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BULLETIN NO. 1

**"Use of controlled environment chambers to simulate
the effects of wheat bulb fly larvae (*Delia coarctata*)
on developing winter wheat plants"**

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Foreword

This previously unpublished scientific paper was written in 1975 by our late mother Dr Margaret G. Jones, co-authored with K. E. Fletcher. At that time both authors were members of the Entomology Department at Rothamsted Experimental Station, Harpenden, Hertfordshire, UK; Margaret was employed there as a research entomologist (mostly part time). The manuscript was reviewed and cleared for publication by Rothamsted Experimental Station in early 1976. Our mother died suddenly in June 1980 without publishing it. We discovered the manuscript among the documents left by our late father, Dr Frederick G. W. Jones, following his death in September 2003. He worked at Rothamsted Experimental Station from 1956 to 1979, staying on there in a retired capacity until 1987. He was Head of the Nematology Department throughout his time at Rothamsted, taking on the additional role of Deputy Director of Rothamsted for the period 1971 to 1979.

This unpublished manuscript represents a valuable, carefully conducted and detailed study worthy of publication, which describes experimental data of considerable potential benefit to other researchers in the Entomology field. We therefore decided to publish it as the first in a monograph series of historical bulletins containing previously unpublished manuscripts by members of our family. The manuscript is published in its entirety, without any attempt to bring it up to date by referring to more recent scientific publications on this subject since 1976. It is, therefore, a posthumously published historical document.

Roger Jones
Susan MacDougall
November 2006

Note: This article is available on the family web site,
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**Use of controlled environment chambers to simulate the effects
of wheat bulb fly larvae (*Delia coarctata*)
on developing winter wheat plants**

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1976

Summary

Winter wheat (cv. Cappelle Desprez) plants were inoculated with newly hatched wheat bulb fly (*Delia coarctata*) larvae at seven different growth stages, and placed in controlled environment chambers. The seven growth stages ranged from one shoot with one leaf (stage (a)) to three shoots with eight leaves (stage (g)). Ninety seven percent of the plants attacked at the one shoot with one leaf stage died. Thereafter, the older the plants when they were attacked, the greater the survival rate, until the four leaf stage, when wheat plants with only one shoot all withstood feeding because their lateral buds produced tillers. At all stages with only one shoot at the time of the initial attack, in surviving plants larval feeding decreased the numbers of shoots and leaves produced, slowed the rate of growth in height, delayed ear production and reduced ear weights. Removal of unattacked plants allowed compensatory growth so that ears, although produced later, were heavier. When attacked or unattacked plants with two or more shoots were infested, they were less affected; none died, and there was little difference between the number of leaves or shoots produced by attacked and unattacked plants with main shoots or tillers. Plants which lost their main shoot grew in height more slowly and produced lighter ears one to two weeks later than unattacked plants; attacks on tillers had little effect. When unattacked plants were removed to allow compensatory plant growth, differences between attacked and unattacked plants were less than where there was only one shoot at the time of initial attack. Also, although earing was delayed, the mean weight of

ears on attacked plants was similar to that on unattacked plants, and greater than when attacked plants were in competition with unattacked plants.

Introduction

In England, wheat bulb fly (*Delia coarctata* (Fall.)) is an important pest of winter wheat which reduces plant stand and grain yield (Raw & Lofty, 1957; Bardner, 1968; Bardner *et al.*, 1972). Eggs are laid in soil during late July and August and, after development to the first instar, the larvae remain in diapause within the chorion until late January or February of the following year, when hatching occurs. On contacting a winter wheat plant, the individual larva bores into the central shoot, feeds on the growing point and may eventually kill the attacked shoot. The shoot growth stage at the time of initial attack determines whether the shoot dies. Bardner (1968) found that, on October-sown wheat plants with two shoots when attacked, few plants were killed and there was little effect on grain yield, whereas with late-sown plants with only one shoot by February, many were killed and grain yield was reduced by 22%. Larval feeding reduced the number of ear-bearing shoots per hectare by killing some plants and restricting the number of new shoots on others, although surviving plants partially compensated for the loss by producing more shoots with heavier ears. In heavily infested crops, Bardner *et al.* (1969) found that 95% of unattacked plants survived to harvest, compared with only 22 - 40% of attacked plants; more attacked plants survived when wheat was sown very early.

This bulletin reports the effect of feeding by wheat bulb fly larvae on developing wheat plants at different growth stages. It also shows how controlled environment chambers can be used to simulate the effects of wheat bulb fly to provide an improved understanding of natural wheat bulb fly attacks in the field. Plants outdoors may be injured by other animals or frost. To avoid these hazards, unattacked and attacked wheat plants were grown in controlled environment chambers and subsequent growth monitored to obtain detailed information on the reactions of wheat plants when attacked by wheat bulb fly larvae during the development cycle of the plant.

