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# Biology, ecology and management of *Diuraphis noxia* (Hemiptera: Aphididae) in Australia

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**Running title:** Review of *Diuraphis noxia* in Australia

## Abstract

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko ex Kurdjumov) is one of the world's most economically important pests of grain crops and has been recorded from at least 140 grass species within Poaceae. It has rapidly dispersed from its native origin of Central Asia into most major grain producing regions of the world including Africa, Asia, Europe, the Middle East, North America and South America. *Diuraphis noxia* was first found in Australia in a wheat crop in the mid-north of South Australia in May 2016. Since then, *D. noxia* has been recorded throughout grain growing regions of South Australia, Victoria, New South Wales and Tasmania. The distribution will continue to expand, with climatic suitability modelling suggesting *D. noxia* can persist in all key grain regions, including large parts of Western Australia and Queensland. Australian populations of *D. noxia* appear to be anholocyclic, with no sexual stages being observed. The aphids can reproduce year-round as long as host plants are available. Australian farmers have generally adopted prophylactic insecticide seed treatments and/or foliar sprays to manage *D. noxia*. Research is required to fully understand yield impacts, host preferences, and host plant resistance associated with *D. noxia*. Cultural control through managing alternate host plants over summer, agronomic crop management, biological control and developments in host plant resistance should provide considerable future benefits.

*Keywords: Russian wheat aphid, exotic pest, invasion, management, review*

## Introduction

Following outbreaks of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko ex Kurdjumov) (Hemiptera: Aphididae), in South Africa in 1978, Mexico in 1980 and the USA in 1986, the Australian grains industry became concerned about the potential arrival of this pest into Australia. The Wheat Research Council commissioned the Commonwealth Scientific and Industrial Research Organisation (CSIRO) to develop a National management plan as a response to the threat (Evans *et al.* 1989). CSIRO compiled a detailed literature review of existing information (Hughes 1988; Hughes 1996) and conducted preliminary research, including modelling likely areas of establishment within Australia (Hughes & Maywald 1990). Early models predicted the Australian climate was highly suitable for *D. noxia*, even more so than the USA and South Africa where populations were known to grow rapidly. Links with overseas institutions were established to examine the susceptibility of Australian cultivars to *D. noxia* (Wellings *et al.* 1993). Potential parasitoids of *D. noxia* were studied for importation to be established on alternative aphid species in cereal production areas as a pre-emptive strategy (Aeschlimann & Hughes 1992; Hughes *et al.* 1994). In 1987, CSIRO stated *D. noxia* is “certain to arrive in Australia”, likely through wind dispersal or cargo and passenger travel from the USA (Dobbyn 1987). The impact on Australian cereals, if it established, was predicted to be significant (Hughes & Maywald 1990).

In 2016, these early predictions proved correct, with *D. noxia* discovered infesting a wheat (*Triticum aestivum*) paddock in South Australia (Yazdani *et al.* 2017). Since that time considerable local data has been acquired. Here, we review the current knowledge of *D. noxia* in Australia and throughout the world. We examine the aphid’s biology, ecology and feeding behavior. We place particular focus on control options being employed by Australian farmers and use this information to suggest future research directions.

## Description

Originally named *Brachycolus noxius*, the Russian wheat aphid (now known as *D. noxia*) was first recognised as a separate species by Mordvilko in a paper by Kurdjumov (1913). Detailed descriptions of *D. noxia* have been provided by Blackman & Eastop (1984) and Stoetzel (1987). In brief, *D. noxia* has an elongated, spindle-shaped body, with the tips of the legs and distal third of the (distinctively short) antennae black. The wings and thorax of alates are also dark in colour (Nematollahi 2017). Distinctive features include: (i) six-segmented antennae measuring half the length of the body, (ii) pale, inconspicuous, and truncated (50-60μm long) cornicles, (iii) elongate cauda, and (iv) a supracaudal process on the 8th abdominal tergite, that has the appearance of a second cauda (Stoetzel 1987). This supracaudal process is almost equal in length to the cauda on apterae but is smaller and less conspicuous in alates and nymphs. The four instars (or nymph stages) of *D. noxia* have been described in detail (Aalbersberg *et al.* 1987b; Blackman & Eastop 1984; Olsen *et al.* 1993).

### *Global distribution*

First described in Russia on barley (*Hordeum vulgare*) (Grossheim 1914), *D. noxia* acquired the name 'Russian' wheat aphid (Walters *et al.* 1982). *Diuraphis noxia* is endemic to central Asia, Russia, Iran, Afghanistan and countries bordering the Mediterranean Sea (Dolatti *et al.* 2005; Durr 1983; Hewitt *et al.* 1984), gaining recognition as a global cereal pest when, in the 1970s, it began to rapidly spread to several continents over a □15-year period (Halbert & Stoetzel 1998; Kovalev *et al.* 1991; Smith *et al.* 2004; Stary 1999a; Zhang *et al.* 2014). It has since extended its range throughout Africa, Asia, Europe, the Middle East, South America, the USA (Clua *et al.* 2004; Souza 1998; Stary 1996; Walters *et al.* 1982; Zhang *et al.* 2001) and in 2016, was first reported in Australia (Table 1).

The success of these invasions has likely been influenced by the large number of compatible host plants, the high degree of phenotypic plasticity of *D. noxia*, and its capability of rapid population growth achieved through parthenogenetic reproduction (Burd *et al.* 2006; Clua *et al.* 2004; Shufran & Payton 2009). Zhang *et al.* (2014) provided evidence to suggest the colonisation of South Africa and the New World arose from a single, accidental introduction of *D. noxia*. The mode of entry into Australia has not been ascertained, although human-mediated movement seems most likely given the large geographic distance to the nearest known country with *D. noxia,* and the huge volume of trade with many potential 'source countries' (United Nations 2008).

### *Australian distribution*

In May 2016, *D. noxia* was identified in a wheat crop in South Australia. In less than 12 months, it had been reported at locations across South Australia, Victoria, parts of southern New South Wales and Tasmania (Yazdani *et al.* 2018). Since that time, field surveillance has continued across the country, with the distribution continuing to expand, particularly in a northerly direction in New South Wales. *D. noxia* is known to cover a geographic area of at least 490,000 $km^2$ (Fig. 1), although monitoring efforts in some regions have been sporadic, so, it is likely *D. noxia* is even more widespread than this. Avila *et al*. (2019) recently improved the precision of the CLIMEX model created by Hughes & Maywald (1990), using distribution data of *D. noxia* in countries outside the original model's scope. Their findings suggest that, within Australia, the distribution of *D. noxia* could become much more widespread than previously predicted (Fig. 1), with natural dispersion likely to render quarantine conditions inadequate in most areas.

There are several factors that may act to constrain the movement of *D. noxia*. This includes: (i) the geographic isolation from regions where *D. noxia* is not yet present (particularly Western Australia), (ii) the different agro-ecological characteristics of the three grain production regions in Australia (Northern, Southern, and Western regions), and (iii) the preference of *D. noxia* to areas of low and medium annual rainfall (Chemeda 2015). In the short time *D. noxia* has been present in Australia, populations have been observed to decline considerably after heavy rainfall, suggesting humidity and/or precipitation reduce survival and reproduction of this pest, either directly or indirectly (van Helden & Heddle, unpub. data). Findings by Mulatu *et al.* (2011), which indicate *D. noxia* populations increase with periods of moisture stress support these early field observations.

