1986).

Bromus is from *bromos*, a Greek word for oat, and *broma* which means food (Jaeger 1966). The species name *diandrus* is from the Greek prefix *di* (two) and plant part *andro* (male or stamen); the reason for *diandrus* is uncertain as most florets have three stamens. *B. diandrus* has many common names including ripgut brome, ripgut grass, giant brome, slands grass, jabbers, Kingston grass and brome grass but its accepted common name is great brome (Hartley 1979). *Rigidus* is Latin for stiff or rigid and describes the erect nature of the inflorescence of *B. rigidus* and, hence, it is aptly called rigid brome (Williams 1986). *B. rigidus* has been known also as ripgut brome, ripgut grass, brome grass and great brome. Part of the confusion between *B. diandrus* and *B. rigidus* is due to the casual use of common names.

Identification

Bromus spp. are very similar in their seedling and vegetative stages of growth (Smith 1970; 1983; 1985). Even in the mature stages (Fig. 1) the species can be misidentified if observations are not sufficiently critical (Williams 1957; 1986; Gill and Carstairs 1988; Kon and Blacklow 1988). This has resulted in confusion in the taxonomy of *B. diandrus* and *B. rigidus* in the monographs on the floras of various countries (Post 1933; Hitchcock 1935; Maire and Weiller 1955; Tsvelev

1983). In the United States, *B. rigidus* and *B. diandrus* are considered to be synonymous (Weed Science Society of America 1985).

Examination of the local and exotic materials held in the Australian herbaria showed that many specimens were misidentified particularly before the 1950s (Kon and Blacklow 1988). Two different *Bromus* species on the same mount were sometimes incorrectly named as a single species. *B. diandrus* was commonly named as *B. maximus*, *B. sterilis* or *B. madritensis* while *B. rigidus* was named as *B. gussonii*, *B. sterilis*, *B. madritensis*, *B. rubens* or, most frequently, *B. diandrus*.

Williams was the first botanist in Australia to study the two species. In 1952 with the help of Hubbard at the Royal Botanic Gardens, Kew, the materials collected from the Meningie district of South Australia were, for the first time, correctly identified and named as *B. diandrus* and *B. rigidus* (Williams 1957). If the work of Williams had been published in a more widely-read journal, Burbidge may not have written that 'the latter (*B. rigidus*) had not been collected locally (in Australia)' (Burbidge 1966). As a consequence of these events, most taxonomists and weed researchers between 1966 and 1986 believed that *B. rigidus* did not exist in Australia until Williams (1986) updated his work on *Bromus* in the 'Flora of South Australia'.

B. diandrus has been differentiated from *B. rigidus* on morphologies of the spikelet branches and the abscission scar on the rachillae, and on somatic chromosome numbers (Hubbard 1968; Ovadiahu-Yavin 1969; Smith 1980; Williams 1957; 1986). Other methods potentially useful for identifying *B. diandrus* and *B. rigidus* are electrophoretic identification of allozyme-phenotypes (Kahler *et al.* 1981) and serological identification of seed proteins (Smith 1983).

We detailed seven characters (Table 2) useful for field identification of *B. diandrus* and *B. rigidus* (Kon and Blacklow 1988). In addition, we have distinguished two biotypes of *B. rigidus* that differ in awn length and time of flowering (Kon and Blacklow 1988). When mature, the drooping habit of *B. diandrus* contrasts with the erect habit of *B. rigidus*; the more erect habit of *B. rigidus* is due to the short, stiff spikelet branches (Fig. 2).

Consistent, microscopic characters for discriminating between the two species are the shapes of the lemma callus and abscission scar on the rachilla (Fig. 3). The abscission scar of *B. diandrus* is circular and its lemma callus is short (1 mm) and spherical with a rounded tip. The abscission scar of *B. rigidus* is elliptical and its lemma callus is elongated (> 1 mm) and compressed with a pointed tip (Fig. 3). Chromosome numbers of all the Australian materials of *B. diandrus* and *B. rigidus* were respectively $2n = 8x = 56$ and $2n = 6x = 42$ but counting chromosomes of polyploids was tedious and slow (Kon and