Methods

During November and December 1974, winter wheat (cv. Cappelle Desprez) seed, treated with a fungicide, was sown at weekly intervals in 13 cm diameter clay pots containing a 5:1 mixture of EFF soil-less compost to Kettering loam soil to provide seven different plant growth stages (Feeke's scale 1 - 3 (Large, 1954)) by mid-January (Table 1). The different growth stages were (a) one shoot with one leaf; (b) one shoot with two leaves; (c) one shoot with three leaves; (d) one shoot with four or five leaves; (e) two shoots with five or six leaves; (f) two shoots with seven or eight leaves; and (g) three shoots with eight leaves. At each growth stage, there were eighteen pots each containing ten wheat seedlings. These eighteen pots were divided into three groups of six.

Between 8 and 10 January 1975, the pots in groups 1 and 2 were inoculated. Each pot in group 1 was inoculated with five newly hatched wheat bulb fly larvae. In group 2, five larvae were again used, but after four weeks the unattacked plants were removed. No larvae were added to the pots in group 3. The pots were then placed in two Saxcil controlled environment chambers: three pots from each group of six within each cabinet. The plants were watered daily. Initially, the chambers were lit for 12 hours/day (08 am - 08 pm) at 100 Wm^{-2} visible radiation and kept at 5°C . At the beginning of the sixth week, the temperature was raised to 8°C and, in the eighth week, day length was increased to 14 hours/day. At the beginning of the ninth week, the temperature was increased to 10°C and illumination to 16 hours/day at 125 Wm^{-2} visible radiation. At the beginning of the twelfth week, day temperature was raised to 12°C (78% relative humidity), the night temperature remaining at 10°C . Finally, at the beginning of the fifteenth week, the day temperature was increased to 15°C and the night temperature to 12°C . Thus, field conditions were simulated but accelerated. Additional nitrogen was supplied by adding 'Liquid-manure' (Boots ®) in weeks 5, 7 and 9. By the eighteenth week, many plants had produced ears, and the pots were removed to a glasshouse where the ears ripened, and, when dry, they were removed and weighed.

Individual plants were examined weekly and those killed by wheat bulb fly larvae noted. The number of shoots per plant was counted throughout the period, and the number of leaves from the third to ninth weeks. Plant height was measured from the tenth to the eighteenth week. The dates when the ears appeared were also recorded.

Results

Stage of attack and survival

(Table 1)

The effects of larval feeding were visible 2 - 3 weeks after inoculation. In no plant group did every larva succeed in attacking a young plant. The greatest success in attacking plants was in growth stages (e) and (g) when twenty-eight out of thirty larvae (93%) entered host plants (Table 1). In stage (a), all but one of the attacked plants were killed; the sole survivor was in a pot with reduced competition where unattacked plants had been removed. In stage (a), the larvae emerged from the dead shoots of attacked plants and entered the main shoots of unattacked ones, but by this time the unattacked plants had two or more shoots with more than three leaves and so they survived (Fig. 1). In stage (b), seven plants survived with competition and six without (33% and 30% respectively). In stage (c), all but three plants survived and these were in pots without competition. By stage (d), some plants had tillered and in stages (d) to (g) all attacked plants survived. Thus, plants which had reached the three-leaf stage usually survived, and all those attacked at the four-leaf stage did so.