## Development and reproduction

*Diuraphis noxia* live for 60-80 days, producing up to 80 offspring at an average temperature of 20°C (Ma & Bechinski 2009; Merrill *et al.* 2009). At this temperature, pre-imaginal growth typically takes around eight days (Aalbersberg *et al.* 1987a). After their fourth moult, aphids develop into either wingless (apterous) or winged (alate) adults, with alates possessing a higher reproductive capacity than apterae, producing 4-5 nymphs per day for a 3-4 week period (Chemeda 2015). As with most aphid species, *D. noxia* populations are made up of mainly apterous individuals, with wing formation occurring when host plant quality declines, however, crowding appears to have little effect (Baugh & Phillips 1991).

Within Australia, *D. noxia* has only been observed reproducing asexually, with no evidence of males, sexual females or eggs. All reproduction is presumed to be anholocyclic, with females producing live young parthenogenetically. Although some induction of oviparae has been observed in the USA (Puterka *et al.* 2012), similarly, no successful sexual reproduction has been reported. Asexual reproduction of *D. noxia* within Australia has been observed year round, but only when suitable host plants are available and the climatic conditions (particularly during the summer months) are not lethal (van Helden, unpub. data).

## Ecology

### *Host plants*

*D. noxia* feeds on numerous members of the Poaceae (grasses) (Hughes & Maywald 1990; Hughes 1996), and the first reported infestation in South Australia appears to have started on volunteer wheat (Yazdani *et al.* 2018). Large numbers of aphids were also supported on wild *Hordeum* species, such as *leporinum, glaucum, murinum* as an early germinating summer/autumn host. This is consistent with overseas observations that *H. murinum* can be an important host, carrying aphid populations post-harvest (Elmali 1998). To date, the plant hosts on which the majority of *D. noxia* have been found in Australia are wheat, barley and durum wheat (*Triticum turgidum*), consistent with findings from elsewhere around the world (Elmali 1998; Girma *et al.* 1993; Robinson 1994; Webster *et al.* 1993).

A number of other cereal crops can act as secondary hosts for *D. noxia*, including oat (*Avena sativa*), rye (*Secale cereale),* rice (*Oryza sativa),* sorghum (*Sorghum bicolor*) and corn (*Zea mays*) (Harvey & Kofoid 1993; Kindler & Springer 1989; Stoetzel 1987; Webster *et al.* 1987; Yazdani *et al.* 2018). On these crops, final instar and adult aphids are able to feed, however it is unclear if other instars can feed, or whether aphids can successfully reproduce. Rice, sorghum and corn seem particularly poor hosts, but may support small numbers of aphids, particularly at the seedling stage (Harvey & Kofoid 1993; Kindler & Springer 1989; Stoetzel 1987; Webster *et al.* 1987). Furthermore, low numbers of *D. noxia* can survive on many grasses (Table 2), but larger colonies only develop on a limited number of species. Barley grass and *Bromus* species (both common in Australia) are capable of sustaining *D. noxia* colonisation (Yazdani *et al.* 2018), indicating these are important host plants in Australian grain systems. Sampling of *D. noxia* on grasses within Australia, as well as laboratory testing of potential Australian grass hosts is ongoing.

### *Dispersal*

Aphids move by walking among leaves, tillers, and from plant to plant, or disperse over longer distances via the flight of alates. Aerial dispersal of alates is governed by wind, however particular environmental conditions are required for both short- and long- distance dispersal, and can result in high mortality (Parry 2013). *D. noxia* tend to limit their long-distance dispersal, remaining on a plant as long as the host quality is acceptable, often building up to high population densities. Within crops, limited movement from tiller to tiller occurs, often resulting in isolated tillers with damage symptoms on a plant. Later in the season, as the crop growth stage progresses, aphid population densities increase, prior to ripening (Umina *et al.* 2017). In turn, aphids migrate in search of alternate summer hosts before the crop becomes too poor for aphid infestation and feeding (Hewitt *et al.* 1984). Populations survive over summer on volunteer plant hosts, where they will subsequently migrate onto cereal hosts in autumn.

Suction trap data from Australia indicates *D. noxia* flights occur when temperatures exceed 20°C, limiting winter dispersal in most cropping regions (van Helden, unpub. data). Alates will still form outside of these conditions, although the potential for short distance dispersal (i.e. from paddock to neighbouring paddock) via alates, is largely unknown. Knowledge of *D. noxia* dispersal is limited in Australia, although data from a suction trap located in Kapunda (South Australia) shows a distinct migration period between September and November, during which time winter active grasses and crops are ripening. Small numbers of *D. noxia* may also migrate between February and April, shortly preceding the winter cereal sowing period (Fig. 2).

### *Environmental factors influencing ecology*

Australia's main cereal cropping regions are characterised by warmer, drier climates which provide a suitable condition for *D. noxia* to thrive. As for all aphids, temperature is the main factor influencing *D. noxia* development. Though *D. noxia* will survive very low temperatures (Butts 1992; Butts & Schaalje 1997; Harvey & Martin 1988), the optimal temperature range is between 10°C and 25°C (Ma & Bechinski 2009). Although supercooling points range from -26.8°C for 1st instars to -24.9°C for adults, most winter mortality occurs at temperatures much higher than these (Butts 1992). In Australia, temperatures never drop to these supercooling points, and therefore *D. noxia* populations do not need to re-establish after overwintering periods.

Rainfall events can cause mortality by washing aphids off plants (Hughes 1963; Maelzer 1977), however unlike many other aphid species, *D. noxia* are often protected inside leaf whorls and thus remain largely unaffected. Nevertheless, rainfall can still affect the dispersal success of *D. noxia*. High humidity appears to have a negative effect on *D. noxia*, possibly due to the occurrence of entomopathogenic fungi, for which soft-bodied insects like aphids are particularly vulnerable (Shah & Pell 2003). Frost events, which are common in cereal cropping areas in Australia, cause aphid mortality, particularly in anholocyclic populations (Havelka *et al.* 2013). Given this is the reproductive strategy exclusively found in Australia (Yazdani *et al.* 2018), frost is likely to be a key contributing factor influencing *D. noxia* population dynamics.

## Damage and yield loss

### *Feeding behaviour and symptoms*

Aphids penetrate the plant with their stylets in search of phloem vessels to establish feeding. In general, they rely on gut endosymbionts to provide some of the essential amino acids that are lacking in the plant phloem (Douglas 2006). *Diuraphis noxia*, however, appears to have a different strategy, whereby the aphids inject toxins from their salivary glands, causing a strong reaction (and symptoms) from the plant, but also, and more importantly for the aphid, modifying the phloem composition to improve its nutritional quality (Luna *et al.* 2018). Such a plant response may be essential for *D. noxia* populations to increase (Telang *et al.* 1999).

