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Diuraphis noxia: reproductive behaviour in Argentina

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Abstract

Diuraphis noxia (Kurdjumov) (Rhynchota Aphididae) is an important aphid pest of wheat and barley crops in many countries. Populations of Russian wheat aphid (RWA) from different origins show different reproductive behaviour, but the situation in Argentina was unknown. The aim of the current research was to determine the reproductive behaviour of RWA in Argentina based on samples from populations at six different localities with contrasting land use, altitude and climate. RWA were collected from cultivated and wild grasses from February to December 2005, and 10-15 colonies of aphids were established by collecting parthenogenetic adult females from each population. These colonies were kept under natural conditions at La Plata (36°36′ South Latitude) from 21 December 2005 to 21 December 2007. In more than half of the colonies, oviparous females and eggs were recorded in both years when temperatures were low and the photoperiod either short or increasing and relatively long. Consequently, oviparous females and eggs were recorded from early autumn (April) until the following spring (October), when day length was 11:33 and 13:44 hours, respectively. In both years the temperature and the altitude at the place of origin were highly correlated with the timing of sexual development. The production of eggs enables RWA to survive periods of adverse conditions and generate variability. Thus, by reproducing sexually, RWA may be able to adapt to new environmental conditions and give rise to new, more aggressive biotypes, which can overcome the current resistant varieties of wheat.

Key words: *Diuraphis noxia*, Russian wheat aphid, sexual reproduction, temperature, photoperiod, altitude.

Introduction

Aphids evolved 200 million years ago. Current species are considered to have descended from species with relatively simple life cycles. Major events in their evolution include: the origin of parthenogenesis and vivipary, the loss of the sexual phase from their life cycle and development of polyphenism (Heie, 1967; Morán, 1992). They can have a complex life cycle (Dixon, 1998) in which the development of mating females (oviparae) and males is induced in autumn by long nights and low temperatures (Lees, 1989).

Sexual morphs mate and lay eggs, often on the same species of plant that the other stages of the life cycle live in summer (monoecious), or on a different species of plant, usually a tree (heteroecious). In spring, the eggs hatch and initiate new parthenogenetic lines. In many holocylic species there are anholocyclic clones that are parthenogenetic all year round. In addition, certain lineages are able to produce only males (androcyclic) or oviparous females (gynocyclic). Some clones produce some sexual individuals and other forms that can over-winter parthenogenetically. These are designated intermediate clones (Llewellyn *et al*., 2003).

Multiple phenotypes in genetically identical individuals, or polyphenism, are commonly induced by environmental stimuli. This allows the organism to maximize its reproduction and fitness (Halkett *et al*., 2004). Numerous authors have studied the influence of photoperiod on reproductive behaviour. They have shown that night length is a key factor in the determination of this behaviour (Lees, 1973; 1987; Steel and Lees, 1977; Simon *et al*., 2002).

The relative frequency of asexual and sexual reproduction within a species varies geographically. This is determined essentially by differences in winter temperatures (Newton and Dixon, 1988; Dedryver *et al*., 2001). Adult and nymphal aphids are unable to survive a severe winter whereas the survival of aphid eggs is unaffected by the severity of winter (Helden and Dixon, 2002). The co-occurrence of holocyclic and anholocyclic clones in populations of the same species in temperate regions is determined genetically (Blackman, 1972).

Aphids are important agricultural pests, mainly because of their reproductive characteristics and their great capacity for exploiting host plants (Powell *et al*., 2006). *Diuraphis noxia* (Kurdjumov) (Rhynchota Aphididae) the Russian wheat aphid (RWA) is a native of Central and Eastern Russia, Afghanistan and Western China (Kiriac *et al*., 1990). In late 1978 the species was accidentally introduced into South Africa and in early 1980 to North America. It now occurs in most wheat- and barley-producing areas in the world, except Australia (Basky and Jordaan, 1997). This aphid was recorded for the first time in Argentina by Ortego and Delfino (1992).

The reproductive behaviour of RWA differs in the different parts of its current world-wide distribution. RWA is reported to be holocyclic in Hungary and Russia (Basky and Jordaan, 1997), and to be gynocyclic and possibly holocyclic in the USA (Kiriac *et al*., 1990), as these authors could not find males and/or eggs. In South Africa, RWA is reported to be anholocyclic (Aalbersberg *et al*., 1987). Oviparae of this aphid were recorded for the first time in Argentina by Ortego (1997) and this was corroborated by Clúa and colleagues in 2004.