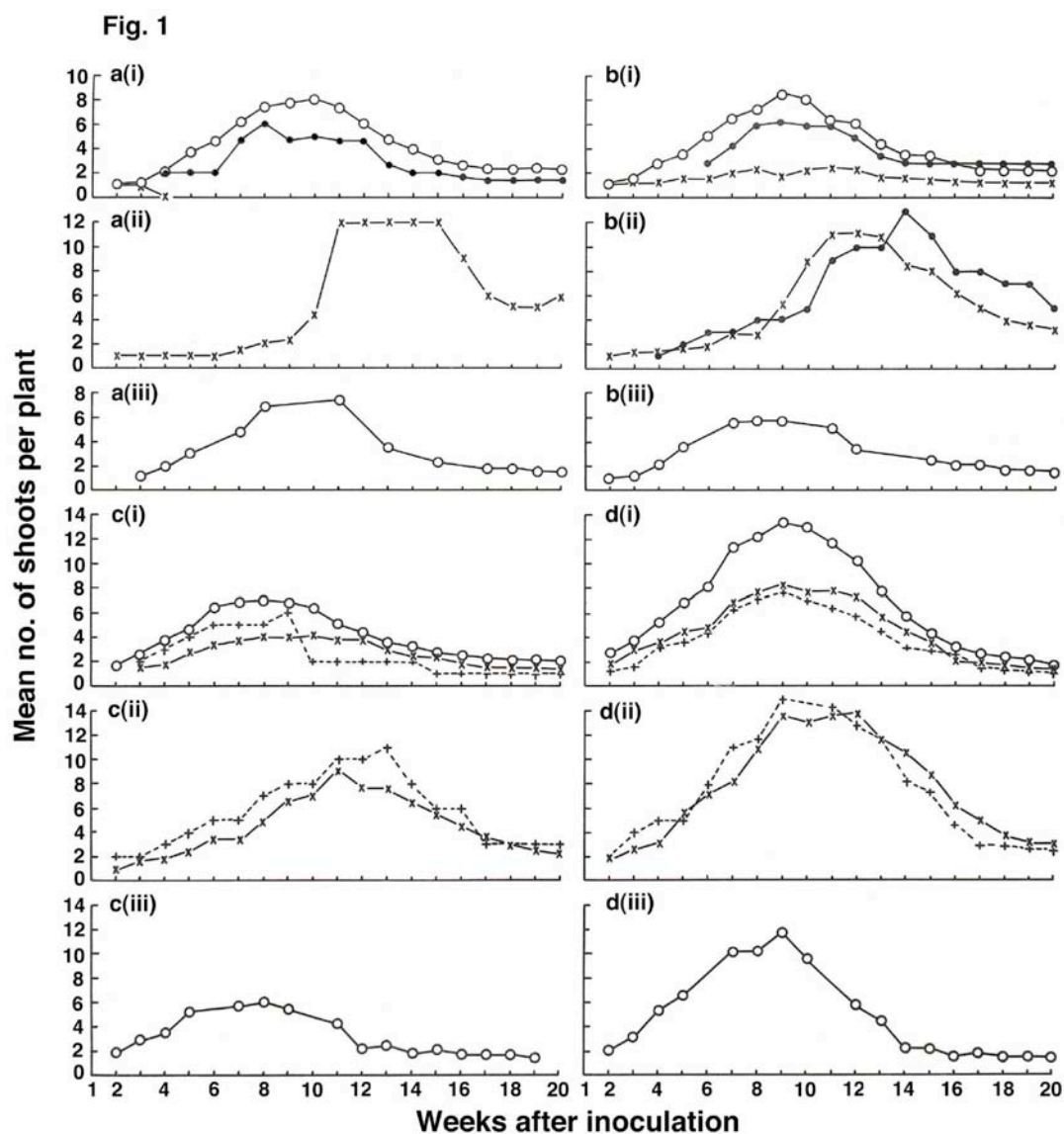
The effect of larval attack on the number of shoots produced

(Figs 1 and 2)

The numbers of shoots produced by attacked plants in growth stages with only one shoot (i.e. (a) to (d)) were reduced by larval attack (Fig. 1).

Table 1. *The number of winter wheat plants surviving attack by newly-hatched wheat bulb fly larvae*

Growth stage	Plant growth	No. pots per stage	No. plants per pot	Larvae per pot	No. of plants first attacked				Total no. of plants killed by first larval attack			
					with competition		reduced competition		with competition		reduced competition	
					main	tiller	main	tiller	main	tiller	main	tiller
a	1 shoot 1 leaf	6	10	5	14	-	21	-	14	-	20	-
b	1 shoot 2 leaves	6	10	5	21	-	20	-	13	-	14	-
c	1 shoot 3 leaves	6	10	5	20	-	23	-	0	-	3	-
d	1 shoot 4 to 5 leaves	6	10	5	12	6	13	3	0	0	0	0
e	2 shoots 5 to 6 leaves	6	10	5	11	17	13	12	0	0	0	0
f	2 shoots 7 to 8 leaves	6	10	5	11	8	8	11	0	0	0	0
g	3 shoots 8 leaves	6	10	5	15	13	17	6	0	0	0	0



Legend to Fig. 1:

Mean number of shoots produced by wheat plants with and without attack by newly-hatched wheat bulb fly larvae: (a) plants attacked at the one-leaf stage; (b) plants attacked at the two-leaf stage; (c) plants attacked at the three-leaf stage; (d) plants attacked at the four- or five-leaf stage.

