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Oviposition by the rice-infesting weevil, *Oryzophagus oryzae* (Costa Lima, 1936) (Coleoptera, Curculionidae): influence of water depth and host-plant characteristics

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ABSTRACT: Following characterization of the egg-laying site, oviposition site selection by the rice-infesting weevil *Oryzophagus oryzae* (Costa Lima, 1936) (Coleoptera, Curculionidae) was studied in relation to water depth, age and density of rice in outdoor tanks. Experimental units consisted of plastic pots that were filled with different soil amounts to obtain the desired water depths in the tanks. Most eggs were laid in the submerged portions of the leaf sheath within the leaves' internal air space (aerenchyma). Oviposition rates increased linearly from 10.9 to 54.5 eggs per plant with an increase in water depth from 0 to 12 cm. There was a significant interaction between water depth and host plant age, and tiller density. In water varying from 4 to 12 cm deep, females oviposited significantly more eggs on 60-day old plants (average > 75 eggs per plant) than on 15-day old plants (average < 30 eggs per plant). Oviposition was negligible on 105 and 150-day old plants. Oviposition rates increased with tiller density in the 4-12 cm water depth interval. The data indicate that females oviposit preferentially on tillering rice plants in relatively deep water, and that egg density is directly related to the number of tillers per plant.

Key Words: Rice water weevils, oviposition behavior, host plant selection, cultural control.

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INTRODUCTION

Oryzophagus oryzae (Costa Lima, 1936) is a major insect pest of irrigated rice, *Oryza sativa* L., in southern Brazil (MARTINS & FERREIRA, 1980; RAMOS, 1985; CAMARGO, 1991). This species shares some biological characteristics with the rice water weevil of the northern hemisphere, *Lissorhoptrus oryzophilus* Kuschel (for a description of *L. oryzophilus* biology, see ISELY & SCHCWARDT, 1934; GRIGARICK & BEARDS, 1965; BOWLING, 1972; MORGAN *et al*., 1984; TSUZUKI *et al*., 1984; HESLER *et al*., 1992). Adults of *O. oryzae* enter diapause and overwinter in clumps of grass, rice stubble, tussocks and bamboo litter (REDAELLI *et al*., 1995; MIELITZ *et al*., 1996). In the spring, they depart from hibernation sites (MIELITZ *et al*., 1996) and enter irrigated rice fields where they feed on rice leaves, producing longitudinal scars (MARTINS, 1976; MARTINS & FERREIRA, 1980). The primary damage to rice is caused by the larval stage. Larvae initially feed upon the rice leaf sheath; later they descend to the roots, which may be severely damaged when the larvae reach their later instars. Larvae of *O. oryzae*, like those of *L. oryzophilus,* have spiracles that are modified into pointed hooks which are inferred to have a primary respiratory function, since they are introduced by larvae into the rice aerenchyma and are connected internally to large tracheae. Pupation occurs in mud-coated cocoons that are attached to rice rootlets. The cocoons are built in connection with the root air space, and thus gas exchange between the pupa and the rice aerenchyma may also occur (G.R.P.M, unpublished data).

Population levels of *O. oryzae* larvae vary considerably under field conditions (MARTINS, 1976, 1979). Among the factors responsible for this variation are time of planting, variety, abundance of alternative host-plants, age of rice when first flooded and other irrigation practices (MARTINS, 1976; MARTINS & FERREIRA, 1980; MARTINS & TERRES, 1995). Within a given paddy field, spatial distribution of larvae is aggregated, and densities are significantly higher where the water level is deeper (MARTINS, 1979). Thus, soil levelling before planting has been recommended as a control measure, because a uniform water column may lead to a relatively uniform adult dispersion and, as a consequence, to a dilution in damage per unit area within paddy fields (MARTINS & FERREIRA, 1980). However, information identifying the cause for a positive correlation between larval density and water depth is still lacking.