Reproductive strategies have a profound influence on the production of new biotypes, which can overcome the current resistant varieties of wheat. Thus, the aim of the current research was to determine the reproductive behaviour of RWA sampled from populations at six different localities with contrasting land use, altitude and climate in Argentina, when reared under the same natural conditions.

Materials and methods

Environmental conditions

RWA were collected from cultivated and wild grasses from autumn (March) to summer (December) 2005 (table 1). Six populations were sampled in Buenos Aires, Mendoza and Neuquén provinces. When the RWA was collected most of varieties of wheat and barley that hosted the aphids were in the heading stage of development (GS 10-11, Feekes scale; Large, 1954), more specifically the flag leaf stage, except the La Plata population, which was collected from wheat at the tillering stage in the fall. The *Bromus* plants, that hosted RWA in early summer in Mendoza and Neuquén, were in the vegetative stage, (table 1).

La Plata (LP) is in a region of Argentina with the highest average rainfall (1200 mm/year), which experiences moderate winters (average temperature of 11 ºC) and summers (average temperature of 20 ºC) (figure 1a). Tres Arroyos (TA) has a lower rainfall (700 mm/year) with an average winter temperature of 7 ºC. The rainfall at Bahia Blanca (BB) is only 500 mm/year, with a similar average winter temperature (7.5 ºC) and higher average summer temperature (23.2 ºC). Nonetheless, this locality has significantly different minimum (−11.8 ºC) and maximum (43.8 ºC) temperatures. These localities are in the Pampean plain region. Mendoza (M) is a very dry region (less than 400 mm/year) with summer rain, cool winters (average minimum temperature 3 °C) and hot summers (average maximum temperature 31 ºC). Chos Malal (CHM) is the highest place (864 m asl) where aphids were collected. It has an average minimum winter temperature of 8 ºC, summer temperatures can reach 25 ºC and is the driest region with only 200 mm of rain/year. Neuquén (N) with an average winter temperature of 5 ºC and a maximum temperature in summer of 20 ºC has 600 mm of rain per year. The last three localities are in the mountains and the aphids there were collected from wild grasses in undisturbed habitats.

Populations

The reproductive strategy of RWA was studied using 10-15 colonies (replicates) from each population. Each colony was composed of the progeny of a single parthenogenetic adult collected from a particular population. The females were caged individually on a mixture of plants of susceptible cultivars of wheat and barley. To prevent cross-contamination of the colonies, each was placed in a transparent plastic cage with ventilation holes covered with a fine mesh.

In December 2005 the colonies were reared outside at La Plata exposed to natural changes in temperature and day length (figure 1a) and the presence of sexual or/and asexual forms was recorded every other day. The oviparous females were identified with the aid of a stereomicroscope (42x). When 50% of the leaf area of the plants was damaged by the aphids, they were replaced by healthy plants onto which the young forms were transferred using a paint brush.

When the oviparous females were identified in a colony, they were transferred and isolated on another individually labelled plant in order to verify if they laid eggs and record the birth of fundatrices. The colonies were monitored continuously from 21 December 2005 to 21 December 2007. An analysis of variance was performed on the variation in the traits studied (SAS, 1998) and the differences between the mean values assessed with the standard error (SE).

Procedures

For every clone the date on which the first oviparous female was observed (D_F), the photoperiod (hours of light) (P_F) and the mean temperature at that time (MT_F) were recorded. Similarly, the date on which the last ovipara was observed (D_L), the photoperiod (hours of light) (P_L), the mean temperature at the time (MT_L) and the percentage of facultative parthenogenetic clones (FP), were recorded. The MT_F and the P_F were correlated with the date of the last ovipara (D_L). Similarly, the number of oviparous females produced by each population in 2006 and 2007, the number of days between the appearance of the first ovipara, the peak number of oviparae and the appearance of the last ovipara, were recorded. Each factor was correlated with the average temperature of the coldest months (June, July and August) and the altitude of the place of origin, using SAS (1998) statistical software.

