AN ABSTRACT OF THE THESIS OF

William Thomas Cram for the Ph.D. in Entomology
(name) (Degree) (Major)

Date thesis is presented February 19, 1964

Title Factors Affecting the Fecundity of the Root Weevils, Brachyrhinus sulcatus (F.), and Sciopithes obscurus Horn

Abstract approved Redacted for Privacy
(Major professor)

Comparisons of the effects of certain physical and nutritional factors on fecundity are made between the introduced black vine weevil, Brachyrhinus sulcatus (F.), which is susceptible to cyclodiene insecticides, and the obscure strawberry root weevil, Sciopithes obscurus Horn, which is tolerant to these insecticides. Both species are economic pests in the Coastal areas of British Columbia, Washington and Oregon.

Methods are given for observing the egg production of these weevils outdoors on detached leaflets and in the laboratory on detached or attached leaflets. A method for obtaining variable diurnal temperature programs is presented. Techniques are described for growing strawberry plants in either vermiculite- or sand-culture in the laboratory under artificial lights.

Observations indicate that although B. sulcatus is much more fecund in nature, it is not so well adapted in British Columbia as S. obscurus which has a lower temperature threshold for oviposition and, therefore, a longer oviposition period.

When the night temperature in cabinets at diurnal temperature programs is minimal at 8°C, the fecundity of these nocturnal species

is maximal at day temperatures of 20° for S. obscurus and 25° for B. sulcatus. Under these diurnal programs B. sulcatus is the more fecund of the two and survives better in continuously high rather than variable relative humidity. S. obscurus is comparatively indifferent to humidity fluctuations.

The feeding rate of B. sulcatus, like fecundity, is higher at higher maximum daily temperatures up to 25°C.

Various levels of the major nutrients: nitrogen, phosphorus and potassium, when fed to the host plant had no significant effect on the fecundity of S. obscurus. Only low levels of nitrogen significantly reduced the fecundity of B. sulcatus. With vermiculite-culture, low artificial light intensity, and restricted drainage the effects of nutrients on B. sulcatus are statistically inconclusive, but indicate a response to nitrogen. The results with detached leaflets from plants fertilised in the field are also indicative of the effect of nitrogen. With sand-culture, high light intensity, and free drainage the effect of nitrogen supplied in either the nitrate- or ammonium-form on the fecundity of B. sulcatus is statistically demonstrated.

FACTORS AFFECTING THE FECUNDITY OF THE ROOT WEEVILS, *BRACHYRHINUS SULCATUS* (F.), AND *SCIOPITHES OBSCURUS* HORN

by

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A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

June 1964

APPROVED:

Redacted for Privacy

Professor of Entomology

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Date thesis is presented _ _February 19, 1964_ _ _ _ _

Typed by Melba Planinsic

ACKNOWLEDGEMENTS

The author wishes to acknowledge the direction of his major professor, Dr. C. H. Martin, Professor of Entomology, Oregon State University.

Facilities for this study were provided by the Research Branch, Canada Department of Agriculture at the Research Station, Vancouver, British Columbia; and previous to 1960 at the Fruit Insect Laboratory, Canada Department of Agriculture, Victoria, British Columbia (now discontinued). These facilities included all the experimental equipment and supplies, as well as certain technical assistance given by the following permanent staff: Messrs. T. L. Theaker (Victoria), L. Chang, M. D. Noble, J. H. Severson (Photographer), and Miss G. V. Armstrong; and summer students: Messrs. A. Clancy and N. Filmer.

Dr. H. R. MacCarthy, Head of the Entomology Section, Vancouver Research Station, gave valuable advice and suggestions during the writing of the thesis.

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INTRODUCTION

The black vine weevil, *Brachyrhinus sulcatus* (F.), and the obscure strawberry root weevil,[1] *Sciopithes obscurus* Horn, (Fig. 1) are economic pests of small fruits especially strawberry, in the Pacific Northwest. *B. sulcatus* is a European species, known there as *Otiorrhynchus sulcatus* F. (28, p.409). It has become widely distributed, damages many crops, and has been studied extensively (8, p.569-579; 9, p.86-91; 22, p.189-202; 28, p.409-437; 42, p.1-45; 50, p.1-109). *S. obscurus* is a native species, and also of the Brachyrhininae. It feeds on many undershrubs in forests of the Pacific coastal areas of the United States and Southern Canada (47, p.89). These two parthenogenetic, non-flying weevils have similar life histories but differ in certain habits and responses, some of which will be discussed. The purpose of this study was to measure the fecundity or production of eggs, a very sensitive index of response to conditions (37, p.151), of both species under the influence of various physical and nutritional factors. Besides adding to information on the ecology of the two weevils, their responses might

[1]This common name has not been approved by the Entomological Society of America.

suggest lines of study that would explain the susceptibility of B. sulcatus and the tolerance of S. obscurus to cyclodiene insecticides (9, p.89; 10, p.7; 14, p.3). This work was conducted in British Columbia at Victoria from 1956 to 1959 and at Vancouver from 1960 to 1962.

GENERAL METHODS AND MATERIALS

Special methods, materials and procedures will be discussed in their particular section.

Collecting

Adults of B. sulcatus were collected from strawberry near Saanichton, 15 miles north of Victoria, on Vancouver Island; and on Lulu Island, at the mouth of the Fraser River, 5 miles south of Vancouver. Since strawberries are usually planted in soil treated with aldrin or heptachlor to control B. sulcatus (9, p.86; 14, p.3), this species was difficult to find except where growers had neglected the treatment.

Adults of S. obscurus were collected only near Saanichton where they were abundant in strawberry plantings on treated soil near woodlands.

Usually, both species were collected in early June, shortly after they emerged from the soil, by sweeping them from the leaves of plants where they climb to feed after dusk (8, p.572). Sweepings were transferred in the field to brown paper sacks and examined the following day to recover the weevils which were usually teneral. Where large populations were discovered, adults were collected during the day either by searching at the crown of plants, or by carefully crumbling soil and removing newly-transformed adults from their cells, or by collecting large clumps of soil containing pupae and recovering the adults as they emerged in the laboratory.

Attempts were made to rear a clone of each species on potted strawberry plants in the greenhouse to overcome some of the individual variability in egg production in B. sulcatus (22, p.191). After five weeks of oviposition by eight clonal adults of B. sulcatus and four clonal adults of S. obscurus, the results were as follows:

Species	Eggs per Weevil							
B. sulcatus	33	117	191	253	303	358	392	440
S. obscurus	180	239	247	249				

The egg production of adults in the B. sulcatus clone was so extremely variable that this laborious, lengthy and expensive method of obtaining adults in quantity was abandoned. The egg production of adults in the S. obscurus clone was more uniform but not different from that previously observed with field-collected adults.

Caging

Cages were devised for confining individual adults with either detached or attached strawberry leaflets. In early work glass shell vials containing detached leaflets were used for both species (Fig. 2A, 1). These vials were 8.5 cm long by 2 cm in diameter with a bronze screen stopper that was moulded to fit snugly inside the mouth of the vial. When adults of S. obscurus were caged on attached leaflets a plastic vial cage (Fig. 2A, 2) was used (10, p.640). For B. sulcatus a modification of this cage was used, consisting of a plastic medicine vial, 6 cm long by 3.2 cm in diameter with a soft plastic snap-on lid (Crystalite Snap-cap R_x vial no. 12 from Jones Box and Label Co. Ltd., London, Canada) with a single notch for the petiole cut in the lip of the vial. A 100-mesh brass strainer cloth (C.O. Jelliff Mfg. Corp., Southport, Connecticut) was welded to the lid and bottom of the vial (10, p.640) to provide ventilation and prevent the loss of eggs (Fig. 2A, 3). Similar vials without screening or the petiole notch were used as unventilated cages for confining B. sulcatus with detached leaflets in one experiment (Fig. 2A, 4).

Foliage from the strawberry variety British Sovereign was used in all experiments. Detached leaflets were replaced twice weekly in the ventilated cages. Those with petioles in water, and those in unventilated cages were replaced weekly.

Recording

Andrewartha and Birch (3, p.171) define fecundity as the number of eggs laid during an animal's lifetime, as opposed to the number of eggs produced during a unit of time. Allee et al. (1, p.289) define fecundity merely as egg production. In this study the term fecundity refers to the number of eggs laid per weevil during the period of the particular observation. In some experiments the observations were, in fact, made for the lifetime of the weevils. However, most observations were terminated when egg-laying declined, the host plant was consumed, or there was no difference apparent in the fecundities between different treatments.

B. sulcatus laid single eggs indiscriminately either on the surface of the leaflet or wall of the cage.

S. obscurus laid eggs in clusters at the edge of a leaflet, folding a serration of the leaflet over the cluster and cementing it down. In the field these eggs were observed on the soft membranous stipe at the base of a petiole. In early trials in the laboratory, eggs were laid more readily on pieces of smooth tissue paper than on the thicker leaflets. Accordingly, a 3-cm square of tissue paper, folded accordion-fashion, was included in each cage. Nearly all the eggs were laid in the tissue which greatly facilitated immediate counting or later counting of frozen eggs.

The viability of B. sulcatus eggs was determined by removing the weevil and keeping the used cage with the eggs and old foliage at room temperature under a plastic hood at above 85 percent relative humidity for four days before counting (Fig. 2J). By this time viable eggs had darkened from white to amber.

The viability of S. obscurus eggs was determined by keeping the tissue paper with eggs in upright open shell vials under the humidity hood for at least 14 days. By this time viable eggs had hatched and larvae and unhatched eggs were counted. Unlike B. sulcatus the larvae of S. obscurus cannot climb vertical glass, therefore, it was not necessary to close the shell vials.

To determine the significance of the effects on fecundity of various physical and nutritional factors, the cumulative numbers of eggs laid (per weevil) were analyzed by Duncan's multiple range test (13, p.1-7). The probability level for significance in all cases was p=.05. Square root transformations were applied to highly variable data (43, p.315).

PHYSICAL FACTORS AFFECTING FECUNDITY

These non-flying, nocturnal, leaf-eating weevils are subjected to a comparatively narrow range of heat and dry stress in nature. They confine their activities to microclimates where the humidity is always near saturation, such as on damp soil beneath plant debris during the day and on relatively dense foliage at night. For this reason the effect of humidity has been studied here only incidentally and under relatively constant conditions, usually above 75 percent relative humidity. Oviposition occurs during six months in the summer (11, p.4) when diurnal temperatures vary widely. Therefore, the fecundities were determined under constant, prevailing outdoor, and various diurnal temperature conditions.

EFFECT OF A CONSTANT AND OUTDOOR CONDITIONS ON THE FECUNDITY OF BOTH SPECIES

To determine and compare the general patterns of egg production, observations were made on both species caged in the laboratory at a constant condition and outdoors at the prevailing weather conditions at Saanichton from 1956 to 1958.

Methods and Materials

Teneral adults of B. sulcatus were collected from pupation cells in the soil on June 5, 1956. Ten were caged singly (Fig. 2A, 1) and kept in a climate cabinet at $20 \pm 1^{\circ}C$ and 85 percent relative humidity with 12 hours of light per day. Another 10 were caged in the same way but were placed outdoors on the soil under a double-slatted baffle to simulate conditions beneath a strawberry plant (Fig. 2B). The temperature under the baffle was recorded continuously by a Weksler recording soil thermometer in 1956. The daily mean temperatures, based on 24 hourly readings, were similar to those recorded at the Victoria International Airport, less than one mile from the location of the cages. The latter means were recorded for this study.

Adults of S. obscurus were collected by sweeping on July 19, 1956. Ten were caged singly in the climate chamber and 10 were caged in the same way outdoors near the B. sulcatus.

Eggs were counted at weekly intervals until the weevils died. Weevils which survived the winter outdoors were observed during the subsequent season.

Results and Discussion

Table 1 shows the egg production of individual weevils, the mean egg production, and the coefficients of variability of these means for each species at both $20^{\circ}C$ and outdoors. The average weekly egg production of the survivors of each species and the weekly mean temperatures at both conditions appear in Fig. 3.

B. sulcatus was much more fecund at $20^{\circ}C$ than outdoors (Table 1).

TABLE I

THE FECUNDITY OF B. SULCATUS AND S. OBSCURUS WHEN 10 OF EACH SPECIES WERE CAGED SINGLY, FED DETACHED STRAWBERRY LEAFLETS, AND KEPT EITHER AT A CONSTANT 20°C OR OUTDOORS AT SAANICHTON, B.C.

Total eggs per weevil									
20°C[1]		Outdoors							
B. sulcatus	*S. obscurus*	*B. sulcatus*				*S. obscurus*			
1956	1956	1956	1957	1958	Total	1956	1957	1958	Total
738	203	141	D[3]	—	141	142	D	—	142
774	292	220	D	—	220	149	D	—	149
855	296	257	D	—	257	175	D	—	175
938	298	274	D	—	274	192	D	—	192
1194	302	336	D	—	336	201	D	—	201
1436	340	347	D	—	347	223	D	—	223
1475	343	258	309	D	567	163	78	D	241
1494	358	196	430	303	929	114	184	D	298
1512	433	420	604	D	1024	167	423	D	590
1696	—[2]	277	467	408	1153	130	587	D	717
Mean 1211	318	273	452	356	525	166	318	—	293
%C.V.[4] 29.4	19.6	29.5	26.9	20.9	71.0	19.2	72.4		67.5

[1]85 percent relative humidity and 12-hour photoperiod.

[2]Weevil escaped.

[3]Indicates a weevil that died while overwintering.

[4]Percent coefficient of variability of the mean.

