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Alatae production in the cereal aphid Sitobion avenae

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Abstract

Crowding of L_3, L_4 and apterous adults of *Sitobion avenae* results in an increase in production of alate offspring. Crowding of L_1 and L_2 results in a slight increase in their number becoming alatae. Fewer alatae are produced by apterae on ears before and during flowering than in later ear developmental stages or on seedling leaves.

On ears before and during flowering reproduction was higher than on the leaves and later ear growth stages. Brown forms often produce alatae less readily than green forms.

Additional keywords: Crowding, host plant, colour form.

Introduction

The development of predictive models of cereal aphid population development (Rabbinge et al., 1979; Carter, 1978) necessitates study of emigration. Aphid populations reach their peak before doughy ripe (80 on decimal scale) (Ankersmit and Carter, 1981) and collapse under the combined effects of natural enemies, disease and emigration. Host plant effects can be expected but, as with other aphids, crowding too may play a role in development of winged emigrants. Therefore the importance of nutritional and contact stimuli in the production of alatae by Sitobion avenae on winter- or summer wheat was studied.

Material and methods

Stock cultures of a green strain of *S. avenae* were maintained on seedlings of winter wheat (cv. Arminda) in a greenhouse at 18 °C and at a daylength of 18 h. In the autumn of 1978 and 1979 one aphid was taken from this culture and with its offspring a clone was established that was kept in a climate room at 18 °C, 18 h of light per day and 70% relative humidity. This clone consisted of 100 individually reared aphids. On the first day that 100 newly born larvae were found a new solitarily reared generation was started. Experiments were done with these aphids or their offspring. Crowding experiments were always started on the leaves of 2-3 week old wheat seedlings, cv. Arminda, in leaf cages as were described by Vereijken (1979).

Crowding was studied by confining 10 aphids for 24h at 18 °C in a glass vial (diam. 15 mm, height 50 mm) and keeping 10 others for a similar period separately in similar vials.

Effects of host plant were studied by keeping aphids in the leaf cages on seedling leaves for 2 days; subsequently, they were transferred to the specific plant stage to be studied. Developmental stages of summer wheat, cv. Opal, reared in the greenhouse under artificial light, were used for this purpose.

Results

Morph production without crowding. Stability in morph production without crowding was studied in the culture of 100 solitarily reared aphids. Production of apterous offspring varied considerably (Table 1). It was 89% (mean) in 1978-1979 and 66% in 1979-1980. During the course of the study it varied from 40 to 100%. This variability in type of morph produced was found in many trials.

Morph production with crowding. Crowding effects in L_1 were tested with seven replicates of 10 aphids each and in L_2 with five similar replicates. The treatment caused some mortality in transferred aphids. Out of a total of 70 crowded L_1, 9 died; in L_2 out of 50 aphids in the uncrowded group, 9 died and among the crowded ones 7 died.

The results (Table 2) indicated a small increase in the number of L_1 and L_2 developing into alatae because of crowding (χ^2 test $P < 0.01$). Crowding of L_2

Table 1. Percentage apterous *S. avenae* when reared almost completely isolated on leaves of 2-3 week old wheat seedling (L18:D6), 18 °C.

Date	Apterae (%)	Date	Apterae (%)
20 Sept. 1978	91	6 Nov. 1979	53
27 Sept.	77	16 Nov.	51
6 Oct.	96	27 Nov.	82
14 Oct.	89	10 Dec.	62
23 Oct.	79	21 Dec.	59
3 Nov.	94	2 Jan. 1980	79
13 Nov.	91	15 Jan.	40
22 Nov.	90	25 Jan.	70
30 Nov.	81	4 Feb.	100
8 Dec.	97	14 Feb.	60
18 Dec.	98		
27 Dec.	88		
4 Jan. 1979	90		
15 Jan.	92		
23 Jan.	82		
1 Feb.	100		
9 Feb.	72		
16 Feb.	83		
24 Feb	100		
3 March	98		

Tabel 1. Percentage ongevleugelde A. avenae onder solitair op 2-3 weken oude tarwezaailingen gekweekte bladluizen (L18:D6), 18 °C.