Table 1. Locality, province, geographical location, altitude, average annual rainfall and host plant from which the aphid was collected, and the number of colonies of RWA from each location established and maintained for two years under natural conditions of temperature and day-length at La Plata (36°36' South Latitude).

Locality	Province	Coordinates	Altitude m asl	Average annual rainfall (mm)	Host plant	Number of colonies
Tres Arroyos	Buenos Aires	38°22'S - 60°16'W	99	700	*Hordeum vulgare*	10
Bahía Blanca	Buenos Aires	38°44'S - 62°14'02"W	83	500	*Triticum aestivum*	15
Neuquén	Neuquén	39°56'S - 71°05'W	765	600	*Bromus* sp.	10
Chos Malal	Neuquén	37°20'51"S - 70°17'01"W	864	200	*Hordeum* sp.	10
Mendoza	Mendoza	33°08'S - 68°28'W	666	400	*Bromus* sp.	10
La Plata	Buenos Aires	34°54'24"S - 57°55'56"W	15	1200	*T. aestivum*	10

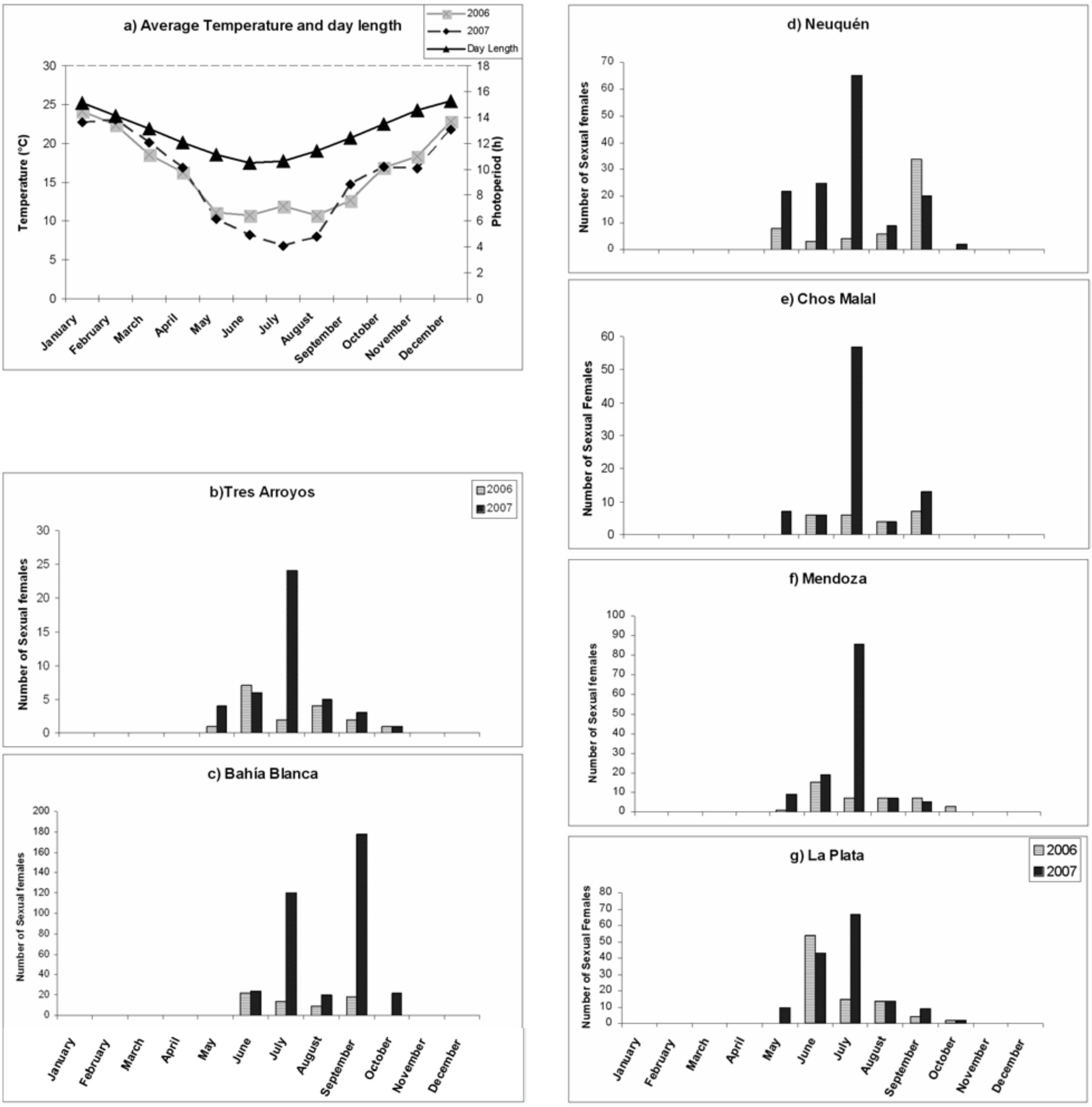

Figure 1. (a) Monthly average photoperiod and temperature in 2006 and 2007 at La Plata (36°36' South Latitude); (b-g) Number of oviparous females produced by the RWA colonies established at La Plata from aphids collected at: (b) Tres Arroyos, (c) Bahía Blanca, (d) Neuquén, (e) Chos Malal, (f) Mendoza, (g) La Plata.

Results

Most colonies produced sexual forms but there were highly significant differences between years and colonies (ANOVA not shown). In 2006, 50% to 70% of the colonies produced sexual forms with a significantly greater proportion in 2007 (60% to 100%). In both 2006 and 2007, the total numbers of oviparous females produced by the populations collected from wild grasses (in Neuquén and Mendoza) and cultivated cereals were significantly different (SE, $P \leq 0.05$) (table 2). The highest numbers of oviparae were recorded in both years in the colonies from BB and LP, which were originally collected from wheat. Similarly, the lowest numbers of oviparae were recorded in the colonies from TA and CHM, originally collected from barley (table 2).