The total egg production at 20°C was completed in an average period of 30 weeks (range 27 to 32) of continuous oviposition (Fig. 3). The oviposition of both species was interrupted outdoors by a period of quiescence during the winter (Fig. 3). Quiescence was involved in overwintering, rather than diapause as defined by Way (49, p.595). This was confirmed in other work when specimens collected in the fall after egg laying had ceased, resumed ovipositing in the laboratory at 20°C after a period averaging 58 days.

In the three seasons outdoors, oviposition by B. sulcatus stopped in September when the weekly mean temperatures dropped to 12, 15, and 13°C, respectively; and resumed in the spring when the weekly mean temperatures were 14 and 10°C, respectively (Fig. 3).

S. obscurus was not significantly more fecund at 20°C than outdoors (Table 1). At 20°C eggs were laid for an average period of only 14 weeks (range 10 to 27). This wide range indicated that the constant conditions were in some way detrimental to maximum egg production.

In the first season outdoors, S. obscurus oviposited one week longer, and in the second season, five weeks longer (weekly mean temperatures of 12 and 10°C, respectively) than B. sulcatus (Fig. 3). Moreover, S. obscurus resumed oviposition four weeks earlier (weekly mean temperature of 8°C) than B. sulcatus.

At 20°C B. sulcatus was significantly more fecund than S. obscurus (Table 1). Outdoors B. sulcatus was significantly more fecund than S. obscurus during the first season but not during the second season or when the total egg productions were compared (Table 1).

Conclusions

Under the conditions of these observations the following general conclusions are drawn:

1. B. sulcatus is much more fecund at 20°C than it is outdoors.
2. S. obscurus is only slightly more fecund at 20°C than it is outdoors.
3. B. sulcatus is more fecund than S. obscurus, and the difference is more pronounced at 20°C than outdoors.
4. S. obscurus oviposits later in the fall and resumes earlier in the spring than B. sulcatus indicating a lower temperature threshold for oviposition in the former species.

EFFECT OF CONTROLLED DIURNAL CONDITIONS ON THE FECUNDITY OF BOTH SPECIES

Studies on the effects of temperature and humidity on organisms conducted at constant conditions have been criticized because conclusions were drawn from these unnatural and uncompensated environments (36, p.1002). In 1961, observations were made on the number of eggs laid by B. sulcatus and S. obscurus under simulated outdoor conditions of temperature, humidity, and light.

Methods and Materials

Four special insulated cabinets (Fig. 2C) were built using fluorescent lights operated by time switches to give various fluctuating climatic programs. The cabinets were about 6 feet long by 4 feet high by 2½ feet deep. Three were located in a large cold room

(21 by 18 by 8 feet) held at 8$\pm$ 2°C and the fourth in a similar cold room at 15$\pm$ 2°C. Temperature programs in the cabinets were obtained by adjusting openings in the cabinet walls and varying the number of 4-foot fluorescent tubes inside. All cabinets were operated on a 16-hour photoperiod from 5 A.M. to 9 P.M. Small circulating fans ran continuously. The diurnal temperature programs were (Fig. 4): 8 to 15° (2 tubes), 8 to 20° (2 tubes), 8 to 25° (4 tubes) and 15 to 33°C (2 tubes).

Eight weevils of each species were confined singly in vial cages (Fig. 2A, 2) on strawberry leaflets with their petioles in water, and the 16 cages were enclosed in a cylindrical plastic ('Kodapak') cage 12 inches in diameter and 6 inches high (Fig. 2D). Wet and dry bulb thermometers (Taylor 'Humidiguide') and a beaker of water with a tissue paper wick were placed in each large plastic cage which was covered with a sheet of glass. The temperature inside this closed cage fluctuated similarly to that in the cabinet (Fig. 4) but the relative humidity was near saturation at all times.

Another eight weevils of each species were confined singly but not enclosed in a plastic humidity cage. Instead, these were subjected to the atmospheric conditions in the cabinet to observe the effects of fluctuating humidity as well as different diurnal temperatures.

For these observations the B. sulcatus were collected by sweeping on June 7, and the S. obscurus on June 12. Teneral adults were weighed before caging and selected for uniformity of size and age. Eggs were counted and foliage provided at weekly intervals. The mature foliage was collected on June 7 and 28 and stored in closed plastic bags at 0°C.

Comparative observations on fecundity were terminated after the weevils had oviposited for 11 weeks.

To observe the effect of changing the temperature program, the surviving _B. sulcatus_ in the high relative humidity groups were transferred to other temperature programs for 5 weeks.

Results and Discussion

Table II shows the mean egg production per week of survivors, the number of survivors, and the mean egg production per weevil for 11 weeks for each species at the various environmental programs. The effects of these conditions on fecundity are indicated in Fig. 4.

In constant high humidity, _B. sulcatus_ produced significantly fewer eggs at the lowest temperature program than at the other temperature programs. A difference in programs of only 5°C during the day was sufficient to produce this effect. This observation apparently does not conform to the general statement of Messenger (33, p.187). Insects that oviposit at night, he claims, are restricted in this activity by nocturnal temperatures, the best measure of which is the mean minimum daily temperature. There were no significant differences in egg production between the various temperature programs when the humidity also fluctuated. Under these conditions some leaves became slightly desiccated and this possibly contributed to the low fecundity and high mortality (Table II). When the means

TABLE II

THE FECUNDITY OF B. SULCATUS AND S. OBSCURUS WHEN EIGHT TENERAL ADULTS OF EACH SPECIES WERE CAGED SINGLY ON DETACHED STRAWBERRY LEAFLETS IN WATER AND KEPT IN CABINETS AT DIURNAL ENVIRONMENTAL PROGRAMS, 1961

Programs[1]															
		B. sulcatus													
Temp. °C	Humidity	Eggs per survivor per week: 1	2	3	4	5	6	7	8	9	10	11	Eggs per weevil[2]		Survivors
8 to 15	High	0	0	1	4	5	0	0	0	0	0	0	8a		7
	Fluct.	0	0	2	21	34	18	8	8	4	1	0		92a	5
8 to 20	High	1	17	32	60	61	63	56	64	56	48	32	476 b		5
	Fluct.	0	9	16	9	22	62	57	55	68	20	-		149a	0
8 to 25	High	5	21	41	34	64	91	84	91	80	53	79	596 b		6
	Fluct.	2	20	8	-	-	-	-	-	-	-	-		30a	0
15 to 33	High	2	20	35	84	80	63	83	73	44	4	0	470 b		4
	Fluct.	7	6	8	10	42	38	48	28	14	-	-		62a	0
												Mean	388	83	
		S. obscurus													
8 to 15	High	4	10	5	3	4	1	3	0	4	0	8	31a		5
	Fluct.	4	11	3	8	6	8	7	4	5	8	6		60a	5
8 to 20	High	21	30	24	3	7	12	19	11	3	1	12	126 b		4
	Fluct.	18	8	1	0	5	5	3	5	33	11	16		51a	2
8 to 25	High	15	10	3	5	4	7	13	0	7	13	13	38a		1
	Fluct.	22	18	6	8	5	5	2	2	6	0	5		67a	4
15 to 33	High	6	12	9	3	9	15	11	23	4	0	-	47a		0
	Fluct.	27	18	9	10	6	21	2	9	10	3	0		103a	3
												Mean	60	70	

[1] All at 16-hour photoperiod. See Fig. 4. High humidity refers to a constant relative humidity of about 90%.

[2] Means in the same species column with the same letter are not significantly different ($p = .05$). Differences between humidities are significant for B. sulcatus only. All data were transformed to $\sqrt{x}$ for analysis.

of the egg productions at all programs for each humidity regime were compared, high constant humidity resulted in significantly higher fecundity than fluctuating humidity.

Surviving B. sulcatus kept at high humidity and moved after the initial 11 weeks of observation to different temperature programs responded as shown in Table III. Quiescent weevils moved from 8 to 15° to 8 to 25°C became active and oviposited within the first week. Active weevils moved from 8 to 20° and 8 to 25° to 8 to 15°C gradually became quiescent.

In constant high humidity S. obscurus produced significantly more eggs at 8 to 20° than at any other program (Table II), and it oviposited readily at 8 to 15°C. Together these observations indicated that this species had a lower temperature threshold for oviposition than B. sulcatus. In fluctuating humidity, the fecundity of S. obscurus was not significantly different at the various temperature programs nor was there any significant difference between the humidity regimes when the means of the egg productions at all temperatures were compared.

Conclusions

Under the conditions of these observations the following conclusions are drawn:

1. B. sulcatus is more fecund and survives better in an environment kept continuously near saturation than at one where the humidity fluctuates with temperature. S. obscurus appears to be better adapted to fluctuating humidity and can probably withstand greater

TABLE III

THE FECUNDITY OF B. SULCATUS FOR FIVE WEEKS AFTER MOVING THE SURVIVORS OF 11 WEEKS OF OVIPOSITING AT CONSTANT HIGH RELATIVE HUMIDITY TO A DIFFERENT TEMPERATURE PROGRAM, 1961

First program			Second program							
°C	Eggs per survivor[1]	Survivors	°C	Eggs per week 1	2	3	4	5	Eggs per survivor	Survivors
8 to 15	10	9	8 to 25	5	55	47	40	56	196	6
8 to 20	532	5	8 to 15	40	18	4	0	0	62	5
8 to 25	659	6	8 to 15	45	26	36	14	0	120	6

[1]During first 11 weeks of egg-laying.

exposure to drying conditions during the day than B. sulcatus.

2. B. sulcatus is capable of laying very few eggs before becoming quiescent when the diurnal temperature is 8 to 15°C; but this nocturnal species is very fecund in high humidity when the day temperature rises above 15° by as little as 5°, e.g. in a program of 8 to 20° and is still more fecund at 8 to 25°, decreasing slightly at 15 to 33°C.

3. In high humidity S. obscurus is significantly more fecund at 8 to 20° than at the other temperature programs described but oviposits readily at 8 to 15°C indicating a lower temperature threshold for oviposition than B. sulcatus. In fluctuating humidity S. obscurus shows no significant differences in fecundity at the different temperature programs described nor is there any significant difference between high and fluctuating humidity at all programs.

EFFECT OF CONTROLLED CONSTANT AND DIURNAL TEMPERATURES ON THE FEEDING AND FECUNDITY OF B. SULCATUS

The rate of feeding and fecundity were shown to be closely associated in the rape flea beetle, Psylliodes chrysocephala (L.), at different temperatures (5, p.454). Since B. sulcatus was available in large numbers in 1961, an experiment was conducted to determine if the same association exists with this species at various temperature programs.

Methods and Materials

The cabinets already described were used for diurnal temperature programs. Constant temperature conditions were available at 8, 13, 18 and 22°C. The two lower temperatures were those of the two cold rooms described. A large air-conditioned insect rearing room and a climate cabinet (26, p.1154) provided constant conditions of 18° and 22°C, respectively. All locations received 16 hours of light from fluorescent lamps.

Teneral adults of B. sulcatus were swept on June 7, 1961. Twenty-five were placed in lantern-globe cages (Fig. 2D) with three trifoliate leaves on June 16. The removable top of the cage was bronze screen-door netting welded by heat to the edge of a 'Kodapak' ring as follows: a strip of the plastic 0.7 cm wide was stapled into a ring to fit the globe snugly, the ring was placed on the globe which was then inverted and the edge of the plastic ring was pressed lightly into the hot screening, which was heated on an electric hot plate. The bottom of the cage was rubber dam held in place by a heavy rubber band. The dam was punctured with a dissecting needle and the leaf petioles inserted from inside the globe. The cage was set on a one-liter beaker filled with water to keep the foliage fresh and the humidity in the cage high. Three cages were used in each location and foliage was changed weekly. Observations were made on feeding and the number of eggs laid until July 7.

Results and Discussion

Differences in feeding rate and oviposition were apparent (Fig. 5). Most feeding and oviposition occurred at the constant temperature of 22°C. A comparison between constant and diurnal programs with similar mean temperatures showed that feeding and initial oviposition were higher at the diurnal programs up to 8 to 25°C. At 15 to 33° there was considerable mortality and fewer eggs than at either a constant 22° or a diurnal 8 to 25°C. At 18° only 20 eggs per cage and moderate feeding occurred, whereas 568 eggs per cage were laid at 22°C and most of the foliage was consumed. Thus a change of only 4° at constant conditions caused a marked effect. An effect was also apparent between 8 to 20° and 8 to 25°C in the diurnal programs.

Conclusions

Under the conditions of these observations on *B. sulcatus* the following conclusions are drawn:

1. The optimum constant temperature for feeding and initial oviposition is 22° and the optimum diurnal program is 8 to 25° (mean

of 21.5°C).

2. Mortality is high and initial oviposition low at diurnal temperatures of 15 to 33°C (mean of 24°C).

3. Feeding is reduced and oviposition retarded when day temperatures do not exceed 15°, but both increase at mean temperatures as low as 14° provided the maximum temperature reaches 20°C during the day.

PLANT NUTRITIONAL FACTORS AFFECTING FECUNDITY

In 1952 the author observed B. sulcatus larvae in outbreak numbers in strawberry plantings where sawdust had been used as a mulch and nitrogen applied in relatively large amounts to restore that lost from the soil by the decomposition of the sawdust. Experiments were conducted to determine if host plant nutrition affects the fecundity of either B. sulcatus or S. obscurus.

