17. ECOLOGICAL STUDIES ON THE RICE GALL MIDGE IN CEYLON

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Introduction

The last review of available information on the rice gall midge, *Pachydiplosis oryzae* was prepared by Reddy (1967) in 1964. It confirmed that many aspects of the ecology of this important pest of rice were poorly understood. Since then the results obtained by a number of workers in Ceylon have shed some light upon this problem. Perera and Fernando (1968 & 1969) developed a technique for the laboratory culture of *P. oryzae* and studied the ecology of this pest, the response of the rice plant to its attack and gall midge resistance in rice varieties. Wickremasinghe (1969) studied the field ecology of this pest while Modder and Alagoda (1970) investigated the basis of resistance of *P. oryzae* attack in one rice variety. The ecological data to be presented in this paper is a summary of the results obtained by those five workers.

General Description of *P. oryzae* and its Damage

The rice gall midge, *P. oryzae,* is a minute mosquito-like insect, the females of which are orange to orange-brown in colour and the males considerably smaller and pale brown in colour. Under natural conditions adult emergence takes place from rice plant galls at night or early dawn with copulation immediately following emergence. The male dies within 12 to 18 hours after emergence while the female lives for three days under Ceylon conditions. Oviposition on rice plants commences on the evening following emergence and hatching commences 72 hours later at dusk. First instar larvae work their way under the leaf sheaths to infest terminal and axillary buds at the base of rice plants. The infestation of active buds by midge larvae alters the growth pattern of the former to produce hollow white tubular sheath galls terminating in small leaf laminae of varying lengths. These galls signal the end of growth of the tiller involved so that midge infestation of rice plants up to the end of the productive tiller formation stage can be economically most damaging to crop yields.

Ovipostion, Embryonic Development and Hatching

Oviposition

The gall midge lays its eggs singly or in small groups, predominantly upon the undersides of the leaves with very few upon the leaf sheaths (Table 1) in early seeding rice plants.

Freshly laid eggs are translucent creamish brown, frequently with an orange tinge. The two polar regions are reddish brown in colour. Each egg is elongate, 0.44×0.125 mm.

Oviposition commences on the evening following emergence at about 6.00 p.m., is at a peak at 7.00 to 10.00 p.m. and thereafter tapers off. (Perera and Fernando 1968.) (Table 2.).

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Table 1. Oviposition by *P. Oryzae* on two rice varieties.

Day after infestation	Rice variety	% plants infested	No. of eggs laid		
			On leaves	On leaf sheaths	Average per plant
1	IR 8	62.6	237	6	3.4
	W_1 263	55.6	209	4	3.3
2	IR 8	76.5	354	8	4.1
	W_1 263	69.6	347	1	4.4
3	IR 8	54.1	178	2	3.9
	W_1 263	64.7	257	3	4.7
4	IR 8	38.5	74	0	2.5
	W_1 263	28.0	81	0	3.5
5	IR 8	5.1	4	0	1.0
	W_1 263	2.5	2	0	1.0

(Modder and Alagoda, 1971) (adapted)

Table 2. Time of oviposition by *P. oryzae* in oviposition tube.

Time (hr.)	Numbers of eggs laid in tubes No's. 1 to 20																				Females ovipositing	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	No.	Per cent
1400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
1600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
1800	—	—	—	—	36	—	—	—	121	—	11	—	8	136	—	—	—	4	—	6	7	35.0
1900	—	35	—	—	62	9	11	—	44	—	72	—	—	61	—	—	65	136	6	60	11	55.0
2000	—	97	36	2	27	76	10	13	8	63	51	—	—	24	26	—	52	43	10	27	16	80.0
2100	—	68	91	4	31	25	62	14	15	105	12	—	—	—	—	39	51	25	3	24	15	75.0
2200	—	20	69	79	11	28	64	4	5	33	5	—	—	—	—	2	37	12	—	10	14	70.0
2300	—	—	32	33	—	8	39	—	1	—	5	—	—	—	43	7	13	—	—	—	9	45.0
0000	2	—	—	3	—	—	1	—	5	—	7	8	—	—	86	43	—	—	—	—	8	40.0
0200	12	—	—	—	—	—	—	—	—	—	—	13	—	—	18	25	—	—	—	—	4	20.0
0400	10	—	—	—	—	—	—	—	—	—	—	4	—	—	3	4	—	—	—	—	4	20.0
0600	112	—	—	—	—	—	—	—	—	—	—	12	—	—	—	18	—	—	—	—	3	15.0
0800	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	1	—	—	—	—	2	10.0

(Perera and Fernando, 1968)

Numbers of Eggs.

Frequency distribution studies were carried out on 120 gravid midges according to numbers of eggs laid (Perera and Fernando 1968) and the results are summarized in Fig. 1. The number of midges in each group increased to a peak in the 200–225 group, and thereafter decreased steeply. The calculated mean, mode and median values of egg lay are 173.75, 212.5 and 181.25 respectively.

Fertility of Eggs

Under laboratory conditions mean maximum/minimum temepartures and relative

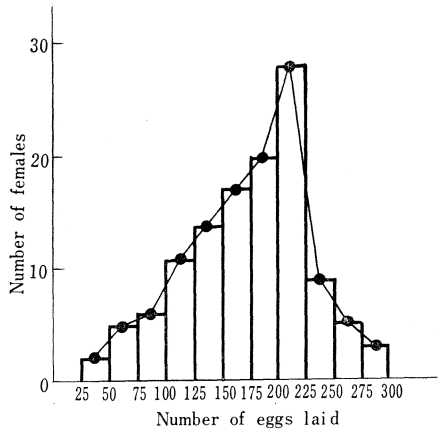

Fig. 1. Frequency distribution histogram and polygon of gravid female *P. oryzae* by total egg lay.
(Perera and Fernando, 1968)

humidities of 27.0/20.5°C and 75–79% respectively were optimal and the fertility rate was almost 100%. However, when mean maximum and minimum temperatures rose to 30.5/20.5 and relative humidity fell to 45–70%, male emergence and survival was low and a sharp drop in the fertility rate was observed.