Sexual reproduction was first recorded (D_F) in April in 2007 and May in 2006 when day length was short and the last sexual individuals (D_L) were recorded in October when day length was long (table 2). In 2006 the D_F of the Tres Arroyos and Chos Malal colonies differed significantly and in 2007 that of Bahía Blanca was significantly lower than those of the Neuquén, Chos Malal and Mendoza colonies (table 2). The aphids originally collected from wild *Bromus* did not differ in D_F in the two years nor did those collected from cereals at La Plata and Chos Malal. The D_L of the colonies from Neuquén, Tres Arroyos, Mendoza and La Plata differed

Table 2. Photoperiod and thermal requirements for the induction of oviparae in the colonies of RWA collected from plants at six locations in Argentina.

2006	Tres Arroyos	Bahía Blanca	Neuquén	Chos Malal	Mendoza	La Plata	SE
FP (%)	60	60	70	60	50	60	--
Total oviparae	17_{f*}	63_b	55_c	23_e	40_d	89_a	1.638
D_F	147 (05/19)	166 (06/05)	157 (05/29)	168 (06/09)	154 (05/26)	160 (06/01)	7.78
P_F (h)	11:06	10:50	10:55	10:49	10:58	10:53	0.36
MT_F (°C)	11.1	10.8	11.1	10.8	11.1	10.8	0.16
D_L	285 (10/04)	280 (09/27)	273 (09/22)	276 (09/19)	285 (10/05)	285 (10/06)	5.2
P_L (h)	13:25	13:16	12:59	12:51	13:27	13:30	0.54
MT_L (°C)	16.8	16.8	16.8	12.7	16.8	16.8	2.14
Eggs (months)	July	June to October	August to September	August	July	July to September	
2007	Tres Arroyos	Bahía Blanca	Neuquén	Chos Malal	Mendoza	La Plata	SE
FP (%)	70	100	100	70	100	90	--
Total oviparae	43_{e*}	353_a	138_b	87_d	126_c	145_b	3.29
D_F	140 (18/05)	125 (04/27)	158 (05/30)	167 (05/29)	157 (05/29)	138 (05/08)	15.7
P_F (h)	11:08	11:40	10:54	10:55	10:55	11:22	0.54
MT_F (°C)	10.3	16.9	10.3	10.3	10.3	10.3	2.14
D_L	287 (14/10)	278 (09/30)	280 (09/30)	269 (15/09)	265 (09/15)	296 (14/10)	5.01
P_L (h)	13:44	13:16	13:16	12:44	12:44	13:44	0.61
MT_L (°C)	17	14.7	17	14.7	17	17	3.74
Eggs (months)	July	June to October	August to September	August	July	July to September	

*Same letters indicate no significant difference.