The effect of host plant nutrition on insects and mites has been comprehensively reviewed (40, p.149-167). Friend (16, p.68) considers that such studies have limited value in determining precise nutritional requirements and warns that the results should not be interpreted solely in terms of mineral deficiency since the plants may contain organic compounds in atypical concentrations. Workers generally conclude that increased nitrogen in the host plant is associated with increased fecundity (15, p.570; 41, p.303; 30, p.147; 3, p.507; 2, p.397; 19, p.110; 39, p.371; 17, p.63; 7, p.45; 29, p.779; 34, p.555; 20, p.136; 35, p.757; 21, p.504). The fecundity of certain mites has been shown to be affected by different levels of phosphorus

(38, p.524), and potassium (38, p.525 and 34, p.556). Lord and Stewart (31, p.927) suggest that outbreaks of phytophagous mites are unlikely to result from increased application of nitrogenous fertilizers to apples in Nova Scotia. Maltais and Auclair (32, p.320) have demonstrated that varieties of peas susceptible to aphid attack contain more nitrogen than resistant varieties.

Experiments with Detached Leaves

In the present study caging weevils on attached leaves outdoors proved unsatisfactory. Small leaf cages became hot and moist during the day and large cages made recovery of eggs impossible. The use of detached leaves, although widely used for mites (39, p.370 and 21, p.504), has been adversely criticized (4, p.582 and 25, p.653) because rapid changes occur in the constituents of the leaves (6, p.274). Nevertheless, to obtain some indication of the effect of plant nutrients outdoors, it was necessary to detach the leaves and feed the weevils under laboratory conditions.

EFFECT OF NITROGEN, PHOSPHORUS AND POTASSIUM IN FIELD CULTURE ON THE FECUNDITY OF BOTH SPECIES

A preliminary study was conducted in 1958 at Saanichton in which commercial fertilizers containing one of the elements nitrogen, phosphorus or potassium were applied in a 2 X 2 X 2 factorial experiment (51, p.14) to four strawberry plants in a randomized block design. A trifoliate leaf was detached from each plant at weekly intervals. Two leaflets were fed to four B. sulcatus per vial and the third leaflet to four S. obscurus per vial kept at constant conditions of 20°C, 75 to 85 percent relative humidity and 16-hour photoperiod. The mean egg productions after nine weeks although not significantly different, strongly indicated that even though the variability was high the application of fertilizers had some effect especially on B. sulcatus (Table IV). On the strength of this preliminary study the following more extensive experiment was conducted at Vancouver from 1960 to 1962.

Methods and Materials

Virus-free strawberries were planted on May 25, 1960 at the University of British Columbia farm on Alderwood sandy loam soil of inherent low fertility but somewhat improved by general use. The design was a randomized block with five plants at 36-inch intervals per row-replicate and four blocks each with seven fertilizer treatments and a check, comprising a 2 X 2 X 2 factorial experiment (51, p.14). Commercial fertilizers (Table IV) were applied by hand around each plant and worked in lightly on the following dates: June 21, 1960, April 13 and July 25, 1961, and May 3, 1962. The plants were irrigated by sprinklers following the applications and all necessary cultural practices were followed. The blossoms were removed in the first summer. The yields were recorded in 1962. No sprays were applied.

In 1960, teneral S. obscurus were swept on June 26 and caged singly on June 30 in glass vials, each with a leaflet from one of the 160 plants. B. sulcatus were difficult to find and were not

TABLE IV

THE FECUNDITY OF *B. SULCATUS* AND *S. OBSCURUS* WHEN CAGED WITH DETACHED LEAFLETS FROM STRAWBERRY PLANTS FERTILIZED OUTDOORS AT SAANICHTON, 1958

Fertilizer treatments[1]		Eggs per weevil[2]	
Elements	Grams per plant	*B. sulcatus*	*S. obscurus*
N	4.5	147	62
P	6.0	130	64
K	5.4	118	64
PK	6.0-5.4	111	50
NP	4.5-6.0	130	85
NK	4.5-5.4	78	68
NPK	4.5-6.0-5.4	157	64
None	-	64	50
% coefficient of variability		53.3	29.9

[1]N as ammonium nitrate (33.5-0-0); P as superphosphate (0-19-0); K as potassium chloride (0-0-60).

[2]After nine weeks of egg-laying; means of four replicates. No significant differences in either species (p =.05).

swept until July 6. Since only 120 were available, these were caged singly with leaflets from only 3 plants of each treatment in one replicate and from four plants in the other three replicates. The vial cages were kept at 20°C and closed with loose-fitting corks in an effort to keep the humidity high and the leaves succulent for one week when they were replaced and the eggs counted. Egg production was recorded for six weeks with both species.

In 1961, the second year, only B. sulcatus was studied. Teneral adults were swept on June 13 and caged singly on June 14 in plastic leaf cages with a leaflet from one of the 160 plants. The petioles were immersed in water by inserting them through holes in a sheet of plastic over a tray of water (Fig. 2E). To maintain a high humidity, another plastic sheet was placed loosely over the cages. The trays were kept in the laboratory at room temperature of between 20 to 25°C. The leaves were renewed and the eggs counted weekly for six weeks.

In 1962, the third year, again only B. sulcatus was studied. Teneral adults were collected in the laboratory as they emerged from clumps of infested soil. Two methods of caging were used: A trifoliate leaf was taken weekly from only three of the five plants per replicate. One leaflet was placed in a closed plastic cage (Fig. 2A, 4) with a weevil and kept at 20°C with 16 hours of light. No leaching of nutrients was possible in this cage. Another leaflet was oven-dried for later chemical analysis. The third leaflet, still attached to the petiole, was caged with a weevil in a plastic leaf cage with screen ends (Fig. 2A, 3). The petioles were immersed in tap water in individual 50-ml erlenmeyer flasks which were covered by a 'Kodapak' plastic hood to maintain high humidity (Fig. 2F), and kept at room temperature. Egg production was recorded weekly for six weeks with both methods. The viability of all eggs was determined.

The leaflets were analyzed for protein nitrogen by the semi-micro method of Ward and Johnston (48, p.11) from foliage detached on July 11, 1961 and August 21, 1962.

Results and Discussion

Table V shows the mean number of eggs produced by weevils of both species.

There was no significant difference between the numbers of eggs produced by S. obscurus fed foliage from differently fertilized plants in 1960 (Table V). The coefficient of variability of the overall mean was 28.8 percent and only one weevil of the 160 died, indicating both low variability between individuals and low stress on the population during the experiment. On the basis of these results no further experiments were conducted with this species and field-grown foliage.

The effect of the fertilizers on the fecundity of B. sulcatus was evident in the first season when the non-fruiting plants were becoming established. The significant differences between main effects are shown in Table V in the column of results for 1960. The highest egg production was observed when nitrogen alone was applied but the production was not significantly different from that obtained with phosphorus or potassium. However, the latter two treatments were not significantly different from the unfertilized treatment or

TABLE V

THE FECUNDITY OF B. SULCATUS IN THREE SEASONS AND OF S. OBSCURUS IN ONE SEASON WHEN CAGED SINGLY WITH DETACHED LEAFLETS FROM STRAWBERRY PLANTS FERTILIZED OUTDOORS AT VANCOUVER, 1960 TO 1962

Fertilizer treatments[1]	Eggs per survivor[2]				
	B. sulcatus				*S. obscurus*
	1960	1961	1962	Mean	1960
N	172a	110a	205a	162a	117a
P	118abc	126a	173a	139a	92a
K	125ab	91a	189a	135a	110a
PK	88 bc	118a	172a	126a	96a
NP	105 bc	131a	142a	126a	110a
NK	91 bc	154a	184a	143a	101a
NPK	74 c	103a	200a	126a	105a
None	84 bc	79a	200a	121a	105a
% coef. of var.	33.6	34.5	25.0		28.8

[1]See Table IV for amounts and text for dates of application.

[2]After six weeks of egg-laying. Initial weevils per replicate: *B. sulcatus* in 1960 was three, in 1961 was five, in 1962 was six (three in each of two types of cages); *S. obscurus* in 1960 was five. Values in the same column with the same letter are not significantly different (p =.05).

the other treatments. The interaction of nitrogen with potassium reduced egg production significantly. Plant growth was not noticeably affected by any of the treatments.

The coefficient of variability of 33.1 percent was low for this species and indicated little variability. These results, unlike those with S. obscurus, were sufficiently encouraging to warrant further studies the next year starting with teneral adults.

No significant differences between egg production were observed during the second season (1961) even though teneral weevils were used (Table V). Analysis of leaves for protein nitrogen showed no wide variation between treatments (general mean of 2.56 percent dry weight). Apparently the inherent soil fertility was sufficient to satisfy the nitrogen requirements of the plants and of the weevils.

Again in the third season (1962) there were no significant differences between egg productions, egg viabilities, or types of cages (Tables V and VI).

The effect on egg production of the fertilizer treatments could not, of course, be shown by the use of detached leaves. It was anticipated, however, that some information could be obtained on differential response between species to verify the results of the preliminary observations at Saanichton in 1958. The first season's results seemed to warrant the subsequent investigations with B. sulcatus, but treatments failed to produce significant differences in fecundity in later years. Possibly an effect could be shown with less fertile soil or with nutrient solution culture.

TABLE VI

THE MEAN FECUNDITY AND VIABILITY OF EGGS OF B. SULCATUS WHEN CAGED SINGLY IN EITHER SCREENED OR CLOSED CAGES WITH DETACHED LEAFLETS FROM STRAWBERRY PLANTS FERTILIZED FOR THREE SEASONS OUTDOORS AT VANCOUVER. MEAN PROTEIN NITROGEN IN THE LEAVES AND YIELD OF FRUIT, 1962

	Screened cages[1]		Closed cages[2]			
Fertilizer treatment[3]	Eggs per weevil[4]	Viability of eggs (%)	Eggs per weevil[4]	Viability of eggs (%)	Protein N in leaves (% dry wt.)	Yield per plot (oz.)[5]
N	202	81	208	80	1.72	21.1ab
P	179	74	166	73	1.30	28.8a
K	178	75	200	78	1.68	27.5a
PK	157	79	185	79	1.46	28.3a
NP	144	72	142	66	1.70	15.8 b
NK	181	74	187	77	1.78	20.2ab
NPK	203	86	196	85	1.67	23.5ab
None	176	64	224	77	1.67	29.6a
% coef. var.	41.3		34.8			

[1]On leaflet with petiole in water at room temperature.

[2]Leaflet in capped vial kept at constant 20°C.

[3]See Table IV for amounts and text for dates of application.

[4]Sum of the means of six weekly counts of four replicates each starting with three weevils.

[5]Means with the same letter not significantly different (p =.05).

In the third season plants receiving no fertilizer gave the highest yield differing significantly from those receiving nitrogen with phosphorus (Table VI). The factorial effects of nitrogen significantly reduced yield.

Conclusions

On the basis of these experiments the following conclusions regarding fecundity are drawn:

1. The application of nitrogen applied to strawberry plants in the first season is associated with an increase in the egg production of B. sulcatus fed detached leaflets. However, this effect is not evident when nitrogen is reapplied in two succeeding seasons.

2. The egg production of S. obscurus is not affected when the adults are fed detached leaflets from plants fertilized outdoors in the first season.

3. The egg production of B. sulcatus is not significantly different whether weevils are caged with detached leaflets in closed plastic vials or in vials with screen ends and the petioles in water.

Experiments with Attached Leaves

A preliminary experiment with B. sulcatus was conducted in an insectary in 1958 using potted plants grown in Shawnigan gravelly sandy loam soil of inherent low fertility. The plants were set in 6-inch clay pots on May 7 and fertilized with nitrogen, phosphorus, or potassium in a 2 X 2 X 2 factorial experiment comprised of eight treatments in eight blocks (Table VII). Teneral B. sulcatus were collected on

May 22 and caged singly in plastic leaf cages on a leaflet of each of the 64 plants. Weevils were moved to fresh leaflets at weekly intervals and the eggs counted. Plants were subjected to prevailing environmental conditions which were apparently too hot and dry during the day as only 39 of the 64 weevils survived for 11 weeks of egg-laying. The application of nitrogen alone or with potassium was associated with increased egg production by the survivors, although differences between treatments were not significant when analyzed by the method of unequal subclass numbers (43, p.232). Further detailed experiments were conducted in the laboratory at Vancouver from 1960 to 1962.

EFFECT OF NITROGEN, PHOSPHORUS, AND POTASSIUM IN VERMICULITE-CULTURE ON THE FECUNDITY OF BOTH SPECIES

Various workers have used vermiculite-culture for testing the effect of concentrations of specific elements on fecundity, especially of mites (30, p.146) and grasshoppers (41, p.298). Leroux questions the value of leaf analysis in this type of work because of the variation in the amounts of constituents present in the same foliage at different times even during the same day (30, p.149). The experiment reported here was designed to compare the effects of two levels of nitrogen, phosphorus, and potassium in all possible combinations on the fecundity of B. sulcatus and S. obscurus. Soil culture was included for comparison.

TABLE VII

THE FECUNDITY OF B. SULCATUS WHEN CAGED SINGLY ON ATTACHED LEAFLETS OF STRAWBERRY PLANTS GROWN IN FERTILIZED SOIL IN AN INSECTARY AT SAANICHTON, 1958

Fertilizer treatments		Eggs per survivor[3]	Survivors
Elements[1]	Grams per plant[2]		
N	3.0	213	7
P	4.6	111	5
K	3.6	95	4
PK	4.6-3.6	142	6
NP	3.0-4.6	183	3
NK	3.0-3.6	244	7
NPK	3.0-4.6-3.6	169	2
None	-	129	5
% coefficient of variability		55.8	

[1]Same formulations as in Table IV.

[2]Applied in three equal applications on May 9, 27 and July 31.

[3]After 11 weeks of egg-laying; starting with eight weevils each. No significant differences between means (p =.05).