Habitat diversity and intra-specific variation of host-plants, among other factors, are known to influence host choices of several herbivorous insects (BERNAYS & CHAPMAN, 1994). Soil water regimes are generally recognized as affecting a number of rice plant characteristics, for example, root length and porosity, dry weight of roots and shoots, and nutrient content in shoots (DAS & JAT, 1977; YOSHIDA, 1981). As a consequence, the aggregation of *O . oryzae* larvae may result at least in part from variation in water depth causing habitat diversity for larvae (*e.g.*, in terms of water temperature) or affecting host plant suitability as larval food. Although not examined yet, these factors in turn could influence performance of *O. oryzae*, and thus rice plants should be used selectively by larvae. Since there is no indication that larvae move actively among rice plants, we suspected that the corresponding spatial pattern would be primarily determined through oviposition site selection. Thus, the specific goals of the present study are: 1) to characterize *O. oryzae* oviposition sites and second and 2) to determine whether females select oviposition sites in response to water depth, host plant age or number of tillers per rice plant.

MATERIALS AND METHODS

1. Experimental procedures

The study was conducted in outdoor, concrete water tanks (Fig. 1), located at Itajaí Experiment Station (EPAGRI), Itajaí County, Santa Catarina State, Brazil. The plants used were EPAGRI 106 cultivar, and were supplied by the Rice Breeding Program of Itajaí Experiment Station. Seedlings and tillers used to test water depth and plant density effects were grown in wooden soil-filled boxes that were irrigated daily and maintained in a plastic screen outdoor house. Plants used to test oviposition preference in relation to rice age were randomly collected from the edges of irrigated plots where grain yield was evaluated according to age of transplanting. A preliminary evaluation indicated that the presence of *O . oryzae* was negligible within these insecticide free plots. Plants that showed adult feeding scars were discarded.

Experimental units consisted of 4-liter plastic pots that were placed contiguously in water tanks (n = 32 per tank), and filled with soil to produce the desired water depths (Fig. 1). The amount of water in each tank was controlled by an overflow and a water level regulating drain. The tanks were filled with tap water before tests started, the drains being set in position to adjust the height of the water column at the level of the plastic pot surfaces.

Simultaneous choice trials (*sensus* SINGER, 1986) were performed to evaluate the effects of water depth, plant age and

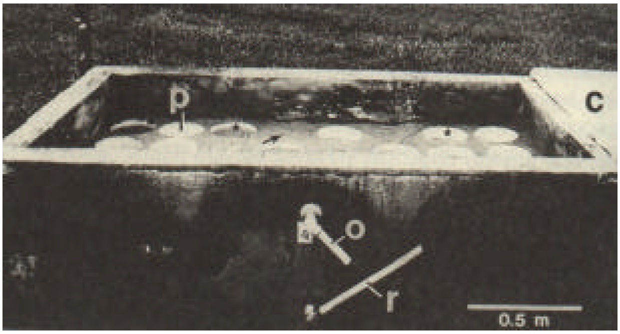

Figure 1. A concrete tank used in the oviposition choice trials. Asterisks indicate partially filled plastic pots (4 and 12-cm water depth treatments). Arrow indicates a plastic pot completely filled with soil (zero water depth treatment). **c**, cloth net covering (partial view); **o,** overflow drain; **p**, plastic pot (experimental unit); **r,** water level regulating drain.

plant density on oviposition site selection. Using one tank at first, ovipositional preference in relation to four water depths (0, 4, 8 and 12 cm) was tested following a one-way, completely randomized design. Young plants (3-4 leaves, 35 cm high, 5 per experimental unit) were used in this choice trial. Subsequently, the effects of these water depths were tested in association with either host plant age or number of tillers per plant, using in each case a two-way completely randomized design. Two tanks were employed in each of these trials (total of 64 experimental units per trial). Rice plants with ages of 15, 60, 105 and 150 days (treatments) were utilized to evaluate plant age effects. In this case, tillers were removed from plants so that there was one tiller per plastic pot (experimental unit = rice plant; n = 256). The influence of the number of tillers per plant on oviposition was examined by using 30-day old tillers (around 40 cm high). The tillers were planted close to each other at densities of 1, 2, 4 and 8 (treatments) per plastic pot (experimental unit = plastic pot; n = 64). It was assumed, by being arranged in such a way, that these treatments represented plants with different numbers of tillers.

Regarding all tests, groups of field collected adults of *O. oryzae* were randomly distributed among tanks and released in their center, at a rate of one mating pair per plant. The tanks were then covered with a fine cloth net (Fig. 1). Trials lasted for three days; then the plants were removed from the plastic plots, cleared of adult beetles, and brought to the laboratory for egg-counting.