These damage symptoms caused by *D. noxia* are unique. The toxin affects epidermal cells and other tissues containing lignin, and also destroys chloroplast membranes which in turn affects the photosynthetic ability of the plant (Fouche *et al.* 1984). Localised damage symptoms include chlorosis and necrosis (Burd *et al.* 1993). Early symptoms visible in plant seedlings include longitudinal rolling of leaves, whitish, yellowish to pink-purple chlorotic streaks along the length of leaves (systemic damage), and a prostrate appearance (Burd *et al.* 1993; Goggin 2007; Hughes & Maywald 1990; Yazdani *et al.* 2018). Viewed from a distance, damage may appear as a general loss of colouration across the affected area. In extreme cases, damage may result in the death of the plant (Hein *et al.* 1990). *Diuraphis noxia* also interferes with normal unrolling of newly emerging leaves, resulting in tightly curled leaves inside of which dense colonies can feed (Hewitt *et al.* 1984; Riedell 1989).

Although it is not entirely clear what causes this combination of damage symptoms (Luna *et al.* 2018), they are clearly visible, and usually the first signal that *D. noxia* are present. Symptoms appear to be limited to the infested tiller and move ‘upwards’, causing the younger leaves to appear more greatly affected. If the aphid disappears the symptoms will persist, however new leaves will show no symptoms. Though very visible, the presence of symptoms in the seedling stage is not directly related to yield loss. In Australia, these symptoms are readily distinguishable from feeding damage caused by other cereal aphids (GRDC 2017), although they can be confused with nutritional deficiencies, herbicide damage or disease symptoms (Wallwork *et al.* 2000).

*Yield impacts*

Preliminary screening work by Wellings *et al.* (1993) found that, of the 200 Australian wheat cultivars and breeding lines, all were susceptible to *D. noxia* and most exhibited severe damage symptoms after infestation. The growth stage of the plant seems to play a major role in its suitability for *D. noxia,* with younger plants being most suitable for population growth (Ma & Bechinski 2009). Cereal seedlings are particularly sensitive to *D. noxia* (Kieckhefer & Gellner 1992), and feeding during early stages can result in yield loss (Kieckhefer *et al.* 1995). Healthy growing cereal plants, especially those at the booting stage are better able to tolerate *D. noxia* infestations, and aphid populations tend to decline once plants mature and senesce (Ma & Bechinski 2009). Drought stress increases the host plant sensitivity, possibly changing the phloem composition (Showler 2014) and impeding the plants ability to withstand the stress caused by aphid feeding (Starý & Lukášová 2002). Moreover, infestations of *D. noxia* may also limit the ability of plants to recover from drought conditions (Riedell 1989).

*D. noxia* is capable of causing high yield losses in cereal crops (Mirik *et al.* 2009). In the USA, yield losses in winter wheat have been estimated to be about 0.5% for every 1% infested tillers, from tillering through flowering (Archer & Bynum 1992). More limited data indicates that losses in barley may be substantially higher, perhaps 0.8% per 1% infested stems (Peairs 2017). There is still a lack of data under Australian conditions, although several field trials have been conducted in recent years. In 2018, a field trial was undertaken at Loxton (South Australia) using *D. noxia* inoculations and exclusion cages in wheat. Yield losses of more than 70% were evident in dry conditions. Similar trials in high rainfall conditions, conducted at the Waite Campus, Adelaide, in the same year showed no yield loss (van Helden & Heddle, unpub. data). Other field trials have been conducted at various localities in South Australia, Victoria, Tasmania and New South Wales, with many of these failing to detect significant yield penalties from *D. noxia* in cereals (van Helden, unpub. data).

It appears yield losses are most likely to occur when several factors are combined: (i) a sensitive crop type (i.e. wheat, barley, durum wheat), (ii) a high autumn infestation of *D. noxia*, and (iii) moisture-stressed plants in spring (Starý & Lukášová 2002). In South Africa, *D. noxia* is reported to cause considerable economic damage in regions where summer rainfall is common-place, but less so in regions with a Mediterranean-type climate such as the Western Cape (Agricultural Research Council 2019).

Unlike many other cereal aphids, *D. noxia* is not considered an important vector of cereal viruses (Damsteegt *et al.* 1992). South African research from 1979 to 1981 showed laboratory transmission of several cereal viruses (including Barley Yellow Dwarf Virus, Brome Mosaic Virus and Barley Stripe Mosaic Virus) by *D. noxia* (von Wechmar 1987), however, there are no published reports of *D. noxia* being associated with field outbreaks of these, or other viruses, in cereal crops (Damsteegt *et al.* 1992).

## Management

### *Monitoring*

The highly visible damage symptoms on infected plants permits relatively straightforward monitoring of *D. noxia* in the field. Plants already stressed are often most susceptible to aphid attack (Li *et al.* 2008), and therefore initial observations are best focused on areas that are likely to contain stressed plants, such as patches affected by water stress, disease or soil compaction. Volunteer plants in or around paddocks, which have not been treated with insecticide should also be monitored as an indicator for *D. noxia* presence in the area.

Within crops, monitoring is best undertaken by first quantifying the percentage of tillers with symptoms. This is achieved by randomly selecting parts of the paddock and counting the total number of tillers and those with symptoms along a 50 cm row length at each sampling point. Next, tillers with symptoms should be checked for aphids, as it is unlikely *D. noxia* will be found on tillers without symptoms. *Diuraphis noxia* will often be hiding at the base of the younger leaves, or inside the rolled leaf or leaf edges, therefore leaves should be carefully unrolled. Often other aphid species, especially *Rhopalosiphum maidis* (Fitch) (corn aphid) and *Rhopalosiphum padi* L. (oat aphid), will be found in sympatry with *D. noxia*, however these species are readily differentiated (Blackman & Eastop 2007). Combining the proportion of tillers with symptoms with the presence of *D. noxia* on symptomatic tillers provides information on the severity of attack within a paddock.

Monitoring for *D. noxia* outside of crops can be more difficult as symptoms are not consistently visible on weed hosts (Hewitt *et al.* 1984; Kindler *et al.* 1992; Kindler *et al.* 1993; Kindler & Springer 1989; Telang *et al.* 1999). A method of vacuum sampling (De Barro 1991) or Berlese sampling (Elberson & Johnson 1995) can be used to confirm the presence of *D. noxia* on weed grasses. Pan traps (Hughes *et al.* 1965; Hughes *et al.* 1964), suction traps (Armstrong *et al.* 1991; Pike *et al.* 1989) and sentinel seedlings (Gilabert *et al.* 2017) may be used to monitor population movements. To manually inspect grasses for *D. noxia* colonies, the base of leaves, particularly where they begin to wrap around the stem, should be checked, and flag leaves should be unwrapped from around emerging grass heads (particularly in the case of *H. murinum*; a highly preferred weed host).