Methods and Materials

On May 24, 1960, 160 virus-free plants were potted in vermiculite ('Terra-lite', horticultural grade, 100 percent vermiculite) and 20 in John Innes soil mixture in 6-inch plastic pots. The pots were placed on aluminum foil saucers, five pots deep and 18 wide, on each of two benches in the laboratory. Every set of five pots comprised one treatment replicate and each bench held two blocks each of nine treatments, designated at random in a 2 X 2 X 2 factorial design. Four, 8-foot, cool white, fluorescent tubes, hung 16 inches above the pots, provided from 200 to 400 foot candles at the leaf level for 16 hours per day. Aluminum foil on cardboard served as a light reflector at all sides of the benches (Fig. 2G).

The plants were watered with tap water until June 1 when 100 ml of nutrient solution was applied from above to the designated pots, and thereafter at weekly intervals. Iron solution, consisting of freshly prepared 0.5 percent ferric chloride stock solution diluted 1:1000, was always applied at 100 ml per pot three days after the nutrient solution. Distilled water was applied to the plants in the soil as required and to the plants in the vermiculite only if re-required. The nutrient solutions (Table VIII) were modifications of Hoagland's solution no. 1 plus minor elements (24, p.31). The solutions were made in 8-liter amounts, or enough for four weeks of feeding, and stored in the dark in covered plastic containers.

No leaf analyses were made.

Teneral adults of S. obscurus were swept on June 18 and caged

(Fig. 2A, 2) singly on June 21 on plants in the first replicate. More were swept on June 25 and caged on the remaining three replicates on June 27. Adults of B. sulcatus were swept on July 2 and caged (Fig. 2A, 3) on July 3. Foliage of similar size and age was selected for the cages. All cages with their leaflets were snipped from the plants at weekly intervals, the eggs were counted or frozen, and the cages were replaced on fresh leaflets. Eggs from S. obscurus were counted for eight weeks and from B. sulcatus for 10 weeks.

Results and Discussion

No significant difference in egg production occurred between the treatment means within either species (Table VIII). In contrast with weevils caged in 1960 with detached foliage from plants fertilized outdoors, B. sulcatus laid more eggs per week on the attached leaves and S. obscurus laid fewer, as follows:

	Leaves attached	Leaves detached
B. sulcatus	20	16
S. obscurus	17	23

These differences were probably related to the lower moisture content of the leaves and the lower humidity in the cages when the leaves were detached. Results already reported indicated that B. sulcatus was less fecund, while S. obscurus was apparently not adversely affected at low humidity (Table II).

In the vermiculite-culture 145 of 180 B. sulcatus and 170 of 180 S. obscurus survived. Death was not related to treatments. The coefficients of variability were low for both species, especially

TABLE VIII

THE FECUNDITY OF B. SULCATUS AND S. OBSCURUS WHEN CAGED SINGLY ON ATTACHED LEAFLETS OF STRAWBERRY PLANTS GROWN IN VERMICULITE-CULTURE AT TWO LEVELS OF NPK AND SOIL, VANCOUVER, 1960

Treatment	PPM[1] N	PPM[1] P	PPM[1] K	B. sulcatus: Eggs per survivor[2]	B. sulcatus: Survivors[3]	S. obscurus: Eggs per survivor[4]	S. obscurus: Survivors[3]
High N	420	31	312	204	17	155	19
High P	210	62	312	200	18	120	20
High K	210	31	624	263	12	160	19
High PK	210	62	624	162	18	128	18
High NP	420	62	312	244	14	143	20
High NK	420	31	624	169	14	130	19
High NPK	420	62	624	200	17	133	18
Std. NPK	210	31	312	142	16	132	19
Soil	-	-	-	221	19	111	18
% coefficient of variability				35.0		15.6	

[1]Modified Hoagland's no. 1 (24, p.31); Ca kept at 480 PPM.

[2]After 10 weeks of egg-laying; no significant differences (p =.05).

[3]Of 20 weevils per treatment.

[4]After eight weeks of egg laying; no significant differences (p =.05).

S. obscurus (Table VIII).

Conclusions

Under the conditions of this experiment, the egg production of either *B. sulcatus* or *S. obscurus* is not significantly affected when weevils feed on attached leaflets of strawberry plants grown in the laboratory in vermiculite-culture at the reported concentrations of nitrogen, phosphorus, and potassium.

EFFECT OF NITROGEN, PHOSPHORUS, AND POTASSIUM IN SAND-CULTURE ON THE FECUNDITY OF *B. SULCATUS*

The failure to demonstrate significant differences in the fecundity of *B. sulcatus* in the previous experiment may have been caused by insufficient spread in the concentrations of nutrients or low illumination of the plants. There was also a possibility that the use of nitrate-nitrogen alone might cause less effect than ammonium-nitrogen or these two forms of nitrogen together. An experiment with *B. sulcatus* in 1961 tested the effect of a wider range of concentrations of elements, higher illumination, and a more uniform population of weevils than in 1960, as well as the two forms of nitrogen.

Methods and Materials

To avoid the possibility of binding the ammonium ion to vermiculite, washed quartz sand of 20- to 40-screen size from Ottawa, Illinois, was used as a root medium.

Plants were selected, washed, and potted in 6-inch plastic pots and placed in aluminum foil saucers on a bench in a ventilated room without windows on May 5. A light bank of 12 cool white 8-foot tubes was suspended 12 inches above the pots (Fig. 2H). The light intensity ranged from 740 to 860 foot candles when cardboard panels faced with aluminum foil were used as side reflectors. The lights were operated for 16 hours per day. The pots were first leached with tap water and then distilled water. Commencing on May 15, nutrient solutions and iron solution were applied weekly as described. The experiment was a completely randomized design with 10 replicates each of a single weevil per plant.

Originally all solutions containing ammonium-nitrogen had equal concentrations of nitrogen as nitrate and ammonium ions. These resulted in pronounced leaf scorching. Plants fed only the ammonium-form died from ammonium ion toxicity and were eliminated from the experiment. Beginning on June 21, solutions of the original concentrations were continued but these had a lower ratio of ammonium to nitrate ions (Table IX), and proved to be less toxic. The nitrate-form of nitrogen was tested at the standard level only (210 p.p.m.).

The number of runners and their growth was recorded on July 5. Leaf analyses for protein nitrogen were made of oven-dried foliage taken on August 28.

Teneral adults of _B. sulcatus_ were collected by searching under plants in about 20 feet of matted row in the field on June 7. Weevils were so abundant that 350 were collected in two hours. Soft weevils of similar weight (70 ± 9 mg) were selected. They were confined

TABLE IX

THE COMPOSITION OF NUTRIENT SOLUTIONS USED IN SAND-CULTURE OF STRAWBERRY, VANCOUVER, 1961

Treatment	Milliliters of 1 M stock solution per liter[1]							PPM[2]				
	KH_2PO_4	KNO_3	$Ca(NO_3)_2$	NH_4NO_3	$CaCl_2$	$NH_4H_2PO_4$	KCl	NH_4-N	NO_3-N	Tot.-N	P	K
<u>N as NO_3</u>												
Standard	1.0	5.0	5.0	-	-	-	-	-	210	210	31	234
<u>N as NO_3+NH_4</u>												
Standard	1.0	-	3.75	3.75	1.75	-	5.0	52	158	210	31	234
High N	1.0	5.0	5.0	22.5	-	-	-	315	525	840	31	234
Low N	1.0	-	2.25	1.5	2.75	-	5.0	21	84	105	31	234
High P	2.0	-	5.0	2.0	-	2.0	4.0	56	168	224	124	234
Low P	0.5	-	3.75	3.75	1.25	-	5.5	52	158	210	16	234
High K	1.0	-	3.75	3.75	1.25	-	23.0	52	158	210	31	936
Low K	1.0	-	3.75	3.75	1.25	-	2.0	52	158	210	31	117

[1] $MgSO_4$ at 2 ml per l; minor element stock solution at 1 ml per l (24, p.30).

[2] Calcium was always at 200 PPM.

singly on the plants on June 8. Daily observations were made to determine the preoviposition periods. Eggs were counted for 10 weeks.

Results and Discussion

Table X shows statistical comparisons of the preoviposition periods, egg productions, runner lengths and content of nitrogen in the leaves, as well as survival of weevils for each treatment. A comparison of the cumulative egg productions appears in Fig. 6.

Short preoviposition periods were associated with solutions of high nitrogen, nitrate-nitrogen standard, nitrate- and ammonium-nitrogen standard, and low or high phosphorus. The longest average preoviposition period was associated with low nitrogen.

High fecundity was associated with solutions of high nitrogen, both standards and low phosphorus. Low fecundity was associated with solutions of high or low potassium but these results were not significantly different from that obtained with the standard solution of both forms of nitrogen.

Plant growth, as measured by runner lengths, was greatest with the standard solution of nitrate-nitrogen and least with that of high nitrogen. The protein nitrogen in the leaves followed an expected pattern in the nitrate- and ammonium-nitrogen series with high and low leaf nitrogen associated with solutions of high and low nitrogen. The protein nitrogen in plants receiving the nitrate-nitrogen standard was significantly lower than in those receiving the nitrate- and ammonium-nitrogen standard.

TABLE X

THE MEAN PREOVIPOSITION PERIOD AND FECUNDITY OF B. SULCATUS WHEN CAGED SINGLY ON ATTACHED LEAFLETS OF STRAWBERRY PLANTS GROWN IN SAND-CULTURE AT THREE LEVELS OF NPK WITH RECORDS OF RUNNER GROWTH AND PROTEIN NITROGEN IN THE LEAVES, VANCOUVER, 1961

Treatment[1]	Preoviposition period (days)	Eggs per survivor[2]	Survivors	Runner length per plant (inches)	Protein N in leaves (% dry wt.)
N as NO_3					
Standard	23.5abc[3]	517a	10	54.0a	1.92 c
N as NO_3+NH_4					
High N	23.1abc	561a	7	10.6 c	3.83a
Standard	21.8a	446ab	9	24.7 bc	2.58 b
Low P	23.0ab	435ab	9	24.9 bc	2.58 b
High P	25.1abcd	395 b	10	12.9 c	2.67 b
Low N	28.6 d	309 b	10	24.3 bc	1.40 d
High K	27.6 cd	273 b	6	34.2 b	2.42 b
Low K	27.2 bcd	269 b	8	23.9 bc	2.94 b
% coefficient of variability		48.2			

[1]See Table IX.

[2]After 10 weeks of egg-laying; starting with 10 weevils each.

[3]Means with the same letter are not significantly different ($p = .05$) within columns.

The treatment which gave the most vigorous plant growth was obviously the nitrate-nitrogen standard. Leaves from these plants were large and showed no sign of marginal leaf scorching which was evident to some degree in all plants receiving solutions containing the ammonium ion. In the latter series leaves were characteristically small, round, and dark green when fed high nitrogen and small, normal-shaped, and pale green with red margins and petioles when fed low nitrogen.

Considering the data in Table X, the treatment most conducive to plant growth, fecundity and survival of the weevils was the nitrate-nitrogen standard. Nevertheless, the total nitrogen in the leaves was relatively low (1.92 percent). The ammonium ion, although associated with high nitrogen in the leaves, was apparently toxic to the plants, since runner growth was retarded in all cases compared with plants receiving only nitrate-nitrogen. Possibly this deleterious effect was responsible for keeping some of the protein nitrogen or other leaf constituents in a form unavailable to the weevils.

The high or low phosphorus solutions appeared to have no effect on fecundity, whereas high or low potassium solutions were both associated with low fecundity compared with the standard levels. All levels of phosphorus and potassium produced plants with similar concentrations of protein nitrogen in the leaves.

Conclusions

Under the conditions of this experiment with *B. sulcatus* the following conclusions are drawn:

1. Fecundity of the weevils and protein nitrogen in the leaves are

high when the plants are fed high nitrogen as nitrate plus ammonium ions and low with low nitrogen in these forms.

2. Fecundity of the weevils is high when the plants are fed a standard level of nitrogen as the nitrate ion only, but protein nitrogen in the leaves is relatively low. With this treatment the plants are more vigorous than when the ammonium ion is also used as a source of nitrogen.

3. High or low phosphorus solutions have no apparent effect on the fecundity of the weevils.

4. High or low potassium solutions appear to reduce the fecundity of the weevils but the protein nitrogen in the leaves is not reduced.

EFFECT OF NITRATE- OR AMMONIUM-NITROGEN IN SAND-CULTURE ON THE FECUNDITY OF *B. SULCATUS*

The phytotoxicity of the ammonium ion already noted prevented a critical comparison of the effects of different forms of nitrogen on the fecundity of the weevils. Hewitt (23, p.96) reported that ammonium toxicity could be avoided by using ammonium citrate as a source of ammonium-nitrogen and by frequent leaching with distilled water. In 1962, an experiment was designed using this method with two concentrations each of nitrate- and ammonium-nitrogen.

Methods and Materials

On February 13, 40 plants were potted as described and placed on inverted plastic dishes to allow free drainage. A light bank of 14 cool white 8-foot tubes was suspended only eight inches above the pots (Fig. 21), so that the light intensity ranged from 800 to 1100 foot candles during a 16-hour photoperiod. A transparent canopy made of 'Kodapak' was suspended beneath the lights and an electric fan directed air between the canopy and the tubes to remove excess heat. A polyethylene curtain hung from the edges of the canopy maintained high humidity among the plants, where the temperature ranged from 20 to 25°C.

The sand was leached with distilled water before the following schedule of feeding per pot was started on February 24:

Monday - leached with 400 ml of distilled water

Tuesday - fed 100 ml of nutrient solution

Thursday - fed 100 ml of iron solution as described

Friday - fed 100 ml of nutrient solution

The experimental design was a randomized block with four treatments of 10 single plant replicates each.