D_F: Number of days to when the first ovipara was recorded in 2006 and 2007 (between brackets the date of appearance of the first ovipara); **P_F**: Photoperiod (hours of light) when the first ovipara was recorded; **MT_F**: Mean Temperature when first ovipara was recorded; **D_L**: Number of days to when the last ovipara was recorded in 2006 and 2007 (between brackets the date of appearance of the last ovipara); **P_L**: Photoperiod (hours of light) when the last ovipara was recorded; **MT_L**: Mean Temperature when the last ovipara was recorded; **FP**: percentage of Facultative Parthenogenesis; **SE**: Standard Error.

significantly in 2006. In 2007 the D_L of the Mendoza and Chos Malal colonies differed significantly from those of the other colonies (table 2).

Since most of the colonies reproduced sexually during this period, the photoperiod requirements for the induction of sexual forms, (P_F, P_L) were similar in both years (table 2). Similarly, the temperature requirements of the colonies over this period (MT_F, MT_L) in 2006 were not significantly different (table 2). In 2007, only the MT_F for the colonies that originated from Bahía Blanca was significantly higher than that of the colonies that originated from other localities. There were no differences in P_F, P_L, MT_F and MT_L of the colonies that originated from aphids collected from cereals and wild grasses (table 2).

Of the colonies that originated from Tres Arroyos (TA), 60% in 2006 and 70% in 2007 produced oviparous females and eggs, and the remainder produced only parthenogenetic forms in both years. Those colonies that produced sexual forms were mainly facultatively parthenogenetic, since only a small proportion of the individuals developed into sexual forms (table 2). Eggs were observed in July when the day length was 10 h 52 min and mean temperature 11.9 ºC (table 2). The beginning and the end of the production of sexual forms by the colonies from TA were associated with similar day lengths in both years (P_F) (table 2). These colonies produced oviparae from June to October in 2006. The period was similar but more sexual females were produced in 2007 (figure 1b). Three colonies reproduced parthenogenetically continuously. Another colony that was parthenogenetic in the first year developed sexual forms in 2007. The number of sexual forms increased tenfold in July (figure 1b) after day length started to increase (from 21 June) and production of oviparae continued until 14 October (table 2).

In 2006 six colonies (60%) from Bahía Blanca (BB) were facultatively parthenogenetic and all were in 2007 (table 2). The production of oviparous females in June and August in 2007 (figure 1c) was 5.6 times greater than in 2006 (table 2). Oviparous females were recorded over a period of 114 days in 2006 and in 2007 the sexual morphs started maturing 38 days earlier and matured over a period of 156 days (figure 1c). Eggs were recorded on plants from June to October in both years (table 2). On 13 September 2006 a fundatrix hatched from an egg.

Of the colonies from Neuquén (N), 70% were facultatively parthenogenetic in the first year and all produced sexual forms in 2007 (table 2). Oviparous females were produced by the N colonies from May to September in both years (figure 1d). As for the colonies from the TA and BB, the first oviparous females were recorded when the day-length was short (May) (table 2) but continued even when the photoperiod increased (from July to September) (figure 1d). Eggs were detected in August and September in both years (table 2).

Table 3. Correlation coefficients of the relationships between the time (days) to the appearance of the first oviparous female recorded for the colonies of RWA from each of the six locations, and photoperiod (**P_F**) and temperature (**MT_F**). P value is in parentheses.

Correlation coefficients	Tres Arroyos	Bahía Blanca	Neuquén	Chos Malal	Mendoza	La Plata
P_F 2006	−0.692 (0.006)	−0.650 (0.01)	−0.274 (0.19)	−0.646 (0.01)	−0.697 (0.005)	−0.606 (0.01)
P_F 2007	−0.632 (0.01)	−0.541 (0.03)	−0.693 (0.006)	−0.530 (0.03)	−0.566 (0.02)	−0.716 (0.004)
MT_F 2006	−0.540 (0.03)	−0.667 (0.008)	−0.445 (0.07)	−0.683 (0.007)	−0.708 (0.004)	−0.538 (0.03)
MT_F 2007	−0.704 (0.005)	−0.637 (0.01)	−0.727 (0.003)	−0.585 (0.02)	−0.621 (0.01)	−0.763 (0.001)