Sowing timing can greatly influence the risk of *D. noxia* colonisation (Elmali 1998), and monitoring should be increased when crop emergence coincides with high risk factors. In Australia, these factors include short, wet summers (resulting in a considerable 'green bridge' of summer grasses) that coincide with weather conditions suitable for autumn aphid migrations (Hughes *et al.* 1964). Crop plants emerging after wet summers should be monitored closely, particularly when preferred grass hosts, such as *H. murinum* and *Bromus* spp., are known to have persisted throughout summer. In warmer and drier regions of Australia, aphid populations are expected to build throughout winter and become highest in spring, so crops emerging in late winter and spring should be monitored regularly. When monitoring for *D. noxia*, beneficial insect activity and mummified aphids (signs of wasp parasitism) should be recorded.

### *Host plant resistance*

Host plant resistance has been deployed as a key management strategy around the world in areas where *D. noxia* is a serious risk. Breeding for wheat varieties resistant to *D. noxia* began in the late 1980s in South Africa, resulting in the identification of the first two resistance genes, Dn1 and Dn2 (Du Toit 1989). To date, at least 14 resistance genes against *D. noxia* have been described, most of which have been mapped to a particular chromosomal region (Table 3). The majority of these genes have been identified in wheat accessions originating from different areas around the world. Within the USA, a major advance in the management of *D. noxia* was the commercial release of 'Halt', 'Prairie Red' 'Prowers 99', and 'Yumar', which have since been succeeded by other *D. noxia*-resistant cultivars (Giles *et al.* 2008). Australian cereals do not possess Dn genes and, based on glasshouse trials, all varieties appear to be susceptible to *D. noxia* at the seedling stage (van Helden, unpub. data).

Globally, there are *D. noxia* biotypes that have overcome many host plant resistances (Puterka *et al.* 1992). Virulent *D. noxia* biotypes have been recorded in Europe (Basky 2003), the USA (Haley *et al.* 2004), South America (Smith *et al.* 2004), Asia (Dolatti *et al.* 2005) and South Africa (Tolmay 2007). Clearly *D. noxia* has an inherent capacity to overcome genetic mechanisms of resistance developed through plant breeding. In response to the incursion of *D. noxia* in Australia, research was undertaken to determine the biotype/s present, in part to assist plant breeders identify effective resistance genes. It was established that there is a single biotype of *D. noxia*, named *D. noxia* RWAau1 (GRDC 2017). Initial seedling screening of commercially available wheat and barley varieties in Australia has indicated some differences in symptom expression, however all were classified as susceptible (van Helden, unpub. data). How this translates to yield loss remains unclear. Early indications from Australian trials suggests germplasm carrying effective resistance genes are likely to be available, however the deployment of resistant traits into commercial plant breeding programs is subject to private sector investment and will take several years before they are commercially available (Umina *et al.* 2017).

### *Cultural control*

In addition to host plant resistance, other cultural practices can play an important role in preventing early season infestations and reducing *D. noxia* damage (Chemeda 2015). Adane (1998) suggested early sowing of summer cereals during the rainy season enabled crop seedlings to escape the majority of damage caused by *D. noxia* in Egypt. This finding is, in part, supported by Sotelo-Cardona (2010), who advocated sowing winter wheat as late as possible and sowing spring crops as early as possible, as a way to manage *D. noxia* in the USA. Agronomic practices can also be used to promote crop vigour and dense canopy growth which inhibit *D. noxia* populations and reduces their impact on crop plants. Sotelo-Cardona (2010) suggests “proper soil fertilization” is required to produce a healthy crop and prevent *D. noxia* from thriving in stressed portions of the paddock.

In Australia, as in other countries, management of so called ‘green bridges’ over summer will help reduce *D. noxia* populations. A green bridge consists of crop volunteers usually from last year’s crop, and weeds emerging from seeds set over many years, or from windborne weed seeds. For *D. noxia*, cereal volunteers (particularly wheat and barley), pasture grasses and wild genera including *Bromus, Hordeum, Lolium, Phalaris* and *Poa* are most important in aiding populations to persist from one cropping season into the next. These summer hosts should be removed through herbicide applications, grazing or cultivation, ensuring no living *D. noxia* host plant is present for a minimum of two weeks prior to sowing (Umina *et al.* 2017). Sowing cereals into standing stubble can also reduce the likelihood of aphids alighting (landing) within the paddock (Verrell 2013) and thus reduce the risk of *D. noxia* infestations.

### *Biological control*

A wide range of natural enemies have been recorded attacking *D. noxia*, with a detailed list provided by CABI (2016). Several authors have listed predators and parasitoids of *D. noxia* in specific countries or areas, however none have compiled a complete global list. Very few natural enemies seem to be restricted to *D. noxia*, to members of the genus *Diuraphis*, or even to cereal aphids (Hopper *et al.* 1998), although Reed & Pike (1991) provided some evidence of specialisation. A diverse range of species are known to attack *D. noxia* in Australia, including those that commonly attack other cereal aphid species (Heddle *et al.* 2016).

Despite the prevalence of natural enemies globally, utilising these organisms within ongoing management is reported to be simpler for other cereal aphids than for *D. noxia.* This is thought to be due to the habit of feeding within the leaf whorls of cereal plants, where natural enemies have limited access (Robinson 1994). To combat this, Stary (1972) proposed a multilateral concept to control *D. noxia*, requiring information that concerns host plants, parasitoids, hyperparasitoids, predators and alternate host aphids. In favour of this multilateral approach, Tanigoshi *et al.* (1995) anticipated management programs would be most successful when using combinations of predators and parasitoids working within a particular habitat type. A further challenge in the control of *D. noxia* using natural enemies is identifying species that are active at different times throughout the growing season, when aphid densities can alter dramatically (Nowierski & Johnson 1995). Overseas, there are some reports that suggest natural enemies have a limited impact in curbing *D. noxia* populations in cropping systems (Aalbersberg *et al.* 1988; Berest 1980; Prinsloo 1990).

A key challenge in cropping landscapes is the lag between pest arrival and the arrival and/or build-up of natural enemy populations in cereal crops (Brier *et al.* 2008; Holloway *et al.* 2008). Perhaps the largest impact natural enemies will have is attacking *D. noxia* on non-crop hosts, particularly between harvest and the following autumn sowings (Nowierski & Johnson 1995).

Predators

An extensive study by Robinson (1992) listed the main groups of *D. noxia* predators in the High Valley of Mexico as predatory beetles (Coccinellidae), predatory bugs (Anthocoridae), hoverflies (Syrphidae), and lacewings (Neuroptera). Similarly, in the USA, 41 species of natural enemies were observed feeding on *D. noxia* by Mohamed *et al.* (2000), which included 15 carabids, 12 coccinellids, six spiders, five syrphids, two nabids (predatory bugs) and two lacewing species, with the most consistently abundant being the coccinellids and nabids. These groups were also observed by Brewer & Elliott (2004), however they found that, regionally, the occurrence and importance of each species within the groups varied. The major arthropod predators in grain crops within Australia are hoverfly larvae, lacewings, predatory beetles (including coccinellids), predatory bugs and spiders (Brier *et al.* 2008), with coccinellids, hoverflies and lacewings likely to be the most important for aphid management (Milne & Bishop 1987). Earwigs (Dermaptera) are listed as predators of aphids, including in winter cereals (Asgari 1966; Skuhravy 1960; Pons & Eizaguirr 2000), however there are no studies that have examined this in Australia.