Solutions with ammonium citrate formed a precipitate overnight, but ammonium acetate was substituted and was satisfactory (Table XI).

The growth of the plants was gauged by measuring the length of runners on April 6. The protein nitrogen content of the leaves was determined from lyophilized foliage taken on April 11.

Adults of _B. sulcatus_ were not available outdoors at this time of year but quiescent weevils kept at a constant 13°C since September, 1961, were available. These were originally collected on June 7, 1961. When they were caged singly on the plants on March 2 they became active and fed voraciously. The eggs were counted at weekly intervals for 10 weeks and their viability determined.

THE FECUNDITY AND VIABILITY OF EGGS OF B. SULCATUS WHEN CAGED SINGLY ON ATTACHED LEAFLETS OF STRAWBERRY PLANTS GROWN IN SAND-CULTURE AT TWO LEVELS OF NITROGEN AS NITRATE OR AMMONIUM IONS WITH RECORDS OF PLANT RUNNER GROWTH AND PROTEIN NITROGEN IN THE LEAVES, VANCOUVER, 1962

Treatment	Milliliters of M stock solution per liter[1]			Eggs per survivor[2]	Survivors	Viability of eggs (%)[3]	Runner length per plant (inches)	Protein N in leaves (% dry wt.)
	$Ca(NO_3)_2$	CH_3COONH_4	$CaCl_2$					
210 PPM N								
as NO_3	7.5	-	-	431a[4]	6	93.4	24.8a	2.71a
as NH_4	-	15.0	7.5	409a	9	93.7	21.0a	2.77a
25 PPM N								
as NO_3	0.9	-	6.6	246b	8	82.4	2.2b	1.22b
as NH_4	-	1.8	7.5	247b	10	80.2	4.4b	1.32b
% coefficient of variability 37.9								

[1] KH_2PO_4 at 1.0 ml; KCl at 5.0 ml; $MgSO_4$ at 2.0 ml; minor element stock at 1.0 ml per liter.

[2] After 10 weeks of egg-laying; starting with 10 weevils each.

[3] Means of seven weekly counts.

[4] Means with the same letter are not significantly different ($p = .05$) within columns.

Results and Discussion

Egg-laying resumed within the first week of feeding. All the weevils fed at about the same rate regardless of the treatments.

Table XI shows the production and viability of eggs, survival of the weevils, the growth of runners, and the total nitrogen concentration in the leaves. The cumulative egg productions appear in Fig. 7.

Significantly more eggs were laid by weevils caged on plants receiving the standard concentrations of nitrogen than on plants receiving low concentrations. No significant difference in egg production occurred between the forms of nitrogen at the same concentrations.

The growth of plants fed the low level of nitrogen was reduced below that of plants fed the standard level and was reflected in the length of the runners (Table XI). The concentration of protein nitrogen in the leaves was lower in plants fed the low level of nitrogen than in those fed the standard level.

Conclusions

Under the conditions of this experiment with B. sulcatus the following conclusions are drawn:

1. Fecundity is positively associated with the concentration of protein nitrogen in the leaves.

2. There is no significant effect on fecundity or on the concentration of protein nitrogen in the leaves whether nitrogen is supplied to the plant in the nitrate- or ammonium-form.

3. At a concentration of 25 p.p.m. of nitrogen in the nutrient solution the plant growth is greatly reduced and nitrogen deficiency symptoms are evident.

EFFECT OF NITRATE-NITROGEN IN SAND-CULTURE ON THE FECUNDITY OF BOTH SPECIES

Using improved techniques, as described in the previous experiment, a positive association was established between the fecundity of B. sulcatus and the concentration of nitrogen, whether fed to plants or recovered in the leaves. This raised the question of whether or not S. obscurus might be similarly affected. An experiment was conducted later in 1962 with both species.

Methods and Materials

The experimental conditions and the feeding schedules were the same as in the previous experiment except that new Sylvania 'Gro-lux' fluorescent tubes were used. Nitrogen was supplied at four concentrations in the nitrate-form only (Table XII) to plants potted on May 14. There were 10 single plant replicates for each concentration arranged in a randomized block design.

The growth of the plants was compared by measuring the length of the runners cut four times. The leaves were analyzed for protein nitrogen (48, p.10-11), potassium (48, p.19), phosphorus (48, p.21) and ash (48, p.5).

A weevil of both species was caged on each plant. Adults of B. sulcatus were collected in the laboratory as they emerged from clods of soil taken from beneath strawberry plants in a heavily infested planting. Only normal weevils which emerged on June 14 were used. Teneral adults of S. obscurus were collected by searching at the base of strawberry plants on June 28. These were caged singly on the plants with folded tissue paper for oviposition sites. The preoviposition periods were determined by examining the cages daily for eggs. Thereafter, eggs were counted at weekly intervals and their viability determined.

After B. sulcatus had oviposited for 11 weeks, weevils on the plants receiving the highest level of nitrogen were moved to plants receiving the lowest level and vice versa. Eggs were recorded for four more weeks, when the weevils were returned to their original plants and the eggs recorded for a further two weeks. Weevils on the plants receiving the two intermediate levels of nitrogen were not moved.

Results and Discussion

Table XII shows the preoviposition periods, the fecundity, and the viability of the eggs for both species, as well as the plant growth and the content of protein nitrogen in the leaves. The production of viable eggs, for both species is shown in Fig. 8. Comparisons of the amounts of protein nitrogen, potassium, phosphorus, and ash in the leaves in relation to the production of viable eggs of both species appear in Fig. 9.

The beginning of egg-laying by B. sulcatus was significantly delayed at the low nitrogen levels, but there was no apparent effect

TABLE XII

THE MEAN PREOVIPOSITION PERIOD, FECUNDITY AND VIABILITY OF EGGS OF B. SULCATUS AND S. OBSCURUS WHEN CAGED SINGLY ON ATTACHED LEAFLETS OF STRAWBERRY PLANTS GROWN IN SAND-CULTURE AT FOUR LEVELS OF NITROGEN WITH RECORDS OF RUNNER GROWTH AND PROTEIN NITROGEN IN THE LEAVES, VANCOUVER, 1962

Treatment[1] (PPM N)	Species	Preoviposition period (days)	Eggs per survivor[2]	Survivors	Viability of eggs (%)	Runner length per plant (inches)[3]	Protein N in leaves (% dry wt.)
210	B. sul.	33a	506a	9	74a	146a	2.40
	S. obs.	17a	108a	9	77a		
105	B. sul.	36ab	398ab	9	73a	134a	2.18
	S. obs.	19a	163a	8	88a		
52	B. sul.	40b	243bc	9	69ab	94b	1.89
	S. obs.	16a	108a	9	76a		
26	B. sul.	53c	146c	10	44b	16c	1.56
	S. obs.	19a	182a	8	88a		

[1]Molar $Ca(NO_3)_2$ at 60, 30, 15 and 7.5 ml per l, respectively; Ca kept at 300 PPM with $CaCl_2$; other ions as in Hoagland's solution no. 1 (24, p.30).

[2]After 11 weeks of egg-laying; starting with 10 weevils each. The coefficient of variability for B. sulcatus was 52.3%; for S. obscurus 54.2%.

[3]Means of 10 plants trimmed four times.

[4]Means with the same letter are not significantly different (p =.05) within columns and species.

on S. obscurus. B. sulcatus laid significantly more eggs and significantly more of them were viable at the standard level of nitrogen than at the lower levels. The results with S. obscurus did not indicate any association between the nitrogen levels and fecundity (Fig. 8). The plants responded to the four nitrogen levels in the expected manner as indicated by the significant differences in runner growth and in the nitrogen content of the leaves (Table XII). There was no correlation between fecundity and the potassium, phosphorous, or ash content of the foliage (Fig. 9). No obvious or consistent differences were observed in the amounts of foliage consumed by weevils caged on plants receiving different levels of nitrogen.

Table XIII shows the effect of moving B. sulcatus from the plants receiving the standard level of nitrogen to those receiving the lowest level and vice versa. Weevils which had previously laid few eggs on plants receiving the lowest level of nitrogen became very fecund when moved to plants receiving the standard level. These weevils returned to low egg production when they were returned to their original plants. The reciprocal response was observed with weevils moved from the standard to the low and back to the standard level of nitrogen. Weevils on plants receiving the intermediate levels of nitrogen were not moved and their egg productions remained comparable to previous levels.

Conclusions

Under the conditions of this experiment the following conclusions are drawn:

TABLE XIII

THE FECUNDITY OF B. SULCATUS WHEN THOSE CAGED ORIGINALLY ON STRAWBERRY PLANTS RECEIVING THE HIGH AND LOW LEVELS OF NITROGEN WERE EXCHANGED FOR A FOUR-WEEK PERIOD AND THEN RETURNED TO THEIR ORIGINAL PLANTS FOR A TWO-WEEK PERIOD, VANCOUVER, 1962

Treatment (PPM N)	Eggs per survivor per week		
	First 11 weeks on original plants	Next 4 weeks (weevils on high and low levels exchanged)	Last 2 weeks (weevils returned to original plants)
210	46	55	35
105[1]	36	57	38
52[1]	22	34	20
26	13	26	15

[1]Weevils kept throughout on their original plants.

1. The fecundity of S. obscurus is not associated with the level of nitrogen supplied to the strawberry plant but remains relatively unaffected at the levels tested.

2. The fecundity of B. sulcatus and the growth of the plants are positively associated to the level of nitrogen supplied and vary significantly between the various levels tested.

3. Other leaf constituents such as potassium, phosphorus and ash were not associated with the level of nitrogen supplied nor with the fecundity of either species.

GENERAL DISCUSSION

Differences have been demonstrated in the responses of the two species of root weevils to temperature, humidity, and host plant nutrition. The lower temperature threshold for oviposition and the slightly higher tolerance to low humidity of S. obscurus as compared with B. sulcatus indicate that the former native species is the better-adapted to this area. The summer climate in the Pacific Northwest is often quite dry, so that S. obscurus might be expected to survive better than B. sulcatus. However, since both species are active only at night when the humidity is high, this advantage is probably negligible. The greater fecundity of B. sulcatus over S. obscurus outweighs any advantage the latter species has in the longer egg-laying period afforded by its lower temperature threshold for oviposition.

The indifferent response in fecundity of S. obscurus to plants fed various levels of nitrogen, phosphorus, and potassium in the experiments in the laboratory and field indicates that the production of eggs would not be affected by low or high soil fertility. Although experiments in the laboratory with B. sulcatus show that low fecundity is associated with low levels of nitrogen in the host, it is not likely that responses of this magnitude could be obtained under conditions in the field where the supply of nitrogen is usually adequate. Results with detached foliage from field-fertilized plants show significant differences in the fecundity of this species in the first or non-fruiting year, but not in the next two years. Possibly the plants were affected to a greater extent by the fertilizer applications when they were newly established than they were when they became established in subsequent years. The applications of nitrogen proved detrimental to yield in this study, and the practice is not likely to be common in commercial production of strawberries.

The apparent detrimental effect on the fecundity of B. sulcatus of high and low potassium was confusing, therefore an additional experiment was conducted which is not reported here in detail. In this experiment, plants were grown in sand-culture at four levels of potassium (0, 30, 117 and 234 p.p.m.) in the same manner as in the experiment with four levels of nitrogen. Even at this wide range of concentrations of potassium there were no significant differences in fecundity. Therefore, like phosphorus, the effect of potassium on the fecundity of B. sulcatus at the levels tested appears to be negligible.

The difference in fecundity between the two species in response to host nutrition is not unusual in insects where the nutritional requirements for growth may be quite similar but for reproduction may vary widely (12, p.137). The effect of nitrogen, or protein, on reproduction is under active study in Calliphora sp. (27, p.133-136 and 45, p.637-646). The suggestion is made that ingested protein leads to the accumulation of activating substances in the blood which quantitatively stimulate the corpus allatum either directly or via the median neurosecretory cells (44, p.138). Both the corpus allatum and the median neurosecretory cells are generally believed to influence insect reproduction (44, p.137).

The ascorbic acid content of the diet of the boll weevil, bollworm and the saltmarsh caterpillar has recently been shown to affect fecundity (46, p.296). Possibly the ascorbic acid content of the strawberry foliage in the experiments with B. sulcatus was affected by the amount of nitrogen supplied. This aspect was not investigated.

Gordon (18, p.28) has suggested that the nutrition of insects and their tolerance to insecticides could be related. In the root weevils, the tolerance of S. obscurus to cyclodiene insecticides may be related in some biochemical way to the apparent indifference of this species to various levels of protein nitrogen in the diet and vice versa for B. sulcatus. Henneberry (20, p.136) found that the fecundity of resistant two-spotted spider mites was not correlated with nitrogen in the leaf, but a correlation did exist for susceptible mites. Gordon (18, p.38) suggests that, in fact, the biochemical ecology of insects is at present only in the stage of conception.

GENERAL CONCLUSIONS

This study has led to certain definite findings with regard to the behaviour of B. sulcatus and S. obscurus. Under the conditions in the laboratory and in cages outdoors the following general conclusions are drawn:

1. B. sulcatus is much more fecund than S. obscurus under similar conditions in the field and at a constant condition of 20°C and 75 to 85 percent relative humidity in the laboratory.

2. In the laboratory, S. obscurus oviposits at a lower temperature and at more variable humidity conditions than B. sulcatus. Outdoors,

S. obscurus that have overwintered begin to oviposit earlier in the spring and those that emerge in the summer continue to oviposit longer in the fall than B. sulcatus.

3. B. sulcatus is much more fecund at a constant temperature of 20° than it is outdoors, whereas, S. obscurus is only slightly more fecund at 20°C than outdoors.