Table 2. Postnatal effect of crowding 10 L_1 or 10 L_2 on numbers becoming alatae.

Offspring	Stage crowded					
	L_1		N[1]	L_2		N[1]
	apterae	alatae		apterae	alatae	
No crowding	67	1 (1.5)[2]	7	32	9 (22)	5
Crowding	49	12 (17)	7	16	27 (63)	5

[1] N = number of trials with 10 aphids each at beginning
[2] In parentheses, percentage alatae

Tabel 2. Postnatale effect van 'crowding' 10 L_1 of 10 L_2 op het aantal dat gevleugeld wordt.

Table 3. Total numbers alatae and apterous offspring produced in 5 days by four groups of 10 crowded and 10 single apterae treated during L_3 and L_4.

	L_3		L_4	
	apterae	alatae	apterae	alatae
No crowding	223	195 (47)[1]	425	185 (30)
Crowding	63	364 (85)	77	477 (86)

[1] In parentheses: percentage alatae.

Tabel 3. Totaal aantal gevleugelden en ongevleugelden dat in 5 dagen wordt geproduceerd door vier groepen van 10 'crowded' en 10 afzonderlijk gehouden ongevleugelden behandeld als L_3 en L_4.

Table 4. Percentage alatae produced by apterae before and for the 4 days after a crowding stimulus when 3 days old. In each trial 20 aphids were used.

	Age of apterae			
	1-2 days		4-7 days	
	alatae (%)	N[1]	alatae (%)	N[1]
Trial 1	60	220	91	321
2	34	202	64	291
3	1	189	57	252
Total	33	611	72	864

[1] N = total number of aphids born (L18:D6), 18 °C and 80% r.h.

Tabel 4. Percentage alaten geproduceerd door apteren vóór en gedurende 4 dagen na een 'crowding' prikkel toen ze 3 dagen oud waren. In iedere proef zijn 20 dieren gebruikt.

resulted in more alatae produced than apterae but not with L_1. Singly reared *S. avenae* also often produce several alatae (Table 1). Crowding of L_1 or L_2 therefore stimulated the alate course of development but only in the case of L_2 the major part became winged.

Crowding of L_3 or L_4 apteriform always caused a significant (χ^2 test $P < 0.01$) increase in the number of alate offspring produced (Table 3) but did not change the morph of the treated larva.

Crowding of apterae 2 days after the final moult always increased the percentage of alatae produced over the next 4 days (Table 4).

Host plant effects. Apterous adults placed for 2 days on winter wheat seedlings in cages and then transferred for 4 days to a developmental stage of the ear (Table 5) produced significantly more alate offspring on milky or doughy ripe ears than on ears before or during flowering ($P \leqslant 0.05$, t-test after angular transformation of percentages). On doughy ripe ears almost all of the offspring consisted of alatae. On ears before flowering and in the flowering stage fewer alatae were produced than in other stages. Reproduction on ears in middle flowering is somewhat higher than on leaves, milky ripe and doughy ripe ears ($P \leqslant 0.05$, t-test).

Alatae tested similarly always remained apterae producers, but reproduction was lower on older developmental stages of wheat (Table 6). Alatae reproduction was always lower than the reproduction by apterae. It was much higher on seedlings leaves than on the ears in different growth stages.

Table 5. Percentage alatae and total number of offspring produced by 60 apterae on different developmental stages of wheat when 1-2 days and 3-6 days old. Numbers in a column followed by the same letter are not significantly different ($P < 0.05$, t-test).