There are an estimated 500 species of coccinellids in Australia (Slipinksi 2007) and many have been observed attacking *D. noxia* (T. Heddle, unpub. data). However, the most important species and their impact remain unclear. Coccinellids are an important predator of *D. noxia* in many regions of the world. In just a single province of China (Xinjiang), 17 coccinellid species were found predating *D. noxia* (Yu & Liang 1998). In other parts of Asia (and Europe), coccinellids most frequently associated with *D. noxia* include *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Hopper *et al.* 1998). Exposed aphids are more vulnerable to attack from coccinellids, although smaller species, such as *Scymnus* spp., are able to access *D. noxia* within leaf whorls (Kauffman & Laroche 1994).

In Europe, coccinellids and syrphids reportedly comprise 99% of the total number of natural enemies attributed to control *D. noxia* (Farkas & Kozma 2003). Syrphids commonly associated with *D. noxia* in Europe (and Asia) include *Episyrphus balteatus*, *Eupeodes corollae* and *Sphaerophoria scripta* (Hopper *et al.* 1998). *Leucopis* spp., of the dipteran family Chamaemyiidae, have been found in association with *D. noxia* throughout Europe and Asia, however in lower abundance than syrphids. Australia has a low number of syrphid species (Colless & McAlpine 1991; Thompson & Vockeroth 2016), however some, particularly *Melangyna viridiceps*, are known to be abundant in grain crops in south-eastern Australia and routinely prey upon cereal aphids (Horne *et al.* 2001).

In Australia, Neuroptera are another important group of aphid predators (Duelli 2001). Both adult and immature brown lacewings (Hemerobiidae) are predaceous (Brewer & Elliott 2004), while the feeding behaviour of green lacewings (Chrysopidae) varies with life stage (Brodeur *et al.* 2017). Immature forms actively predate on aphids, as do most adults, however, some chrysopid adults feed on aphid honeydew, nectar and pollen (Brodeur *et al.* 2017). *Mallada signata*, a native to Australasia, is the most common green lacewing, although it is often found in such low abundances, that identifying predatory behaviour is difficult (Horne *et al.* 2001). In regions of Australia where *D. noxia* is presently found, the brown lacewing, *Micromus tasmaniae*, is the most common lacewing species in grain crops (Horne *et al.* 2001). Importantly, this species has a relatively low temperature threshold, which allows significant activity of larvae and adults during the winter months (Syrett & Penman 1981).

<u>Parasitoids</u>

In general, hymenopteran parasitoid prevalence has been recorded as low within cereal aphid populations around the world. In the High Valley of Mexico, Robinson (1992) listed the parasitoid wasps associated with *D. noxia* as *Diaeretiella rapae*, *Aphidius ervi*, *Asaphes* sp., *Pachyneuron* sp., *Aprostocetus* sp., *Dendrocerus* sp., and *Alloxysta* sp.. This list includes both primary and secondary parasitoids of *D. noxia*. During his study, Robinson (1992) found *D. rapae* to be the most abundant parasitoid attacking *D. noxia*. This has been corroborated by other authors (Noma *et al.* 2005; Pike *et al.* 1997; Rakhshani *et al.* 2008; Stary 1999b) and has also been recorded in Australia (Heddle *et al.* 2016). Parasitism by *D. rapae* has been shown to decrease as the aphid density declines (Bernal *et al.* 1994), which could be attributed to the volatiles from the plant-host complex, to which the parasitoids are attracted

(Farias 1995; Reed *et al.* 1995). Even though parasitism of *D. noxia* can reach high levels (Farias 1995), there are often only a small number of aphid ‘mummies’ per colony (Chen & Hopper 1997), which makes it difficult for farmers to estimate the levels of parasitism that may be occurring in the field.

Upon establishment in California, it was noted that *D. noxia* acquired polyphagous, opportunistic, parasitoid species (Bernal *et al.* 1993). This is promising for Australia, where there are numerous species of generalist aphidiines, although Bernal *et al.* (1993) expressed concern that a lack of host specificity would reduce the effectiveness of these natural enemies. Several species of aphidiine have been recorded parasitising *D. noxia* in South Australia, including *Aphidius platensis, A. rhopalosiphi*, *Lysiphlebus testaceipes* and *A. colemani*; the latter was also recorded attacking *D. noxia* in Victoria (Heddle *et al.* 2016). In New South Wales, Tasmania and Victoria, *L. testaceipes* appears to be the predominant wasp parasitising *D.* noxia, followed by *D. rapae* (Ward, unpub. data). The combination of multiple parasitoid species’ activity may be important in long-term *D. noxia* population regulation.

In addition to the aphidiines, aphelinids (*Aphelinus albipodus, A. asychis* and *A. varipes*) have been recognised for their control of *D. noxia* (Hopper *et al.* 1995). Bernal & Gonzalez (1993) demonstrated aphidiines have lower developmental thresholds compared with aphelinids, which may be the reason why aphelinids are important parasitoids throughout the summer rainfall areas of the USA and not abundant in the southern regions of Australia. Furthermore, aphidiines may be able to enter a diapause state (Hagvar & Hofsvang 1991; Stary 1970), while the aphelinids appear to lack this ability (Pike *et al.* 1997; Van den Bosch *et al.* 1964; Van den Bosch *et al.* 1959), which is likely to mean aphidiines can be found throughout the year in Australia, whereas aphelinid activity is restricted to a shorter timeframe.

Although several aphelinid species have been recorded attacking multiple species of aphid, none have been identified parasitising *D. noxia* within Australia so far (Heddle *et al.* 2016). This includes *A. varipes,* which was released into Australia in anticipation of the arrival of *D. noxia* (Hughes *et al.* 1994); although there is some confusion surrounding the classification of this released parasitoid. Hughes *et al.* (1994) labelled the species *A. varipes,* however, it was originally collected as *A. hordei* (Prinsloo 1998; Prinsloo & Neser 1994). Prinsloo (2000) referred to this aphelinid species as ‘sp. nr. *varipes’* instead of *A. hordei*, but then in later publications it is again referred to as *A. hordei* (Prinsloo *et al.* 2002; Prinsloo

2006). Importantly, Hopper *et al.* (2017) demonstrated that *A. varipes* does not attack *D. noxia*, unlike *A. hordei*, which has established on *R. padi* and *R. maidis* within Australia (Waterhouse & Sands 2001).

### Pathogenic fungi

Several endophytic fungi that control *D. noxia* have been identified, with Clement *et al.* (1992) proposing their use as biocontrol agents by artificially inoculating uninfected cereal plants. Within natural populations of *D. noxia*, fungal pathogen epizootics seem to be rare, perhaps because *D. noxia* is usually found in dry environments (Wraight *et al.* 1993). Subsequently, the reliable use of these organisms as control agents in semi-arid areas may require manipulation of environmental conditions, for example through irrigation (Wraight *et al.* 1993). Although outbreaks of fungal infections rarely occur in the USA (Feng *et al.* 1991; Wraight *et al.* 1993), six species of entomopathogenic fungi have been recovered from *D. noxia*, including *Beauveria bassiana*, *Verticillium lecanii*, *Conidiobolus obscurus*, *Pandora neoaphidis*, *P. radicans* and *Neozygites fresenii* in southwestern Idaho alone (Feng *et al.* 1990). In South Africa, many of the same species of fungi recorded from the USA can be found infecting *D. noxia*, in addition to *Conidiobolus thromboides* and *Entomophthora planchoniana* (Hatting *et al.* 1999). In Turkey, many species of fungi overlap with the Idaho and South Africa findings (Burton 1988), although their potential role has not been identified (Nowierski & Johnson 1995). Wilson *et al.* (1991), Clement *et al.* (1992) and Wang & Knudsen (1993) have shown that *D. noxia* is adversely affected by various endophytic fungi.