4. B. sulcatus requires a continuously high humidity for survival, whereas, S. obscurus can tolerate conditions in the laboratory where the humidity fluctuates diurnally with temperature.

5. At diurnal temperatures of 8 to 15°, B. sulcatus is quiescent but is very fecund when the temperature during the day is raised by 5°, and is most fecund at 25°C. Fecundity is slightly lower than maximum at a temperature of 15° at night and 33°C during the day. The maximum fecundity of S. obscurus occurs at 8 to 20°C. This species will lay eggs at 8 to 15°C.

6. The feeding rate of B. sulcatus, like fecundity, increases at higher maximum daily temperatures up to 25°C.

7. The fecundity of S. obscurus is not significantly affected; but that of B. sulcatus is significantly reduced, the preoviposition period is increased, and the viability of the eggs is reduced when adults are fed attached foliage of strawberry plants receiving low levels of nitrogen in either the nitrate- or ammonium-form in the laboratory.

8. Phosphorus and potassium at the concentrations tested appear to have no significant effect on the fecundity of either species.

SUMMARY

Comparisons of the effects of certain physical and nutritional factors on fecundity are made between the introduced black vine weevil, Brachyrhinus sulcatus (F.), which is susceptible to cyclodiene insecticides, and the native obscure strawberry root weevil, Sciopithes obscurus Horn, which is tolerant to these insecticides. Both species are economic pests of strawberry in the Coastal area of British Columbia, Washington and Oregon.

Observations indicate that although B. sulcatus is much more fecund in nature, it is not so well adapted in British Columbia as S. obscurus which has a lower temperature threshold for oviposition and, therefore, a longer oviposition period.

When the night temperature in cabinets at diurnal temperature programs is minimal at 8°C, the fecundity of these nocturnal species is maximal at day temperatures of 20° for S. obscurus and 25°C for B. sulcatus. Under these diurnal conditions B. sulcatus is the more fecund of the two and survives better in continuously high rather than variable relative humidity. S. obscurus is comparatively indifferent to humidity fluctuations.

Various levels of the major nutrients: nitrogen, phosphorus, and potassium, when fed to the host plant had no significant effect on the fecundity of S. obscurus. Only low levels of nitrogen significantly reduced the fecundity of B. sulcatus. With vermiculite-culture, low artificial light intensity, and restricted drainage

the effects of nutrients on B. sulcatus are statistically inconclusive, but indicate a response to nitrogen. The results with detached foliage from plants fertilized in the field are also indicative of the effect of nitrogen. With sand culture, high light intensity, and free drainage the effect of nitrogen supplied in either the nitrate- or ammonium-form on the fecundity of B. sulcatus is statistically demonstrated.

It is suggested that the different responses of the two species to the application of nitrogen to the host plant might lead to a line of study to explain their different susceptibilities to cyclodiene insecticides.

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APPENDIX

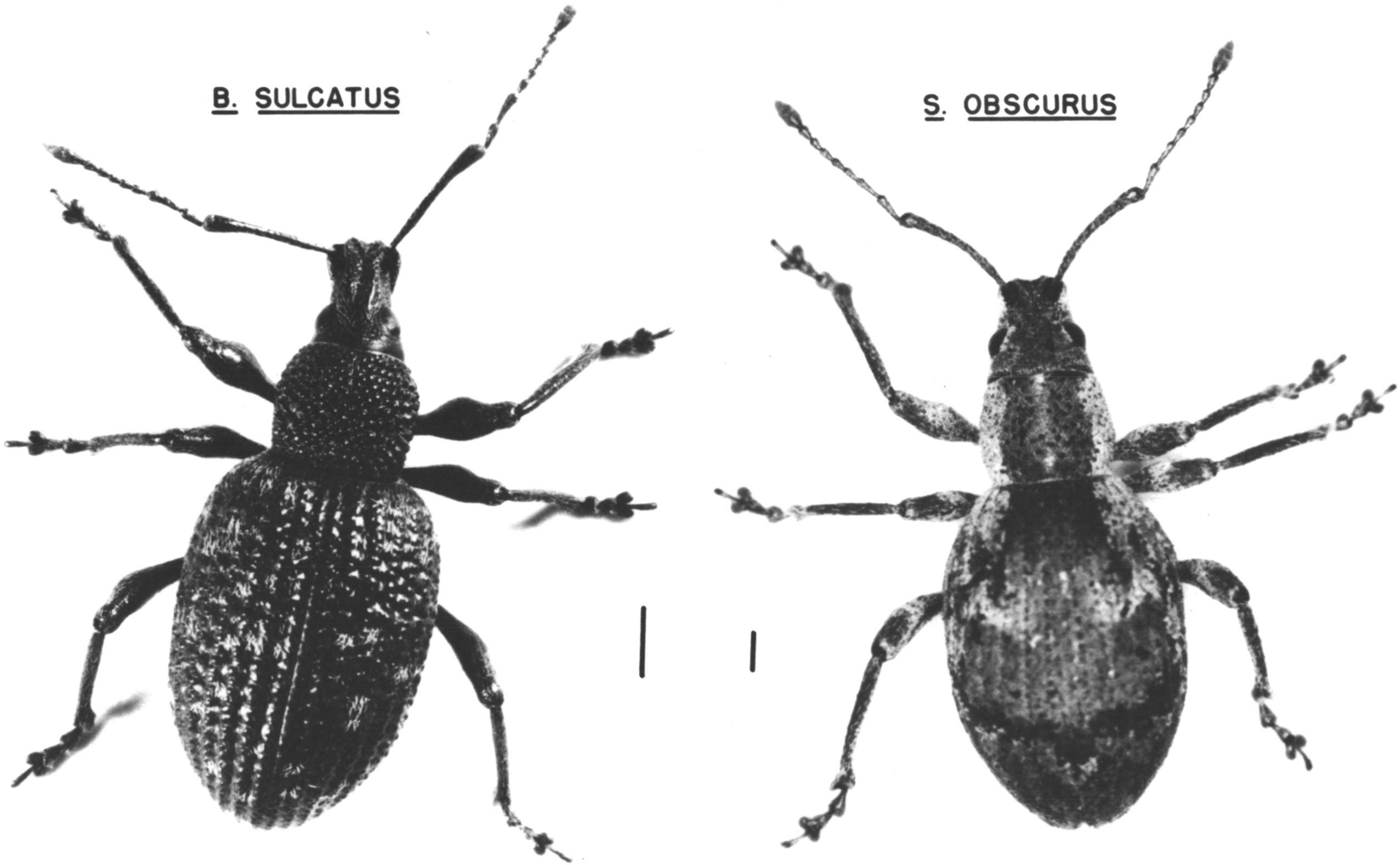

FIG. I. ADULT WEEVILS. VERTICAL LINES INDICATE ACTUAL LENGTHS.

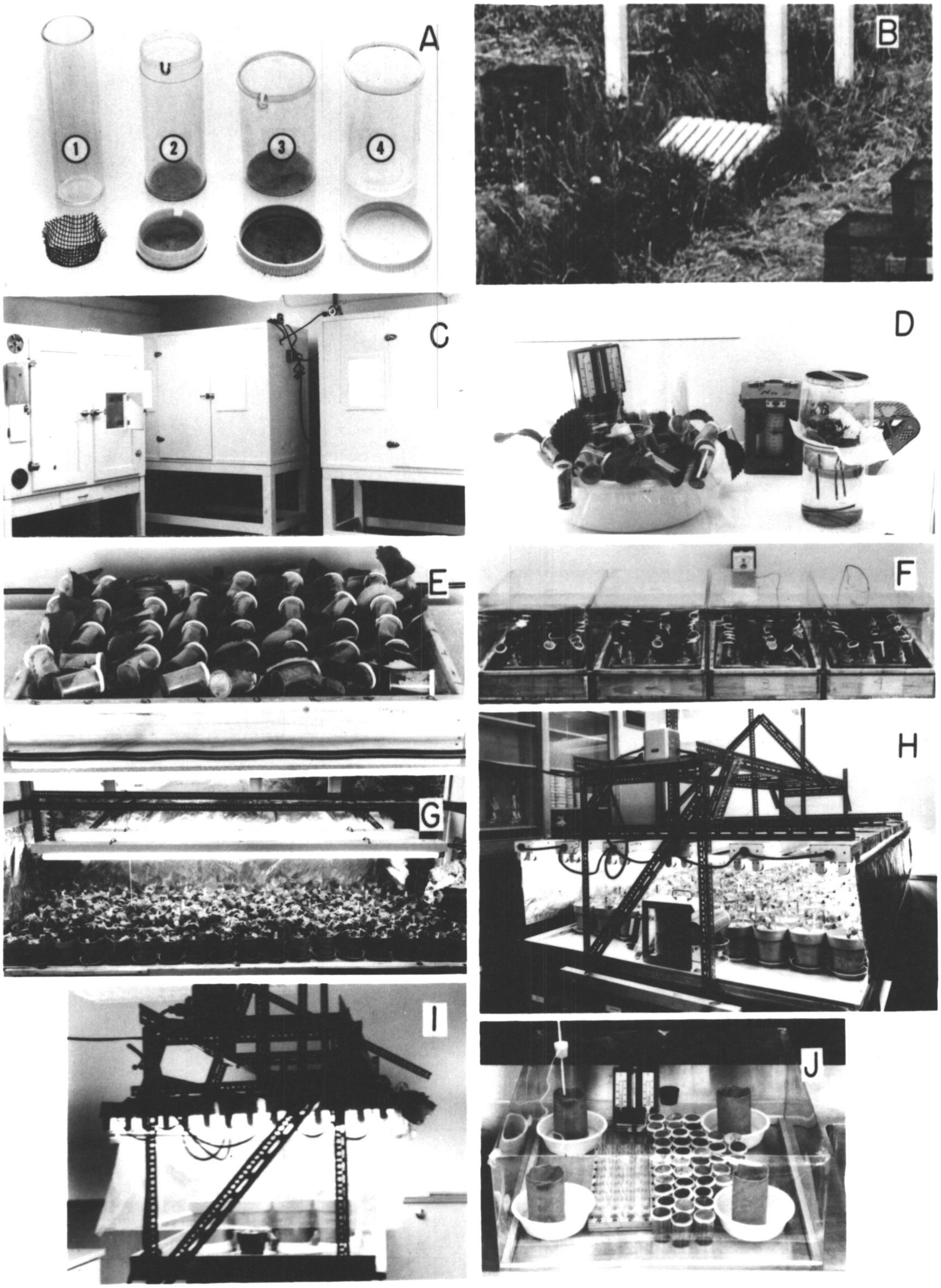

FIG. 2. A. VIAL CAGES. B. LOCATION OF CAGES OUTDOORS UNDER BAFFLE. C. REARING CABINETS IN COLD-ROOM. D. CAGES ON DETACHED LEAFLETS IN CABINET. E. CAGES ON DETACHED LEAFLETS FROM FERTILIZER EXPERIMENT, 1961. F. 1962. G. VERMICULITE-NUTRIENT SOLUTION CULTURE, 1960. H. SAND-NUTRIENT SOLUTION CULTURE, 1961. I. 1962. J. HIGH HUMIDITY INCUBATOR.

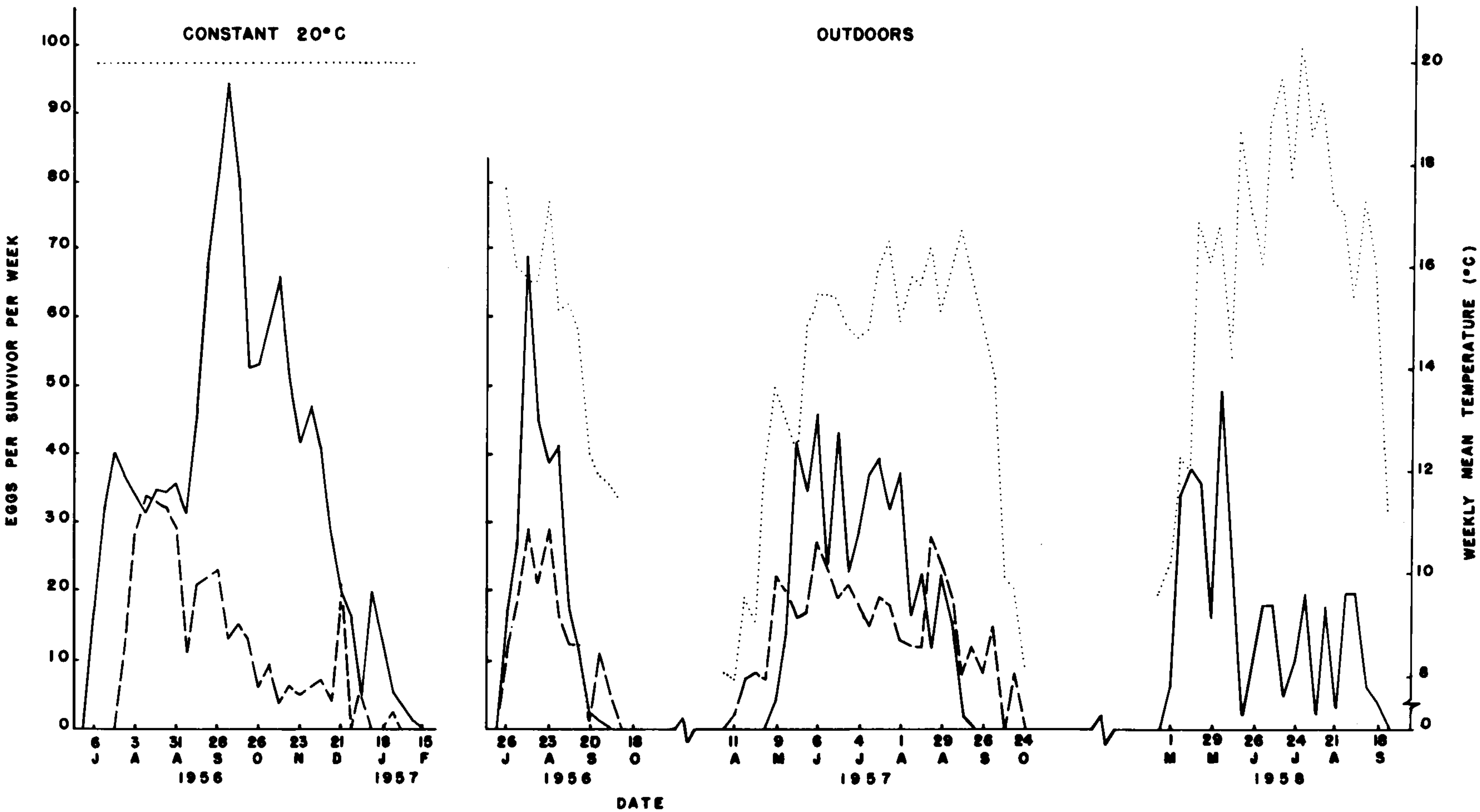

FIG. 3. MEAN WEEKLY EGG PRODUCTION OF THE SURVIVORS OF 10 *B. SULCATUS* (SOLID LINES) AND 10 *S. OBSCURUS* (BROKEN LINES) CAGED SINGLY UNTIL ALL DIED. WEEVILS FED DETACHED STRAWBERRY LEAFLETS AND KEPT EITHER AT A CONSTANT 20°C. OR OUTDOORS AT SAANICHTON, B.C. WEEKLY MEAN TEMPERATURE RECORDED BY DOTTED LINES.

