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Effects of feeding on healthy and diseased corn plants on a vector and on a non-vector insect*

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Abstract. Insect-transmitted plant pathogens can have positive, negative or no effects on the vector insect. Effects could be direct (caused by the pathogen) or indirect (mediated by changes in the plant). Pathogen effects on non-vector insects are less well known. *Peregrinus maidis* (Ashmead) (Homoptera: Delphacidae), an insect that is not a vector of the corn stunt spiroplasma (CSS), weighed less 15 days after feeding on CSS-infected corn plants relative to insects feeding on healthy corn plants. Fecundity of non-vector insects that were removed from diseased plants was higher than for insects coming from healthy plants. For *Dalbulus maidis* (DeLong & Wolcott) (Homoptera: Cicadellidae), an insect that transmits CSS, there were no differences in weight, longevity, eggs per day, weekly or total fecundity after feeding on healthy or on CSS-infected corn plants. Significant differences in some phloem amino acids were detected between healthy and CSS-infected plants. Infected plants also showed an increased phloem acidity as disease symptoms progressed. Feeding on CSS-infected corn plants by an insect that does not vector the pathogen infecting the plant can have favorable consequences as evidenced by an increased fecundity.
Key words. Cicadellidae; Delphacidae; Homoptera; leafhoppers; mollicutes; planthoppers; *Spiroplasma*.

A plant infected by a plant pathogen can respond in several ways, including the synthesis of secondary chemicals, changes in the amino acid and carbohydrate content, changes in color and architecture, and cell wall modifications[1,2], among others. These pathogen-induced plant changes could influence a plant's suitability for insect herbivores[3], and can be referred to as indirect effects, in contrast to the direct effects of pathogen acquisition by the insect. An indirect effect could be increased plant suitability due to a higher amino acid content[4], while a direct effect can be any cytopathological change in the insect caused by the pathogen[5,6]. Most investigations on the indirect effects of plant pathogens on insects have studied the insect vectors of the pathogen. Vector responses to feeding on infected plants have been positive[7–18], negative[14,19–32] or neutral[29,30,33].

In contrast to the wealth of information on vector insects, we only found seven studies that report responses of non-vector insects after feeding on plants infected with pathogens transmitted by insects[7,8,33–37]. Other studies have looked at the response of non-vector insects to pathogens not transmitted by insects[32,38–47]. The lack of information on non-vector response to feeding on plants infected with insect-vectored plant pathogens is noteworthy, first, because of the commonness of plant disease[48], and second, because most insect herbivores do not serve as vectors for plant pathogens. For example, of 53 insect species reported as pests of bean, 94% are non-vectors; of 40 reported as pests of alfalfa, 79% are non-vectors; of 56 reported as pests of tobacco, 90% are non-vectors; and of 54 reported as pests of tomato, 83% are non-vectors[49]. Most studies (on vectors and non-vectors) do not differentiate between the direct effect of the pathogen and its plant-mediated effects on herbivores.

In this study, we were interested in the effects that feeding on infected plants had on an insect that is not a vector of the pathogen infecting the plant. As a vector insect, we used the corn leafhopper *Dalbulus maidis* (DeLong & Wolcott) (Homoptera:Cicadellidae) the principal vector of the phloem-limited mollicute[50] corn stunt spiroplasma (CSS, *Spiroplasma kunkelii*[51]). The corn planthopper *Peregrinus maidis* (Ashmead) (Homoptera:Delphacidae), a phloem feeder[52] that can transmit viruses but does not transmit CSS[33] was used as the 'non-vector' insect. We selected these organisms because CSS is phloem-limited[50] and both *D. maidis* and *P. maidis* feed on the phloem. Thus, any pathogen-induced change in the chemistry of the plant that is expressed in the phloem should be experienced by both insects during feeding. We determined changes in weight, longevity, eggs per day, weekly fecundity and

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total fecundity for *D. maidis* and *P. maidis* after feeding on CSS-infected plants. We also analyzed the phloem of healthy and infected corn plants for amino acid and pH levels.

Materials and methods

The original batch of insects from which colonies were started was provided by L. R. Nault (The Ohio State University). Insect colonies had been maintained for about 15–20 generations on corn in the greenhouse before their use in this experiment. To standardize age of insects used in the experiment, first-second instars of *D. maidis* and second instars of *P. maidis* were taken from the stock cages and transferred to healthy corn or to corn plants showing strong CSS symptoms (e.g., severe stunting and striping in leaves[53]). Before nymphs eclosed into adults, they were sexed to isolate virgin females and kept on healthy or CSS-infected plants. When the experiment was initated, all insects (starting as nymphs) had been exposed to healthy or diseased corn plants for a total of 15 days.