Of the fungi listed above, *B. bassiana, V. lecanii*, *C. obscurus*, *P. neoaphidis***,** *P. radicans, N. fresenii, C. thromboides* and *E. planchoniana* are present in Australia (or Australasia), or can be purchased commercially within Australia. Furthermore, CABI (2016) lists *Conidiobolus coronatus*, *Erynia neoaphidis* and *Paecilomyces fumosoroseus* as natural enemies of *D. noxia*; all of which are present in either Australia or Australasia (ALA, 2019). Pathogenic fungi have been observed attacking *D. noxia* in Australia. For example, fungi that were favoured by high rainfall during the 2016 growing season, played a role in the unexpected and sharp decline of *D. noxia* populations in South Australia and Victoria in the spring of that year (Umina *et al.* 2017). Similar reductions in *D. noxia* populations due to pathogenic fungi have been observed in other countries (e.g. Hopper *et al.* 1998). Further research is required to identify the extent of the role pathogenic fungi play in helping to manage *D. noxia* in Australia.

*Chemical control*

Insecticides have been used for many years to successfully combat *D. noxia* infesting cereal crops in almost all countries it inhabits. The majority of insecticides recommended for *D. noxia* are organophosphates, such as chlorpyrifos and dimethoate, synthetic pyrethroids, such as alpha-cypermethrin, and the carbamate, pirimicarb. These chemicals are commonly used to control other cereal aphids in Australia (Edwards *et al.* 2008). Although highly effective, the use of foliar insecticides should consider the cost of control, the estimated crop return, and the correlated, predicted yield loss. Little research into the benefits of chemical control of *D. noxia* in Australia has been conducted and therefore most knowledge is based on overseas data. Economic thresholds have been adapted to help guide spray decisions, and these have been widely recommended to Australian farmers (GRDC 2017). Chemical control is thought to be justified if *D. noxia* infestations exceed 20% of seedlings infested at the start of tillering or 10% of tillers during the period of stem elongation to soft dough (GS31-85) (Peairs 1998). During this latter growth stage, protection of the top three leaves is a priority for minimising yield loss. Research is currently underway to validate these economic thresholds under Australian conditions and with Australian cereal varieties.

Because *D. noxia* are typically hidden in rolled leaves, they are somewhat protected from contact insecticides. Consequently, chemicals with systemic and/or vapour activity are preferred options for control. In Australia, the first chemical Emergency Use Permits made available to farmers were for chlorpyrifos and pirimicarb (Umina *et al.* 2017) and these remain the most commonly applied foliar sprays for *D. noxia.* Insecticide seed treatments have some advantages over foliar chemical applications, and are highly effective at curbing early aphid invasion and feeding damage in vulnerable establishing crops. Seed treatments can also provide longer and more persistent protection than insecticide sprays and reduce the risk of chemical exposure to farmers and spray operators (Dewar & Denholm 2007). There have been numerous studies investigating the use of seed treatments in combating cereal aphids. Abd-Ella (2016) and Liu *et al.* (2005) found imidacloprid and thiamethoxam provide the longest period of protection for wheat cultivars against aphids. Wilde *et al.* (2001) found that the aforementioned seed treatments were successful in controlling *D. noxia* in early infestations in winter wheat, however less consistently for spring infestations. They also showed that fipronil was not effective against *D. noxia*. Burd *et al.* (1996) found *D. noxia* was controlled for 45 days after planting wheat seedlings grown from seed treated with imidacloprid. A recent Australian study examined the length of protection provided by several insecticide seed treatments against *D. noxia* in wheat and compared this with *R. padi* (Kirkland *et al.* 2018). All seed treatments examined were effective at controlling *D. noxia* up to 49 days after wheat emergence, however the responses differed between *D. noxia* and *R. padi*. In most instances, *R. padi* was able to colonise wheat at an earlier growth stage than *D. noxia*, suggesting *D. noxia* is more sensitive to these seed treatments (Kirkland *et al.* 2018). This trial, however, was undertaken within a shadehouse and therefore results may differ in the field.

Insecticide seed treatments in cereals have become commonplace in parts of south-eastern Australia where *D. noxia* is present (Kirkland *et al.* 2018; Umina *et al.* 2019). In part this is due to farmers' uncertainty about the impacts *D. noxia* can have and the inability to confidently assess crop risk (Umina *et al.* 2017). Historically in Australia, insecticide seed treatments in cereals have been largely used to minimise the risk of plant viruses, particularly in high rainfall zones (McKirdy & Jones 1997). While Australian farmers have found currently registered insecticide seed treatments effective in minimising the early colonisation of *D. noxia* in cereal crops (Umina *et al.* 2017), further research is needed to ascertain when seed treatments are warranted. Despite their long-term use in *D. noxia* management overseas, the benefits of seed treatments to crop yield remain unclear. Wilde *et al.* (2001) showed no yield benefits of any insecticide seed treatments in *D. noxia* trials conducted over four years at two locations in Kansas, USA. Other studies have found higher yields and/or increased profit. For example, Tolmay *et al.* (1997) confirmed increased wheat yields when imidacloprid was applied to aphid- resistant and susceptible varieties in field trials in South Africa. Furthermore, increased profit was reported in South Africa when *D. noxia* was controlled using imidacloprid seed treatments (Van der Westhuizen *et al.* 1994).

While insecticide seed treatments have less pervasive effects on natural enemies than conventional high-volume insecticide sprays, they can still adversely impact arthropod predator and parasitoid communities. One exposure route through which natural enemies are exposed to seed treatments is by eating tainted prey. For example, Douglas *et al.* (2015) found that after grey field slugs, *Deroceras reticulatum*, feed on soya beans grown from thiamethoxam-treated seed, they delivered a lethal dose of the insecticide to predatory ground beetles. This is despite the insecticide having no (or very little) harmful effect on the slugs. In this case, the reduction in predators due to neonicotinoids resulted in an increase in slug numbers and lead to a reduction in crop yield (Douglas *et al.* 2015). Further research is required to understand the long-term impacts of insecticide seed treatments in lieu of their increased usage in Australia because of *D. noxia*.

