Effect of Silicon and Host Resistance on Sheath Blight Development in Rice

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ABSTRACT

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Rice cultivars high in partial resistance (Jasmine, LSBR-5), moderately susceptible (Drew and Kaybonnet), and susceptible (Lemont and Labelle) to sheath blight were grown in a silicon-deficient Histosol with and without calcium silicate slag. The treatment with silicon increased the concentration of this element in plant tissue by 80% over all experiments. Fertilization with silicon significantly reduced the severity of sheath blight, and the total area under the vertical lesion extension progress curve on moderately susceptible and susceptible cultivars compared to those cultivars high in partial resistance without silicon. The percentage of infected tillers was significantly reduced by 82, 42, 28, 41, 26, and 17% respectively for Jasmine, LSBR-5, Drew, Kaybonnet, Lemont, and Labelle, when silicon was applied, over all experiments. Dry matter accumulation was significantly greater with added silicon. In the absence of disease, silicon enhanced dry matter accumulation by 15% over the control, whereas silicon more than doubled the mean dry matter accumulation in infected plants. The application of silicon to complement host resistance to sheath blight appears to be an effective strategy for disease management in rice, especially when the soil is low or limiting in plant-available silicon.

Additional keywords: calcium silicate, *Oryza sativa*, *Rhizoctonia solani*

Sheath blight, caused by *Rhizoctonia solani* Kühn (*Thanatephorus cucumeris* (Frank) Donk), anastomosis group 1 IA (AG-1 IA) (25), is a potentially devastating disease of rice (*Oryza sativa* L.) in all temperate and tropical rice production regions, especially in irrigated production systems (4,8,14,26,29). Symptoms of sheath blight include lesions on the base of the leaf sheath near the waterline which are elliptical or oval-shaped and greenish-gray with yellow margins (8,14). High levels of nitrogenous fertilizers, double cropping, high plant populations per unit area, and the utilization of early-maturing, short-stature, high-tillering compact, susceptible cultivars have intensified the severity of this disease in most rice-growing regions in the world (4,14,26,29).

Although control strategies for sheath blight have centered around the use of foliar fungicides (10), their use is limited due to perceived environmental problems,

expense, and potential risk of emergence of pathogen populations that could become resistant. Development of cultivars resistant to sheath blight has been slow because the pathogen has an extremely wide host range, resistance shows low heritability, and resistance is linked with poor-yield performing characteristics such as tall plant stature, late maturity, and poor milling quality (15,19,23,26). The highest level of resistance among cultivars grown in the southwestern United States is found in the short- and medium-grain types. These are more like the Japonic rices, although long-grain cultivars, such as Labelle, Bluebelle, and Lebonnet, tend to be more susceptible (18,29).

Resistance to sheath blight is expressed partly as a reduced number of infection cushions produced by *R. solani*, subsequently resulting in fewer and smaller lesions (9). Cultivars with an adequate level of resistance to sheath blight are currently available to farmers in the United States (21,36). Several cultural practices have been applied to minimize the intensity of sheath blight. They include crop rotation, solarization, reduced close spacing of hills in transplanted rice, biological control with potential agents such as *Trichoderma* spp. and fluorescent pseudomonads, and induced resistance with avirulent strains of *R. solani* or different chemicals and nutrients (1,28).

Other alternatives need to be investigated for sheath blight management. Silicon

fertilization may offer an important and viable alternative for sheath blight control or as a supplement to the use of fungicides, especially where soils are deemed to be low or limiting in plant-available silicon (Si). Some economically important diseases in rice such as blast (*Magnaporthe grisea* (Hebert) Barr), brown spot (*Cochliobolus miyabeanus* (Ito and Kuribayashi in Ito) Drechs ex Dastur), stem rot (*Magnaporthe salvinii* Catt.), scald (*Monographella albescentis* Theum), and grain discoloration had their intensities reduced by Si (5,13,31,34). Si also has been shown to suppress the development of sheath blight (20,35).

The purpose of this study was to measure levels of disease development in rice cultivars grown with and without Si that are high in partial resistance, moderately susceptible, and susceptible to sheath blight. In addition, we wanted to determine whether fertilization with Si could augment inherent host resistance of susceptible and moderately susceptible cultivars to the same level of resistance exhibited by those cultivars high in partial resistance without Si. A portion of this study was previously published (27).