The experiment was conducted with 24 females per species (*Dalbulus maidis* or *Peregrinus maidis*), twelve of which had fed for 15 days on healthy plants (treatment = healthy) and 12 which had fed for 15 days on diseased plants (treatment = diseased). Two males and one virgin female of each species were introduced in each of 12 separate cylindrical cages containing healthy corn seedlings (*Zea mays* L. cv. 'Aristogold Bantam Evergreen') at the 4–6 leaf stage. Cylindrical cages were made of transparent cellulose butyrate (30 cm × 7.5 cm dia.), with four 5 cm dia. holes on opposite sides covered with organdy to allow for air passage. The top of the cage was also covered with organdy. Females' weight was determined before introducing them in the cages. Males were removed 15 days after they were introduced in the cage. Although repeated mating is important in some planthoppers[54], fecundity in *P. maidis* is not affected by repeated matings, i.e., only a single mating is required per female[55]. *D. maidis* females mate only once[56]. Every 3 or every 4 days, females were transferred to a new corn seedling in the 4–6 leaf stage. To facilitate egg counting, seedlings on which the females had oviposited were kept in the greenhouse for 3 additional days, placed in boiling water for 5–7 min, submerged in 95% ethanol for 3 days (to remove chlorophyll) and placed in acid fuchsin for 24 hours[57]. The use of acid fuchsin was discontinued, as it was not necessary to visualize eggs. Greenhouse conditions during the experiment averaged 25 °C and 70% R.H.. Natural daylength was supplemented with 16 alternating cool-white and Gro-Lux fluorescent tubes. These were placed 0.5 m above the cages and turned on from 06.00 until 18.00 h.

Treatment effects on weight (15 days after being on healthy or diseased plants), longevity (days), total number of eggs, and eggs per day (EPD = total eggs/longevity) were estimated in ANOVA's which had treatment and replicate as main effects and longevity as a covariate for total eggs and EPD. For weekly fecundity, a repeated measures split-plot ANOVA was run with treatment, treatment nested within replicate, week and treatment x week as sources of variation. Treatment differences for each week were tested by t-tests where the treatment by week interaction was significant and by Bonferroni's methods where the interaction was not significant.

Amino acid and pH experiment

To obtain CSS-infected corn plants, infective *D. maidis* were placed on corn seedlings (*Zea mays* (L.) cv. Aristogold Bantam Evergreen) at the 2–4 leaf stage for a 7 day inoculation period. Immediately after inoculation, plants were shipped from the University of Maryland to Washington State University in Pullman, where the experiments were conducted. Corn seedlings of the same cultivar had been planted in Pullman within the same week as the plants that were shipped from Maryland and were used as healthy controls. In Pullman, plants were planted in 20 cm pots using equal volumes of vermiculite, perlite, and potting soil, and placed in a temperature-controlled greenhouse with the following settings: 30 °C max and 28 °C min during the day; 30 °C max and 26 °C min during the night. All plants were fertilized using 500 ppm N-P-K once a week. Plants grew under natural photoperiod.

One month after plant inoculation, phloem exudates were collected. At this point, plants were starting to show striping of leaves, a characteristic CSS symptom. Small colonies (ca. 50) of the bird cherry-oat aphid (*Rhopalosiphum padi*) were placed on the abaxial side of the third flag leaf of healthy and CSS-infected corn plants. Insects were allowed to remain on leaves until the following day, when their stylets were cut by radiofrequency microcautery[58]. Exudate was allowed to air-dry on the leaf surface (reaching approximately 75% dry matter under our growth conditions; estimated by drying samples in the oven) on 3 dates. The accumulated exudate was collected by dissolving it in a few μl of distilled water and stored at −80 °C until analysis. If the phloem on a specific plant stopped exuding, a new aphid colony was placed on the same leaf and the stylets were cut. Fisher and Macnicol[59] have shown that incubation of phloem exudates for extended periods of time at room temperature does not affect amino acid composition. In addition, Fisher et al.[60] have shown that the protein content of exudate left to semi-dry on the plant is unaffected.