Development of Eggs

As embryonic development progresses the eggs become darker orange–brown in clour. Thirty six hour old eggs show the outline of the developing larva through the chorion with two deep red to crimson kidney shaped eye spots located anterodorsally. When the egg is nearly 72 hours old the two eyespots become adjacent in the antero-middorsal line forming an X-shaped structure.

Hatching of Larvae

Hatching commences after 72 hours of development at dusk, reaches a peak at about 10.00 p.m. and is almost completed by midnight. This is an important adaptive feature for larval survival as will be discussed later.

Description of Immature Stages

(1) The First Instar Larva

The description which follow are based on those given by Perera and Fernando (1969). The first instart larva is approximately fusiform, on average 0.50 mm long and 0.127 mm broad at its widest part and is 13 segmented (Fig. 2.1). The integument is colourless and transparent. The reduced head bears a pair of antennae. The oral region is of a light amber colour and appears heavily selerotized. As with the second instar larva no sternal spatula is present. An X-shaped eyespot is located mid-dorsally in the third segment. The midgut, visible through the integnment, is deep orange coloured. Segments 12 and 13 have spin-bearing tubercles postero-laterally. Segment 12 has two small spines of equal size while on each side of segment 13 there are four spines one of which is markedly longer than the other three. These spines characterize the first instar larva and apparently coupled with the colourless slimy substance which covers the body serve for locomotion of this very active immature stage of the pest. The duration of the first instar is 3–4 days.

(2) The Second Instar Larva

Maximum length and width 1.5 mm and 0.4 mm respectively. Head similar to that

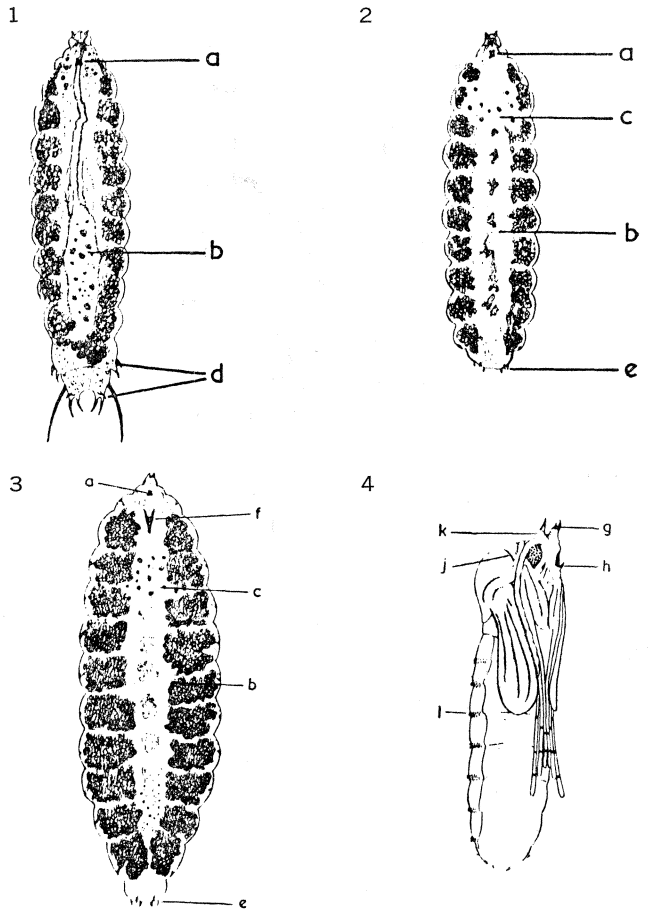

Fig. 2. 1–4: Immature stages of *P. oryzae*. 1. first-instar larva; 2. second-instar larva; 3. thire-instar larva; 4. pupa. (a. eye-spot; b. mid gut; c. salivary glands; d. spine-bearing tubercles; e. short spines; f. sternal spatula; g. cephalic horns; h. sub-ocular spine; j. thoracic spine; k. post-occipital spine; l. abdominal tergal spines.)
(Perera and Fernando, 1969)

of first instar larva. Body 13-segmented, rounded at both ends, segment 13 with three very short spines on each side. Body colour translucent white, midgut brown. Duration 3–4 days (Fig. 2.2).

(3) The Third Instar Larva

Maximum length and width 3.2 and 0.8 mm respectively. Head similar to first and second instar larva. Y-shaped sternal spatula located mid-ventrally between first and second body segment. Pair of spiracles on body segments 2 and 4–12, segment 13 with three pairs of very short spines. Duration 6–7 days (Fig. 2.3).

Prepupa

Prepupa similar to late third—instar larva, but with anterior end rounded expanded and filled with translucent fluid and with kidney-shaped eyespot on each side dorsolaterally. Duration about 24 hours.

Table 3. Effects of relative humidity on development and hatching of eggs of *P. oryzae*.

Age of eggs used in experiment (hr.)	Concentration of KOH in 100 ml. of water (gm)	Relative humidity (%)	Total No. of eggs used	No. of infertile eggs	No. of eggs collapsed		No. of eggs with red spot after 60 hr. indicative of complete development	No. of larvae hatched noted after 84 hr.	Hatch of fertile eggs (%)	Condition of hatched larvae in chamber
					After 1 day	After 3 days				
12	0	100	190	37	2	2	153	148	96.7	Normal
12	2.5	98.4	264	67	6	6	197	173	87.8	Normal
12	5.0	96.8	321	15	4	4	306	268	87.5	Normal
12	7.5	94.8	232	6	9	9	226	195	86.7	Sluggish
12	10.0	92.9	280	10	11	11	270	226	73.7	Sluggish slightly contracted
12	15.0	88.8	201	19	20	20	182	141	77.4	Sluggish contracted
12	20.0	83.8	243	59	83	123	184	144	78.2	Immobile contracted
12	25.0	78.7	220	14	37	157	206	86	41.7	Immobile contracted
60	7.5	94.8	413	3	—	—	410	406	99.0	Immobile contracted
60	10.0	92.9	523	8	—	—	515	492	94.5	Immobile contracted
60	15.0	88.8	530	0	—	—	530	516	97.3	Immobile contracted

(Perera ane Fernando, 1968)

Pupa

Male, 3.2 mm long and 0.8 mm wide; female, 3.6 mm long and 0.9 mm wide. Exarate; occipital region with two large cephalic horns each bifurcating to form heavily chitinized spines, behind each cephalic horn a small hairlike spine, below each compound eye a large heavily chitinized spine recurved towards cephalic spines; anterior margin of mesothorax with heavily chitinized spines directed backwards. Posterior-margins of abdominal tergites 2–8 with numerous, minute, heavily chitinized spines. Male pupa distinguished from female pupa by smaller size, and claspers developing in last abdominal segment. Duration 6–7 days (Fig. 2.4).