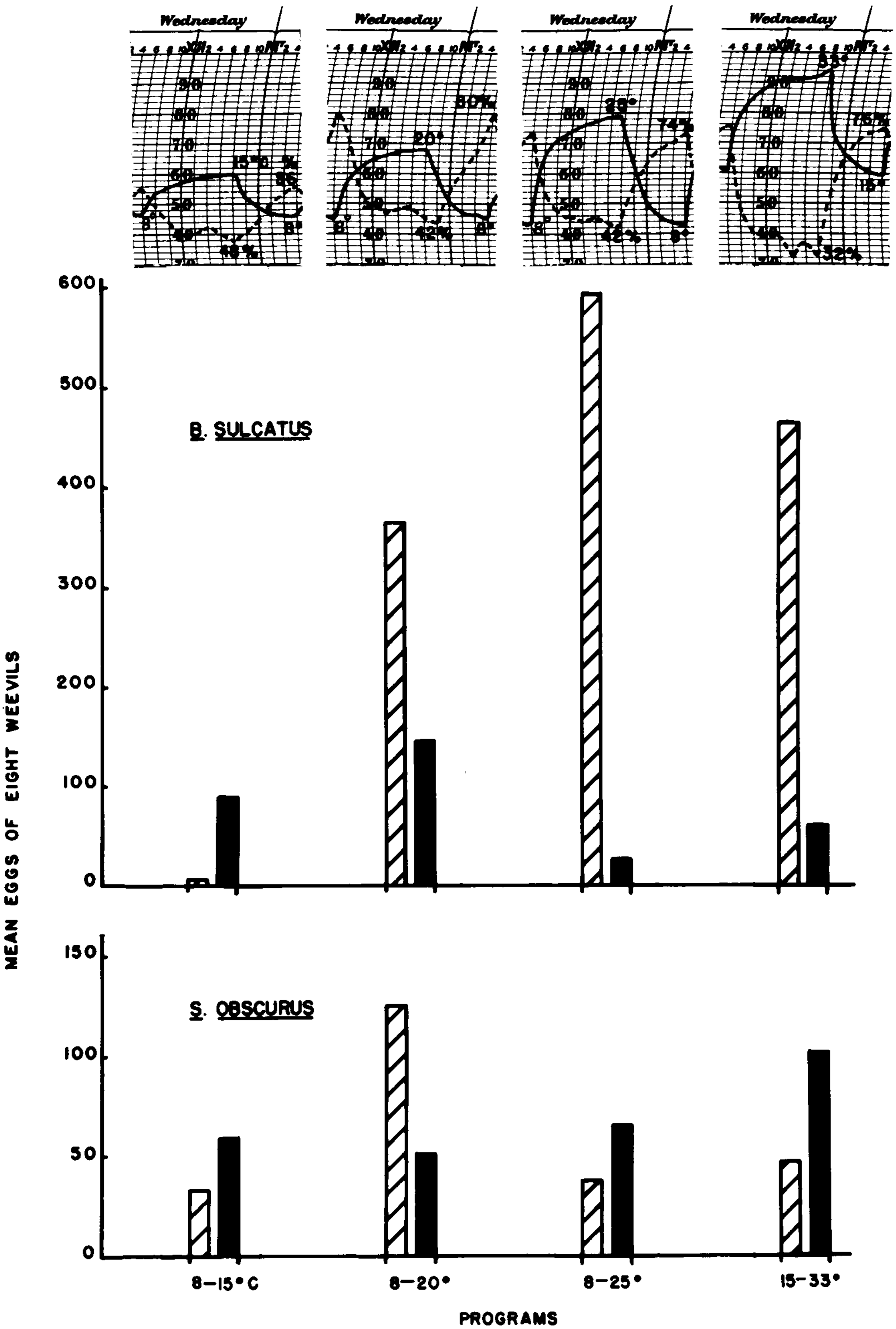

FIG. 4. THE FECUNDITY OF B. SULCATUS AND S. OBSCURUS WHICH OVIPOSITED FOR 11 WEEKS AT THE INDICATED DIURNAL PROGRAMS (SOLID BARS) OR AT THE SAME TEMPERATURE PROGRAMS BUT AT A CONSTANT HIGH RELATIVE HUMIDITY (HATCHED BARS).

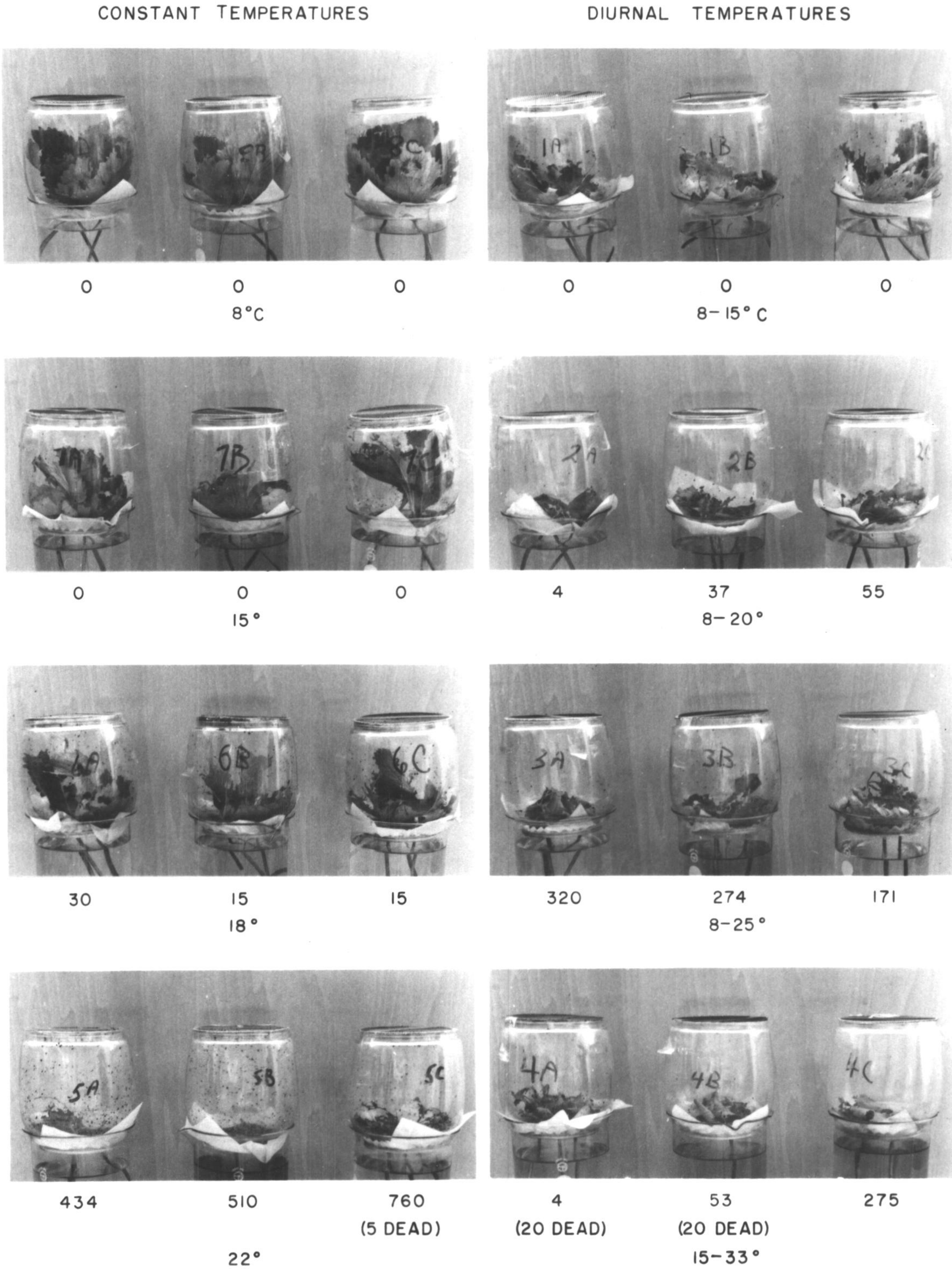

FIG. 5. FEEDING RATE AND NUMBER OF EGGS LAID BY 25 B. SULCATUS PER CAGE TO JULY 7; THREE CAGES KEPT AT THE INDICATED CONSTANT OR DIURNAL TEMPERATURES, 1961.

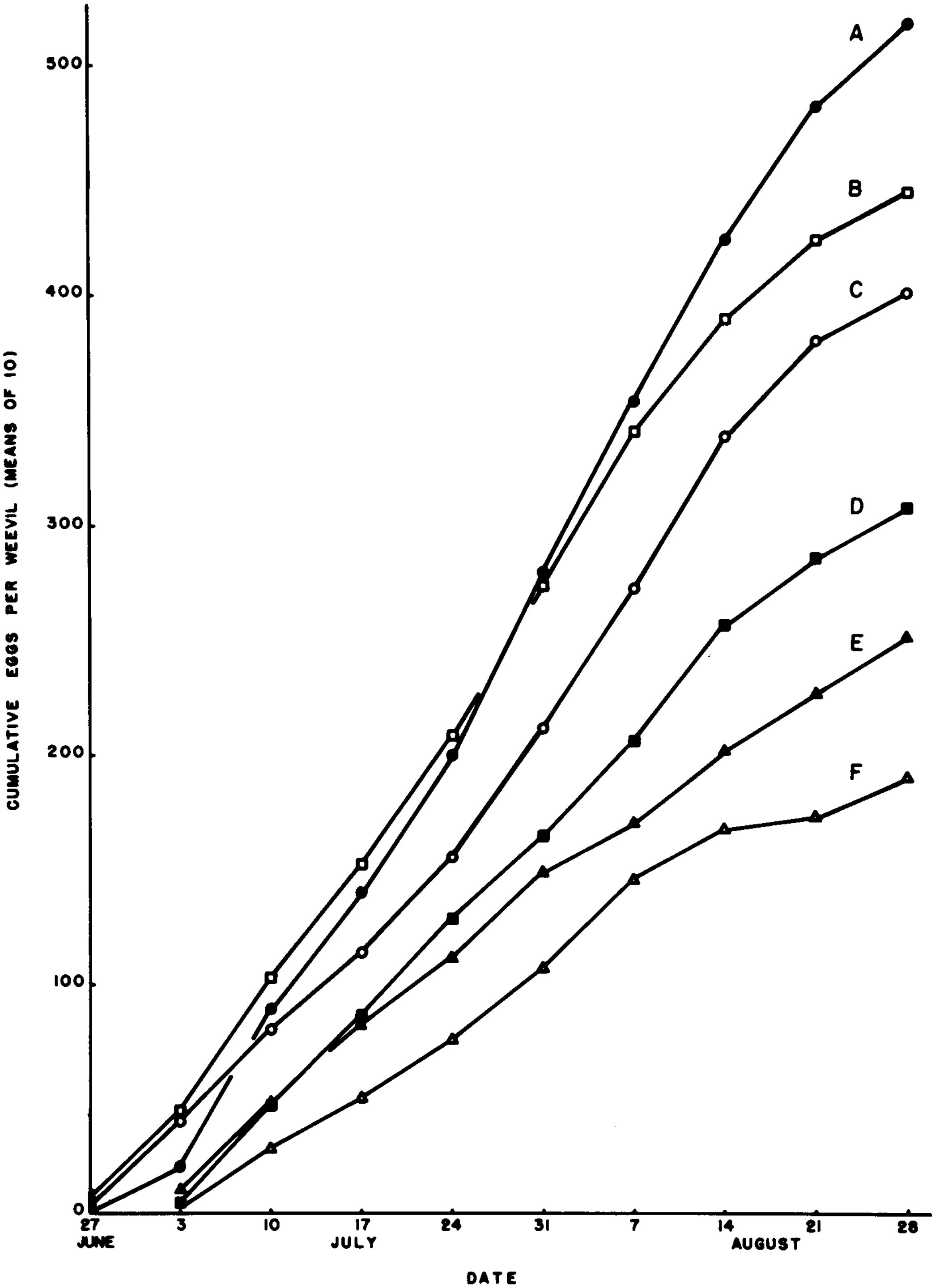

FIG. 6. CUMULATIVE EGGS PRODUCED BY B. SULCATUS FOR 10 WEEKS WHEN CAGED ON STRAWBERRY LEAFLETS GROWN IN SAND-NUTRIENT SOLUTION CULTURE, 1961. A. NO_3^--NITROGEN AT 210 PPM (STANDARD). B. NO_3+NH_4-NITROGEN AT 840 PPM (HIGH). C. NO_3+NH_4-NITROGEN AT 210 PPM (STANDARD). D. NO_3+NH_4-NITROGEN AT 105 PPM (LOW). E. NITROGEN AS IN C BUT POTASSIUM AT 117 PPM (LOW). F. POTASSIUM AT 936 PPM (HIGH). RESULTS WITH PHOSPHORUS AT 15·5 PPM (LOW) AND 124 PPM (HIGH) WERE SIMILAR TO C.