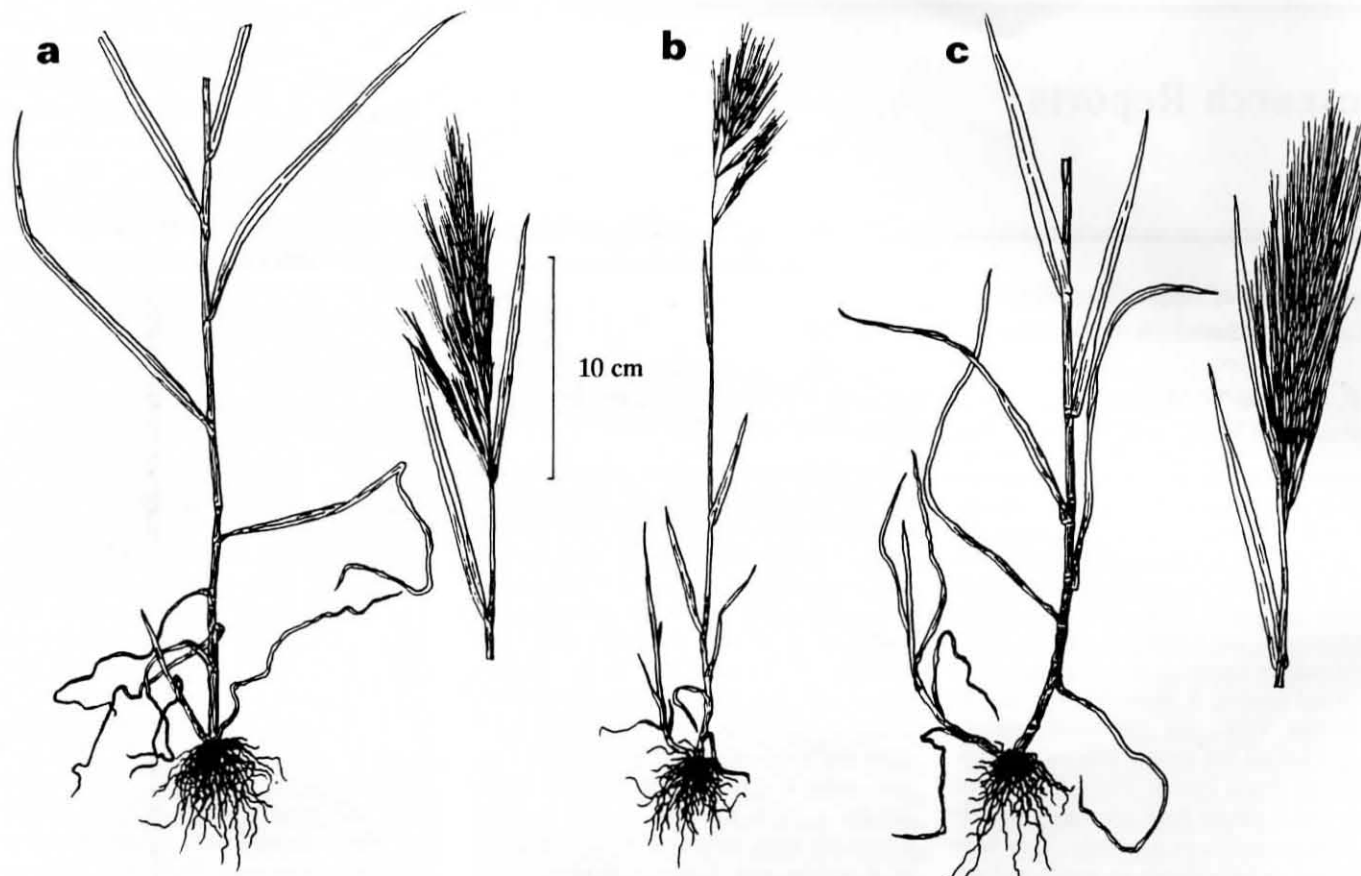


Figure 1. Mature plants of (a) *B. diandrus*; (b) *B. rigidus*, short-awned biotype and (c) *B. rigidus*, long-awned biotype. The number of culms per plant increases at low levels of inter- and intra-plant competition. The 'loose and nodding' form of the inflorescence of *B. diandrus* is not displayed by the herbarium specimen

Blacklow 1988). Furthermore, Ovadiahu-Yavin (1969) recorded an octoploid of a subspecies of *B. rigidus* in Palestine. Gill and Carstairs (1988) reported also on the chromosome numbers of *B. diandrus* and *B. rigidus* from the northern wheatbelt of Western Australia.

Descriptions

We support the descriptions for *B. diandrus* and the short-awned biotype of *B. rigidus* of Williams (1986) with the additions shown; the description for the long-awned biotype of *B. rigidus* is from our studies (Kon and Blacklow 1988; Kon and Blacklow, unpublished data):

B. diandrus : 'Strongly growing annual, 30-90 cm high (Fig. 1), with erect usually stout stems, hairy below the panicle; leaves to 10 mm wide, rough with some long hairs; sheath loose, with spreading hairs; ligule prominent, membranous; panicle usually loose and nodding, to 25 cm, with rough branches, some at least as long as the spikelet, in half whorls of three or four (Fig. 2), each bearing a single (rarely two) spikelet(s); spikelets to 35 mm, at first tightly enclosed by the glumes, becoming cuneate at maturity; lower glume one-nerved, 15-20 mm, linear-lanceolate, the upper three-nerved, 20-27 mm, lanceolate; lemma 25-28 mm, five-nerved, lanceolate, with a toothed apex 5-7 mm above the insertion of the awn;

callus scar (called the abscission scar by Kon and Blacklow 1988), where floret is detached from the rachilla, circular (Fig. 3); awn 35-55 mm long (Fig. 2), straight, scabrid and flattened' (Williams 1986). We would add to this description: lemma callus short, ≤ 1 mm, spherical with a rounded tip (Fig. 3); chromosome number, $2n = 56$ (Kon and Blacklow 1988).

Short-awned *B. rigidus* : 'Erect annual 15-55 cm high (Fig. 1); stem pubescent;

leaves with sparse hairs, c. 80 x 2-4 mm; sheaths with spreading or retrorse hairs; ligule prominent, torn; panicle 55-80 x 20-25 mm, erect; branches in half whorls of two to four, 4-14 (rarely 20 mm) long (Fig. 2), pubescent, rigid, erect, with one (sometimes two) spikelets; spikelets to 30 mm, often heavily pigmented with reddish to black; lower glume 14-16 mm, one- or weakly three-nerved, upper 20-27 mm, prominently three-nerved; lemma 20-32 mm, weakly five-

Table 2. Characters that enable identification of *B. diandrus* and the biotypes of *B. rigidus* (Kon and Blacklow 1988).

Character	<i>B. diandrus</i>	<i>B. rigidus</i> biotypes	
		short-awned	long-awned
Hairs of first leaf, adaxial surface ^A	long (0.4-0.8 mm), dense (100-750 cm ⁻²)	short (0.1-0.3 mm), sparse (100-350 cm ⁻²)	short (0-0.4 mm), sparse (0-250 cm ⁻²)
Panicle length	150-200 mm	90-150 mm	110-210 mm
Panicle form	loose and nodding	compact and erect	
Spikelet branches	longer than spikelets	shorter than spikelets	
Rachilla abscission scar	circular	elliptical	
Lemma callus	short (≤ 1 mm), spherical with rounded tip	elongated (> 1 mm), compressed with pointed tip	
Awn length	35-55 mm	29-38 mm	50-78 mm
Chromosome number	$2n = 56$	$2n = 42$	

^A Examination of specimens in the herbaria showed that hairiness of the leaves of later growth stages was too variable to be useful in discriminating between *B. diandrus* and *B. rigidus*.

