

The biological characteristics and distribution of the greenbug, *Schizaphis graminum*, and Russian wheat aphid, *Diuraphis noxia* (Hemiptera: Aphididae), in Argentina and Chile

ARIEL CLUA¹, ANA M. CASTRO^{1*}, SILVIA RAMOS¹, DANIEL O. GIMENEZ¹, ARACELI VASICEK¹,
HUGO O. CHIDICHIMO² and ANTHONY F.G. DIXON³

¹Department of Natural Sciences, Facultad de Ciencias Agrarias y Forestales, UNLP. CC 31 (1900) La Plata, Argentina; e-mail: amcastro@isis.unlp.edu.ar.

²Department of Plant Production, Facultad de Ciencias Agrarias y Forestales, UNLP. CC 31 (1900) La Plata, Argentina

³School of Biological Sciences. University of East Anglia, Norwich, NR4, 7TY, U.K.

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Abstract. The aphids *Schizaphis graminum* (Rondani) (greenbug) and *Diuraphis noxia* (Mordvilko) (Russian wheat aphid, RWA) were collected from several localities in Argentina and Southern Chile. Clones were established from aphids collected at each location. The host preferences were studied in free choice tests. Biotypes were characterized on the basis of aphid antibiosis and host plant tolerance. The production of sexuals was assessed under natural conditions, from March to November in 1997–2001, at La Plata (34°55' S, 57°57' W). The greenbug distribution ranged from 24°40' to 43°28' S, and was bounded between isothermals 18–20°C and 8–10°C, and isohyets 400–600 mm and greater than 1200 mm. The aphids at all localities were collected from a wide range of cultivated and wild hosts. The biotypes in ten out of thirty-four populations were identified. One population was obligatorily parthenogenetic, the remainder cyclically parthenogenetic. No correlation was found between the region they came from and the period required for the induction of sexuals. RWA was found between 26°50' and 43°28' S, bounded by the isothermals 20–22°C and 8–10°C, and isohyets 400–600 mm and 2000 mm. In Chile, this aphid was only found in Osorno County, which lies on isothermal 8–10°C and is bounded by the isohyets 1000 mm and 2000 mm. Only a few RWA genotypes (clones) produced sexuals irrespective of the host they were collected from, period of the year, region, current host, or the day length and average temperature of the rearing conditions. For the first time, RWA was found infesting cultivated as well as wild oats in South America. At low latitudes, populations of both aphid species were found only infesting wild *Sorghum halepensis* (L).

INTRODUCTION

The greenbug, *Schizaphis graminum* (Rondani) and the Russian wheat aphid, RWA, *Diuraphis noxia* (Mordvilko) are the two economically most important insect pests of wheat and barley throughout much of the Americas. The greenbug is well adapted to conditions in the Americas, whilst the RWA is the last of several recent aphid introductions into Argentina and Chile. Russian wheat aphid was first discovered in Texas, USA, in 1986, and is now widespread in the USA and Canada (Kindler & Springer, 1989; Peairs et al., 1989). This species was first found in Chile in 1988 and in Argentina in 1992 (Ortego & Delfino, 1994). It was found in the main cereal producing region of Argentina, south of Buenos Aires province, in 1994 (Bellone & Almaraz, 1995), and then spread northwards and eastwards infesting barley and wheat (*Triticum aestivum* and *T. durum*) in 1995 (Castro et al., 2000, 2001). Parasitoids and chemicals failed to control this pest, possibly because it causes the leaves to curl tightly, which protects the enclosed aphids (Burd et al., 1998). Although RWA prefers cereal crops (Butts & Paken-dorf, 1984), it also feeds on other cultivated and wild grasses (Kriel et al., 1984; Kindler & Spomer, 1986).