Transfer	Age of apterae (days)					
	1-2 (on leaf)			3-6 (on other crop stages)		
	alatae (%)	N[1]	M[2]	alatae (%)	N[1]	M[2]
From leaf to leaf	52	531	8.9	70^{af}	757^{a}	12.6
From leaf to ear before flowering	45	544	9.0	30^{bc}	840^{ab}	14.0
From leaf to ear middle flowering	50	548	9.0	36^{ac}	852^{e}	14.2
From leaf to watery ripe	54	583	9.7	71^{ef}	796^{ab}	13.3
From leaf to milky ripe	50	542	9.0	87^{d}	717^{ad}	12.0
From leaf to doughy ripe	44	535	9.0	94^{d}	473^{c}	7.9

[1] N = total number of aphids born.
[2] M = mean number born per adult.

Tabel 5. Percentage alaten en totale aantal nakomelingen geproduceerd door 60 apteren, op verschillende ontwikkelingsstadia van tarwe, als ze 1-2 en 3-6 dagen oud zijn. Getallen in een kolom gevolgd door dezelfde letter zijn niet betrouwbaar verschillend. ($P \leqslant 0.05$, t-test).

Table 6. Number of offspring produced by individual alatae on different developmental stages of wheat when 1-2 days and 3-6 days old.

Transfer	Age of alatae (days)	
	1-2	3-6
From leaf to leaf	4.0	8.3
From leaf to ear (middle flowering)	3.5	4.0
From leaf to ear (watery ripe)	3.6	3.7
From leaf to ear (milky ripe)	4.4	2.7
From leaf to ear (doughy ripe)	4.1	2.1

Tabel 6. Aantal nakomelingen geproduceerd per gevleugelde bladluis op verschillende ontwikkelingsstadia van tarwe als ze 1-2 en 3-6 dagen oud zijn.

Table 7. Total number of offspring and percentage alatae produced by brown and green forms collected in the field and kept for 4 days in a leaf cage on a seedling leaf at about 20 °C and natural daylength.

Date	Number collected	Morph	Number of offspring	Alatae (%)
19 June	19	Alatae green	275	4.4
	18	Apterae green	237	70.5
	18	Apterae brown	216	36.6
22 June	14	Apterae green	318	92.8
	19	Apterae brown	303	53.8
26 June	14	Apterae green	153	77.1
	16	Apterae brown	260	63.5
29 June	13	Apterae green	268	80.1
	12	Apterae brown	220	48.2

Tabel 7. Totaal aantal nakomelingen en percentage gevleugelden geproduceerd door bruine en groene vormen van S. avenae die in het veld waren verzameld en 4 dagen afzonderlijk in een bladkooi op zaailingblad waren gehouden bij 20 °C en natuurlijke daglengte.

Colour forms and development of alatae. Brown and green apterae and alatae were collected in the field and kept isolated in leaf cages on 2-3 week old seedlings for 4 days. Table 7 shows that green alate morphs produced predominantly apterous offspring. The green apterae had fewer apterous descendants than the brown ones.

Solitary reared colour forms crowded in vials when 3 days old gave a high alate production in the green form and a lower one in the dark brown form (Table 8). The light brown form at first resembled the green form and then the brown form. Crowding has only little effect in this form but it produced more alatae with and without crowding than the dark brown form.

Table 8. Percentage and mean number of alatae produced per aphid (apterae) by three colour forms when 4-8 days old with or without a 24-h crowding stimulus when 3 days old. Within a trial, numbers in the same row or the same column followed by the same letter are not significantly different (P < 0.05 t-test).

	Colour form					
	green		light brown		dark brown	
	alatae (%)	number	alatae (%)	number	alatae (%)	number
Trial 1						
No crowding	77	6.8^{a}	78	7.4^{a}	8	0.8^{c}
Crowding	91	9.1^{b}	86	8.0^{ab}	54	5.1^{d}
Trial 2						
No crowding	63	9.9^{a}	8	1.0^{c}		
Crowding	93	14.9^{b}	17	2.6^{c}		

Tabel 8. Percentage en aantal gevleugelden geproduceerd per bladluis (ongevleugeld) door drie kleurvormen als ze 4-8 dagen oud waren, met of zonder 'crowding'-prikkel op de derde dag.