Voucher specimens of *O. oryzae* adults are deposited in the Museum of Fundação Zoobotânica of Rio Grande do Sul State, Porto Alegre, numbers 163881 to 163900.

2. Egg counts

Preliminary dissections revealed that most eggs were inserted in the submerged portion of the leaf sheath. Some eggs were deposited on the proximal emerged portion of the leaf sheath, which is located just above the water surface, and thus egg counts were also made on such parts.

Counts were performed on an individual leaf basis under a dissecting stereomicroscope. To determine the spatial distribution of eggs in relation to plant height, leaf sheaths were placed against a ruler and cut into 1-cm long sections, which were inspected for eggs. Eggs were removed from the leaf tissue with fine needles. To facilitate the localization of the eggs, plants were first blanched in hot water for 5 min, and then placed in 70% alcohol for further bleaching (EVERETT & TRAHAN, 1967). After 5 days, they were transferred to a rose bengal alcohol solution (200 mg per liter in 70% ethanol) for staining and preservation. Rose bengal is taken up by leaf tissue and *O. oryzae* eggs, but is concentrated to a deep pink in the latter.

3. Oviposition site description

To characterize the oviposition site of *O. oryzae*, pieces of leaf sheath stained with rose bengal were directly examined and photographed under a Wild M-5 stereomicroscope. To show the position of eggs in the leaf air space, additional pieces were transversely sectioned. Then they were immersed in liquid nitrogen and freeze dried. Pieces containing exposed eggs were attached with double stick tape to aluminum stubs and gold-coated with a Balzers Union sputter coater. They were then examined and photographed in a Jeol 5800 scanning electron microscope.

4. Statistical analysis

For analyses of variance, data from plant age and density trials were transformed into $\sqrt{y} + \sqrt{y+1}$, following criteria suggested by FREEMAN & TUKEY (1950). Where analyses of variance were significant, differences among treatments were tested using Tukey multiple comparison tests, according to the procedures described by SOKAL & ROHLF (1981). Non-parametric tests were conducted according to CONOVER (1980). The Lilliefor's modification was adopted while performing Kolmogorov goodness-of-fit tests for normality. Unless noted, results are expressed as average ± standard errors.

RESULTS

Eggs were laid primarily in the submerged part of rice plants, mostly close to the middle rib of the outermost leaf sheath. They were inserted directly into the leaf aerenchyma, where they could be detected by transparency and counted under a stereomicroscope (Fig. 2).

Figure 2. *Oryzophagus oryzae* egg inserted into the rice aerenchyma as seen in light and scanning electron microscopy, respectively; in a bleached leaf sheath (A) and through a transverse section of leaf sheath (B). **e**, egg; **s**, leaf air spaces (chambers); **t,** diaphragm (transverse wall across the chambers); $\mathbf{v_1}$ **,** middle rib of outermost leaf; $\mathbf{v_2}$, middle rib of first overlapped leaf seemed by transparency. Bars = 1.5 and 0.2 mm, respectively.

Eggs were normally distributed in relation to leaf sheath height for all water depths tested (Fig. 3). The pattern of egg distribution moved from the water surface (0 cm water level) to the middle of the water column in 12-cm water depth. Average egg density per leaf sheath portion varied from 0 to 16 per cm with no indication that such variation was related to water depth. On the other hand, the portion of the leaf sheath most preferred for oviposition increased with increase in water depth (Fig. 3). As a consequence, oviposition rates per plant increased linearly with an increase in water depth (Fig. 4), varying on average from 10.9 eggs per plant in the 0 cm depth to 54.5 eggs per plant in the 12 cm water depth.