MATERIAL AND METHODS

Experiments were conducted under greenhouse conditions from March to June of 1997 at the University of Florida, Everglades Research and Education Center, Belle Glade. The soil type used in all experiments was a Si-deficient Histosol (Terra Ceia muck), collected from the Everglades Agricultural Area, with 3.97 mg dm⁻³ plant-available Si. Each pot was filled with 2 kg of muck soil and amended with calcium silicate slag at the rates of 0 and 10 g pot⁻¹ (approximately 10 metric tons per hectare) 2 days before sowing. Available soluble Si from calcium silicate slag was approximately 22%.

Rice cultivars Jasmine and LSBR-5 (high level of partial resistance), Drew and Kaybonnet (moderately susceptible), and Lemont and Labelle (completely susceptible) were chosen from previous field experiments to represent a range of resistance types to sheath blight (16,30). All cultivars tested were tropical *japonicas* except for Jasmine, which is an *indica* type (17,30). Seeds of each cultivar were sown at the rate of 12 seeds per pot. Ten days after

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sowing, each pot was thinned to four plants. No modifications were made to the pots to allow for drainage, and plants were kept under flooded conditions until the end of the experiment.

A virulent isolate of *R. solani* (AG-1 IA), obtained from symptomatic rice plants and provided by F. Lee, University of Arkansas, was used to inoculate plants. The isolate was maintained on acid potato dextrose agar medium (APDA). Inoculum was obtained as follows: the isolate of *R. solani* was grown on APDA and incubated for 10 days at room temperature to produce mycelia. Wooden toothpicks, 1 cm in length, were placed in Erlenmeyer flasks containing a shallow layer of potato broth and autoclaved. After autoclaving, 15 toothpicks and five agar plugs, 5 mm in diameter, obtained from the margin of an actively growing colony of *R. solani*, were transferred to APDA plates. Plates were allowed to incubate for 8 days at room temperature so that *R. solani* could colonize the toothpicks.

Plants (42 days old, maximum tillering stage) were inoculated by placing a 1-cm toothpick colonized by *R. solani* into the lowest inner sheath of the main tiller. Immediately after inoculation, all plants were transferred to a plastic mist chamber inside a greenhouse for 20 to 29 days, depending on the experiment. For all three experiments, temperature and relative humidity were measured using a traceable relative humidity/temperature meter (Fisher Scientific, Atlanta, GA) and recorded three times per day. In experiment 1 (March-April), the temperature inside the chamber ranged from 19.4 to 21.2°C, 21.6 to 24.8°C, and 22.8 to 23.4°C, respectively, at 8 AM, 12 AM, and 5 PM. In experiment 2 (April-May), the temperature ranged from 23.7 to 25.7°C, 32.7 to 35.1°C, and 26.9 to 34.5°C, respectively, at 8 AM, 12 AM, and 5 PM. In experiment 3 (May-June), the temperature ranged from 28.1 to 29.6°C, 34.8 to 36.4°C, and 27.4 to 35.8°C at 8 AM, 12 AM, and 5 PM respectively. For all experiments a 12-h relative humidity period was

maintained within this plastic mist chamber, ranging between 89 and 96% with a humidifier (Herrmidifier 500 Co., Inc., Lancaster, PA). Plants also were maintained under natural light.

Sheath blight progress on the plant was evaluated by measuring the vertical lesion extension (mm) in the inoculated sheath as well as on the two sheaths above. In experiment 1, the evaluations in the inoculated sheath were made at 4, 5, 6, 7, 8, 9, and 10 days postinoculation; for the second sheath at 10, 12, 15, 17, 19, 21, and 23 days postinoculation; and for the third sheath at 21, 23, 24, 27, and 29 days postinoculation. In experiment 2, the evaluations in the inoculated sheath were made at 4, 5, 6, 7, and 8 days postinoculation; for the second sheath at 5, 6, 7, 8, 10, 12, 14, and 15 days postinoculation; and for the third sheath at 12, 14, 15, 16, 19, and 20 days postinoculation. In experiment 3, the evaluations in the inoculated sheath were made at 4, 5, 6, 7, and 9 days postinoculation; for the second sheath at 5, 6, 7, 9, 11, 14, 16, and 18 days postinoculation; and for the third sheath at 14, 16, 18, 20, and 21 days postinoculation. Data from each sheath in each treatment and experiment were used to construct the vertical lesion extension progress curve. Area under the vertical lesion extension progress curve (AUVLEPC) for each sheath in each plant, replication, treatment, and experiment was computed using the trapezoidal integration of vertical lesion extension progress curve over time using the formula proposed by Shaner and Finney (33). Total AUVLEPC represents the sum of the AUVLEPC from all sheaths.