The biology and ecology of both these aphid pests has been studied in the United States (Puterka et al., 1988, 1993; Shufran et al., 1991, 1997, 2000; Shufran & Wilde, 1994; Kieckhefer et al., 1995; Ullah & Peters, 1996). However, no information is available on the distribution or population biology of these

aphids in South America. Important outbreaks of greenbug occurred in 1989, 1990 and 1995 in the centre of Argentina (Arriaga, pers. comm.). In 1998, outbreaks of RWA occurred in Buenos Aires and Córdoba provinces. No change in biotype composition occurred in the greenbug populations collected in the centre of Argentina (Córdoba and Santa Fe provinces) (Almaraz et al., 1990). However, considerable variation was found in their isoenzymes (Gimenez et al., 1991; Castro et al., 1996). The aphids collected from Córdoba and Santa Fe were subsequently analysed for mt (mitochondrial) DNA polymorphisms by Martínez et al., (1993) and Castro (1994). The values of their genetic distances (Nei, 1987) were similar to those found by Powers et al., (1989) for B and C biotypes in the USA. Nonetheless, mtDNA haplotypes of Argentinean and Spanish clones showed no relationship with biotype characterization (Martínez et al., 1993; Castro 1994), which accords with recent results published by Anstead et al. (2002). Since both aphid species are important pests of cereals and virus vectors (Ferreter et al., 1993; Pérez et al., 1995), a better understanding of their biology is likely to facilitate their control.

The objectives of this paper were to: 1) study the distribution of the greenbug and RWA in Argentina and Chile; and 2) determine the variability, within and between populations, in biotype composition, the incidence of sexual reproduction and host preferences.

* Corresponding author.

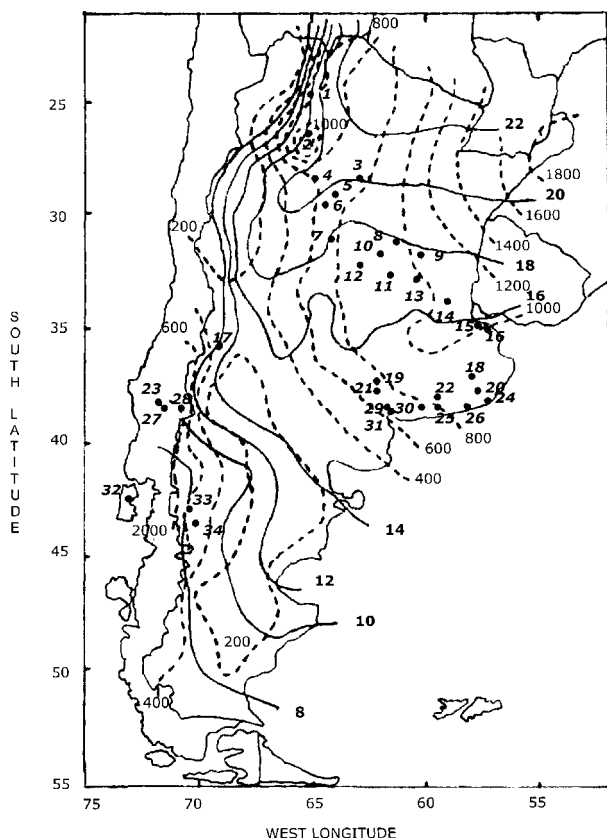


Fig. 1. Isohyets (-----), isothermals (—) and the geographical location of the collection site of *Schizaphis graminum* and *Diuraphis noxia* in Argentina and Chile.

MATERIAL AND METHODS

Aphids were collected from 34 localities in Argentina and southern Chile, including dry steppe (Fig. 1, locations 10, 12, 19, 21, 29, 31, 34), deserts (3 and 4), humid subtropical regions with warm summers (1, 2), localities with a moderate climate and all year rain fall (8, 9, 11, 13–16, 18, 20, 22–26, 30, 32, 33) and undifferentiated mountains (5–7, 17, 27, 28). The designation of the localities follows the classification used by Koppen (1923). Samples of varying numbers were collected from cereal crops and wild grasses every 50 to 100 km (Table 1), in autumn and spring, from 1996 to 1999.