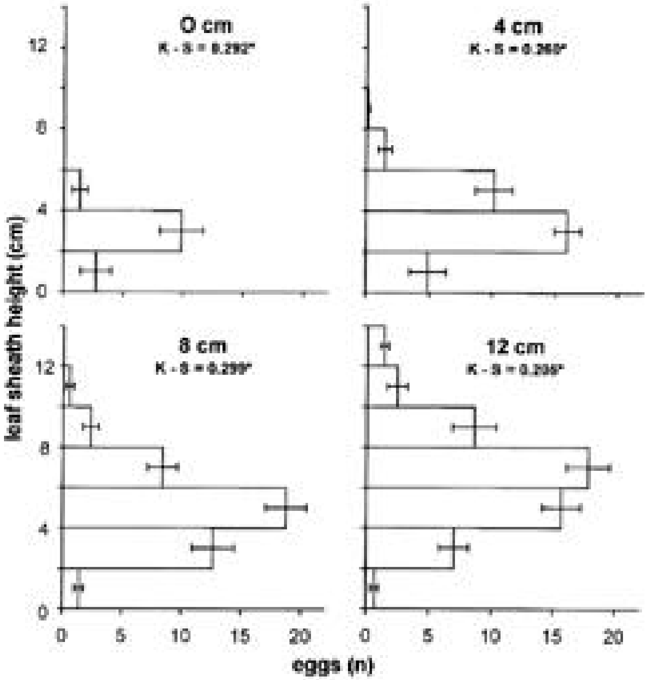

Figure 3. Oviposition of *Oryzophagus oryzae* as a function of leaf sheath height and water column depth. Bars represent the average number of eggs per 2 cm of leaf sheath, and corresponding 95% confidence intervals. All distributions do not differ from normality (K-S values, Kolmogorov goodness-of-fit test, alpha = 0.05).

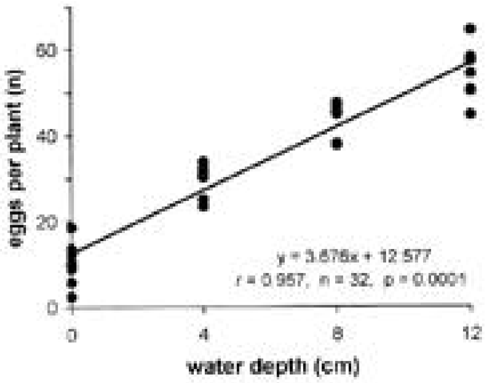

Figure 4. Oviposition of *Oryzophagus oryzae* in relation to water depth.

There was a significant interaction between water depth and both plant age and tiller density in the two-way designs (Table 1). Thus, in these cases statistical comparisons were only performed within each water depth treatment. Oviposition was negligible in reproductive tillers (flowering and milk stages) but was significantly greater in the tillering (average > 75 eggs per plant) than in the emergence/transplanting stage (average < 30 eggs per plant), in the 4-12 cm water depth intervals (Fig. 5). Number of eggs laid per tiller did not change significantly among treatments in all water depths tested (Table 1; Fig. 6). As a consequence, oviposition rates per plant rose linearly with the increase in number of tillers per plant, in the 4-12 cm water depth interval (Table 2).

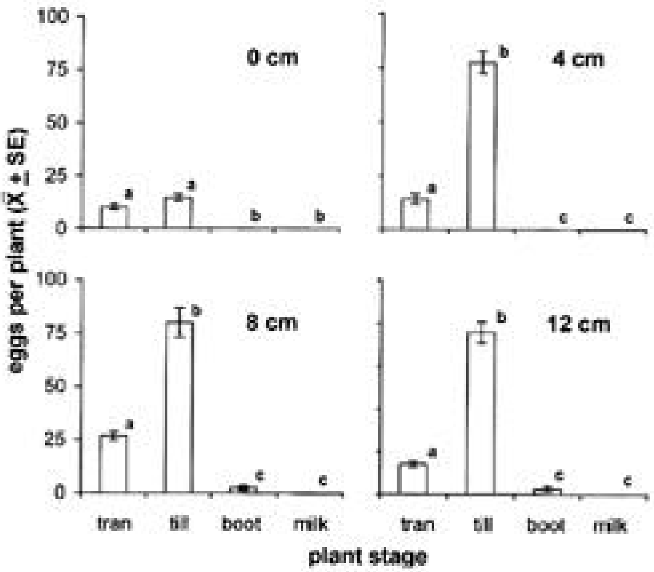

Figure 5. Egg-laying response of *Oryzophagus oryzae* in relation to rice plant age under different water depths (0-12 cm). Bars followed by the same letter within a given water depth are not significantly different (One-way Anova, alpha = 0.05; Tukey multiple comparison tests, alpha = 0.05). **tran**, transplanting; **till**, tillering; **boot,** booting (reproductive stage); **milk** , milking (maturation stage).