*Insecticide resistance*

There is no evidence to suggest *D. noxia* has evolved insecticide resistance globally. There has, however, been relatively low historic selection pressure using foliar insecticides in cereal crops and very limited research in relation to the potential for resistance evolution. Variability in *D. noxia* susceptibility to chlorpyrifos in the USA led Brewer & Kaltenbach (1995) to propose *D. noxia* may evolve insecticide resistance. Furthermore, *D. noxia* displays significant chromosomal heterogeneity (Nicholson *et al.* 2015) and has repeatedly shown rapid evolution of new biotypes in response to plant resistance genes (e.g. Puterka *et al.* 1992) which makes it likely that genetically-based insecticide resistance can occur under high selection pressure. Australian farmers have been advised to only use insecticides when warranted and always adhere to product labels. Unfortunately, within Australia there is very limited opportunity to rotate cereal seed dressings with neonicotinoid-free products as there are, effectively, no other classes of insecticide seed dressings targeting the same pest spectrum (Umina *et al.* 2019). Protecting natural enemies associated with *D. noxia* will help decrease the potential for insecticide resistance by reducing the intensity of chemical applications.

## Conclusions

The arrival of *D. noxia* in Australia was inevitable, given its history of invasion around the world. Preparatory research was undertaken prior to its arrival and a great deal has been achieved since being detected in 2016. With the high likelihood of *D. noxia* distribution continuing to expand into all major grain regions of Australia, it is important that future efforts focus on sustainable management practises given the somewhat indiscriminate use of insecticides to control *D. noxia* to date. Research across multiple years is required to better understand population dynamics, yield impacts, host preferences and host plant resistance opportunities. Observations and experiments involving natural enemies, particularly pathogenic fungi and parasitoids, would inform future biological control options within Integrated Pest Management programs. Regular testing of field populations to understand if insecticide resistance is likely to evolve is also warranted.

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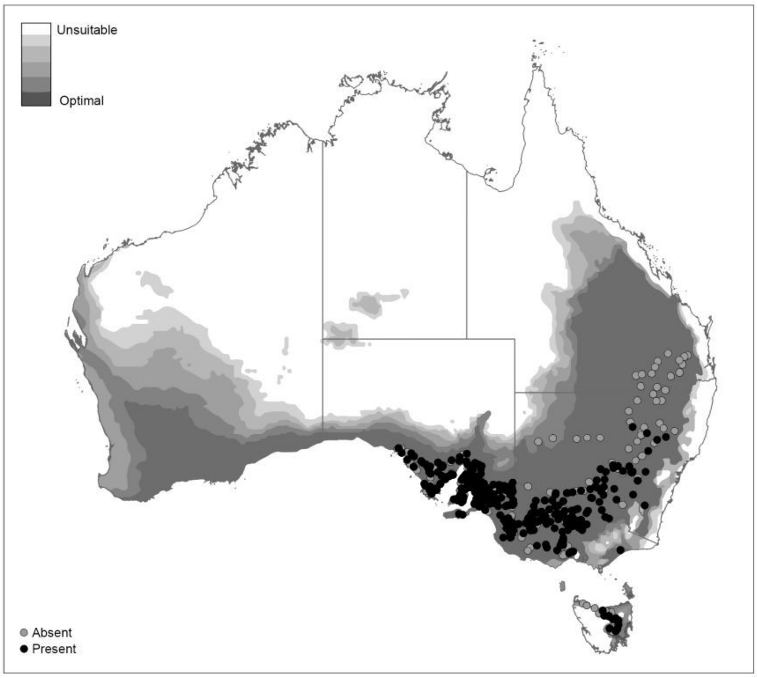

Figure 1. Known distribution of *D. noxia* in Australia, overlaid with the Avila *et al.* (2019) CLIMEX model where darker colours indicate higher climate suitability. Black circles indicate areas where *D. noxia* has been identified between May 2016 and August 2019. Grey circles indicate areas where active surveillance has failed to locate *D. noxia* (Source: E. Pirtle, J. Maino, T. Heddle and M. van Helden, unpub. data).

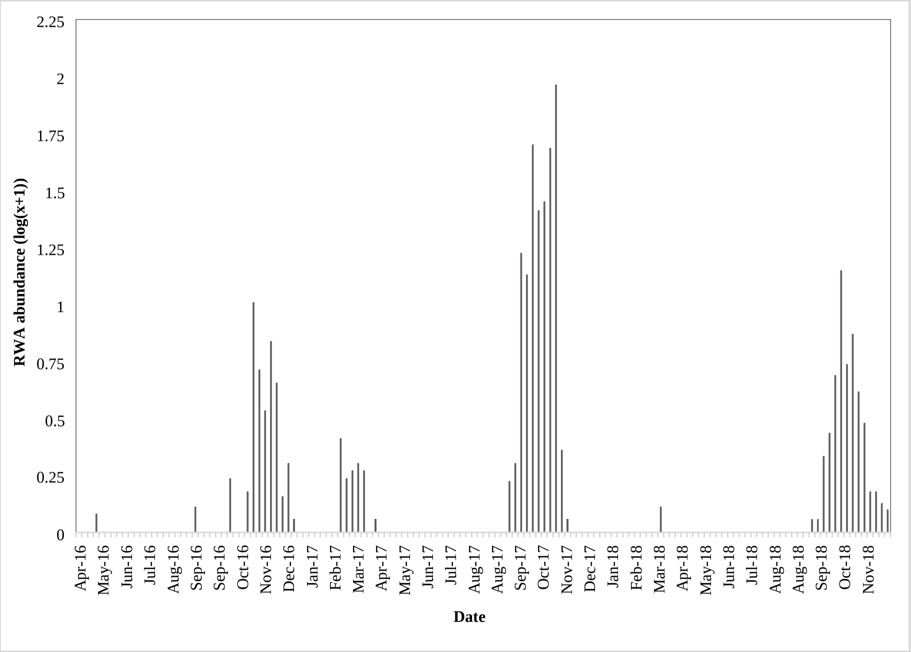

Figure 2. Logged number of *D. noxia* captured at weekly intervals between April 2016 and November 2018 by suction trap at Kapunda, South Australia (Source: T. Heddle and M. van Helden, unpub. data).

Table 1. First published records of *D. noxia* around the world.

| **Country** | **Date** | **References** |
|---|---|---|
| Russia | 1900 | (Kovalev *et al.* 1991; Kurdjumov, 1913) |
| Spain | 1947 | (Alfaro 1947) |
| Ethiopia | 1972 | (Adugna & Megenassa 1987) |
| Yemen | Late 1970s | (Evans *et al.* 1989) |
| South Africa | 1978 | (Basky & Jordaan 1997; Walters *et al.* 1984) |
| Mexico | 1980 | (Basky & Jordaan 1997; Gilchrist *et al.* 1984) |
| USA | 1985* | (Morrison & Peairs 1998; Webster & Starks 1987) |
| | 1986* | (Zerene *et al.* 1988) |
| Chile | 1987* | (Evans *et al.* 1989; Ortego & Delfino 1994) |
| | 1988* | |
| Canada | 1988 | (Evans *et al.* 1989; Morrison 1988) |
| Hungary | 1989 | (Basky & Eastop 1991) |
| Argentina | 1992 | (Ortego & Delfino 1994) |
| Czech Republic | 1993 | (Stary 1996; Vošlajer 1999) |
| Australia | 2016 | (Baker *et al.* 2016) |

* Conflicting evidence of the first recording of *D. noxia* in the USA and Chile. Presumably the earlier dates are correct.