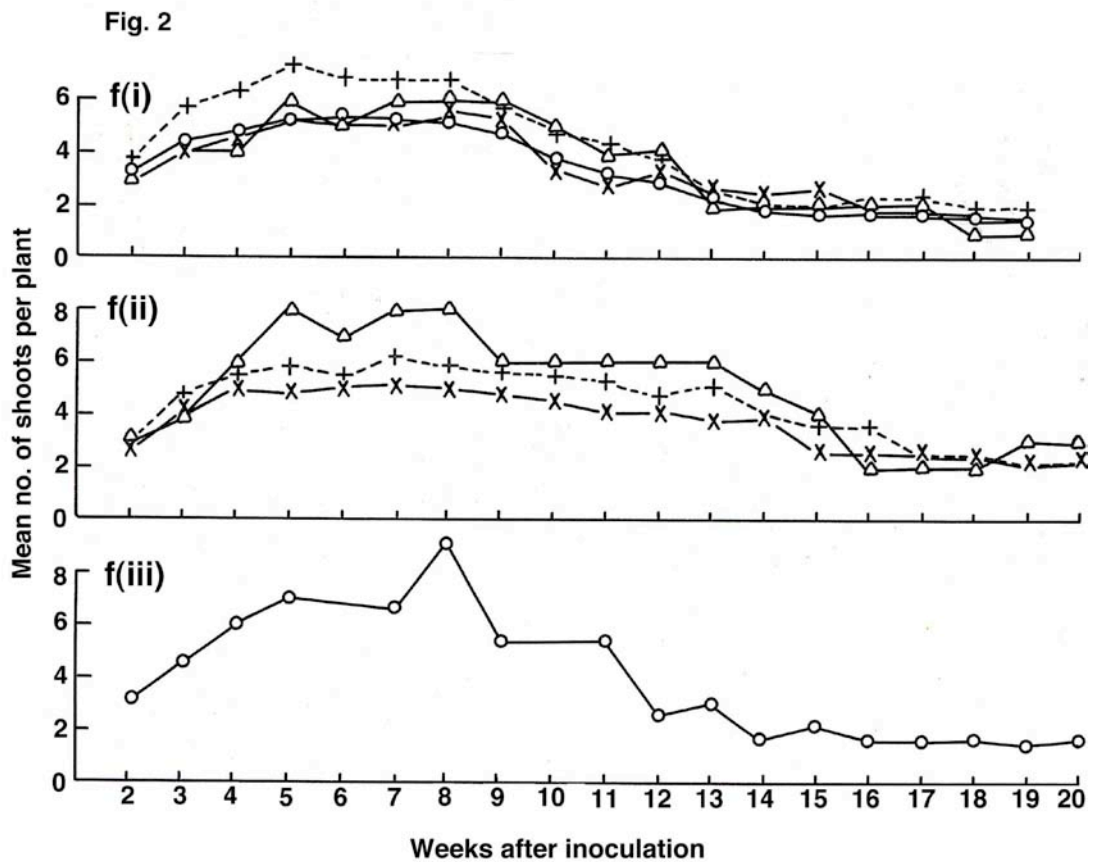
(i) Attacked and unattacked plants in competition; (ii) attacked plants with unattacked plants removed; (iii) uninoculated plant controls. O — O unattacked plants, X — X main shoot attack, ● — ● secondary attack by older larvae on the main shoot, + --- + tiller attack.

In stage (a), after the death of all but one of the first plants attacked, larvae entered the main shoots of other plants at a later stage of development (Fig. 1, a(i)), causing fewer shoots to develop than in unattacked plants. The maximum number of shoots was produced earlier by unattacked plants and their excess shoots died off sooner. Plants attacked in stages (b) to (d) produced fewer shoots than unattacked plants, but when unattacked plants were removed and there was less competition, more shoots were produced with peak numbers occurring later (Fig. 1, b - d). In the uninfested control pots, competition was greater and fewer shoots were produced than in the less dense stands of surviving unattacked plants in inoculated pots.

The effect of feeding on main shoots and tillers was less marked in stages (e) to (g). These plants all had two or more shoots when first attacked and did not produce as many tillers as did younger plants. The numbers of shoots produced by unattacked plants, and those with a main shoot attack, tiller attack, or main shoot and tiller attack differed little (Fig. 2). In the absence of competition, attacked plants produced most shoots. After 18 - 20 weeks each plant had only one or two shoots, the others having died. Plants in uninoculated control pots and unattacked plants in inoculated pots grew similarly.

There were always more unattacked than attacked plants in the pots. The variability in the numbers of unattacked plants, as shown by the coefficients of variation of the mean number of shoots ten weeks after inoculation, was: unattacked shoots, 8%; plants with the main shoot attacked, 15%; plants with tiller attack, 14%; and plants with both main shoot and tiller attack, 28%. Significantly, fewer shoots were produced by plants with the main shoot attacked when compared with unattacked plants in stages (a) to (d) ($P < 0.01$, < 0.001 , < 0.02 , < 0.001 , respectively), but not in the older growth stages (e), (f) and (g).

These results showed that plants attacked when they had one shoot and up to four or five leaves were more severely affected than those with two shoots and five leaves or more.



Legend to Fig. 2:

Mean number of shoots produced by wheat plants with and without attack by newly hatched wheat bulb fly larvae added to plants with two shoots or more; results from (f) only. (i) Attacked and unattacked plants in competition; (ii) attacked plants with unattacked plants removed; (iii) uninoculated controls. Symbols as for Fig. 1, and $\Delta - \Delta$ main and tiller attack.

The effect of the feeding by larvae on the production of leaves

(Table 2)

Leaves were counted on each plant from the third to the ninth or tenth week after inoculation (Table 2). In growth stages (a) to (d), the number of leaves produced by unattacked plants in competition with attacked plants was always significantly greater ($P < 0.01$, < 0.001 , < 0.01 , < 0.001 , respectively) than the number produced by plants with the main shoot attacked. When there was no competition, plants with the main shoot attacked produced leaves slowly at first, but thereafter the attacked plants always had fewer leaves than unattacked ones except in stage (d), where plants grew most vigorously. There was little difference between the numbers of leaves produced by plants in the uninoculated control pots and the unattacked plants in the inoculated pots.