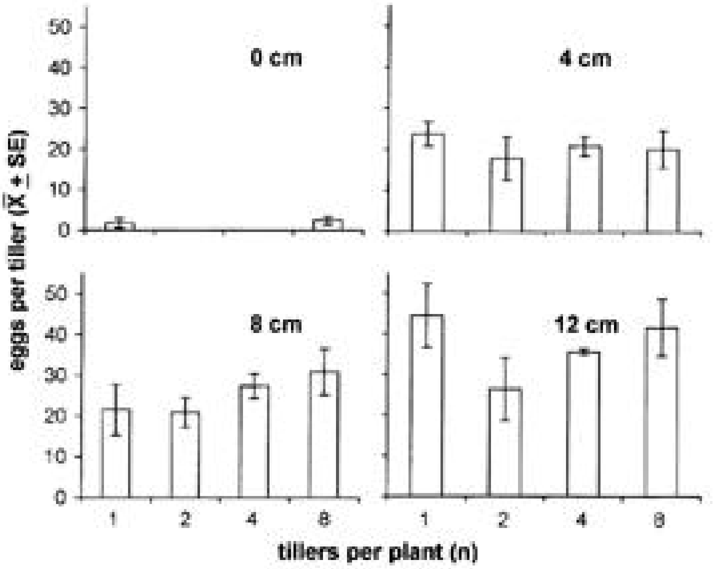

Figure 6. Number of *Oryzophagus oryzae* eggs laid per tiller in response to number of tillers exposed to four water depths (0-12 cm). Within any water column treatment, averages are not significantly different (One-way Anova, n = 64, alpha = 0.05).

Table 1. Summary of two-way ANOVA of age and number of tillers in rice plants, and water depth, on oviposition rates by *Oyzophagus oryzae*

Response variable	**Source**	**Sums of Squares**	**df**	**F**	***p* > F**
Eggs/plant	Age of plants	8381.475	3	609.91	0.00001
	Water depth	665.164	3	48.40	0.00001
	Interaction	862.643	9	20.92	0.00001
	Error	1099.371	240		
Eggs/plant[a]	Number of tillers	2706.549	3	73.47	0.0001
	Water depth	3171.838	3	86.10	0.0001
	Interaction	501.857	9	4.54	0.0002
	Error	589.411	48		
Eggs/tiller[b]	Number of tillers	33.395	3	3.28	0.0282
	Water depth	922.014	3	90.54	0.0001
	Interaction	24.342	9	0.79	0.6219
	Error	162.942	48		

[a] total number of eggs per experimental unit;
[b] average number of eggs per tiller per experimental unit;

Table 2. Regression equations of number of tillers per plant (x) on *Oryzophagus oryzae* oviposition rates per plant, under different water column levels

Water depth (cm)	Equation	r^2	n	F	p > F
0	$y = 0.959x - 0.376$	0.703	16	8.628	0.005
4	$y = 2.175x + 7.956$	0.976	15	44.309	0.00001
8	$y = 3.119x + 6.796$	0.987	16	91.150	0.00001
12	$y = 3.416x + 8.981$	0.983	16	109.319	0.00001

DISCUSSION

For the first time, it was showed that most of the *O. oryzae* eggs are inserted in the submerged portion of the leaf sheath, similar to the oviposition behavior of *L. oryzophilus* (GRIGARICK & BEARDS, 1965; EVERETT & TRAHAN, 1967; BOWLING, 1972). Before starting this study, it was unclear whether *O. oryzae* eggs were primarily laid in rice roots or leaves (see MARTINS, 1976; MARTINS & FERREIRA, 1980; RAMOS, 1985). Additional studies carried out in our laboratory suggest that the eggs are laid preferentially in the middle rib which is the portion of the rice leaf sheath where the number and size of air spaces are greater. Furthermore, they may not be inserted into the leaf sheath of overlapped leaves, because the ovipositor of *O. oryzae* is not long enough to reach them (G.R.P.M., unpublished data).

Results from this study showed clearly that during tillering stage, when located in relatively deep water, rice plants are preferred for oviposition by *O. oryzae*. Thus, high densities of *O . oryzae* larvae in areas of irrigated rice fields with high water levels are at least in part determined by oviposition site selection. The interaction between water depth and both plant age and tiller number demonstrates that these variables can not be dissociated, both being important. The effect of low water level on oviposition was expected, because the presence of water is necessary for development of *O. oryzae* immature stages (G.R.P.M., unpublished data).