Severity of sheath blight was scored using a scale ranging from 0 to 9, which is based on relative lesion height on the whole plant (12). The scale is as follows: 0 = no infection; 1 = lesions limited to lower 20%; 3 = lesions limited to lower 20 to 30%; 5 = lesions limited to lower 31 to 45%; 7 = lesions limited to lower 46 to 65%; and 9 = lesions infecting more than 65% of plant height. Percentage of infected tillers, dry matter accumulation for inoculated and noninoculated plants, and silicon concentration in straw also were determined.

Dry matter accumulation of plants was determined at 62 to 71 days after sowing, depending on the experiment. Leaves and culms were ground to pass through a 40-mesh screen with a Thomas-Wiley mill (Thomas Scientific, Swedesboro, NJ). The concentration of silicon in tissue samples was determined by first digesting 0.1 g of dried tissue, then performing automated colorimetric analysis (6). Results obtained were expressed in decagrams (dag) of Si per kg of plant tissue.

A 2 × 6 × 2 factorial experiment, consisting of two levels of Si, six cultivars, and inoculated and noninoculated (control) plants, was arranged in a completely randomized design with five replications. Val-

Table 1. Concentration of Si (dag kg⁻¹) in straw of rice cultivars grown in pots nonamended and amended with Si^a

Cultivars	Experiment 1		Experiment 2		Experiment 3	
	– Si	+ Si	– Si	+ Si	– Si	+ Si
Jasmine	0.56	2.10	0.72	2.98	0.76	3.15
LSBR-5	0.52	2.90	0.70	3.33	0.87	3.92
Drew	0.50	2.70	0.67	3.82	0.80	4.05
Kaybonnet	0.56	2.46	0.62	3.83	0.84	4.48
Lemont	0.52	3.48	0.70	4.03	0.83	4.53
Labelle	0.50	3.08	0.65	3.72	0.76	4.27
FLSD ($P \leq 0.05$)	0.06	0.32	0.08	0.36	0.09	0.30

^a Si analysis in the rice straw was determined by first digesting 0.1 g of dried tissue, then performing automated colorimetric analysis.

Table 2. Influence of silicon and host plant resistance on severity of sheath blight^a

Cultivars	Experiment 1		Experiment 2		Experiment 3	
	– Si	+ Si	– Si	+ Si	– Si	+ Si
Jasmine	1.70	1.20	2.50	1.00	2.92	1.00
LSBR-5	1.60	1.20	3.40	1.00	3.17	1.25
Drew	1.80	1.30	4.70	2.20	6.00	2.58
Kaybonnet	2.13	1.40	5.60	2.10	6.50	2.67
Lemont	2.50	1.70	7.90	4.00	7.75	3.33
Labelle	2.85	1.65	6.70	3.70	7.42	3.17
FLSD ($P \leq 0.05$)	0.71	0.49	1.07	1.05	0.55	0.67

^a Severity of sheath blight was scored on a scale ranging from 0 to 9, which is based on the relative lesion height on the whole plant.

Table 3. Influence of silicon and host plant resistance on the total area under the vertical lesion extension progress curve^a

Cultivars	Experiment 1		Experiment 2		Experiment 3	
	– Si	+ Si	– Si	+ Si	– Si	+ Si
Jasmine	97.59	36.90	154.58	48.83	203.15	126.25
LSBR-5	121.45	47.43	132.00	69.28	203.08	112.94
Drew	98.30	78.43	201.21	114.30	426.25	253.94
Kaybonnet	105.91	69.58	244.28	63.62	385.89	278.83
Lemont	123.14	77.03	283.30	228.00	528.54	236.11
Labelle	122.03	81.95	251.75	149.43	415.80	231.39
FLSD ($P \leq 0.05$)	20.60	42.90	70.49	58.93	75.98	54.11