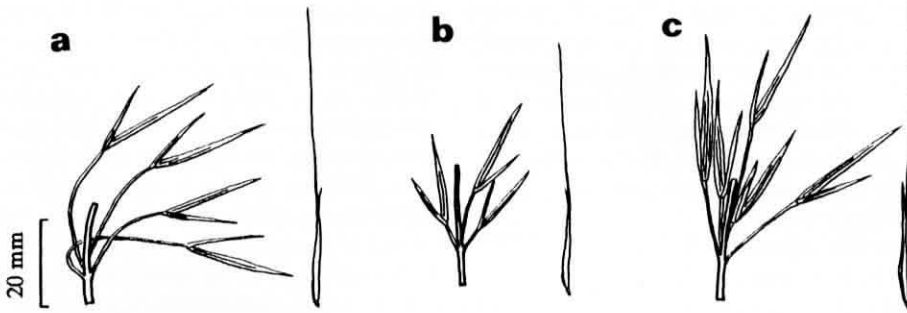


Figure 2. First whorls of spikelet branches of the inflorescences and detached seeds of (a) *B. diandrus*; (b) *B. rigidus*, short-awned biotype and (c) *B. rigidus*, long-awned biotype.

nerved, scabrous; awn inserted 2.5-5 mm below the two-fid apex of the lemma, 30-45 mm long (Fig. 3), flattened and scabrid towards the base' (Williams 1986). We would add to this description: abscission scar, elliptical; lemma callus elongated, > 1 mm, compressed with a pointed tip (Fig. 3); chromosome number, $2n = 42$ (Kon and Blacklow 1988).

Long-awned *B. rigidus*: Erect annual 50-90 cm high (Fig. 1); stem pubescent; leaves with dense hairs, c. 350 x 12-18 mm; sheaths with spreading or retrorse hairs; ligule prominent, membranous; panicle 110-205 x 30-60 mm, erect; branches in half whorls of four to seven, 5-40 (few greater than 20 mm) long (Fig. 2), pubescent, rigid, erect, with one (sometimes two or three) spikelets; spikelets to 35 mm, often heavily

pigmented with reddish to black; lower glume 15-22 mm, one- or weakly three-nerved, upper 25-34 mm, prominently three-nerved; lemma 22-32 mm, weakly five-nerved, scabrous; awn inserted 8-9 mm below the two-fid apex of the lemma, 50-78 mm long (Fig. 3), flattened and scabrid towards the base; abscission scar, elliptical; lemma callus elongated, > 1 mm, compressed with a pointed tip (Fig. 3); chromosome number, $2n = 42$ (Kon and Blacklow 1988).

Distribution

Origins and world distribution

The genus *Bromus* originated in Eurasia (Henrard 1941; Smith 1970; Stebbins 1981). *B. diandrus* is indigenous to the Mediterranean region, centred in Turkey, Cyprus,

Syria, Lebanon, Israel, Jordan, Egypt, Iraq and the Caucasus and Uzbekistan of Russian central Asia (Bor 1968; Ovadiahu-Yavin 1969). *B. rigidus*, also of a Mediterranean origin, is found mainly in the coastal areas of Turkey, Cyprus, Syria, Lebanon, Israel, Jordan, Egypt, Crete, Greece, the Aegean Islands, Caucasus, Turkestan and Caspian Sea (Ovadiahu-Yavin 1969).

From their origins, *B. diandrus* and *B. rigidus* spread into Mediterranean and temperate Europe, northern Africa and Britain (Maire and Weiller 1955; Smith 1980). Later, continental explorations, new settlements and agriculture spread these species into North America, South Africa and Australia (Hitchcock 1935; Chippindall 1955; Williams 1986). *B. diandrus* is also recorded in New Zealand, South Korea, Japan and Ussuri in eastern Russia (Lambrechtsen 1975; Hafliker and Scholz 1981; Tsvelev 1983).

The species are most common in areas with a Mediterranean climate, typified by mild, wet winters and hot, dry summers. Although the European distributions of both species overlap considerably, *B. rigidus* is restricted more to coastal regions than *B. diandrus* (Henrard 1941; Smith 1980).

Invasions into Australia

Mueller (1873) wrote that the *Bromus* spp. were introduced into Australia in 1847 but specimens or literature have not been located to support Mueller's observation

Table 3. Earliest records of *B. diandrus* and *B. rigidus* in the National Herbarium of New South Wales (NSW), National Herbarium of Victoria (MEL), Tasmanian Herbarium (HO), State Herbarium of South Australia (AD), Western Australian Herbarium (PERTH) and Mallee Research Station (MRS). Herbarium abbreviations as in Holmgren *et al.* (1981).

State	<i>B. diandrus</i>	<i>B. rigidus</i> (short-awned biotype)	<i>B. rigidus</i> (long-awned biotype)
NSW	1875 Riverina district (MEL)	1880 Jerilderie district (NSW)	1880 Jerilderie district (NSW)
VIC	1882 Alexandra (MEL)	1983 Mallee district (MRS)	
TAS	1876 Hobart (HO)		
SA	Pre-1900 Clarendon (AD)	1906 Norwood, Adelaide (NSW)	1974 Marion Bay (AD)
WA	1893 Darling Range (NSW)	1938 Swanbourne, Perth (PERTH)	1969 Bibra Lake, Perth (PERTH)
QLD	1916 Stradbroke Island (NSW)		
NT	1985 Alice Springs (NSW)	1979 Pridmore Bore (AD)	

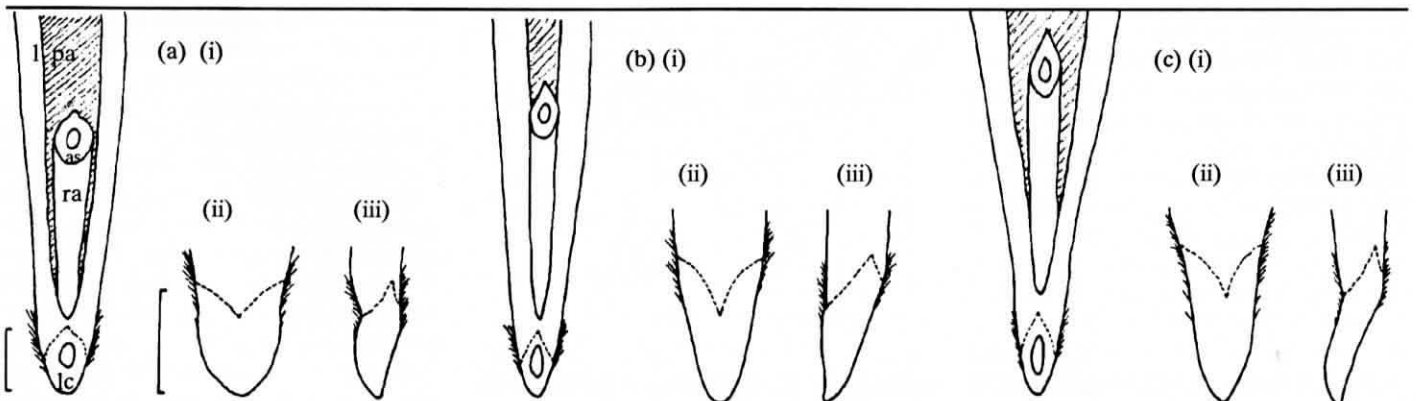


Figure 3. Abscission scars and lemma calluses of (a) *B. diandrus*; (b) *B. rigidus*, short-awned biotype and (c) *B. rigidus*, long-awned biotype (after Kon and Blacklow 1988). (i) ventral; (ii) dorsal; (iii) lateral views.