Phloem analysis was done following the methodology of Kuo-Sell[61], with one modification (i.e., CSS removal). Briefly, phloem samples were freeze dried, taken up in 2 ml 0.7% NaCl solution and centrifuged for 2 h at

2500 rpm in a Centrisart I micro tube (Sartorius SH 13229, GmbH, Göttingen, Germany). The Centrisart micro tube contains a 5000-dalton membrane used to remove CSS. Removal of the spiroplasma was done to prevent clogging of the column in the amino acid analyzer. Twenty nmol of norleucine were added as an internal standard to one ml of the phloem sample and frozen at −25 °C followed by freeze drying and the addition of 100 µl of lithium citrate buffer (pH 2.2). The total volume was then injected in an automatic amino acid analyzer. Exudate pH measurements were made with a small glass combination pH electrode (Microelectrodes, Inc., Londonberry, New Hampshire, USA) capable of making measurements in volumes down to about 3 µl. Phloem exudate (for amino acid and pH analyses) was collected on 3 different dates using 4 replicates per date for CSS-infected plants and 3 replicates per date for healthy plants. Data were analyzed as a repeated measures completely randomized design. ANOVA[62] on each amino acid and on pH was conducted using the following sources of variation: treatment, treatment nested within replicate, date, and treatment x date.

Results

Linear regressions were fit for each treatment and species for the effects of weight on longevity, total number of eggs and EPD. The only significant ($p < 0.05$) regression slope was for weight effects on EPD for *D. maidis* in diseased plants. We examined the data closely and found an individual that weighed only 0.9 mg and laid 107 eggs but lived 44 days (EPD = 2.4). When this individual was deleted from the analysis the initial weight was no longer related ($p > 0.10$) to EPD. This individual was therefore considered an outlier and left out from further analysis.

Dalbulus maidis that fed on diseased plant had an average weight of 1.36 mg and those that fed on healthy plants weighted 1.48 mg, a non-significant difference ($F = 2.77$, $df = 1,10$, $p = 0.13$). For *P. maidis*, insects that fed on diseased plants weighted significantly less (table 1) than those that fed on healthy plants ($F = 35.35$, $df = 1,10$, $p < 0.01$). Longevity (days) was not affected by replicate or treatment in *D. maidis* (table 1; replicate: $F = 1,10$, $df = 11,10$, $p = 0.45$; treatment: $F = 1.03$, $df = 1,10$, $p = .33$) or in *P. maidis* (table 1; replicate: $F = 1.30$, $df = 11,11$, $p = 0.34$; treatment: $F = 0.01$, $df = 1,11$, $p = 0.92$).

Table 1. Means (± SE) for weight (mg), longevity (days), eggs per day (EPD), weekly fecundity, and total number of eggs for *Dalbulus maidis* and *Peregrinus maidis* that had fed for 15 days on healthy or CSS-infected corn plants.

	Dalbulus maidis (vector)		
	Healthy	Diseased	p-value
Weight	1.36 ± 0.07	1.48 ± 0.06	> 0.10
Longevity	42.3 ± 3.9	37.3 ± 3.2	> 0.10
EPD	13.4 ± 0.8	12.2 ± 1.1	> 0.10
Weekly fecundity	99.3 ± 5.8	93.8 ± 6.8	> 0.10
Total # eggs	588 ± 67	477 ± 72	> 0.10
	Peregrinus maidis (non-vector)		
	Healthy	Diseased	p-value
Weight	2.52 ± 0.1	2.00 ± 0.1	< 0.01
Longevity	25.8 ± 2.6	24.8 ± 2.3	> 0.10
EPD	6.3 ± 0.8	8.9 ± 1.3	< 0.05
Weekly fecundity	55.9 ± 6.0	75.6 ± 9.1	> 0.10
Total # eggs	177 ± 32	239 ± 46	= 0.05

EPD was examined in a model which included replicate, treatment, and the linear effect of longevity. None of the three soures of variation had a significant effect on *D. maidis* EPD (replicate: $F = 0.64$, $df = 11,9$, $p = 0.76$; treatment: $F = 0.21$, $df = 1,9$, $p = 0.66$; longevity: $F = 3.87$, $df = 1,10$, $p = 0.08$). For *P. maidis* both treatment and longevity had a significant effect (treatment: $F = 5.48$, $df = 1,10$, $p = 0.04$; longevity: $F = 6.44$, $df = 1,10$, $p = 0.03$), but replicate did not ($F = 1.27$, $df = 11,10$, $p = 0.36$).

For weekly oviposition, treatment had no effect on *D. maidis* (table 2). Comparisons within treatments for each week were made with Bonferroni's method[63] but no significant differences were found. For *P. maidis* there was a significant ($p = 0.02$) treatment by week interaction (table 2). Comparisons of treatments within each week were made by t-tests of least-squares means and in weeks 1 and 2 the insects that had fed on the

Table 2. Repeated measures split plot analysis of variance for weekly number of eggs laid by *Dalbulus maidis* or *Peregrinus maidis* that had fed for 15 days on healthy or CSS-infected corn plants.