Aphids were reared on susceptible wheat (cv. 'Buck Ombú') and barley (cv. 'Bordenave Ranquelina') plants growing in pots (500 cc) covered with a plastic cage. Individuals from each population (i.e., collected on the same host and locality in each season) were allowed to reproduce parthenogenetically under controlled conditions (20–22°C, 60–70% relative humidity and 16 h photophase) and then 20 to 30 individuals from each population were used to establish single asexual lineages ("clones"). In most of the regions sampled, greenbug and RWA were found accompanied by *Sitobion avenae* (Fabricius), *Rhopalosiphum padi* (Linnaeus), *R. maidis* (Fitch) and *Metopolophium dirhodum* (Walker). There were twelve localities in which RWA was not found, but only one where greenbug was absent (Table 1, locality 28).

Aphid clones were reared separately on different cultivars of cereals (following Porter et al., 1997) and the aphid biotype identified by its antibiotic responses (reproductive rate, mortality and duration of immature period, compared with that recorded for the same clone on a susceptible cultivar; Ramos et al., 1998, 2003) and the tolerance of the plants to the aphid

(chlorotic damage, plant height and number of expanded leaves; Noriega et al., 1998, 2002).

The ability of aphids to produce sexuals was studied by subjecting them to natural conditions from 1st March to 30th November at La Plata (34°55' S, 57°57' W) and recording every other day the presence of sexuals (males and oviparae) and eggs over a four year period, 1997–2001. Populations and clones derived there from were placed outdoors on susceptible plants growing in pots (1000cc) and covered with a plastic, transparent tube with a top made of voile ®.

Aphid host preferences were studied by giving aphids a free choice of plants at the same growth stage (second leaf fully expanded) and each growing in a pot (5 cm diameter × 10 cm high). Ten different host plants were randomly placed in a circle, with their leaves directed towards the centre of the circle. One hundred adult apterous aphids, equivalent to 10 aphids per plant, were placed in the lid of a Petri dish (20 cm diameter), which was inverted over the leaves in the centre of the circle, following the methodology of J. Pettersson, (pers. comm.). In order to avoid the direction of light influencing plant selection, this assay was carried out in the dark. Each combination was replicated ten times. After 2 h and again after 24 h, the number of adult aphids on each plant was recorded. Since both recordings were not significantly different ($P = 0.05$), only the results after 24 h are presented (Table 2). For a particular host, the average of the recordings after 24 h was used (Table 2). The cultivars tested were susceptible cultivars of wheat (*Triticum aestivum* L.) (cv. 'Buck Ombú'), barley (*Hordeum vulgare* L.) (cv. 'Bordenave Ranquelina'), rye (*Secale cereale* L.) (cv. 'Don Enrique'), oats (*Avena sativa* L.) (cv. 'Buck 152'), sorghum (*Sorghum bicolor* M.) (cv. 'NTK147'), triticale (*Triticumsecale*) (cv. 'Pampeano'), tritordeum (*Triticum x Hordeum chilense* M.) (cv. 'Cdb197-2'), bromus (*Bromus catharticus* L.) (cv. 'Miguel'), *Hordeum murinum* (L.) (cv. 'FA194'), *Poa pratensis* (L.) (cv. 'FA4796') and a selection of *Sorghum halepensis* (cv. 'FA1992/96').

Data were analysed by ANOVA, whilst the Duncan's Multiple Range Test was used to compare differences between clones, and the effect of host, region and time of the year when the aphids were collected (SAS, 1998).

RESULTS AND DISCUSSION

Schizaphis graminum

The distribution of the greenbug ranged from 24°40' to 43°28' S, bounded by isothermals 18–20°C and 8–10°C and isohyets 400–600 mm and >1200 mm (Fig. 1).

This aphid was collected from many plant species (Table 1). At low latitudes it was found mainly on *S. halepensis* (localities 1, 2, 4 and 5).