P_F: Photoperiod when the first ovipara was recorded; **MT_F**: Mean Temperature when first ovipara was recorded

Of the colonies from Chos Malal (CHM), 40% were obligatorily parthenogenetic in 2006, whereas a small proportion of the individuals in the other colonies reproduced both sexually and parthenogenetically (table 2). Most of these colonies were obligatorily parthenogenetic in 2007. Some of the colonies that originated from CHM were similar to those from TA, in producing a low proportion of oviparae in both years (figure 1e), compared to those from the other locations (table 2). In both years, the temperature associated with the induction of the last sexual female was lower for the colonies from CHM than those from the other locations (table 2). The period over which oviparous females were induced was shorter than that recorded for colonies from other locations: 102 days and 108 days in 2006 and 2007, respectively. Eggs were recorded in August in both years (table 2).

Compared to the colonies from other locations, a lower percentage (50%) of those from Mendoza (M) reproduced parthenogenetically in the first year (table 2). In 2007, every colony was facultatively parthenogenetic and produced a three-fold greater number of oviparous females than in 2006 (table 2). The last oviparous female was recorded on 5 October, when day length was long (13 h 27 min, figure 1f). In 2007, oviparous females were recorded one month earlier than in the first year and produced continuously from June to 15 September, when the last sexual forms were recorded when the day length was 12 h 55 min, (table 2). Eggs were recorded in July in both years (table 2).

As for most of the populations analyzed, 60% of the La Plata (LP) colonies were facultatively parthenogenetic in 2006 and 90% in 2007 (table 2). Sexual reproduction started one month earlier in 2007 (figure 1g), probably because the mean temperature in May was rather similar to that recorded in June 2006 (figure 1a). Eggs were produced between July and September in both years (table 2).

For the colonies from Tres Arroyos, the production of sexual forms was significantly associated with the day length in both years and the mean temperature in 2007 (table 3). As lower average temperatures were recorded in 2007 (figure 1a), it is likely that this accounted for the increase in the production of sexual females in that year. For the colonies from Bahía Blanca, the number of days to the appearance of the first oviparous female was significantly correlated with the photoperiod and the temperature in both years (table 3). For the colonies from Neuquén, the number of days required for the induction of the first oviparous female was negatively correlated with temperature and photoperiod only in 2007 (table 3). Correlation coefficient values recorded for the colonies from Chos Malal and Mendoza for both, temperature and photoperiod, in 2006 were significantly higher than those recorded in 2007 (table 3). The highest correlation coefficients were recorded for the colonies from La Plata in the second year (table 3).

The correlation analysis of the results for all colonies showed that oviparous production in 2007 was correlated negatively with the mean temperature of the coldest months (June, July and August) at the places from which the colonies originated (r: −0.75, P: 0.043). This correlation indicates that the lower the temperature at the place of origin, the higher the production of sexual individuals. There was also a significantly negative correlation between the number of oviparous females and the period of time over which they were produced (r: −0.99, P: 0.0001 in 2007). This relation was not significant in 2006 (r: −0.70, P: 0.06). The numbers of oviparous females produced in 2006 and in 2007 were significantly correlated (r: 0.84, P: 0.018), thus, this trait may be inherited. In 2006, the number of days that elapsed before the highest production of oviparae occurred, was significantly correlated with the mean temperature at the place of origin (r: −0.81, P: 0.025), with the lower the temperature the longer period. Similarly, the altitude of the place of origin was negatively correlated with the number of days to the appearance of the last oviparae in 2006 (r: −0.86, P: 0.014) and the first oviparae in 2007 (r: −0.93, P: 0.0035), with the higher the altitude the lower the number of days to the appearance of the last and the first sexual individuals, respectively. The mean temperature at the place of origin was negatively correlated with altitude at the place of origin (r: −0.94, P: 0.0026) (table 3).

Discussion

Influence of environment on reproductive behaviour

The coexistence of both sexual and asexual reproduction within the same species is uncommon. Our results indicate that obligatory and facultative parthenogenesis can coexist in RWA populations in Argentina. When the colonies from different localities were transferred to the same place, the environmental conditions in the new place induced different percentages of sexual individuals in both years. Similar results are reported by Halkett *et al.* (2006) for *Rhopalosiphum padi* L. (oat aphid), which produced sexual and facultative parthenogenic lineages that coexisted in time and space with asexual lineages.