The data also show that, when water depth and the number of tillers per plant are constant, there is no significant difference in the number of *O. oryzae* eggs laid either per leaf sheath portion or per tiller. First, this implies that *O. oryzae* females assess egg-load and alter their oviposition rates per plant according to host-plant availability, reaching a nearly uniform dispersion of eggs in these situations. Second, the greater egg density in plants located in the deep water columns, and in those plants bearing higher numbers of tillers, may result directly from a greater amount of submerged leaf sheath tissue available for oviposition per plant in both situations. The ability of ovipositing females to discriminate between host plants with differing egg loads has been recognized for a number of herbivorous insects (see JONES, 1991; MUGRABI-OLIVEIRA & MOREIRA, 1996), including other beetles, for example, *Callosobruchus maculatus* (MESSINA & RENWICK, 1985). Third, egg-load assessment leading to a uniform distribution of eggs among host plants may obscure the corresponding female preferences (see SINGER, 1986), and should be taken into account in future investigations regarding *O. oryzae* oviposition site selection.

The proximate causes for *O . oryzae* females selecting irrigated rice plants based upon water depth, age and number of tillers per plant, and underlying mechanisms remain to be investigated. There is strong evidence that these ovipositional choices made by *O. oryzae* females are adaptive. Aerenchyma formation is a typical physiological response of plants to flooding, which provides an air conducting system between aerial parts of the plant and the root system (DAUBENMIRE, 1974; KAWASE & WHITMOYER, 1980; YOSHIDA, 1981; PEZESHKI, 1994). Thus, it is reasonable to assume that the amount of air space formed in the submerged parts of rice leaves vary proportionally with the water depth in which plants are located. Rice tillers and roots emerge from the same node at the same time, and thus roots are produced at the greatest rate during tillering (YOSHIDA, 1981). As a consequence, leaf area and dry weight of rice plants are directly correlated with number of tillers. Furthermore, concentration of some nutrients (*e.g.*, nitrogen and phosphorous) are generally high at early growth stages in the vegetative parts, and progressively decrease with the advent of maturity (YOSHIDA, 1981). As showed by DAS & JAT (1977), an increase in root porosity is associated with greater root length, increased dry weight of roots and shoots, and higher nutrient levels in shoots. Larvae and pupa of *O. oryzae* depend upon rice aerenchyma for respiration. I have found coccons attached primarily to young roots. Young larvae feed on the leaf sheath and later instars on the roots (G.R.P.M, unpublished data). Thus, rice plants during the tillering stage, with a high number of tillers and when located in deep water columns may provide a more favorable oviposition sites for *O . oryzae*, because they offer the appropriate amount of air space for respiration and a greater availability of nutritional food for development.

Control of rice water weevil in Southern Brazil has been achieved primarily through application of chemical insecticides (MARTINS *et al*., 1996). The results obtained in this study support the recomendation of MARTINS & FERREIRA (1980) that soil levelling before planting should decrease damage by *O. oryzae*. In other words, egg and subsequent larval distribution should be more evenly distributed among rice plants in such a situation. Also, results indicate that the use of low water column levels in association with soil levelling should reduce damage. Finally, the earlier rice fields are irrigated the greater should be the propensity for damage by *O. oryzae*. In fact, delaying irrigation has been a practice recommended for reducing rice water weevil damage in irrigated rice (MORGAN *et al*., 1989; HESLER *et al*., 1992). Unfortunately, in southern Brazil farmers are moving from traditional seed sowing methods and delayed irrigation, to sowing soaked seeds on permanently irrigated fields. This practice should substantially enhance the pest status of *O. oryzae*, because oviposition occurs preferentially on young plants, even on seedlings. Finally, our data point to alternative control practices within an integrated pest management approach. For example, they support application of localized control practices, in areas of deep water, where adults and larvae aggregate. This procedure could be used to attract ovipositing females to susceptible cultivars in small flooded areas, and planting resistant varieties (MARTINS & TERRES, 1995) in the remaining fields. However, these control measures remain to be tested experimentally.

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