Ten populations included known biotypes (Table 1). Samples from locality 16 included biotypes B, C, E and F, whereas those from localities 15, 18 and 30 consisted only of biotypes B and C in the ratios 1:1, 1.7:1 and 1:2, respectively. In twenty four of the populations the aphids could not be assigned to a biotype (Ramos et al., 1998, 2003).

There was no apparent correlation between the locality from which aphids were collected and the period required for the induction of sexuals. Most of the populations required an extended period for sexual induction, ranging from 120 days (localities 1 and 2) to 180 days (localities 10, 11, 15, 16, 18, 20, 21, 23, 29, 31, 32, 33). The most precocious populations in this respect were those from localities 3 and 26 (36 days), 4 (42 d), 27 (43 d), 22 and 24 (54 d), 25 (63 d), 30 (67 d), and aphids from locality 34 did not produce sexuals.

TABLE 1. The place, geographical location in Argentina and Chile (by latitude and longitude), aphid species, biotypes, number of individuals collected and host plant (wheat: *T. aest.*; barley: *H. vulg.*; oat: *A.sat.*; *Hordeum* spp: *H. murinum*, *H. marinum*, *H. chilense*; Sorghum: *S. halepensis*, *S. bicolor* and *S. sacharata*).

Populations	GPS Data		Aphids	Biotype	Number of individuals on each host plant ¹
	South Lat.	West Long.			
1. Salta	24°40'	65°03'	<i>S. graminum</i>		<i>S. halepensis</i> -5
2. Tucumán	26°50'	65°12'	<i>S. graminum</i>		<i>S. halepensis</i> -5
			<i>D. noxia</i>		<i>S. halepensis</i> -5
3. Ceres	28°36'	62°57'	<i>S. graminum</i>		<i>Hordeum</i> spp-1, <i>S. halepensis</i> -2
			<i>D. noxia</i>		<i>Bromus</i> -2, <i>S. halepensis</i> -2
4. Frías	28°39'	65°09'	<i>S. graminum</i>		<i>S. halepensis</i> -5
			<i>D. noxia</i>		<i>S. halepensis</i> -5
5. Cruz del Eje	29°10'	64°20'	<i>S. graminum</i>		<i>S. halepensis</i> -5
			<i>D. noxia</i>		<i>S. halepensis</i> -5
6. L.V. Mansilla	29°48'	64°43'	<i>S. graminum</i>		<i>Bromus</i> -2, <i>Setaria</i> -1
			<i>D. noxia</i>		<i>Bromus</i> -1, <i>Setaria</i> -1
7. La Cumbre	30°59'	64°29'	<i>S. graminum</i>		<i>Hordeum</i> spp-5, <i>Bromus</i> -5
			<i>D. noxia</i>		<i>Hordeum</i> spp-5, <i>Bromus</i> -5
8. Rafaela	31°10'	61°28'	<i>S. graminum</i>		<i>Sorghum</i> -5
9. Paraná	31°52'	60°29'	<i>S. graminum</i>		<i>T. aest.</i> -6, <i>Sorghum</i> -6, <i>Bromus</i> -6
10. Córdoba Norte	31°40'	62°20'	<i>S. graminum</i>		<i>Sorghum</i> -5, <i>A. sat</i> -5
11. Córdoba Sur	32°40'	61°53'	<i>S. graminum</i>		<i>H. vulg.</i> -5, <i>A. sat</i> -5
			<i>D. noxia</i>		<i>H. vulg.</i> -5, <i>A. sat</i> -5
12. Va. María	32°25'	63°15'	<i>S. graminum</i>		<i>A. sat</i> -5
13. Rosario	32°57'	60°39'	<i>S. graminum</i>		<i>T. aest.</i> -6, <i>H. vulg.</i> -6, <i>Bromus</i> -5, <i>Sorghum</i> -5
14. Baradero	33°49'	59°30'	<i>S. graminum</i>		<i>Sorghum</i> -5, <i>A. sat</i> .-5.
15. Los Hornos	34°55'	57°57'	<i>S. graminum</i>	B, C	<i>A. sat</i> -6, <i>H. vulg.</i> -6, <i>Poa</i> -6