In stages (e) to (g), differences between the number of leaves produced by unattacked plants, those with a main shoot attack, those with tiller attack, and those with both main shoot and tiller attack, were less marked than in stages (a) to (d). Leaf production by plants differed little whether there was competition or not and, although leaf production was apparently stimulated most in those plants which had both main shoot and tiller attack, this difference was not statistically significant. Only when plants were attacked in the first four growth stages were the numbers of leaves produced by plants with a main shoot attack significantly fewer than in unattacked plants. Thus, the younger the plant attacked, the greater the harm to early leaf production.

The effect of larval attack on plant height

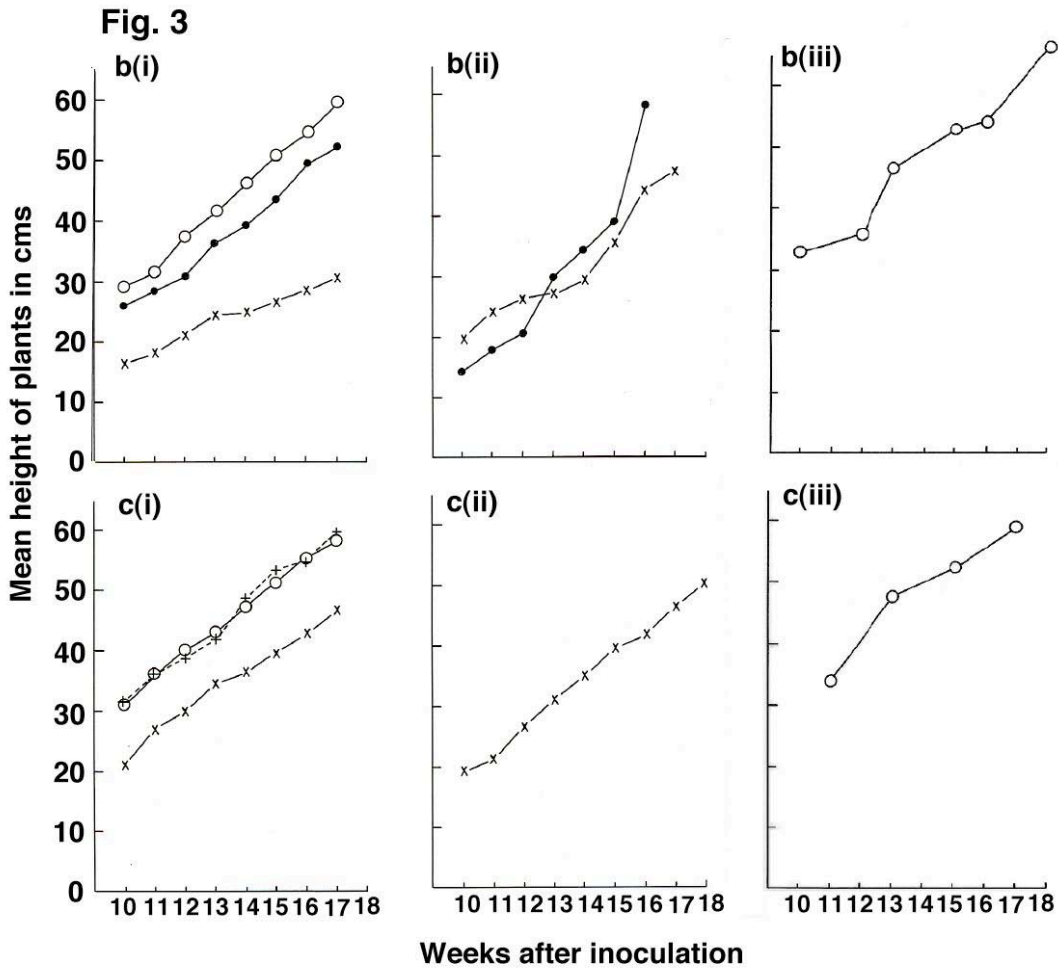
(Figs 3 and 4; Table 3)

The height of the plants was measured from the tenth week after inoculation by larvae until emergence of the ears (Fig. 3). The rate of growth followed much the same pattern as for the leaves and shoots in stages (a) to (d), those plants with the main shoot attacked growing more slowly. The height of plants with tiller attack was little affected. When competition was less,

Table 2. Number leaves per of winter wheat plant 8[†] or 9[‡] weeks after inoculation with newly-hatched wheat bulb fly larvae