	Dalbulus maidis			*Peregrinus maidis*		
SOV	df	MS	p	df	MS	p
Treatment	1	11459	0.15	1	1329	0.52
Rep (trt)[1]	22	5165		22	3070	
Week	7	22958	< 0.01	4	21932	< 0.01
Trt × week	6	1149	0.24	3	2111	0.02
Residual[2]	96	849		45	571	

[1]Error term for treatment effects.
[2]Error term for week and trt × week effects.

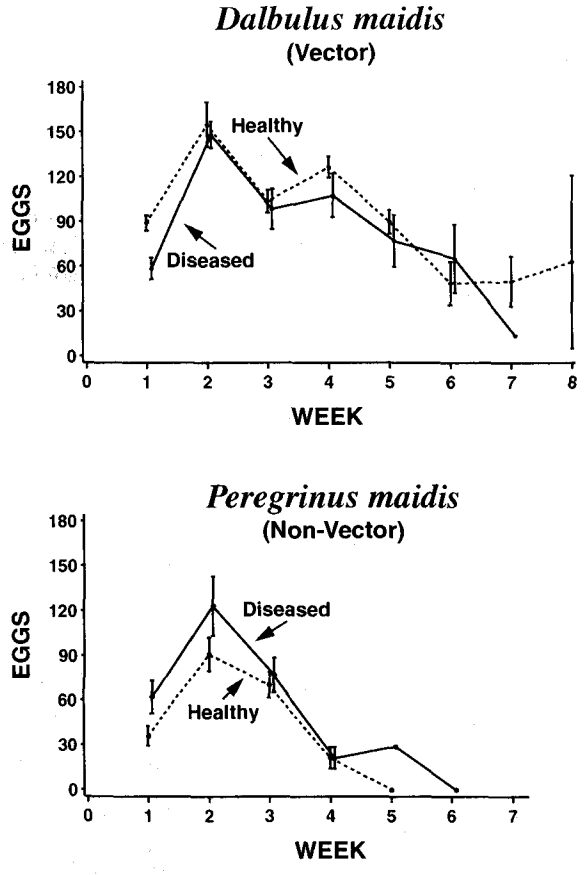

Figure 1. *Dalbulus maidis* and *Peregrinus maidis* weekly fecundity (± SE) after feeding on healthy or diseased corn plants for 15 days. Insects were moved to healthy corn seedlings after the 15 days of feeding.

diseased plants laid more eggs than the insects that had fed on healthy plants (fig. 1).

Weekly number of eggs was analyzed by linear regression starting on the second week, when egg laying had reached its peak. Comparisons (by t-test at $p < 0.05$) showed that in *D. maidis* the regression lines were parallel (i.e., the slopes were not different). The average number of eggs laid weekly by *D. maidis* declined at a similar rate (≈ 19 eggs per week) for both treatments. The rate of egg decline of *P. maidis* eggs was faster ($p < 0.05$) for insects that had fed on diseased plants (≈ 45 eggs per week) than that for insects that fed on healthy plants (≈ 34 eggs per week).

Total number of eggs was evaluated in each species in a model which included replicate, treatment, and the linear effect of longevity. For *D. maidis*, replicate or treatment did not have a significant effect on total number of eggs (table 1; replicate: $F = 0.91$, $df = 11,9$, $p = 0.57$; treatment: $F = 0.61$, $df = 1,9$, $p = 0.45$), but longevity did ($F = 30.68$, $df = 1,9$, $p < 0.01$), with insects that lived longer laying more eggs. Longevity had a partial regression coefficient of 15.7 eggs per day of survival. Longevity was run within treatment and found to be the same between treatments (t-test of regression coefficients). For *P. maidis*, the total number of eggs was not affected by replicate ($F = 1.38$, $df = 11,10$, $p = 0.31$) but was affected (at the $\alpha = 0.06$ level) by treatment (table 1; $F = 4.74$, $df = 1,10$, $p = 0.0544$) and longevity ($F = 19.41$, $df = 1,10$, $p < 0.01$). Each additional day of survival was associated with an additional 12.60 eggs ($p < 0.01$ by partial regression analysis). The regression coefficients were found to be the same.

Amino acid and pH results

Thirty seven amino acids were detected in the phloem of both healthy and diseased corn plants (table 3). Diseased plants had significantly higher levels ($p < 0.05$) of T-aminobutyric acid, tryptophan and unknown amino acid #1, but significantly lower levels ($p < 0.05$) of glycine, glutamic acid, ammonia, arginine and unknown amino acids #5 and #6 (table 3). Unknown amino acids #1, #3, #4, and #5 have been reported in oats[61]. Retention time data suggest that unknown amino acid #1 and #3 are probably cysteine and α-aminopimelic acid, respectively, but confirmation requires further identification.