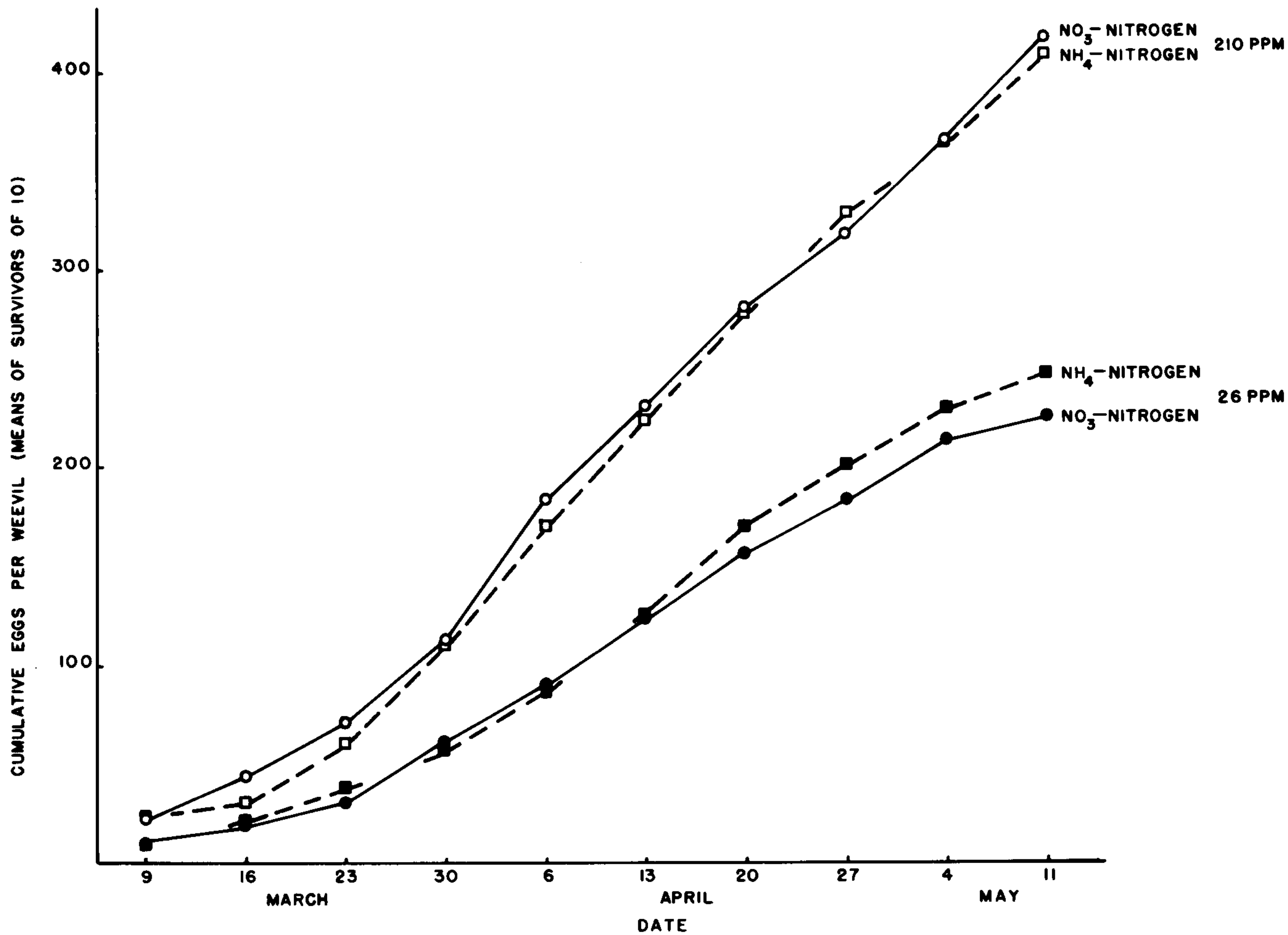

FIG. 7. CUMULATIVE EGGS PRODUCED BY B. SULCATUS FOR 10 WEEKS WHEN CAGED ON STRAWBERRY LEAFLETS GROWN IN SAND-NUTRIENT SOLUTION CULTURE AT 210 OR 26 PPM OF NITROGEN IN EITHER THE NO_3– OR THE NH_4– FORM, 1962.

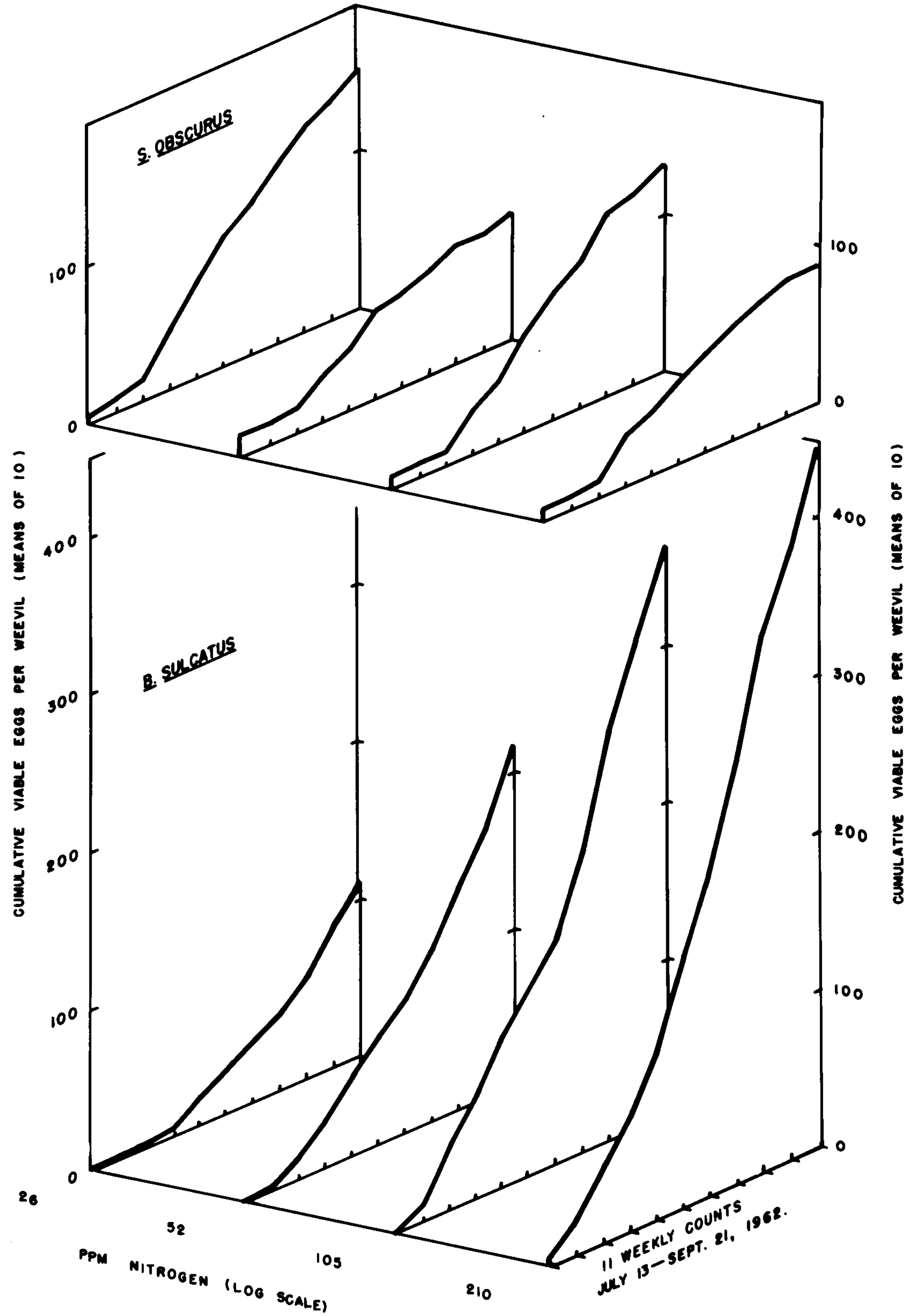

FIG. 8. CUMULATIVE VIABLE EGGS PRODUCED BY S. OBSCURUS AND B. SULCATUS FOR 11 WEEKS WHEN CAGED ON STRAWBERRY LEAFLETS GROWN IN SAND—NUTRIENT CULTURE AT FOUR LEVELS OF NO_3^--NITROGEN.

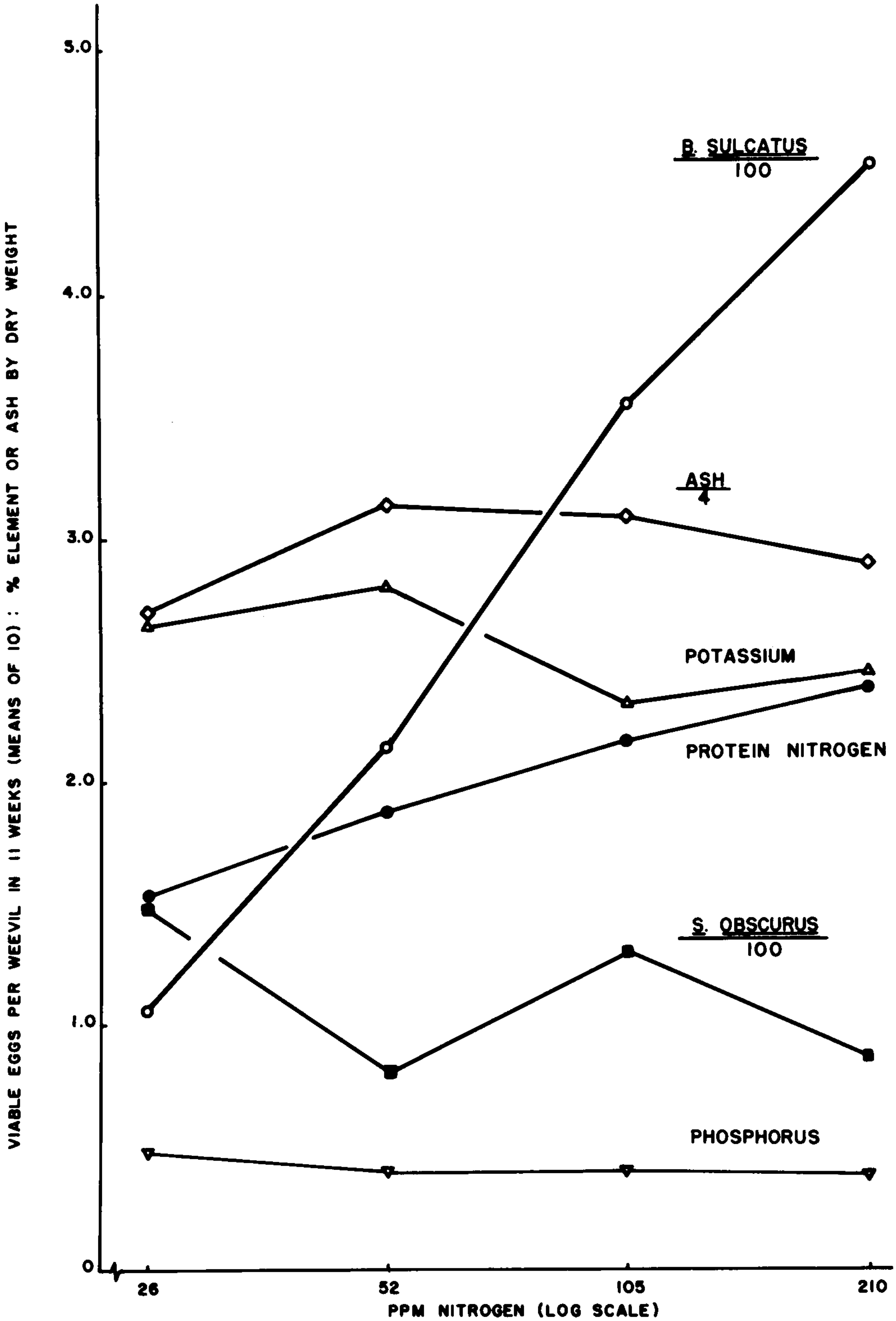

FIG. 9. THE PRODUCTION OF VIABLE EGGS BY B. SULCATUS AND S. OBSCURUS WHEN CAGED ON STRAWBERRY LEAFLETS GROWN IN SAND-NUTRIENT SOLUTION CULTURE AT FOUR LEVELS OF NO_3-NITROGEN AND THE ANALYSIS OF THESE LEAFLETS FOR PROTEIN NITROGEN, PHOSPHORUS, POTASSIUM, AND ASH, 1962.