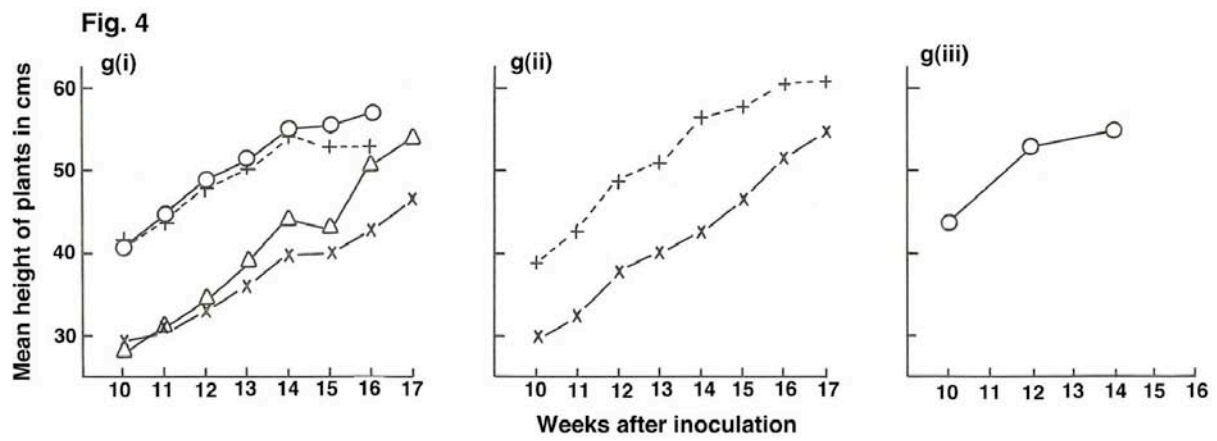
Growth stage		Group	No. of plants	Mean no. (\pm S.E.) of leaves per plant		Growth stage		Group	No. of plants	Mean no. (\pm S.E.) of leaves per plant		
a (i) [‡]	No plants removed	Unattacked	39	20.5	± 1.16	e (i) [†]	No plants removed	Unattacked	34	7.6	± 0.40	
		1st main attack	0	-	-			Main attack	8	7.6	± 0.65	
		2nd main attack	4	10.3	***			± 3.30	Tiller attack	13	7.2	± 0.84
				Main and tiller attack	3			8.0	± 1.16			
(ii)	Unattacked plants removed	Main attack	1	15.0	-	(ii)	Unattacked plants removed	Main attack	9	11.6*	± 1.28	
								Tiller attack	9	8.0****	± 0.89	
								Main and tiller attack	3	13.0***	± 1.33	
b (i) [‡]	No plants removed	Unattacked	30	21.6	± 1.09	f (i) [†]	No plants removed	Unattacked	39	13.3	± 0.84	
		1st main attack	14	3.6	****			± 0.71	Main attack	11	13.6	± 1.51
		2nd main attack	8	15.9*	± 2.29			Tiller attack	8	16.3	± 2.31	
				Main and tiller attack	1			13.0	-			
(ii)	Unattacked plants removed	Main attack	6	14.2	± 2.94	(ii)	Unattacked plants removed	Main attack	8	13.3	± 2.30	
								Tiller attack	11	16.2	± 1.76	
								Main and tiller attack	1	21.0	-	
c (i) [‡]	No plants removed	Unattacked	38	17.8	± 0.70	g (i) [†]	No plants removed	Unattacked	40	7.9	± 0.54	
		Main attack	17	10.8	***			± 1.96	Main attack	5	8.4	± 1.12
		Tiller attack	4	13.0	*			± 0.91	Tiller attack	13	6.5	± 0.87
				Main and tiller attack	2			8.0	-			
(ii)	Unattacked plants removed	Main attack	20	12.3	± 2.12	(ii)	Unattacked plants removed	Main attack	16	10.6	± 0.67	
		Tiller attack	1	12.0	-			Tiller attack	6	8.8	± 1.22	
d (i) [‡]	No plants removed	Unattacked	42	26.3	± 0.81							
		Main attack	13	15.5****	± 2.06							
		Tiller attack	6	25.7	± 2.09							
(ii)	Unattacked plants removed	Main attack	14	23.4	± 2.70							
		Tiller attack	2	30.0	± 6.02							

* $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$, **** $P < 0.001$



Legend to Fig. 3:

Mean heights of wheat plants from tenth week after inoculation to production of the ears for stages (b) and (c). Symbols and numbers as for Fig. 1.



Legend to Fig. 4:

Mean height of wheat plants from tenth week after inoculation to the production of ears for stage (g). Symbols and numbers as for Fig. 2.