Symbols: lemma, l; palea, pa; rachilla, ra; abscission scar, as; lemma callus, lc. Measurement bars are 1 mm long.

Table 4. Diseases of *B. diandrus* and *B. rigidus*.

Pathogen/agent	Type ^A	Part attacked	Reference ^B
<i>Claviceps purpurea</i> (Fr.) Tul.	F	panicle	6
<i>Cochliobolus sativus</i> (Ito & Kurib.) Drech. ex Dast.	F	whole plant	6
<i>Erysiphe graminis</i> DC.	F	stem, leaf	6
<i>Gaeumannomyces graminis</i> (Sacc.) v. Arx & Oliv.	F	seedling, stem, leaf	1,2,10
<i>Leptosphaeria michotii</i> (West.) Sacc.	F	leaf	9
<i>Leptosphaeria nodorum</i> Müller	F	stem, leaf, glume	2
<i>Pleospora</i> spp.	F	leaf	9
<i>Puccinia bromoides</i> Guyot	F	stem, leaf	4
<i>Puccinia elimi</i> Westd.	F	stem, leaf	9,10
<i>Puccinia graminis</i> Pers.	F	stem, leaf	6
<i>Puccinia recon dita</i> Roberge ex Desm.	F	stem, leaf	5
<i>Pyrenophora bromi</i> (Died.) Drechsler	F	leaf, glume	6
<i>Pyrenophora teres</i> Drechsler	F	leaf, glume	2
<i>Rhizoctonia solani</i> Kühn	F	root, stem	2
<i>Tetraploa aristata</i> B. & Br.	F	leaf	9
<i>Tilletia caries</i> (DC.) Tul.	F	panicle	6,8
<i>Urocystis</i> spp.	F	leaf and glume	6
<i>Ustilago bullata</i> Berk.	F	panicle	6,7
<i>Heterodera avenae</i> Woll.	N	root	2
<i>Meloidogyne</i> spp.	N	root	3
Cereal yellow dwarf virus	V	whole plant	5
Lucern dwarf virus	V	whole plant	5

^A F, fungus; N, nematode; V, virus.

^B 1, Chambers (1971); 2, Cocks (1975); 3, Khair (1986); 4, Kon and Blacklow (1988); 5, MacFarlane (1968); 6, Morschel (1964); 7, Peeper (1984); 8, Richardson (1979); 9, Talbot (1964); 10, Williams (1957).

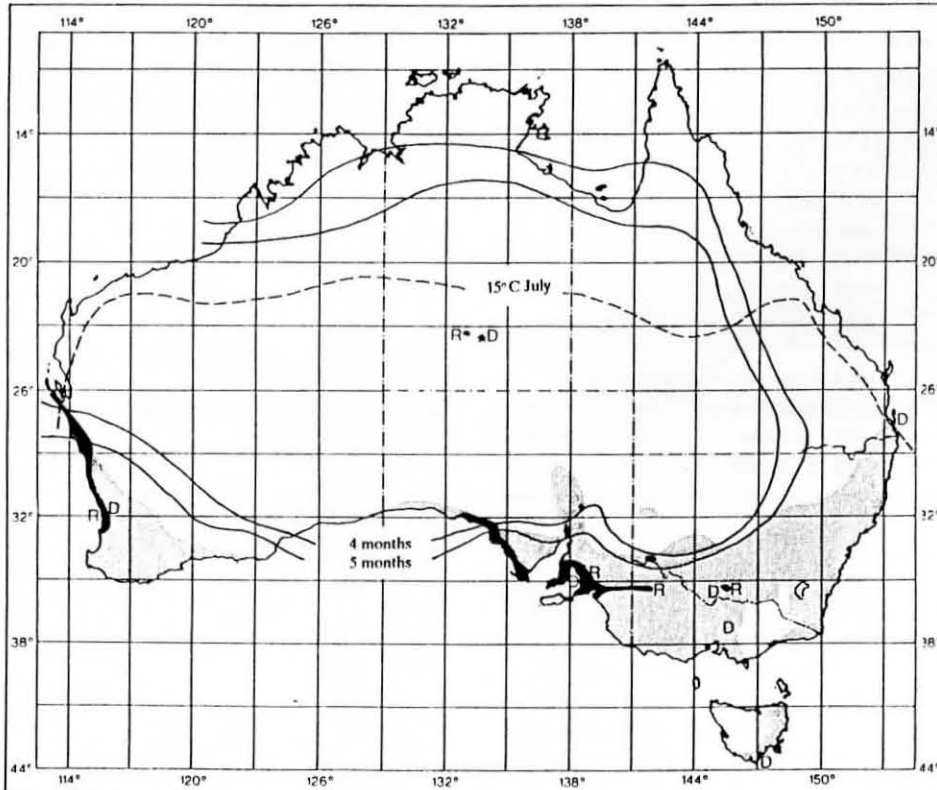


Figure 4. Estimated distribution of *B. diandrus* and *B. rigidus* based on herbaria specimens lodged between 1875 and 1988. Earliest records of *B. diandrus* (D) and of *B. rigidus* (R) as in Table 2. Symbols are *B. diandrus* (●); *B. rigidus* (●). Isohyetochrone (solid lines), 4 or 5 months growing season; isotherm (broken line), 15°C mean July temperature.