Effect of Relative Humidity and Moisture on Eggs and First Instar Larvae

That relative humidity and moisture played a vital part in the abundance of *P. oryzae* was suspected in the past but no evidence was available as to how exactly this environmental factor acted upon eggs and first instar larvae to limit gall midge populations.

Experiments on the effects of a range of relative humidities between 78% and 100% on midge eggs and first instar larvae have elucidated this point (Perera and Fernando 1968). The results of these studies with 12 hour old eggs are presented in Table 3. Percent hatch was positively correlated with increase in relative humidity and below a relative humidity of 83.8% the hatch decreased steeply. Eggs shrink and collapse at relative humidities below 90% (although some of these hatch) and as the humidity decreases below 90% the number of collapsed eggs increases.

The effect of relative humidity upon first instar larvae is of special significance. At relative humidities below 94.8% freshly hatched first instar larvae are capable of only limited locomotion. Thereafter they become sluggish and contracted and finally the colourless slimy sceretion which covers the body surface thickness and hardens into a creamish substance which provides a solid protective encasement for the larva and also cements it to the surface on which it is located. In this condition the larva is completely dormant. Revival of such larvae is possible within 24 hours and is immediate if they are wetted with water. Within seconds of such treatment the alimentary tract shows peristalsis. The longitudinal body muscles then begin contractions and the larvae appear normal within ten minutes of the wetting. Very high relative humidity associated with a moist substratum are hence essential for normal activity of the freshly hatched first instar larva (Perera & Fernando 1968).

Gall Formation and Ecology of Immature Stages

Entry of First Instar Larvae into Rice Plants

Eggs commence hatching at dusk about 72 hours after oviposition. The first-instar larvae which hatch out on leaves and leaf sheaths reach the terminal and axillary shoot apices without boring into plant tissue, either by following an irregular, progressively narrowing spiral pathway between consecutive leaf sheaths or by a vertical descent under the leaf sheath of the leaf on which it hatches and a subsequent decreasing irregular circular pathway between the bases of the leaf sheaths.

Most larvae reach the terminal shoot apex, whilst a few reach the axillary shoot apices. Infestation of axillary shoot, apices takes place when there is a large number of larvae hatching on a single rice seedling. Larvae reach the shoot apices in a two-week-old rice seedling 6–12 hours after hatching. High relative humidity, enough to cause condensation on the leaf surface, is essential for larval movement. At lower humidities the body surface hardens and desiccation and death follow unless high humidity is restored within 24 hours as mentioned earlier. First instar larvae were never

observed to bore into leaf sheath or meristematic tissue. They feed at the base of the growth cone between this structure and the youngest leaf primordium, the body lying vertically with the head downwards (Perera & Fernando 1969).

Normal Gall Formation and Behaviour of Immature Stages

The presence of active first-instar larvae at the terminal shoot apices stimulates the formation of a gall and suppresses development at the growth cone. Normally leaf primordia envelope the growth cone tightly (Fig. 3.1). The first sign of gall formation is the development of a space between the base of the growth cone and the youngest leaf primordium (Fig. 3.2). As the larva reaches the second instar, (Perera & Fernando 1969) radial ridges caused by cell proliferation appear on the inner surface of the yougest leaf primordium in a zone immediately above the level of the posterior end of the larva and below the area of ligule differentiation (Fig. 3.3-4). This zone of cell proliferation defines the upper limit of the gall. The radial ridges grow inwards and fuse to form a plug of tissue, below which the gall primordium, consisting entirely

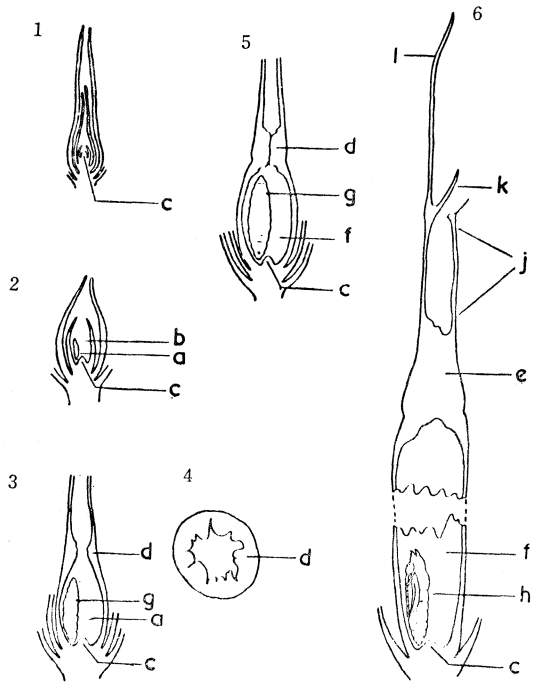

Fig. 3. 1–6: Stages in gall formation. 1. longitudinal section (LS) uninfested shoot apex; 2. LS infested shoot apex with first-instar larva; 3. LS infested shoot apex after radial ridge formation; 4. transverse section region of radial ridges; 5. LS infested shoot apex after fusion of radial ridges; 6. LS infested shoot apex showing elongated gall after pupation. (a. space formed by suppression of leaf primordial differentiation; b. first-instar larva; c. growth cone; d. zone of cell proliferation forming radial ridge; e. plug of tissue delimiting gall cavity; f. gall cavity; g. late second-instar larva; h. pupa; j. portion of leaf sheath above plug; k. ligule; l. shortened lamina.) (Perera and Fernando, 1969)

of leaf sheath tissue, encloses the larva (Fig. 3.5). At this stage the gall cavity ranges up to 2 mm in length (under optimal conditions of high humidity and day temperature of about 30°C), and the larva continues to feed at the base of the growth cone during instars 2 and 3. When pupation approaches, the third-instar larva stops feeding and turns round inside the gall by means of the sternal spatula so that it head points away from the growth cone (Perera & Fernando 1969). During the third larval and early pupal stages the length of the gall cavity increases to about 9 mm and 133 mm, respectively, and towards the end of pupation it reaches a length of about 190 mm.* The fully formed gall consists of a long ivory-white tube which terminates in a solid plug of white tissue. Above this plug the rest of the leaf sheath is delimited from a shortened lamina by a distinct ligule (Fig. 3.6). Leaves of infested plants show symptoms of yellowing typical of nitrogen deficiency unless they are grown on nitrogen-rich soils.