Table 3. Height of winter wheat plants in cms, 15 weeks after inoculation with newly-hatched wheat bulb fly larvae

Stage	Group	No. of plants	Mean height (\pm S.E.) per plant	Stage	Group	No. of plants	Mean height (\pm S.E.) per plant		
a(i)	No plants removed	Unattacked	39	46.0 \pm 0.67	e(i)	No plants removed	Unattacked	31	53.7 \pm 0.69
		1st main attack	0	-			Main attack	6	37.4**** \pm 4.63
		2nd main attack	4	36.0**** \pm 5.07			Tiller attack	12	51.1 \pm 2.37
						Main and tiller attack	3	41.4**** \pm 7.85	
(ii)	Unattacked plants	Main attack	1	35.0 -	(ii)	Unattacked plants removed	Main attack	9	45.4 \pm 1.84
b(i)	No plants removed	Unattacked	33	50.8 \pm 0.98			Tiller attack	9	52.3* \pm 2.13
		1st main attack	10	28.8**** \pm 4.17			Main and tiller attack	3	44.4* \pm 1.98
		2nd main attack	4	39.2*** \pm 8.97	f(i)	No plants removed	Unattacked	38	47.5 \pm 1.70
(ii)	Unattacked plants removed	1st main attack	6	36.9 \pm 2.64			Main attack	11	38.4**** \pm 1.54
		2nd main attack	1	39.2 -			Tiller attack	8	52.1 \pm 2.02
c(i)	No plants removed	Unattacked	32	52.1 \pm 1.20		Main and tiller attack	1	36.0 -	
		Main attack	17	36.1*** \pm 2.99	(ii)	Unattacked plants removed	Main attack	8	38.3 \pm 3.90
		Tiller attack	4	53.8 \pm 2.12			Tiller attack	11	49.9** \pm 2.15
						Main and tiller attack	1	46.0 -	
(ii)	Unattacked plants removed	Main attack	20	41.1 \pm 3.16	g(i)	No plants removed	Unattacked	40	55.7 \pm 1.41
		Tiller attack	1	59.0 -			Main attack	5	40.0**** \pm 6.01
d(i)	No plants removed	Unattacked	35	35.2 \pm 1.14			Tiller attack	13	52.9 \pm 1.45
		Main attack	13	33.1* \pm 1.39			Main and tiller attack	2	43.0 \pm 4.01
		Tiller attack	5	41.9 \pm 2.55	(ii)	Unattacked plants removed	Main attack	16	46.3 \pm 1.64
(ii)	Unattacked plants	Main attack	13	32.6 \pm 1.89			Tiller attack	6	57.9**** \pm 1.24
		Tiller attack	3	35.0 \pm 0.72			Main and tiller attack	0	-

* $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$, **** $P < 0.001$

attacked plants partly compensated but nevertheless remained shorter than those unattacked.

In stages (e) to (g), plants with main shoot, or main shoot and tiller attack grew more slowly in competition than unattacked or tiller attacked plants (Fig. 4), while those with tiller attack differed little from the unattacked plants. In the pots only containing attacked plants, those with tiller attack were taller than either plants with main shoot or with main shoot and tiller attack (Fig. 4, Table 3). In every growth stage, plants with the main shoot attacked were always shorter than plants with tiller attack alone or uninfested plants.

*The effect of larval attack on the production of ears and the
weight of grain
(Tables 4 and 5)*

The date of appearance of the first ear varied from 14 to more than 22 weeks after inoculation with larvae (Table 4). With competition, ears appeared from one to 5 weeks later on plants with early main shoot attack than on unattacked plants, and those with tiller attack eared either at the same time or later than those that were unattacked. With reduced competition, dates of earing were less affected. The few plants with double attack (main shoot and tiller) eared either at the same time or 1 week later than those with only the main shoot attacked. Between the eighteenth and twenty-first week, most plants had produced ears. Plants from stage (a), the latest sown, were the last to ear. Those from stage (d) which produced large numbers of shoots (Fig. 1) were late producing ears. Possibly the excessive tillering delayed their heading.

After the plants were removed to the glasshouse, they were left until completely dry. The ears were then removed and weighed (Table 5). The weights were not comparable with those from plants grown in the field, but nevertheless showed that when plants with main shoot attack were in competition with unattacked plants, the weight of ears was consistently smaller than in unattacked plants, while for plants with tiller attack it

Table 4. *Emergence of ears from winter wheat plants either unattacked or attacked by newly-hatched wheat bulb fly larvae*

Growth stage		Appearance of first ear. Weeks after inoculation by larvae			% of plants bearing ears 18-21 weeks after inoculation by larvae		
		With compe- tition	Reduced compe- tition	Control	With compe- tition	Reduced compe- tition	Control
a	Unattacked	20	-	20	51	-	30
	1st main attack	-	>22	-	-	-	-
	2nd main attack	>22	-	-	-	67	-
b	Unattacked	17	-	16	57	-	54
	1st main attack	22	19	-	22	17	-
	2nd main attack	19	20	-	71	0	-
c	Unattacked	16	-	16	77	-	85
	Main attack	18	17	-	60	35	-
	Tiller attack	17	20	-	50	0	-
d	Unattacked	19	-	17	17	-	36
	Main attack	20	22	-	8	0	-
	Tiller attack	19	22	-	50	-	-
e	Unattacked	16	-	15	77	-	84
	Main attack	19	18	-	25	78	-
	Tiller attack	16	17	-	62	78	-
	Main and tiller attack	20	19	-	0	67	-
f	Unattacked	17	-	17	74	-	51
	Main attack	19	18	-	18	25	-
	Tiller attack	18	17	-	75	55	-
	Main and tiller attack	19	19	-	0	100*	-
g	Unattacked	15	-	14	100	-	88
	Main attack	18	17	-	40	19	-
	Tiller attack	15-16	17	-	75	100	-
	Main and tiller attack	19	-	-	0	-	-