16. B. Bavio	35°05'	57°44'	<i>S. graminum</i>	B, C, E, F	<i>A. sat</i> -6, <i>Sorghum</i> -6, <i>Hordeum</i> spp. -6
17. Malargue	35°30'	69°35'	<i>S. graminum</i>		<i>Rye</i> -3, <i>Bromus</i> -5, <i>Hordeum</i> spp. -5
			<i>D. noxia</i>		<i>Rye</i> -2, <i>Bromus</i> -5, <i>Hordeum</i> spp.-5
18. Ayacucho	37°08'	58°29'	<i>S. graminum</i>	B, C	<i>Hordeum</i> spp.-3, <i>Poa</i> -5.
19. Puán	37°33'	62°46'	<i>S. graminum</i>	C	<i>T. aest.</i> -5, <i>H. vulg.</i> -5, <i>Rye</i> -5
			<i>D. noxia</i>		<i>T. aest.</i> -5, <i>H. vulg.</i> -6, <i>Rye</i> -6, <i>Triticale</i> -5
20. Balcarce	37°50'	58°17'	<i>S. graminum</i>	C	<i>T. aest.</i> -3, <i>H. vulg.</i> -3, <i>Triticale</i> -3
			<i>D. noxia</i>		<i>T. aest.</i> -3, <i>H. vulg.</i> -3, <i>Triticale</i> -3
21. Bordenave	37°51'	63°01'	<i>S. graminum</i>	B, C, F	<i>H. vulg.</i> -5, <i>A. sat</i> -5, <i>Rye</i> -5, <i>Triticale</i> -5
			<i>D. noxia</i>		<i>H. vulg.</i> -5, <i>A. sat</i> -5, <i>Rye</i> -5, <i>Triticale</i> -5
22. G. Chavez	38°02'	60°05'	<i>S. graminum</i>		<i>T. aest.</i> -6, <i>Bromus</i> -6, <i>A.sat</i> -6, <i>H.vulg.</i> -6, <i>T. durum</i> -6
			<i>D. noxia</i>		<i>T. aest.</i> -6, <i>Bromus</i> -6, <i>A.sat</i> -6, <i>H. vulg.</i> -6, <i>T. durum</i> -6
23. Osorno ²	38°13'	72°20'	<i>S. graminum</i>		<i>Rye</i> -6, <i>T.aest.</i> -6
			<i>D. noxia</i>		<i>Rye</i> -6, <i>T.aest.</i> -6
24. Miramar	38°15'	57°50'	<i>S. graminum</i>		<i>T. aest.</i> -5, <i>H. vulg.</i> -5, <i>Bromus</i> -5
25. Tres Arroyos	38°23'	60°17'	<i>S. graminum</i>		<i>T. aest.</i> -6, <i>T. durum</i> -6, <i>H. vulg.</i> -6, <i>Triticale</i> -6
			<i>D. noxia</i>		<i>T. aest.</i> -6, <i>T. durum</i> -6, <i>H. vulg.</i> -6, <i>Triticale</i> -6
26. La Dulce	38°25'	58°42'	<i>S. graminum</i>	F, C	<i>A. sat</i> -6, <i>H. vulg.</i> -6, <i>T. aest.</i> -6
			<i>D. noxia</i>		<i>A. sat</i> -6, <i>H. vulg.</i> -6, <i>T. aest.</i> -6, <i>T. durum</i> -6
27. Temuco ²	38°20'	72°20'	<i>S. graminum</i>		<i>T. aest.</i> -5, <i>A. sat</i> -5
			<i>D. noxia</i>		<i>T. aest.</i> -5, <i>A. sat</i> -5
28. Lonquimay ²	38°26'	71°21'	<i>D. noxia</i>		<i>A. sat</i> -5
29. Cabildo	38°30'	61° 54'	<i>S. graminum</i>	C	<i>T. aest.</i> -5, <i>Tritordeo</i> -5
			<i>D. noxia</i>		<i>T. aest.</i> -4, <i>Tritordeo</i> -5
30. Copetonas	38°30'	60° 28'	<i>S. graminum</i>	B, C	<i>T. aest.</i> -5, <i>H. vulg.</i> -5, <i>A. sat</i> -5
			<i>D. noxia</i>		<i>T. aest.</i> -5, <i>H. vulg.</i> -5, <i>A. sat</i> -5
31. Bahía Blanca	38°44'	62°16'	<i>S. graminum</i>	C	<i>T. aest</i> -5, <i>T. durum</i> -5
32. Castro ²	42°29'	73°45'	<i>S. graminum</i>		<i>T. aest</i> -5, <i>T. durum</i> -5
			<i>D. noxia</i>		<i>Dactylis</i> spp. -5
33. Esquel	42°55'	71° 20'	<i>S. graminum</i>		<i>T. aest</i> -5
			<i>D. noxia</i>		<i>T. aest</i> -5
34. Teka	43°28'	70°50'	<i>S. graminum</i>		<i>T. aest</i> -5, <i>Bromus</i> -5
			<i>D. noxia</i>		<i>T. aest</i> -5, <i>Bromus</i> -5