Gall formation by *P. oryzae* has so far been recorded only at vegetative shoot apices. In the course of this study, infestation by midge larvae of the reproductive shoot apices has occasionally been found to cause gall formation in parts of the panicle.

As adult emergence approaches, the pupa wriggles upwards within the elongated gall cavity using the spines on its body surface and bores a hole, mainly with the cephalic and subocular spines, immediately below the plug at the upper and of the gall cavity (Perera & Fernando 1969). Through this hole the anterior portion of the pupal body is protruded and adult emergence takes place.

Effect of Cessation of Larval Feeding Following Insecticidal Action

Treatment of rice plants with an effective insecticide such as diazinon or fenitrothion either killed the larvae soon after or rendered them moribund for as much as 30 days before death. In either case larval feeding ceased. The various effects observed in infested rice plants depended upon the larval stage that had been subjected to insecticidal action.

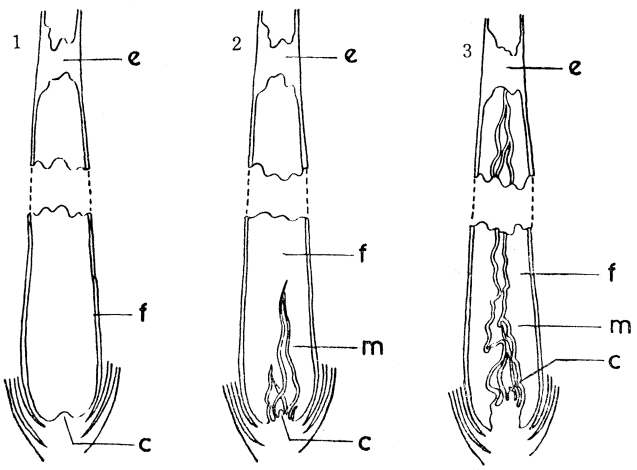

Fig. 4. 1–3: Regeneration of shoot apex within gall following death of late second-instar larva of *P. oryzae*. (m. developing leaves; other symbols as in Fig. 3. 1–6)
(Perera and Fernando, 1969)

* All measurements given here for gall primordia and galls are those for plants grown in pots in the first 5 weeks of growth under relatively crowded conditions in the laboratory.

At the stage before the radial ridges have fused, cessation of feeding by early second-instar larvae resulted in a elongation of the incipient gall and renewed activity of the growth cone within three days. Differentiation of leaf primoridia and elongation of the gall after killing of the second-instar larvae at first followed the same course, but the leaf primordia differentiated and grew within the gall until they reached the upper limit of the gall cavity and then became wrinkled due to lack of space (Fig. 4.1-3 9–11). Application of nitrogenous fertilizer promotes sufficient growth for the leaves to burst through the gall. The first leaf to emerge thus is permanently wrinkled, and the plant tillers more vigorously than is normal. The gall produced under such conditions appears as a shortened deep green leaf sheath terminated by a similarly shortened lamina (Fig. 5), Killing third-instar larvae or pupae resulted in a greater elongation of the gall (to 175 mm), but the growth cone was not re-activated and the plant grew further only by tillering.

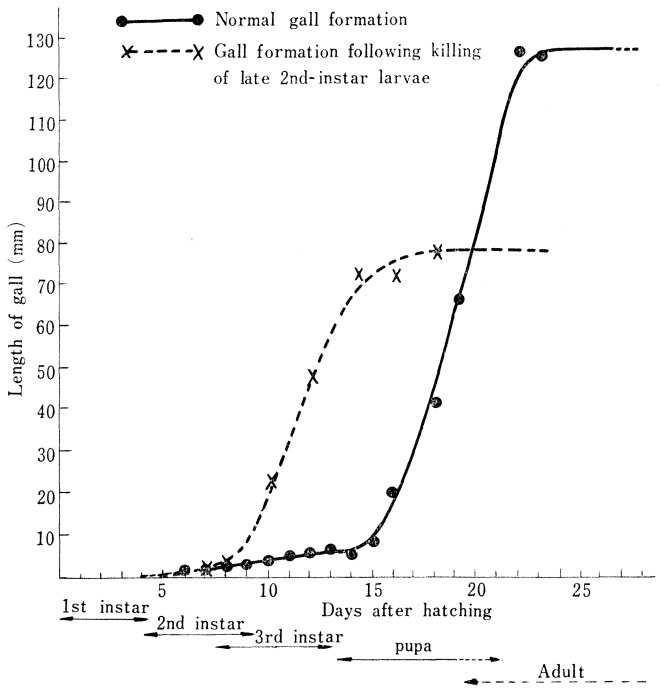

Fig. 5. Growth of normal galls compared with that of galls in which larvae of *P. oryzae* were killed in late second instar. (Perera and Fernando, 1969)

Multiple Infestation

Two types of multiple infestation of shoot apices have been observed (Perera & Fernando 1969). In one type two or more larvae may be found at a single shoot apex, while in the other, one or more larvae may be found in more than one shoot apex of the same plant. In the first type, under high adult population pressure in the laboratory, up to 18 or more first-instar larvae have been found around a terminal shoot apex. However, in a single gall primordium only three such larvae survived to the second instar, two to the third instar and one to the pupal stage.