Several authors have studied the role of environmental factors in regulating the production of sexual morphs. Photoperiods below certain critical values, combined with low temperature, induce sexual reproduction and the production of eggs prior to the onset of winter (Dixon, 1972; Lees, 1973; 1987; 1989). In Argentina, the day length starts to increase from 21st June. In this study the production of oviparae started in April when day-length was short (11:33 h) and continued until October (13:44 h). Eggs were recorded only in winter (July-August) for three of the populations (Tres Arroyos, Chos Malal and Mendoza), but the other populations continued to produce eggs until September/October (spring). Clonal differences in the tendency to produce sexual or asexual morphs when subjected to identical environmental conditions are reported for several species of aphid (Blackman, 1971; MacKay, 1989; Mittler and Gorder, 1991; Wegorek and Dedryver, 1987; Papura *et al.*, 2003; Vorburger *et al.*, 2003; Vorburger, 2004).

Moreover, in both 2006 and 2007, the number of days to when the first and the last oviparae matured and the peak in the production of sexual forms, were strongly associated with the mean temperature and altitude at the place of origin of the colonies. That is, when reared under the same conditions the differences in the reproductive behaviour of the different colonies reflected the differences in the environmental conditions at their places of origin. On the other hand, the production of oviparous females was associated with the host from which the colonies were collected. In both years those aphids that were collected from barley produced the fewest oviparous females and those collected from wheat the greatest number. As all the colonies were reared on wheat it is likely this influenced the number of sexuals they produced. Moreover in this study RWA was reared continuously on the same host whereas in the field this species often colonizes a different wild or cultivated host when the host matures. Rearing this aphid on a different host in the two years might have resulted in it producing more oviparae and becoming better adapted to the new environment (temperature, photoperiod and host).

There are several biotypes of RWA in South Africa and USA, where genetic diversity is rare or absent (Shufran and Payton, 2009). Only RWA biotypes 1 and 2 are recorded in Argentina, which are characterized by different sets of *Dn* resistance genes (Almaraz *et al.*, 2003; Ricci *et al.*, 2006), which is interesting, given the fact that no RWA-resistant wheat varieties are grown in Argentina. It is likely that the genetic variation in RWA in Argentina is due to sexual reproduction, which permits aphids to adapt to different climates and a wide range of hosts.

Comparison of populations

Some colonies, mainly those from the Andes (Neuquén, Mendoza and Chos Malal), are from populations that are probably holocyclic at their place of origin because of the extreme climate conditions prevailing there. The colonies from other populations could be functionally parthenogenetic, although every colony produced sexuals. Thus, sexual reproduction might be the mechanism by which this aphid species adapts to different environments. *D. noxia* is a monoecious species living on winter and summer gramineae in Argentina (Clúa *et al.*, 2004) and it is likely that its phenotypic plasticity enabled it to adjust its life cycle to that of its hosts (coevolution) and to different environmental conditions.

Of the colonies established from samples of *D. noxia* collected in the former Soviet Union, more than half of those collected in Moldova and the Crimea produced sexual forms. In contrast, only nine percent of those collected from close to Odesa and Kherson in the Ukraine, produced sexuals. In addition, less than 1% of those collected in Idaho and Oregon produced oviparae (Kiriac *et al.*, 1990). *D. noxia* collected in Moldova and reared at 20 ºC and an 8:16 (L:D) photoperiod produced sexual forms, but those collected from Syria, France, Turkey, Jordan and Kirghizstan did not. The latter only produced sexuals and eggs at 16 ºC and a phothoperiod of 14:10 (L:D) (Kiriac *et al.*, 1990). In Argentina similar temperatures and photoperiods induced RWA populations to produce sexuals.

Conclusions

Phenotypic plasticity may have enabled RWA to adapt to the very different environments and hosts in Argentina. It is possible that selection, acting on the extent and timing of sexual reproduction, enabled this species to synchronize its life cycle with the availability of potential host plants at a wide range of localities experiencing very different environmental conditions. Sexual reproduction and facultative parthenogenesis contribute to the genetic variability and the evolution of noxious biotypes of *D. noxia* in Argentina.

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