(Kloot 1983). Bentham's study (Bentham 1878) of the collections (*B. sterilis sensu auctorum non* according to Kloot (1983)) sent by Mueller from Parramatta, New South Wales; Yarra River, Victoria; Swanport, Ravenswood and King Island, Tasmania, indicated there were *Bromus* specimens before 1878 but they have been lost (Kloot 1983). Ewart (1930) wrote that the earliest record of *B. diandrus* (*B. villosus sensu auctorum non*) in Victoria came from the Yarra River in 1860. Our studies of specimens in the national herbaria showed that *B. diandrus* has been collected between 1875 and 1985 and *B. rigidus* between 1880 and 1983 (Table 3). Although the earliest herbarium records of *B. diandrus* and *B. rigidus* were 1875 and 1880, respectively (Table 3), *B. diandrus* and other awned *Bromus* spp. were widespread weeds by the mid 1800s (Francis 1859).

B. diandrus and *B. rigidus* were most likely introduced into Australia in ship ballasts and as contaminants of crop seeds, forages, wool or attachments to livestock (Kloot 1986a, b; 1987a). *B. diandrus* in England and *B. tectorum* in the United States were known to have been introduced via contaminated seed supplies (Salisbury 1964; Forcella 1985).

Mediterranean annuals spread across southern Australia with the alienation of new land for farming (Kloot 1985). The *Bromus* spp. were preadapted to the disturbed ground of annual crops and pastures that became the farming systems of this region. The *Bromus* spp. are aggressive and the time from introduction to naturalisation can be as short as one growing season (Kloot 1983). In South Australia, the rate of naturalisation of *Bromus* spp. between 1802 and 1965 was 0.06 species per year (Kloot 1987b).

Distribution in Australia

B. diandrus and *B. rigidus* are distributed between latitudes 23° and 44°S, in areas of greater than 250 mm of mean annual rainfall and at least four months of growing season with less than 15°C of mean July temperature (Fig. 4). These species become less dominant as rainfall decreases, being replaced by *B. madritensis* and *B. rubens* in drier areas (Rossiter 1966). *B. diandrus* is widespread across southern Australia from south-eastern Queensland to south-western Western Australia. The distribution of *B. rigidus* is, presently, more limited than *B. diandrus*. The short-awned biotype of *B. rigidus* is found mainly around the regions of Dirk Hartog Island, Geraldton, Streaky Bay to Fowlers Bay, Adelaide, Meningie and the Victorian Mallee. The long-awned biotype of *B. rigidus* is common from Lancelin to Mandurah, particularly around metropolitan Perth, while only two specimens have been recorded outside Western Australia; i.e. Jerilderie, New South Wales, in 1880 and

Marion Bay, Yorke Peninsula, South Australia, in 1974 (Table 3).

B. diandrus tolerates a wide range of climatic and edaphic conditions and grows on acidic or alkaline sandy to loamy soils, particularly those enriched with nitrogen and phosphorus (Tiver and Crocker 1951; Rositer 1966; Mock and Amor 1982). Our studies of herbarium specimens support observations that *B. diandrus* is found on many soil types but *B. rigidus* is more common on calcareous sandy soils (mapping units Bc1, Bc2 and Ca1 in Atlas of Australian Resources 1980), especially along coastal areas; this edaphic limitation may explain why the distribution of *B. rigidus* is more restricted and patchy than that of *B. diandrus* (Fig. 4). Both species have been collected from a diverse range of habitats including croplands, pastures, waste places, roadsides, hill tops, coastal sand dunes, national parks and reserves, and to 1500 m altitude. In Western Australia, the adaptation of *Bromus* spp. to sandy soils was attributed to their capacity to extract nitrogen from these deficient soils (Gladstone and Loneragan 1975) but it is likely to include also a number of attributes of their phenology.

The *Bromus* spp., particularly *B. diandrus*, have been serious weeds across southern Australia only recently (Mock and Amor 1982; Blacklow 1983; Anderson 1984; Gill and Blacklow 1984a; 1985; Harradine 1986; Cheam 1986; Gill and Carstairs 1988; Kon and Blacklow 1988). *B. diandrus* has proliferated because of increased frequencies of cereal crops sown with minimum cultivation but without effective herbicides for its selective control. Furthermore, competition with other weeds, including grasses, has decreased because they have been controlled by selective herbicides (Blacklow 1983). More generally, the modern, reduced tillering cereals sown at low densities in areas of low rainfall are open to invasion by weeds such as the *Bromus* species; they are quick to germinate at the break of the winter season from high densities of germinated seeds (Amor and de Jong 1983; Blacklow 1983).

Growth and Development

Seed dormancy and germination

Seeds (caryopses) of *B. diandrus* are innately dormant but after-ripening ensures high germinability by the usual time of opening winter rains (Anderson 1984; Gill and Blacklow 1984b; 1985; Cheam 1986; Harradine 1986; Gill and Carstairs 1988; Kon and Blacklow 1988). The loss of innate dormancy is under genetic control and ecotypes are adapted to the variable environments across southern Australia (Gill and Blacklow 1985).

Seeds of *B. diandrus* also exhibited enforced dormancy when exposed to high temperatures and low soil moisture, but there was little induced dormancy and high ger-

minabilities were restored when favourable conditions were renewed (Gill and Blacklow 1985; Cheam 1986; Harradine 1986). Low germination of seeds of *B. diandrus* on the soil surface was due to a lack of imbibition rather than dormancy imposed by light (Gill 1985; Cheam 1986). Ungerminated seeds of *B. diandrus* can remain viable in the field, especially in the surface soil layer, for two to three years (Cheam 1987; 1988). However, seed viability decreased with increased humidity during storage (Harradine 1986).

Some populations of *B. rigidus* also lost innate dormancy over the summer period (Gill and Carstairs 1988; Kon and Blacklow 1988). However, a short-awned population of *B. rigidus*, collected from East Chapman, W. A., had a 30% residual, innate dormancy after April (Kon and Blacklow 1988). Gill and Blacklow (1985) also reported residual dormancy in another accession of short-awned *B. rigidus* (*B. diandrus sensu auctorum non*) from Geraldton, W. A.. Residual dormancy in this accession of *B. rigidus* was broken on removal of the palea and lemma from the caryopsis and by gibberillic acid. These results indicate that innate dormancy is more variable between populations of *B. rigidus* than those of *B. diandrus*.