^a Total area under the vertical lesion extension progress curve was obtained by summing the area under the vertical lesion extension for all three sheaths in each experiment.

ues obtained for each variable were analyzed by analysis of variance (ANOVA). For dry matter accumulation, ANOVA included the factor of inoculated and noninoculated

plants. Mean comparisons were conducted with Fisher's protected least significant difference (FLSD, $P \leq 0.05$) test. Single degree-of-freedom contrasts were used to

make comparisons between specific cultivar groups, nonamended and amended with Si. Arcsine transformation was used in the analysis of the percentage of infected tillers.

Fig. 1. Vertical lesion extension (mm) progress curves on rice cultivars Jasmine, LSBR-5, Drew, Kaybonnet, Lemont, and Labelle fertilized (+ Si) or not (– Si) with silicon. Data points are means of 20 plants in five replications for each sheath in each treatment. Evaluations started 4 days postinoculation when the first lesion was observed on sheath 1 (inoculated sheath). Bars represent standard deviation of the mean. Three experiments were conducted with consistent results and the data presented represent the third experiment.

The experiment was repeated three times and data from repeated experiments were not pooled for analysis because there was no interaction between experiment and treatment effects. Data were subjected to analyses using the Statistical Analysis System (SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

Silicon and cultivar treatments had highly significant effects ($P \leq 0.05$) on silicon concentration in straw, severity of sheath blight, total area under the vertical lesion extension curve, and percentage of infected tillers in all experiments (data not shown). The cultivar $\times$ silicon interaction was also significant ($P \leq 0.05$) for these variables, requiring the analysis of Si means by cultivar.

Mean Si concentration in straw increased markedly with addition of calcium silicate slag (range of 73 to 85%, 76 to 84%, and 76 to 82%, respectively, in experiments 1, 2, and 3 over all cultivars), as compared to Si-nonamended treatments (Table 1). Variation among cultivars was significant ($P \leq 0.05$) for Si concentration in Si-nonamended treatments only in experiments 2 and 3. However, the range among cultivars was very narrow. For the Si-amended treatment, cultivars varied significantly ($P \leq 0.05$) for Si concentration in plant tissue (Table 1). In experiment 1, Jasmine had the lower plant-tissue Si concentration and differed significantly from other cultivars. In experiment 2, the highest Si values were determined on Drew, Kaybonnet, Lemont, and Labelle, which differed significantly from Jasmine and LSBR-5. In experiment 3, only Kaybonnet, Lemont and Labelle, with the greatest values of Si concentration, differed significantly from Jasmine and LSBR-5. Genotypic differences for concentration of Si in Jasmine and LSBR-5 observed in all experiments could have resulted in differential uptake and utilization of this element in comparison to the other cultivars.

Increasing Si concentration in straw significantly reduced the severity of sheath blight on cultivars Jasmine and LSBR-5 that are high in partial resistance; on the moderately susceptible cultivars Drew and Kaybonnet, and on the susceptible cultivars

Lemont and Labelle, by 27, 29, and 37% respectively in experiment 1; 66, 58, and 47% in experiment 2, and 63, 58, and 57% respectively in experiment 3, as compared to these cultivars without Si (Table 2).

Total AUVLEPC also decreased significantly on cultivars high in partial resistance, moderately susceptible and susceptible by 62, 28, and 35% respectively in experiment 1; 59, 60, and 30% in experiment 2, and 41, 34, and 51% respectively in experiment 3, as compared to these cultivars without Si (Table 3 and Fig. 1).