In the second type of multiple infestation the course of larval development from a single batch of eggs differs in terminal and axillary shoot apices. In the terminal shoot apices the first instar is completed in 3–4 days, but at axillary shoot apices first-instar larval development is arrested for 15 days or more, i.e. until the shoot apices become active. Thus a larva at the terminal shoot apex may have reached the pupal stage while those at the axillary shoot apex may still be in the first instar, the rate of development of the first instar depending upon the activity of the shoot apices (Table 4). Once the first instar is completed, larval development proceeds normally in axillary shoot apices. On any one plant, individuals hatching simultaneously from a single batch of eggs may thus be in any of the four immature stages (Fig. 6).

Table 4. Multiple infestation of rice plants by *P. oryzae* showing stage of development and numbers of larvae in various types of shoot apices.

Date	Mean* length of primary gall cavity (mm)	Number and development stage of larvae in various shoot apices of single plants**						
		Terminal shoot apex	Primary axillary shoot apices					Secondary axillary shoot apices
			No. 1	No. 2	No. 3	No. 4	No. 5	
30. v. 68	No gall	2 (1)	0	0	1 (1)	0	0	0
1. vi.	No gall	1 (1)	0	1 (1)	1 (1)	3 (1)	0	0
2. vi.	Gall initiation	1 (2)	0	0	1 (1)	0	0	0
4. vi.	1.0	1 (2)	0	0	1 (1)	1 (1)	2 (1)	0
5. vi.	1.9	1 (3)	0	1 (1)	3 (1)	4 (1)	0	0
9. vi.	4.6	1 (3)	0	3 (1)	2 (1)	7 (1)	0	0
10. vi.	5.3	1 (3)	0	0	1 (1)	4 (1)	0	0
11. vi.	5.7	1 (P)	0	2 (1)	0	3 (1)	0	0
13. vi.	9.1	1 (P)	0	0	2 (2)	4 (1)	0	0
14. vi.	21.7	1 (P)	0	1 (3)	2 (2)	2 (1)	0	0
16. vi.	24.2	1 (P)	0	0	0	1 (1)	0	0
17. vi.	66.5	1 (A)	0	0	1 (3)	0	0	0
18. vi.	88.5	1 (A)	0	1 (2)	0	1 (1)	0	0
20.	126.4	1 (A)	0	1 (3)	0	0	0	0
21. vi.	125.3	1 (A)	0	1 (3)	1 (1)	0	0	0
22. vi.	141.5	1 (A)	0	0	0	1 (2)	0	3 (1)

(Perera and Fernando, 1968)

* Mean of 8–10 galls.

** (1), (2), (3), (P) and (A), first-, second- and third-instar larvae, pupae and adults, respectively. Details from one plant for each date.

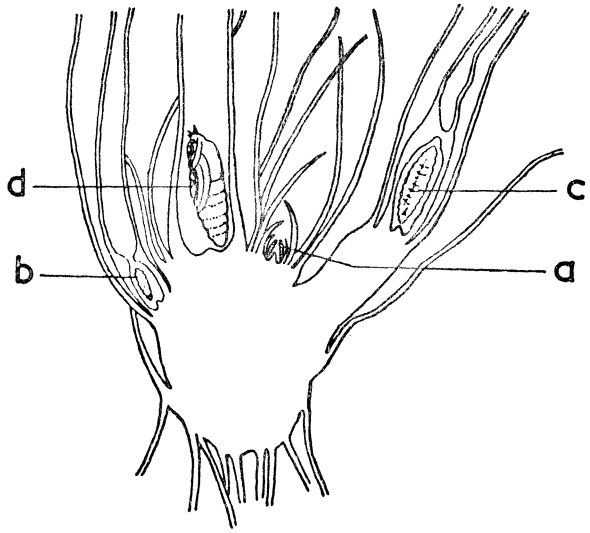

Fig. 6 Vertical section of base of rice seedling showing multiple infestation of terminal and axillary shoot apices by *P. oryzae*. (a. first-instar larva at axillary shoot apex; b. second-instar larva at axillary shoot apex in developing gall; c. third-instar larva at axillary shoot apex within gall primordium; d. pupa at terminal shoot apex in elongated gall.) (Perera and Fernando, 1969)

Resistance to Gall Midge in Rice Varieties

High levels of resistance in rice varieties to gall midge, based upon field observations, were reported in a number of Eswarakora crosses (Warangal 1251, 1253, 1257, 1263) from India. (A.I.C.R.I.P. Report 1967). Since then workers in India have demonstrated gall midge resistance in several other rice varieties (A.I.C.R.I.P. Report 1969).

The Eswarakora crosses were subjected to intensive laboratory screening for gall midge resistance by Fernando and Perera (1969) and were found to show varying levels of resistance. Essentially these workers found that in a proportion of the Erawarakora plants first instar larval development was retarded and mortality of this stage continued for over a month after infestation. In IR 8, a midge-susceptible variety, the first instar lasted only about 4 days when transformation into the second instar took place. Fernando (1969) saw a strong resemblance up to a point between the first instart larval dormancy in inactive axillary buds of susceptible plants and the retardation of first instar larval development in resitant Eswarakora hybrid, Warangal 1263 plants.

Modder and Alagoda (1971) studied the mecchanism of gall midge resistance in Warangal 1263 using IR 8 as the susceptible variety for comparison. These workers found that gravid female midges showed no oviposition preference for the susceptible IR-8 plants over the resistant Warangal 1263 plants (Table 1).

Modder and Alagoda (1971) also found that in both the IR 8 and the Warangal 1263 plants the freshly hatched first instar larvae were equally successful in reaching the shoot apices (Table 5). This finding precludes the possibility that mechanical barriers on the leaves or between sheaths contribute to gall midge resistance in Warangal 1263.