Establishment

Bromus spp. can establish as cohorts due to protracted germination and because emergence can be from variable depths of seed burial. The establishment of *B. diandrus* was more rapid and uniform when the seed was under a wheat stubble than on the surface of bare soil; seedling establishment was higher if the seed was mixed with the soil by shallow cultivation (Cheam 1986). The establishment of *B. tectorum* was improved by more favourable moistures and temperatures from vegetative cover, stubble retention, seed burial and soil aggregation (Evans and Young 1984). Staggered germination and establishment may be limited but important in species survival of seasonal false breaks and in thwarting control attempts.

Growth

The growth of the *Bromus* spp. is typical of annual grasses. A succession of tillers may be produced in the axils of leaves if plant densities are low, winter temperatures are low, and nutrient supply is high. The tillers of *B. diandrus* are strongly appressed to the soil surface until culm elongation in the spring; the vegetative growth of *B. rigidus* is more erect. The prostrate vegetative habit of *B. diandrus* is typical of winter types and it responds to vernalization (Gill and Blacklow 1985). The rate of tillering of *B. diandrus* was slower than that of wheat (Gill 1985) but at low densities, *B. diandrus* and *B. rigidus* produced more than 50 tillers per plant (Kon and Blacklow 1988). The root systems of *Bromus* spp. are fibrous and concentrated in

the top 15 cm of the soil profile (Rughkla 1987; Supasilapa 1988).

Flowering

Apical meristems of the shoots of *B. diandrus* and *B. rigidus* (Geraldton accession of *B. diandrus sensu auctorum non*) changed to the reproductive stage (double ridge) when they had four to six leaves (Wilkerson 1986). Generally, populations of *B. diandrus* flowered later than those of *B. rigidus* (Williams 1957; Kon and Blacklow 1988) except in the Victorian Mallee (*B. diandrus sensu auctorum non*) (Velthuis and Corbett 1984). There was variability also in time to flowering between populations of both species (Gill and Blacklow 1985; Kon and Blacklow 1988). This variability in *B. diandrus* was significantly correlated with the lengths of growing seasons to which the ecotypes had become adapted. Variabilities in times to panicle emergence between seasons were due to temperature differences; the heat-sum for germination to panicle emergence in the short-awned *B. rigidus* was 1450°C days (Kon and Blacklow 1988). Heritable variabilities of panicle emergence and anthesis within populations of both species was between 29 and 34% and would enable adaptations to new or changing environments (Kon and Blacklow 1988).

Vernalisation of imbibed seeds decreased the time to flowering (Gill and Blacklow 1985), due to earlier floral initiation and shorter periods of development of floral structures (Wilkerson 1986). *B. diandrus* requires long photoperiods for flowering and is classified as a long-day plant (Ashby and Hellmers 1959). However, a period of short days without vernalization followed by exposure to long days promoted flowering in several annual *Bromus* spp. (Finnerty and Klingman 1962). These requirements for flowering, and hence production of seeds, of low temperatures and/or short photoperiods followed by long photoperiods are likely to be the main reasons for the southern distribution of *B. diandrus* and *B. rigidus* in Australia (Fig. 4).

Seed production and dispersal

Although *B. diandrus* flowered earlier than *B. rigidus*, the period between anthesis and seed shedding was 26 days for three populations of each species (Kon and Blacklow 1988). The numbers of seeds per plant of both species were very variable between and within populations and, per plant, ranged from 660 to 3380 seeds of *B. diandrus* and 1160 to 2910 of *B. rigidus*; a large proportion of this variability was due to the phenotypic plasticity of tillers per plant. There were large variabilities also in seed weights between populations but seeds with awns attached of the short-awned and long-awned *B. rigidus* were heavier (13 to 15 mg) than seeds of *B. diandrus* (10 to 13 mg) (Kon and Blacklow 1988).

Seeds of *Bromus* spp. are dispersed by wind while part of the detached culm, and as a light, awned seed when it abscises at the rachilla node (Fig. 3). The persistent, scabrid awn attaches the seed to animals, clothes and machines and, as such, can be transported over long distances. The seed can be difficult to clean from crop and pasture seeds (Mock and Amor 1982; Mock 1987) and can be transported as a seed impurity.

Population Dynamics

Across southern Australia, *B. diandrus* and *B. rigidus* germinate, grow and produce seeds during the winter, spring and early summer and, as dormant seeds, a high proportion (Cheam 1988) survive the hot, dry summers. By the end of the summer following their production, dormancy has dissipated and most seeds germinate with the opening winter rains (Gill and Blacklow 1985). Some seeds may not germinate during the wet seasons because of persistent dormancy (Kon and Blacklow 1988) or, although germinable, failure to imbibe if exposed on the soil surface (Gill and Blacklow 1985). However, viability is lost within a year, or two at the most, if exposed to a humid environment (Harradine 1986). Within this seasonal pattern of activity and dormancy, the densities of plants can vary greatly but the plasticity of culms per plant ensures a high level of seed production even at low plant densities. The objectives for management of these weed species, therefore, is to achieve a high level of seedling deaths over successive years and thus exhaust the residues of seed in the soil.

Genetics

B. diandrus and *B. rigidus* are, respectively, an octaploid ($2n = 8x = 56$) and a hexaploid ($2n = 6x = 42$) (Ovadiahu-Yavin 1969; Smith 1980). Knowles (1944) observed that *B. diandrus* (*B. rigidus sensu auctorum non*) formed 28 ring bivalents at meiosis and, thus, it is likely to be an allopolyploid or segmental allopolyploid of a hybrid of unknown parents with simple disomic inheritance.

B. diandrus and *B. rigidus* are self-compatible hermaphrodites with anthers close to feathery stigmas (Beddows 1931). The lengths of the anthers of *B. diandrus* and *B. rigidus* are 1 to 7 mm and 1 mm or less respectively (Beddows 1931; Smith 1980), and produce small numbers of pollen grains (Smith 1981). Florets are usually cleistogamous but, occasionally, the anthers are exerted from chasmogamous florets to enable occasional outcrossing. Our studies have shown that outcrossing in *B. diandrus* was less than 1% (Kon and Blacklow, unpublished data). Outcrossing in *B. mollis* was 2 to 14% and *B. rubens* showed no outcrossing (Jain *et al.* 1970; Brown *et al.* 1974; Jain 1975). As polyploid annuals with mixed-pollinating systems, *B. diandrus* and *B. rigidus*

can be genetically variable and flexible in their adaptations to changing environments (Young and Evans 1976).