To determine whether the application of Si to moderately susceptible and susceptible cultivars could suppress the severity of sheath blight and the total AUVLEPC to those cultivars high in partial resistance that had not been treated with Si, selected cultivar-Si combinations were compared by single degree of freedom contrasts (Table 4). In all experiments, the combination of Drew and Kaybonnet, Lemont and Labelle, or these cultivars analyzed separately, plus silicon reduced the severity of sheath blight to the same statistical level as that for the cultivars Jasmine and LSBR-5 high in partial resistance without Si. Si fertilization also reduced the total AUVLEPC for Drew and Kaybonnet and Lemont and Labelle in experiment 1; for Drew and Kaybonnet and Labelle in experiment 2, and for Drew and Lemont and Labelle in experiment 3, to the same statistical level as Jasmine and LSBR-5 without Si ($P \leq 0.05$) (Table 4). Little information is currently available for sheath blight control by addition of Si. According to Mathai et al. (20), application of Si had a significant effect in reducing the intensity of sheath blight, even though the difference between the high and low levels of Si was not statistically significant. Winslow et al. (35) reported only that Si reduced the severity of sheath blight in irrigated *indica* rice genotypes as compared to *japonica* upland rice genotypes and intermediate groups. However, in this study, we demonstrated that Si reduced sheath blight development in both tropical *japonicas* and an *indica* type. This suggests that enhanced sheath blight resistance by Si is not limited to *indica* types. Future research needs to be conducted on greater populations of *indi-*

cas and *japonicas* to better understand the scope of Si-responsive genotypes.

Fertilization with Si reduced the percentage of infected tillers by *R. solani* by a range of 20 to 86%, 19 to 85%, and 9 to 76% respectively in experiments 1, 2, and 3, over all cultivars (Table 5). Variation among cultivars was significant in Si-nonamended treatment only in experiments 1 and 2. In all experiments, for the Si-amended treatment, Jasmine and LSBR-5, which are high in partial resistance to sheath blight, had the lowest percentage of infected tillers, as compared to Lemont and Labelle, which are known to be sheath blight-susceptible. The decrease in the number of diseased hills is particularly important to slow the horizontal spread of *R. solani* in the field and consequently reduce yield loss (8,26).

A physical barrier of Si in the cuticle layer of the leaf sheath as affirmed by Yoshida et al. (37) would likely reduce lesion extension, as well as disease intensity in general, on Si-treated plants. Volk et al. (34) hypothesized that blast lesion size could be reduced by organosilicon compounds in the walls of epidermal cells, and Inanaga et al. (11) later proved that Si does indeed form complexes with organic compounds in these cells. Seebold et al. (32) demonstrated that the rate of blast lesion expansion in several rice cultivars decreased from 0.8 to 0.43 mm/day as the rate of calcium silicate slag increased from 0 to 10 T ha⁻¹. An induced resistance by Si might also have contributed to reducing sheath blight intensity, not accounted for by the physical barrier of Si in the cuticle layer. In rice, the exact mechanism(s) by which Si reduces the intensity of sheath blight, and other diseases such as blast, is unknown. Other researchers have suggested that Si acts in crops such as cucumber and barley to stimulate host defense mechanisms to pathogenesis, such as increasing phenol content and the activity of chitinases, β -1,3-glucanases, peroxidase, β -glucosidase, phenylalanine ammonia-lyase, and polyphenoloxidase (2,3,7,22).

A significant interaction was detected between cultivar $\times$ inoculated and non-inoculated plants and silicon $\times$ inoculated and noninoculated plants (data not shown). In all experiments, for all cultivars, non-

Table 4. Single degree of freedom contrasts for comparisons between specific groups of cultivars nonamended and amended with Si on severity of sheath blight (Sev) and total area under the vertical lesion extension progress curve (TAUVLEPC)

Cultivar groups			Sum of square ^a					
			Experiment 1		Experiment 2		Experiment 3	
			Sev ^a	TAUVLEPC	Sev	TAUVLEPC	Sev	TAUVLEPC
– Si		+ Si						
Jasmine and LSBR-5	vs.	Drew and Kaybonnet	1.800 ^{ns}	3571.128 ^{ns}	1.800 ^{ns}	21978.450 ^{ns}	4.167 ^{ns}	96076.760 ^{**}
Jasmine and LSBR-5	vs.	Drew	1.633 ^{ns}	206.719 ^{ns}	0.833 ^{ns}	813.802 ^{ns}	3.361 ^{ns}	41327.501 ^{ns}
Jasmine and LSBR-5	vs.	Kaybonnet	0.833 ^{ns}	6923.602 ^{ns}	1.633 ^{ns}	45610.502 ^{ns}	2.250 ^{ns}	91733.266 [*]
Jasmine and LSBR-5	vs.	Lemont and Labelle	0.013 ^{ns}	3315.313 ^{ns}	39.200 ^{ns}	88711.200 ^{**}	1.041 ^{ns}	28042.091 ^{ns}
Jasmine and LSBR-5	vs.	Lemont	0.033 ^{ns}	3136.519 ^{ns}	32.033 ^{ns}	149495.502 ^{**}	1.361 ^{ns}	22236.101 ^{ns}
Jasmine and LSBR-5	vs.	Labelle	0.133 ^{ns}	1445.602 ^{ns}	20.833 ^{ns}	9946.302 ^{ns}	0.250 ^{ns}	16782.881 ^{ns}