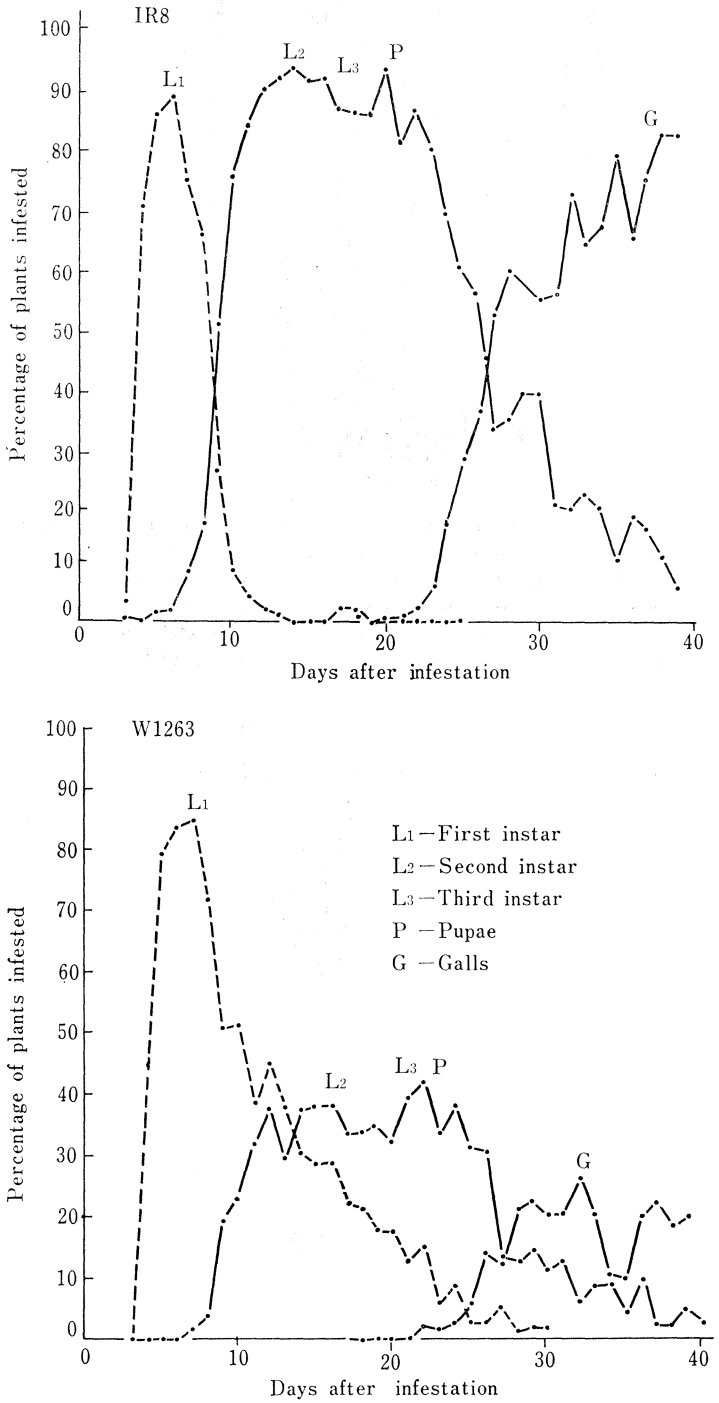

Fig. 7. Comparison of infestation of IR 8 and W1263 by L_1S and later stages. (Adapted from Modder & Alagoda.)

Table 5. Percentage of plants showing presence of first instar larvae at apical meristem.

Day after Infestation	Rice variety	
	IR 8	W 1263
3	1.38	0
4	70.73	41.92
5	85.61	78.46
6	88.52	82.91
7	79.84	84.68
8	69.09	77.30
9	43.51	58.75
10	14.94	61.94
11	11.04	46.75

(Modder and Alagoda, 1971) (Adapted)

In a study of the rate of development of the immature stages of the gall midge in Warangal 1263 and IR-8 plants infested at the same time Modder and Alagoda (1971) obtained very interesting results which are summarized in Fig. 7. By the twelfth day after infestation 90% of the IR 8 plants had second instar larvae whereas in Warangal 1263, 35% contain second instars and over 40% still contain first instars. Furthermore, even after the number of first instars decrease, a delayed increase of later developmental stage is not observed in Warangal 1263. On the basis of these observations Modder and Alagoda (1971) concluded that about 40% of the Warangal 1263 plants are resistant to the gall midge and that the active shoot apices of these plants are capable of preventing transformation of first instar midge larvae into second instar.

Population Fluctuations and Effect on Rice Plants in the Field

Studies on gall formation and incidence in H-4 were carried out under field conditions for three seasons (Wickremasinghe 1969). Although gall production continued in the tillers up to maturity of the crop observations were taken only up till the beginning of the reproductive phase of the plant in the three studies because these galls are of economic significance.

In Fig. 8 the general pattern of gall midge build-up as represented by gall incidence is seen for each of the three seasons. After transplanting there is a gradual increase in gall incidence with a peak occurring during the 5–8 week after transplanting. For a 4-4½ month rice crop such as H-4 this in the period of maximum tiller formation and most of the productive tillers have formed by the 7th week. Unproductive tertiary tillers are formed after this stage.

The distriution of galls in tillers of the various orders is presented in Fig. 9. Gall formation in main culms and primary tillers lasted until the 4th week after transplanting. Thereafter galls appeared only in the secondaries and tertiaries, with more and more damage to unproductive tertiary tillers occurring as the season advanced.

Gall formation following midge attack in rice plants results in activation of normally inactive tiller buds causing both an acceleration and an increase in the total number of tillers produced. Table 6 gives the results of the study and shows that this effect was marked where the primary tillers are damaged. Damage to the main culm may or may not show this effect depending on how early the main axis is infested.