Economic Importance

Benefits

Bromus species are palatable in the vegetative phase and their rapid, early growth from high seed densities provide early season forage (Whittet 1964; McIvor and Smith 1973; Aligianis 1977). The persistent fibrous root system and unpalatable mature shoots can protect the sandy soils, on which they dominate, from wind erosion.

Losses

Bromus spp. are regarded as contaminants of grain, hosts of cereal diseases, and serious weeds of pastures and crops. Dockage of crop seeds due to seeds of *B. diandrus* has increased in Victoria from 5% of the samples inspected in 1977/1978 to 26% in 1985/1986 (Mock and Amor 1982; Mock 1987). In some cases, 30 seeds of *B. diandrus* were found in 100 g samples of barley seeds.

B. diandrus and *B. rigidus*, like other annual weeds, are hosts to a range of pathogenic fungi, viruses and nematodes (Table 4). The cereal diseases that *B. diandrus* is known to co-host include: ergot (*Claviceps purpurea* (Fr.) Tul.); foot rot (*Cochliobolus sativus* (Ito & Kurib.) Drech. ex Dast.); powdery mildew (*Erysiphe graminis* DC.); take-all (*Gaeumannomyces graminis* (Sacc.) v. Arx & Oliv.); septoria glume blotch (*Leptosphaeria nodorum* Müller); black stem rust (*Puccinia graminis* Pers.); brown rust (*Puccinia recondita* Roberge ex Desm.); barley net blotch (*Pyrenophora teres* Drechsler); sharp eyespot (*Rhizoctonia solani* Kühn); bunt (*Tilletia caries* (DC.) Tul.); cereal yellow dwarf virus; cereal cyst nematode (*Heterodera avenae* Woll.); and root-knot nematode (*Melodogyne* spp.). It is likely that *B. rigidus* is a co-host to these diseases also but there may be differences (Morschel 1964; MacFarlane 1968; Chambers 1971; Cocks 1975; Richardson 1979; Khair 1986).

In pastures, the seeds of *B. diandrus* and *B. rigidus* reduce animal productivity by penetrating the soft tissues of eyes, mouths, feet and intestines (Whittet 1964; Bor 1968; Cocks 1975; Aligianis 1977). The seeds damage hides and meat, and are a vegetable fault in wool (Cocks 1975; Aligianis 1977).

B. diandrus and *B. rigidus* compete with crops and pastures for nutrients and water. When sown with wheat at 200 plants m^{-2} , the absorption of nitrogen and phosphorus by *B. diandrus* increased linearly with densities from 100 to 400 plants m^{-2} and caused equivalent losses in absorption by wheat. This competition for nutrients was measured 72 days after seeding and was translated into losses in grain yield. There was evidence from this experiment of competition for wa-

ter during the grain filling phase of wheat (Gill and Blacklow 1984a). *B. diandrus* and wild oats (*Avena* spp.) were the most competitive grass weeds in wheat (Poole and Gill 1987). In Western Australia, wheat yields decreased exponentially with increasing densities of *B. diandrus* and at 100 plants m^{-2} , wheat yield was reduced by 30% (Gill *et al.* 1987). *B. diandrus* competes also with lupins for phosphorus and nitrogen particularly in the early stages of crop growth (Rughla 1987; Supasilapa 1988). The competitive nature of *B. rigidus* has yet to be studied in Australia but is likely to be similar to *B. diandrus*, early competition for nutrients proportional to weed densities. Absorption of nutrients and water during the unpalatable phases of the *Bromus* spp. would not contribute to productivity of the prevailing pasture.

Legislation

B. diandrus and *B. rigidus* are not declared as noxious plants for any part of Australia. In the genus *Bromus*, only *B. commutatus* Schrad. is listed as prohibited from entry into Australia under the federal Quarantine Act 1908 (Groves 1986).

Weed Management

Cultural control

The *Bromus* spp. are weeds of crops and pastures. Options for their cultural control in rotations of crop and pastures include cultivation, fire, grazing, mowing and slashing. In practice, cultural methods may be combined with chemical methods.

Shallow cultivations that expose the roots of *Bromus* seedlings to desiccation are effective in killing them. An established system of cultivation known as 'working-up and working-back' is practised to control a wide spectrum of grass and broad-leaved, annual weeds in the crop-pasture rotations of southern Australia. The first cultivation aims to kill the initial flush of weed seedlings that establish after the opening winter rains. A second cultivation is directed at survivors and a second flush of germination promoted by seed-burial with the first cultivation. This system of cultivation control, and its variations, is being replaced by minimum cultivation, enabled by pre- and post-sowing herbicides, which permits earlier crop establishment with less soil compaction and erosion and more reliable weed control.

The seed of *Bromus* spp. can be burnt or damaged by fire. Crop stubbles and pasture residues are burnt in late autumn to minimise the loss of standing, dry summer feed, and the time that bare soil is exposed to erosion before winter revegetation. Fire destroys some other weed seeds, pests and diseases but it depletes seeds of some desirable species, and organic matter and some nutrients. Furthermore, even superficially buried

seeds can escape a damaging heat if the fire moves quickly through the sparse residues left at the end of summer grazing; for this reason fire is followed usually by other cultural and chemical methods to increase the level of weed control.

The *Bromus* spp. are palatable in the vegetative phases of their growth and, potentially, could be controlled by grazing (Rossiter and Pack 1956). However, high rates of stocking are required to prevent seed production and pasture species suffer also under such stocking intensities; overgrazing may cause an increase in weeds, including *Bromus* spp. (Carter and Day 1970). Furthermore, the bare, disturbed soil is exposed to erosion.

Production of seed by the *Bromus* spp. can be reduced by mowing, or slashing, before viable seed is produced. This method is effective in preventing seed production of other weedy species also but, in practice, it is difficult to choose a single time that will sever all the culms of all unwanted species. Furthermore, the high ratios of growth in the spring of desired pasture species is truncated by this non-selective defoliation. However, mown or slashed material may be conserved as silage or hay.