1. Number of aphids collected: 1 = 10–19; 2 = 20; 3 = 21–49; 4 = 50 ; 5 = 50–100; 6 = > 100

2. Chile

TABLE 2. Number of adult aphids recorded on each of the hosts in the choice test after 24 h for greenbug (A) and RWA (B). Values in brackets are SEs. Values in a column with different letters are significantly different ($P = 0.05$).

A			
Test host	N	Greenbug collected from	
		Cereals*	Grasses*
Barley	10	30.4 ^a (± 4.25)	12.54 ^c (± 1.26)
Wheat	10	22.1 ^b (± 3.20)	9.23 ^d (± 1.03)
Oat	10	10.2 ^c (± 1.32)	15.10 ^b (± 1.14)
Triticale	10	10.3 ^c (± 1.21)	7.10 ^d (± 1.17)
Tritordeo	10	10.0 ^c (± 1.18)	8.09 ^d (± 1.30)
<i>S. bicolor</i>	10	6.10 ^d (± 0.64)	24.23 ^a (± 3.25)
<i>S. halepensis</i>	10	6.09 ^d (± 0.62)	22.12 ^a (± 2.68)
Rye	10	4.17 ^e (± 0.58)	2.03 ^e (± 0.34)
B			
Test host	N	Russian wheat aphid collected from	
		Cereals*	Grasses*
Barley	10	16.83 ^{ab} (± 2.02)	9.54 ^a (± 2.30)
Oat	10	14.17 ^b (± 1.56)	15.46 ^b (± 1.78)
Wheat	10	11.21 ^{cd} (± 1.27)	9.47 ^c (± 1.15)
Tritordeo	10	11.02 ^{cd} (± 1.21)	10.28 ^c (± 1.35)
Triticale	10	9.87 ^{de} (± 1.08)	8.77 ^{cd} (± 1.03)
Rye	10	8.96 ^{ef} (± 0.97)	5.64 ^e (± 0.67)
<i>Bromus</i> spp.	10	7.85 ^{fe} (± 0.84)	7.15 ^f (± 0.82)
<i>Poa</i> spp.	10	7.02 ^g (± 0.87)	7.38 ^{ef} (± 0.88)
<i>Hordeum</i> spp.	10	6.84 ^g (± 0.86)	8.13 ^{de} (± 0.82)
<i>S. halepensis</i>	10	6.29 ^g (± 0.74)	9.68 ^e (± 1.04)

*The host from which the aphids were collected in the field.