Table 2. Reported plants on which *D. noxia* is known to successfully reproduce.

| Scientific name | Common name | References |
|---|---|---|
| *Agropyron cristatum* | Creased wheatgrass | (Armstrong *et al*. 1991) |
| *Agropyron desertorum* | Crested wheatgrass | (Clement *et al*. 1990) |
| *Agropyron elongatum* | Tall wheatgrass | (Kindler & Springer 1989) |
| *Agropyron intermedium* | Intermediate wheatgrass | (Armstrong *et al*. 1991; Kindler & Springer 1989) |
| *Agropyron smithii* | Western wheatgrass | (Armstrong *et al.* 1991) |
| *Agropyron trichophorum* | Pubescent wheatgrass | (Armstrong *et al.* 1991) |
| *Aristida oligantha* | Prairie three-awn | (Armstrong *et al*. 1991) |
| *Avena sativa* | Oat | (Kindler & Springer 1989; Yazdani *et al.* 2018) |
| *Bouteloua curtiendula* | Side-oats grama | (Armstrong *et al.* 1991) |
| *Bouteloua gracilis* | Blue grama | (Armstrong *et al.* 1991) |
| *Bromus arvensis* | Field bromegrass | (Kindler & Springer 1989) |
| *Bromus madritensis* | Spanish broom | (Stoetzel 1987) |
| *Bromus mollis* | Blando bromegrass | (Kindler & Springer 1989) |
| *Bromus* spp. | Brome grass | (Yazdani *et al.* 2018) |
| *Bromus tectorum* | Downy brome | (Armstrong *et al*. 1991) |
| *Calamovilfa longifolia* | Prairie sandreed | (Armstrong *et al.* 1991) |
| *Cynodon dactylon* | Bermuda grass | (Kindler & Springer 1989) |
| *Dactylis glomerata* | Cocksfoot | (Clement *et al.* 1990) |
| *Echinochloa crusgalli* | Barnyard grass | (Armstrong *et al*. 1991) |
| *Elymus arenarius* | European dunegrass | (Kindler & Springer 1989) |
| *Elymus canadensis* | Canada wildrye | (Armstrong *et al.* 1991) |

| | | |
|---|---|---|
| *Elymus triticoides* | Beardless wildrye | (Kindler & Springer 1989) |
| *Elytrigia elongata* | Tall wheatgrass | (Stoetzel 1987) |
| *Eragrostis cilianensis* | Stinkgrass | (Armstrong *et al.* 1991) |
| *Festuca arundinacea* | Tall fescue | (Clement *et al.* 1990) |
| *Hordeum murinum* | Barley grass | (Elmali 1998; Stoetzel 1987; Yazdani *et al.* 2018) |
| *Hordeum pusillum* | Little barley | (Kindler & Springer 1989) |
| *Hordeum vulgare* | Barley | (Kindler & Springer 1989; Stoetzel 1987; Yazdani *et al.* 2018) |
| *Lolium rigidum* | Rye grass | (Yazdani *et al.* 2018) |
| *Oryza sativa* | Rice | (Stoetzel 1987) |
| *Oryzopsis hymenoides* | Indian ricegrass | (Kindler & Springer 1989) |
| *Panicum capillare* | Witchgrass | (Armstrong *et al.* 1991) |
| *Panicum effusum* | Panic grass | (Yazdani *et al.* 2018) |
| *Panicum virgatum* | Switchgrass | (Armstrong *et al.* 1991) |
| *Phalaris canariensis* | Canary grass | (Elmali 1998; Stoetzel 1987) |
| *Phalaris* spp. | Phalaris | (Yazdani *et al.* 2018) |
| *Phleum pratense* | Timothy grass | (Stoetzel 1987) |
| *Secale cereale* | Rye | (Kindler & Springer 1989; Yazdani *et al.* 2018) |
| *Setaria viridus* | Green foxtail | (Armstrong *et al.* 1991) |
| *Sitanion hystrix* | Squirreltail | (Armstrong *et al.* 1991) |
| *Sorghum bicolor* | Sorghum | (Harvey & Kofoid 1993) |
| *Sporobolus cryptandrus* | Sand dropseed | (Armstrong *et al.* 1991) |
| *Stipa comata* | Needle-and-thread | (Armstrong *et al.* 1991) |
| *Stipa viridula* | Green needle-grass | (Armstrong *et al.* 1991) |

| | | |
|---|---|---|
| *Triticum aestivum* | Wheat | (Kindler & Springer 1989; Stoetzel 1987; Yazdani *et al.* 2018) |
| *Triticum cylindricum* | Jointed goatgrass | (Kindler & Springer 1989) |
| *Triticum turgidum* | Durum wheat | (Stoetzel 1987) |
| *Vulpia myuros* | Rattail fescue | (Kindler & Springer 1989) |
| *x Tritosecale* | Triticale | (Stoetzel 1987) |
| *Zea mays* | Corn | (Kindler & Springer 1989) |

Table 3. Identified *D. noxia* resistance genes in cereal plants.

| Gene | Source | Chromosome | Accession | References |
|---|---|---|---|---|
| Dn1 | *T. aestivum* (Iran) | 7D | PI137739 | (Du Toit 1989) |
| Dn2 | *T. aestivum* (Russia) | 7D | PI262660 | (Du Toit 1989) |
| Dn3 | *Triticum tauschii* | * | SQ24 | (Nkongolo *et al.* 1991a) |
| Dn4 | *T. aestivum* (Russia) | 1D | PI372129 | (Nkongolo *et al.* 1991b) |
| Dn5 | *T. aestivum* (Bulgaria) | 7D | PI294994 | (Marais & Dutoit 1993) |
| Dn6 | *T. aestivum* (Iran) | 7D | PI243781 | (Saidi & Quick 1996) |
| Dn7 | *S. cereale* | 1RS,1BL | 94M370 | (Marais *et al.* 1994) |
| Dn8 | *T. aestivum* | 7D/1D | PI294994 derivative | (Liu *et al.* 2001) |
| Dn9 | *T. aestivum* | 7D/1D | PI294994 derivative | (Liu *et al.* 2001) |
| Dnx | *T. aestivum* (Afghanistan) | 7D | PI220127 | (Harvey & Martin 1990) |
| Dny | *T. aestivum* (Stanton CV) | * | PI220350 | (Smith *et al.* 2004) |
| New | *T. aestivum* (USDA) | 1RS,1BL | STARS 02*D. NOXIA*2414-11 | (Peng *et al.* 2007) |
| New | *T. aestivum* (Iran) | 7D | PI626580 | (Valdez *et al.* 2012) |
| New | *T. aestivum* (Tajikistan) | 7D | CI2401 | (Fazel-Najafabadi *et al.* 2015) |
| *Rdn1, 2,3* | *H. vulgare* | 1H,3H,2H | STARS-9577B | (Mittal *et al.* 2008) |

| | | | | |
|---|---|---|---|---|
| *Rdn1, 2* | *H. vulgare* | 1H,3H | STARS-9301B | (Mittal *et al.* 2008) |

* Chromosome unknown