Herbicides

Broad spectrum, non-residual herbicides are used as alternatives to cultivation for weed control, including *Bromus* spp., prior to seeding of crops. Herbicides used in these situations (Anderson and Henderson 1984; Bowran *et al.* 1988) include the non-translocated bipyrindiles (paraquat and diquat) and the translocated herbicides glyphosate and glufosinate-ammonium; seedlings establishing from later germinations are not killed by these non-residual herbicides and escapees may compete with the crop and replenish the pool of seed residues. Data of Cheam (1988) for Geraldton, Western Australia, suggested that 50 plants m^{-2} of *B. diandrus* escaped from a paraquat and diquat treatment prior to seeding wheat, and these escapees added about 5000 seeds m^{-2} to the seed pool; 50% of the seed survived the summer months to ensure a weed problem the following year.

There are no effective and reliable herbicides for the selective control of *Bromus* spp. in wheat. Large areas of wheat in southern Australia are treated with pre- and post-emergence applications of chlorsulfuron for a control of a broad spectrum of weeds. Campion (1982) claimed useful suppression of *Bromus* spp. with chlorsulfuron but results are variable and survivors set sufficient seeds (Kon and Blacklow, unpublished data) to create a potential problem for the next stage in the rotation. Ethyl-metribuzin controlled 90 to 100% of *B. secalinus*, *B. tectorum* and *B. catharticus* in winter wheat (Ratliff and Peeper 1987). If the past is any indication, we can expect herbicides for the selective control of *Bromus* spp. in wheat to

be discovered and then we will need to move on to other weeds that will be adaptable to the changed environment (Blacklow 1983).

A broad spectrum of weeds including the *Bromus* spp. can be selectively controlled in lupins (*Lupinus angustifolius* L.) with simazine. Consequently, lupins can be a cleaning crop for the *Bromus* spp. in the crop-pasture rotations of southern Australia. Simazine is applied prior to seeding the lupins and additional simazine may be applied if residual activity from the initial application is inadequate. Atrazine may be added to the simazine for improved weed control but with some loss in the margin of selectivity. A mixture of paraquat and diquat may be applied simultaneously with the triazines after weed emergence but prior to seeding the crop (Allen 1977; Gilbey 1984a; Bowran *et al.* 1988). Post-emergence herbicides are available also for the control of grass weeds in lupins, including the *Bromus* species; these include fluzifop-butyl, haloxyfop-methyl and quizalofop-ethyl (Seth and Fua 1984; Gilbey 1984b; Davis 1987; Wall and Phimister 1987). Cheam (1988) showed it was possible to reduce the seed density of *B. diandrus* to about 150 m^{-2} at the end of a lupin crop by a herbicide mixture of paraquat, diquat and simazine applied seven days after the opening winter rains, and fluzifop-butyl when *B. diandrus* had 3 to 5 leaves. An admittedly expensive option but, with an assumed 50% survival of seeds over the summer, the densities of *B. diandrus* would be below the economic thresholds for a following wheat crop (Poole and Gill 1987).

Herbicides can replace cultural methods to prevent *Bromus* spp. from producing seed in pastures and, hence, diminish the weed problem in the pasture as well as crops that follow in the rotation. The benefits of non-selective herbicides, such as paraquat, diquat and glyphosate, used to prevent seed production are set against the losses in pasture production in the year of application (Barret *et al.* 1973; Stephensen 1984; Blowes *et al.* 1984; Harradine 1986; Cheam *et al.* 1987), and in the following years because of decreased seeds of pasture species for regeneration (Dear and England 1987). Selective control of grasses in pastures is possible with fluzifop-butyl (Holmes 1984). Selective, or not, available herbicides have little residual activity and, as with cultural prevention of seed production, it is difficult to prevent seed production from species that establish and produce seed over extended periods.

B. tectorum has developed resistance to several triazines (Bandeem *et al.* 1982) but there are no reports of herbicide resistance in *B. diandrus* and *B. rigidus*. However, accessions of *B. diandrus* from Western Australia varied in their response to chlorsulfuron (Gill and Blacklow 1984b). Furthermore, there were heritable variabilities within *B. diandrus* of sensitivities to chlorsulfuron and simazine which would allow shifts within

populations towards tolerance (Kon and Blacklow 1987).

Natural enemies

Pathogenic fungi, viruses and nematodes attack *B. diandrus* and *B. rigidus* (Table 4), although the records may be inaccurate because of difficulties with identification of *Bromus* species. Many of these natural enemies attack cereals also and, thus, are unsuitable as potential biological control agents. However, potential mycoherbicides are *Puccinia bromoides* Guyot and *Ustilago bullata* Berk., particularly the latter, which infects the entire inflorescence, has a narrow host range and is easily cultured (Mordue and Waller 1981).

B. rigidus was more resistant than *B. diandrus* to *Puccinia elymi* Westd. (Williams 1957), *P. bromoides* (Kon and Blacklow 1988) and *U. bullata* (Kon and Blacklow, unpublished data) but inoculations with other races of the fungi are necessary to establish the generality of these observations. *B. rigidus* was resistant to races of *Puccinia coronata* var. *coronata* Cda., *E. graminis*, *C. purpurea* and *P. recondita* (Braverman 1986). Later maturing ecotypes of *B. diandrus* were more highly infected with *P. bromoides* (Kon and Blacklow 1988).

Integrated pest management

Cultural, chemical and biological methods can be integrated to manage a range of pests and disease with minimal use of pesticides for long-term productivity and health of the environment (Wicks 1984). Weeds that have no simple chemical method for their control, such as the *Bromus* spp., have required an integrated approach to their management. Furthermore, these species are alternative hosts of diseases of cereal crops and, therefore, require an integrated approach to pest management; critical levels and periods of reductions required to avoid competition with crops and pastures for nutrients and water may not coincide with those required for disease management. Levels of reduction may appear cosmetic in the short-term but necessary for long-term rotations required for stable and profitable farm production. Integrated approaches to the management of the *Bromus* spp. should continue even if effective herbicides are developed for their control in paddocks where they are observed to be a nuisance.

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identified *Puccinia bromoides* and R. Shivas identified *Ustilago bullata*.

Those seeking specific recommendations for weed management should consult local authorities.

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Errata

In the paper by Kon and Blacklow Vol 4(2) 51-60 the species name *Bromus rigidus* was misspelt in the title.

The editor apologises for these errors.