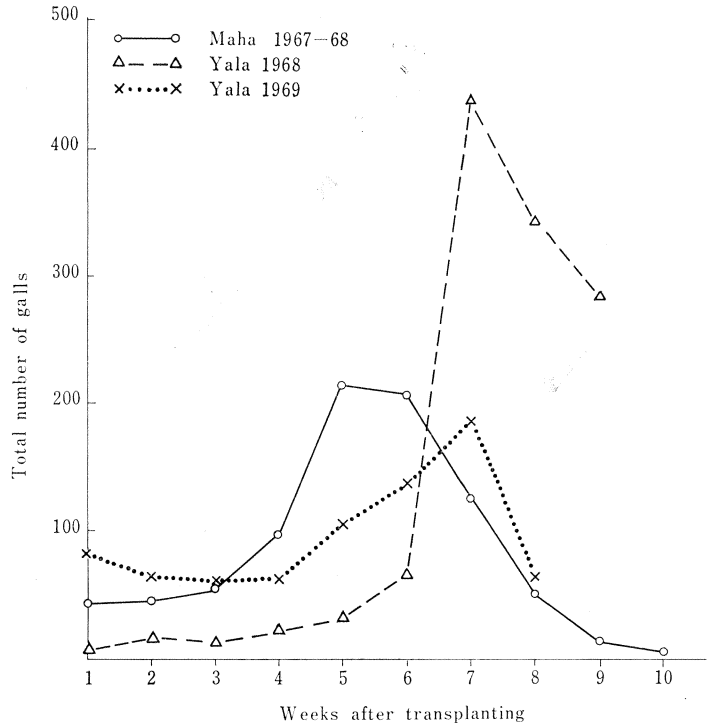

Fig. 8. Population fluctuations of *P. oryzae* during three seasons.

Infestation of the main culm in the first two weeks after sowing can lead to the death of the plant.

Increase in tiller number with increase in panicles occurs only when a low level of midge incidence occurs early in the field affecting the main culm and primary tillers (Table 6). However, even in this instance there was no significant increase in grain

Table 6. Effect of midge infestation of various types of tillers on tillering, panicle number and yield.

Type of tiller attacked	No. of plants studied	Av. No. of galls per plant	Number of tillers if unattacked =100	Av. panicle No. per plant	% Effective tillers of total tillers	Av. grain wt. per plant (oven dried) in gms.
Primary	14	1.0	140	8.4	67	24.6
*Early Secondary	44	1.4	117	6.6	63	22.6
Early Tertiary	11	2.6	114	6.6	64	20.6
Late Secondary	89	1.2	122	6.8	62	21.9
Late Tertiary	126	1.9	119	7.0	65	23.6
Unattacked	52	0	100	7.1	78	23.6
Statistical An.	—	Not analyzed	Not analyzed	Signif. at 5%	Not analyzed	Not Sig.

* Early tillers indicate these tillers which appeared before the end of the sixth week.

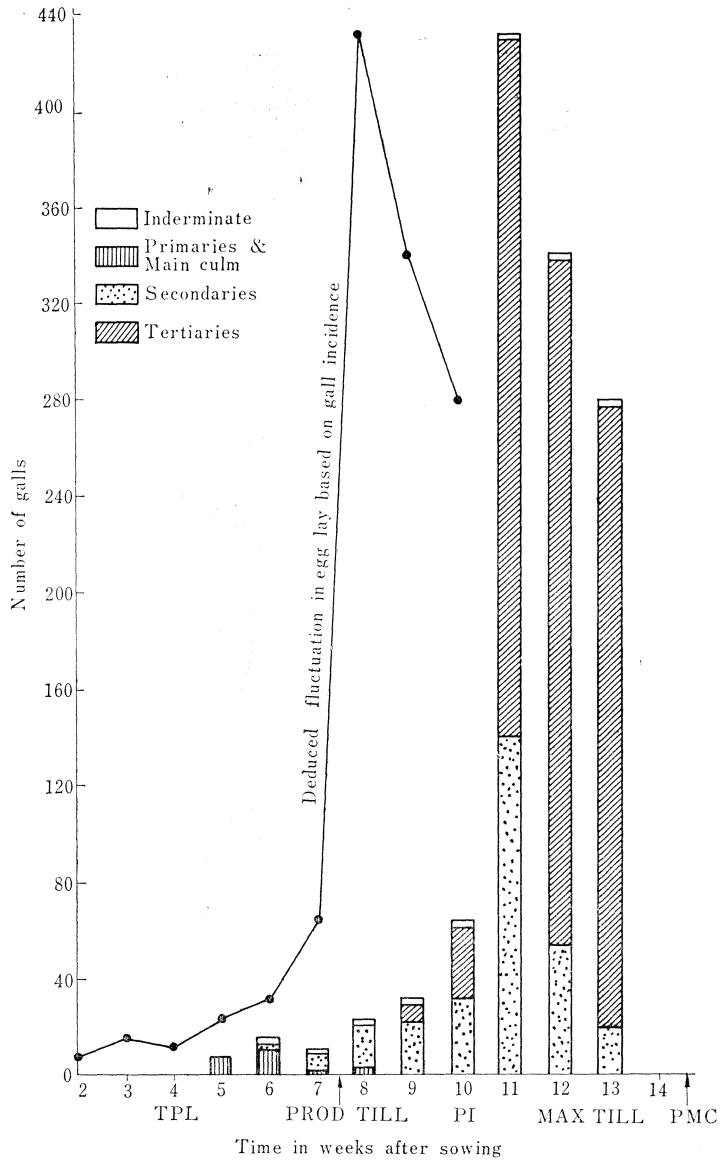

Fig. 9. Incidence and distribution of galls on tiller types.

yield as the heavier main culm and primary tiller panicles were replaced by tillers which produced smaller panicles.

Parasites and Predators

Populations of the rice gall midge are controlled in the field in Ceylon by at least four species of parasites and predators. The carabid beetle, *Cassinoidea interestitialis* and the nabid bug, *Nabis capsiformis* are the predators, the former entering galls and feeding upon the pupae while the latter destroys the adult stage. These two predators are only of minor economic importance. Two hymenopteran parasites, the sceleonid,

Platygaster oryzae and the pteromalid, *Norbanus* sp. have been recorded from *Pachydiplosis oryzae*. *Norbanus* sp. oviposits on second or third instar larvae through the gall primordium, and this is only possible when water is absent in rice fields. This parasite is therefore of very limited importance as a natural controlling factor. *Platygaster oryzae* on the other hand is a very important controlling factor on gall midge populations. This minute parasite lays its eggs into the egg or exposed first instar larvae of the host and emerges in the prepupal stage of the host through larvae of the host and emerges in the prepupal stage of the host through the galls. Parasitization is low early in the season, rises to 40–50% in the tillering phase and reaches 80–95% by the end of the season.