* 1 plant

Table 5. Mean weight (gms) of ears (with S.E) from winter wheat plants either unattacked or attacked by newly-hatched wheat bulb fly larvae

Growth stage		No. of plants	In competition	No. of plants	Reduced competition	No. of plants	Controls
a	Unattacked	34	1.17±0.11	-	-	29	1.1±0.07
	1st main shoot attack	-	-	1	0.35	-	-
	2nd main shoot attack	1	0.43	-	-	-	-
b	Unattacked	28	1.21±0.12	-	-	59	1.13±0.06
	1st main shoot attack	8	0.33±0.09	6	1.67±0.57	-	-
	2nd main shoot attack	3	1.20±0.18	1	2.23	-	-
c	Unattacked	36	1.10±0.09	-	-	49	1.30±0.08
	Main shoot attack	10	0.45±0.05	18	1.40±0.20	-	-
d	Unattacked	30	0.61±0.13	-	-	57	1.05±0.05
	Main shoot attack	9	0.40±0.05	12	1.06±0.17	-	-
	Tiller attack	7	0.8±0.03	3	0.90±0.2	-	-
e	Unattacked	31	0.82±0.17	-	-	56	0.83±0.04
	Main shoot attack	8	0.53±0.12	8	1.10±0.18	-	-
	Tiller attack	13	0.72±0.08	9	1.19±0.22	-	-
	Tiller and main shoot attack	3	0.44±0.02	3	1.10±0.10	-	-
f	Unattacked	38	0.65±0.04	-	-	49	1.04±0.05
	Main shoot attack	10	0.32±0.03	8	0.78±0.18	-	-
	Tiller attack	8	0.84±0.21	11	1.28±0.23	-	-
	Tiller and main shoot attack	1	0.25	1	0.92	-	-
g	Unattacked	42	0.86±0.07	-	-	50	1.08±0.07
	Main shoot attack	6	0.39±0.10	16	1.08±0.13	-	-
	Tiller attack	9	0.81±0.13	7	1.30±0.07	-	-
	Tiller and main shoot attack	1	0.44	-	-	-	-

Table 6. *Effects of newly-hatched wheat bulb fly larvae on winter wheat plants at different stages of growth*

Shoots	Leaves	Attack	% killed	Earing
1	1	Main shoot	> 90)	delayed
	2	"	> 70)	in survivors
	3	"	> 7	delayed
	4	"	none	delayed
2	> 5	"	"	delayed
		Tiller Main shoot and tiller	" "	unaffected delayed
> 3	> 6	Main shoot	"	delayed
		Tiller	"	unaffected
		Main shoot and tiller	"	delayed

was not. The few plants with both main shoot and tiller attack yielded poorly. When the competing plants were removed, yields from all attacked plants improved. The mean weights of the ears from plants from the uninoculated control pots differed little from those of unattacked plants in the inoculated pots.

Discussion

The technique employed in this research has considerable potential for application in future studies with wheat bulb fly. For example, the resulting information is valuable in formulating a procedure for assessing the resistance of wheat cultivars to wheat bulb fly attack. This research also demonstrates how controlled environment chambers can be used to simulate the effects of wheat bulb fly on wheat plants and so provide valuable new information for comparison with known facts about wheat bulb fly attack in the field. Thus, it complements more limited earlier work in the field by Bardner & Griffiths (1967) and Griffiths & Scott (1969), and extends the data collected to the entire development cycle of the wheat plant, including the maturation of the grain.

In field studies, plants attacked by wheat bulb fly larvae at an early growth stage, even when sprayed with insecticide, failed to recover if they had lost the central meristem, while older ones grew away from the damage (Griffiths & Scott, 1969). By comparing the growth of attacked and unattacked wheat plants in controlled environment chambers (summarised in Table 6), we showed that plants attacked after the one and two leaf stages are likely to survive feeding by wheat bulb fly larvae. Thus, plants with three leaves, especially when there was a bud at the base of a leaf, grew away from damage. Plants with four leaves and those with two shoots withstood larval feeding and differed little from unattacked plants in the number of shoots and leaves produced, although main shoot growth was retarded, earing delayed and grain yield reduced. Where there was little or no competition and compensatory growth occurred, the yield per plant was not reduced. In the field, compensatory growth would be greatest if attacked plants were

regularly and evenly distributed. Populations of eggs, larvae, damaged and undamaged plants are nearly random in their distribution which allows for extra growth of unattacked plants (Bardner & Lofty, 1971).

A practical outcome of this research is in helping to pinpoint when to spray wheat plants with insecticide in the field to achieve greatest improvement in grain yield. This would be when plants reach the two shoot stage when the larvae are numerous.

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