Discussion

Both crowding and host plant stage were important in morph determination. Crowding affected all instars but had a strong prenatal effect on L_3 and L_4 and a weak postnatal effect on L_1 and l_2. Adults too could switch to higher alatae productions in response to crowding or by altering the host plant developmental stage upon which the aphids were feeding. What effects were most important in modelling aphid population development? Table 5 showed that during milky ripe stage only few apterous aphids would produce apterous offspring but alatae (Table 6) were always apterae producers. Field counts (Rabbinge et al., 1979) and laboratory studies (Walters and Carter, 1981) indicate no or only minor immigration after flowering. The chance for apterae production by either apterae or by immigrated alatae on the ears of milky ripe wheat therefore seems small. Production of apterae on these growth stages has a poor survival value for the population as the plant soon becomes unsuitable as a host and it would take too much time to obtain alate offspring from apterae born on these late wheat stages. The host plant stage also affected reproduction (Table 5). On ears in growth stage 60-70 (preflowering and flowering) a high rate of reproduction was reached with a low percentage of alatae offspring. This confirmed Watt's results (1979) which also indicated the decline in reproduction during milky ripe. The ripening host plant then stimulated the production of alatae which complete development in time to escape the deteriorating habitat of ripening wheat. Even under uncrowded conditions such a course of events would occur and consequently the host plant stage gave the best cue for modelling alatae production by *S. avenae*. Crowding seemed less safe as a signal for deteriorating host plant conditions. Watt and Dixon (1981) found no good correlation between first occurrence of alatae and earlier aphid density. The ecological significance of crowding is probably more for escape from natural enemies. Several of these accumulate near big colonies of cereal aphids and are then responsible for the aphid population crash.

Indications were that brown forms produced fewer alatae than green forms. This agrees with Phillips' (1916) observation that brown forms are commoner than green near the end of the epidemic. In our observations 1978 and 1981, however, this relative increase in brown forms did not always occur. It was absent in 1978 when throughout the aphid epidemic about 25% of the population was brown but not in 1981 when somewhat more brown forms were found at the end. Within the group of brown forms differences existed (Table 8). The light brown forms are closer to the green forms in alatae production than to the dark brown forms. As the origin of colour difference is still obscure (green forms can be born to brown mothers) prediction of colour form composition of the population and its impact on alatae production in *S. avenae* is still impossible.

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Samenvatting

Produktie van alaten door de graanbladluis Sitobion avenae

Voor de ontwikkeling van populatiemodellen voor de graanbladluis is het noodzakelijk de achtergrond van emigratie te kennen. Hiertoe werden de factoren die het ontstaan van gevleugelden veroorzaken bestudeerd. Bij L_1 en L_2 was een postnataal effect van 'crowding' aanwezig waardoor hieruit meer gevleugelden ontstonden (Tabel 2). Bij L_3, L_4 en volwassen bladluizen werd een prenataal effect geconstateerd (Tabellen 3 en 4). Het ontstaan van gevleugelden werd sterk beïnvloed door het ontwikkelingsstadium van de waardplant (Tabel 5). Op de aar vóór en gedurende de bloei produceerden solitair gekweekte ongevleugelden minder gevleugelde nakomelingen dan op het blad of op latere ontwikkelingsstadia van de aar. Op deegrijpe aren werden vrijwel uitsluitend gevleugelde nakomelingen geproduceerd en de reproduktie nam dan sterk af. Solitair gekweekte gevleugelde bladluizen hadden op alle plantstadia alleen ongevleugelde nakomelingen (Tabel 6).

Bruine vormen van *S. avenae* hadden onder invloed van 'crowding' vaak minder gevleugelde nakomelingen dan groene (Tabellen 7 en 8). Het ontwikkelingsstadium van de waardplant geeft waarschijnlijk de beste aanwijzingen voor het voorspellen van de emigratie.

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