Seven populations and their derived clones did not produce eggs, either because only male individuals were produced (localities 6, 7, and 10) or only sexual females (5 and 17). Moreover, only one sex, either male or oviparae, was recorded for clones collected from localities 3 and 4. From the samples collected at locality 3, six clones produced males, six oviparae and eight produced only parthenogenetic individuals. From the samples collected from locality 4, eight clones produced females, four males and nine only parthenogenetic individuals. In the populations from localities 3 and 4, aphids produced both sexes, but not simultaneously, and consequently did not mate.

For ten of the populations studied, every clone produced sexuals and eggs (1, 2, 8, 9, 14, 20, 23, 24, 26 and 32). For eight localities (16, 18, 19, 25, 28–31), 50–90% of the twenty clones produced sexuals and eggs. The aphids from locality 12 produced eggs, but none of the twenty clones derived from this population produced eggs. Eight of the clones only produced oviparae, four only males and the rest only parthenogenetic individuals. None of the clones produced both sexes. Of the ten clones from locality 11, seven produced sexuals, but only four of these produced eggs as three produced only females. Similar results were obtained for the aphids collected at locality 13 (of over fifteen clones, three produced both sexes, two produced only males, and the rest were obligately parthenogenetic), 15 (all twenty clones produced sexuals but only half produced both sexes), 21 and 33 (90% of twenty clones produced sexuals and 80% eggs), 22 (60% of 20 clones produced sexuals and only

20% eggs) and 27 (60% of 20 clones produced sexuals and 30% eggs).

Whether clones produce sexual forms is under genetic control and subject to environmental modulation, as in other cereal aphid species; however, clones producing only sexual females are not recorded (Simon et al., 1997; Rispe et al., 1999). In those populations composed of clones that produced both sexes and others that produced only females, sexual reproduction occurred, but in the populations from localities 6, 7 and 10, which did not produce sexual females, only parthenogenetic reproduction occurred.

The production of sexuals by greenbugs occurred at day lengths shorter than 9h (mean 8.00h \pm 40') ($P \geq 0.01$). For those clones that required 32–70 days before producing sexuals (clones from populations 3, 4, 22, 24, 25, 26 and 27) this was independent of temperature, as day/night temperatures from March to June ranged from 25–17°C/ 20–12°C in La Plata. Moreover, several of these clones produced sexuals under controlled conditions at a constant temperature (20 \pm 2°C) in an insectary (Noriega et al., 2000). Aphids collected at lower latitudes (localities 1, 2) required a shorter day length for sexual production (they started producing sexuals in July when the photoperiod was 9L : 16D, 120 \pm 3 days from 1st March) than those collected at higher latitudes (160–180 days to elapse before producing sexuals: populations 10, 11, 15–18, 20, 21, 23, 29, 31, 32, 33), since they produced sexuals from 1st August to 20th August when day-length is 10 h to 10 h 30'. Greenbugs collected from grasses at lower latitudes (localities 3, 4, 5, 6) did not differ from those from cereals in the induction period required for sexual production (70.6 \pm 6 days vs 68.4 \pm 7.2 days, respectively, $P \geq 0.05$). However, aphids collected from grasses at higher latitudes, locality 34, did not produce sexuals.

Greenbugs collected from wheat and barley preferred these hosts to oats, rye, triticale and tritordeum in free choice tests (Table 2A), whilst those collected from oats showed a significantly lower preference for wheat and barley. Lastly, aphids from grasses preferred sorghums and oats. This host preference may indicate that *S. graminum* is better adapted to sorghums and oats than to wheat and barley. Sorghums include *Sorghum halepensis*, an aggressive weed that can be found in the field throughout the year in regions with warm winters. It may host aphids that could infest cultivated cereals and possibly transmit virus to other economically important crops of the region, although this has yet to be proven.