Discussion of Results

Pachydiplosis oryzae eggs require a relative humidity of over 90% for normal development. First instar larvae require a relative humidity of over 95% for normal locomotion and a moist surface for free movement to reach the shoot apices for feeding. Hatching which takes place at dusk and at night is therefore adaptive because both guttation and dew condensation at this time of the day provide the relative humidity and moist leaf surfaces essential for first instar larval movement. Cloudy skies and continuous light rainy periods usually favour high gall midge populations probably for the same reasons.

The observations on gall formation and midge larval development suggest that a fluctuating flow of plant nutrients and substances of insect origin underlie both phenomena. The evidence available suggests that first instar larvae are attracted to the shoot apics by a chemical present in both active and dormant buds and that their growth is stimulated by one or more of the auxins, amino acids and sugars characteristically present at actively growing apices. Activity of the growth cone is suppressed by diversion of nutrients to the larvae but nutrients are released again for plant growth either if larval feeding is terminated by insecticidal action or pupation. The release of nutrients allows for gall elongation and also for leaf primoridal differentiation wherever a midge-attacked growth cone has been reactivated by killing of first or second instar larvae. The lesser gall elongation following premature cessation of larval feeding is due to the inadequacy of the available nutrients for both maximum gall elongation and leaf primordial growth. The markedly greater elongation of the gall following pupation is the result not only of the irreversible suppression of the growth cone activity but also possibly the release of a growth promoting substance, by the prepupa at pupation a view which is supported by the complete suppression of the chlorophyll formation in such a gall. Growth of the radial ridges is possibly stimulated by an excretory product of the first instar larva. Similar insect-host relationships have been recorded; for example according to Küster (1911) and Cosens (1912) the excretory produces of *Pontaria viminalis* (L) and *P. hospes* (Walsh), respectively, are capable of stimulating cell division, and La Rue (1935) has observed outgrowths around faecal pellets in contact with the mesophyll of poplar leaves infested with leaf-mining larvae.

Arrested growth of first instar larvae at inactive axillary shoot apices may explain the carry-over of *P. oryzae* populations from season to season and also the continuity of the attack in the field.

The results obtained by Modder and Alagoda (1970) preclude the possibility that oviposition preference or mechanical obstacles to first instar larval movement cotribute to midge resistance in Warangal 1263 rice plants. The active vegetative, meristems of resistant plants in this rice variety prevent the transformation of first instars into second instars and the former eventually die. It is this property in Warangal 1263

which forms the basis of its midge resistance. The physiological basis of this inhibitory action is not yet understood.

The gall midge is a major pest of the present day high-yielding dwarf and semi-dwarf rice varieties. Laboratory and field studies show that the pest attacks the rice plant from the seedling stage but, other than in rare instances, does not affect a rice plant beyond the stage of earhead primordia initiation. They also show that the attack is at its worst at the stage of maximum tillering and subsequent midge attack on unproductive tillers is of no economic significance. A 4½ month rice crop therefore needs to be protected against midge attack only for the first 9 weeks of its life. Several modern systemic insecticides have been found capable of achieving this resulting economically.

Discussion

S. Areekul, Thailand: 1) Have you observed whether parthenogenesis exists in this species of insect? 2) I saw in the first diagram that the insect pupates at the growing point. Is this case quite common? And if so, how do the adults get out of the stem?

Answer: 1) This was investigated very carefully and the results preclude the possibility that parthenogenesis occurs in the rice gall midge. 2) Pupation by the gall midge larva at the terminal shoot apex located at the base of the rice seedling is normal without variation. The pupa wriggles upwards through the gall cavity and in reaching the plug of tissue at the top of the gall, it bores a hole in the gall below this point through which the pupal body is protruded to aid adult emergence. 3) Gall formation occurs at any stage after the second instar when cell proliferation to form a complete plug of tissue at the gall takes place.

M. B. Kalode, India: Did you develop any chemically defined diet for the gall midge? If not so, how are we going to study the effect of inhibitory substance as remarked by you?

Answer: No artificial diets have been developed for the rice gall midge and such a development does not seem likely. With regard to the study of the biochemical basis for gall midge resistance, detailed biochemical analyses will have to be done on resistant and susceptible varieties to observe differences and obtain leads on the nature of the substances involved.

T. Saito, Japan: There are two cases for insect gall formation; one is making giant cells, and another is increasing the number of the cells. Which case is the gall formation in this pest?

Answer: In the case of the rice gall midge, both processes occur in gall formation. For the early stages, cell proliferation takes place and in the late stage of gall elongation, cell expansion takes place.

M. Sakai, Japan: 1) Is it right to understand that insecticides have to be applied before the larvae reach the 2nd instar to depress the gall formation? 2) What kinds of insecticides did you use in the experiments.

Answer: 1) Yes, that is correct. 2) A series of organophosphate insecticides such as Dursban, diazinon, fenitrothion, phorate and many others applied as soil-water treatments kill the larvae and pupae of the gall midge inside the gall.

T. Hidaka, Japan: 1) How about the gall midge incidence in the field in Ceylon? 2) Could you check the sternal spatula for identifying larval instar? 3) What do you think of the formation of the abnormal gall (twisted and curled gall)?

Answer: The midge incidence in Ceylon is generally low with flareups in various areas—roughly about 10% of the areas. 2) Yes, you could distinguish the 3rd instar by the presence of the sternal spatula. The other two instars do not have a sternal

spatula. 3) The twisted gall is possibly the results of incomplete closure of the sides of the gall primordium.

H. A. Custodio, the Philippines: 1) In the light of your discussion on the survival (reversible) of plants when larvae (1st instar) are killed, what specific recommendation could you suggest on the timing of insecticide application? 2) If we could prevent subsequent infestation of tillers, what percentage of the crop could be lost (or recovered)? (loss of primary tiller)

Answer: 1) I could recommend soil/water treatment of nurseries, pre-transplant dip of seedlings for about 12 hours in a series of insecticides diluted at about 30 ppm active ingredient. I would follow these treatments with one treatment in the field at 3–4 weeks after transplanting at 1–2 lbs active per acre. The insecticides of choice are suricide, Dursban, diazinon, phorate etc. 2) I have no data on this question, but I would expect the increase in the field to be in proportion to the extend of the attack by the gall midge and the stage at which control is achieved.

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