^a ns, *, and ** = nonsignificant, significant at 0.05 and 0.01 levels of probability.

inoculated plants had significantly greater dry matter accumulation when compared to inoculated plants (Table 6). Dry matter accumulation for noninoculated plants increased relative to the inoculated plants by a range of 46 to 96%, 45 to 137%, and 24 to 162% respectively in experiments 1, 2, and 3 (Table 6). For inoculated plants, dry matter accumulation on Jasmine and LSBR-5 was significantly higher compared to Lemont in experiment 1, and to Drew, Kaybonnet, Lemont, and Labelle in both experiments 2 and 3 (Table 6). In the absence of disease, Si enhanced dry matter accumulation by 13, 25, and 15% respectively in experiments 1, 2, and 3. However, in the presence of sheath blight, Si more than doubled the mean dry matter accumulation in experiment 3 (38%), had a little effect in experiment 2 (28%), and had no effect in experiment 1 (13%) (Table 6). Increases in dry matter accumulation by Si for inoculated plants could be attributed to a decrease in the intensity of sheath blight, and more favorable plant nutrition for both inoculated and noninoculated plants. It is known that sheath blight infection may change the dynamic balance of synthesis and decomposition of chlorophyll pigments and rate of photosynthesis in rice (24), due to the presence of several large lesions on leaf sheath and leaf blades of the rice plant.

The results presented in this study provide evidence that Si can be used successfully to enhance the level of resistance to sheath blight, especially in moderately susceptible and susceptible cultivars grown

in soils low or limited in plant-available Si. This becomes especially important when cultivars with a satisfactory level of resistance to sheath blight are not available for commercial use.

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Table 5. Influence of silicon and host plant resistance on the percentage of infected tillers^a

Cultivars	Experiment 1		Experiment 2		Experiment 3	
	- Si	+ Si	- Si	+ Si	- Si	+ Si
Jasmine	17.50	2.50	50.00	7.50	90.28	21.87
LSBR-5	12.50	10.00	50.00	20.00	90.28	49.31
Drew	25.00	17.50	62.50	45.00	100.00	72.92
Kaybonnet	28.13	12.50	70.00	42.50	94.45	66.67
Lemont	42.50	35.00	100.00	47.50	95.83	87.50
Labelle	40.00	32.50	65.00	52.50	91.67	79.17
FLSD ($P \leq 0.05$)	22.31	21.52	26.18	25.52	12.05	20.55

^a Values were arcsine transformed before analysis.

Table 6. Influence of silicon and host plant resistance on dry matter accumulation (g per 4 plants)^a

Cultivars	Experiment 1		Experiment 2		Experiment 3	
	Inoculated	Noninoculated	Inoculated	Noninoculated	Inoculated	Noninoculated
Jasmine	11.69	17.10	9.41	13.65	7.86	9.78
LSBR-5	9.79	15.70	9.03	13.83	6.51	11.46
Drew	10.60	18.37	7.47	15.35	5.79	11.82
Kaybonnet	9.87	18.22	7.15	14.85	4.85	12.28
Lemont	8.61	16.05	6.92	15.97	4.57	11.99
Labelle	10.84	21.30	7.24	19.54	5.62	12.75
FLSD ($P \leq 0.05$)	1.17	3.45	0.93	7.59	0.68	1.73
Silicon						
- Si	9.63	16.73	7.05	13.84	4.94	10.86
+ Si	10.83	18.85	9.03	17.34	6.80	12.50
t test ($P \leq 0.05$)	0.67	1.99	0.53	2.36	0.39	0.99

^a Dry matter accumulation was determined 62 to 71 days after sowing depending on the experiment.

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