Diuraphis noxia

RWA was found between 26°50' S to 43°28' S (Table 1), bounded by isothermals 20–22°C and 8–10°C and isohyets 400–600 mm and 2000 mm (Fig. 1). In Chile, this species was only found in Osorno county, which lies on the isothermal 8–10°C, bounded by isohyets 2000 mm and 1000 mm, on crops at an advanced stage of growth in late spring. It was uncommon in the Central Valley and close to the Pacific Ocean, yet abundant above an altitude of 1000 m, where the rainfall is greater than at sea level (Prado, pers. comm.). Ortego & Delfino (1994) report that RWA is found up to an altitude of 1800 m in Chile. Two localities (27 and 28) where RWA was collected in Chile are at 1000 and 2400 m above sea level, respectively, and locality 23 is in the Central Valley. In Argentina, populations were collected at localities 2, 5–7, 17 and 33, which are at different altitudes ranging from 400 to 1200 m.

RWA from locality 34 (43°28' S) was the most southerly population reported, and that found at locality 2 (26°50' S), the most northerly in all of South America (Table 1). The aphid was found in regions with 2000 mm of rainfall (localities 2, 27, 28, 33), which contrasts with the findings in the USA. In the

Northern Hemisphere, this species occurs in areas bounded by the isohyets 750 and 1000mm. On both subcontinents, however, its distribution follows the isotherm 5–10 °C.

In the field RWA colonises a great range of hosts, e.g. rye, barley, triticale and grasses such as *Poa*, *Bromus* and *Hordeum* spp., and in South America even oats, not previously reported as a host (Table 1). At low latitudes, RWA was found infesting *S. halepensis*, and at high latitudes, samples were collected in spring and autumn from cultivated and/or wild grasses.

Only a few of the RWA clones (20%) produced sexuals irrespective of host, the period of year, or region from which they were collected (localities 11, 17, 20, 23, 28, 31). Bellone et al. (1999) report that the low production of sexuals by RWA is independent of the conditions under which they are reared (12% of clones reared under 9.0 h light and 12°C versus 14% of those reared under 9.0 h light and 20 °C). Probably the temperature and extreme short day conditions prevailing at La Plata (34°55' S) are unsuitable for the induction of sexuals, whereas in the field at Mendoza (35°30' S), this species produces sexuals (Ortego, pers. comm.).

RWA collected from cereals and other grasses showed a preference for cereals in the free choice tests (Table 2B), but those collected from *S. halepensis* equally preferred this host, wheat, tritordeum and triticale, as previously reported by Castro et al. (2000). This suggests that *S. halepensis* could be an alternative host to cereals for this aphid.

Genetic structure

Variability in restriction fragment length polymorphisms (RFLPs) of greenbug mtDNA (Martinez et al., 1993; Castro, 1994) and isoenzymes (Giménez et al., 1991; Castro et al., 1996) can be attributed to the long period of colonisation and the existence of sexual reproduction in the region from 24°40' to 42°55' S, and between 57°44' and 73°45' W. One would expect greenbug populations in Argentina and Chile to have a different genetic structure compared to those from the USA, because of the very different and contrasting climates of the two regions.

RWA showed variability in certain traits. This accords with high intra- and interpopulation variability in isoenzymes and allozymes reported by Castro et al. (1997). Such variability may be a consequence of the diverse environments in which both completely parthenogenetic and sexual clones coexist, living on a variety of hosts. Nonetheless, this pest was only recently introduced into the region.

CONCLUSIONS

The present results increase our understanding of the population biology of these two pest aphids in Argentina and Chile, information that may facilitate their control. In greenbug, sexual reproduction is wide-spread throughout Argentina and Chile, and whilst it appears widespread in RWA, only 20% of the clones tested actually produced sexuals. Thus there is the potential for more economically damaging clones to be produced by sexual reproduction. Yet so, further research is required on the relation between host preference, reproductive behaviour and the spatial and temporal distributions of both pest-aphid species in Argentina and Chile.

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