Table 3. Amino acid concentrations (nmol mg^{-1} exudate dry wt; mean ± SE) of CSS-infected and healthy corn plant phloem averaged over 3 dates.

Amino acid	CSS-infected[1]	Healthy
Phosphoserine	0.194 ± 0.026	0.104 ± 0.065
Phosphoethanolamine	1.29 ± 0.12	0.68 ± 0.36
Aspartic acid	0.016 ± 0.016	0.45 ± 0.39
Serine	15 ± 3	20.8 ± 4.3
Asparagine	2.5 ± 2.5	n.d.
Glutamic acid	27.3 ± 4.5*	52.5 ± 9.9
Glutamine	11.7 ± 3.9	7.1 ± 1.3
α-aminoadipic acid	1.6 ± 1.5	0.19 ± 0.14
Glycine	1.40 ± 0.18*	3.85 ± 0.82
Alanine	25.9 ± 3.6	36.6 ± 4.8
α-aminobutyric acid	0.200 ± 0.071	0.029 ± 0.023
Valine	5.2 ± 1.1	3.1 ± 1.1
Cysteine	0.189 ± 0.090	0.044 ± 0.034
Methionine	1.00 ± 0.23	0.207 ± 0.096
Cystathionine	0.29 ± 0.016	n.d.
Isoleucine	2.85 ± 0.57	2.22 ± 0.65
Leucine	2.14 ± 0.47	1.62 ± 0.56
Tyrosine	7.3 ± 1.2	5.8 ± 1.6
Phenylalanine	2.60 ± 0.44	3.0 ± 1.1
β-alanine	0.576 ± 0.090	0.30 ± 0.17
τ-aminobutyric acid	1.47 ± 0.45*	0.058 ± 0.031
Ethanolamine	0.0058 ± 0.0043	n.d.
Ammonia	0.476 ± 0.086**	2.81 ± 0.81
Tryptophan	1.46 ± 0.30**	0.26 ± 0.17
Ornithine	4.11 ± 0.63	1.64 ± 0.27
Lysine	5.83 ± 0.83	6.8 ± 1.9
Histidine	0.94 ± 0.17	0.64 ± 0.30
Arginine	0.72 ± 0.46**	7.8 ± 2.1
Glucosamic acid	0.198 ± 0.035	0.064 ± 0.036
Unknown 1	4.28 ± 0.52*	1.25 ± 0.46
Unknown 3	2.24 ± 0.27	2.66 ± 0.39
Unknown 4	2.80 ± 0.42	1.25 ± 0.43
Unknown 5	0.99 ± 0.26*	4.5 ± 1.8
Unknown 6	0.126 ± 0.080*	7.2 ± 1.9
Unknown 7	1.66 ± 0.47	0.46 ± 0.40
Unknown 8	0.128 ± 0.016	0.090 ± 0.069
Unknown 9	n.d.	0.45 ± 0.22

[1]Significant treatment effect at the $p < 0.05$ level (*) or at the $p < 0.01$ level (**).

Table 4. Mean pH of corn phloem sampled on 3 different dates; pH's within a treatment followed by the same letter are not significantly different ($p = 0.05$).

Date	pH Healthy	Diseased
9/13	7.51a	7.62a
9/16	7.60a	7.13b
9/18	7.38a	6.89b

The peaks for unknown #1, unknown #9, and aminoadipic acid were very close to each other and in many cases appeared together. A similar situation was found for peaks for aspartic acid, unknown #5, unknown #6, and unknown #7. Asparagine, cystathionine, and ethanolamine were not detected in healthy plants, and were present at very low levels in diseased plants. The only amino acid on which date of sampling had a significant effect was α-aminoadipic acid. Using a microscope, CSS was observed in phloem exudates collected by the stylet cutting technique and in samples obtained by cutting the stem with a razor blade, indicating that the plant was infected with the pathogen. An interesting observation was the consistent and striking ease of phloem exudate collection when a razor blade was used on infected versus healthy plants. A similar phenomenon involving an impairment of the sieve tube sealing mechanism has been reported with trees infected with a mycoplasmalike organism[64].

There was a significant date effect for pH in diseased plants ($p < 0.05$), with pH of phloem at the second and third sampling date being significantly lower than that of the first date (table 4).

Discussion

To date, the results of experiments on the effects of plant pathogens on non-vector insects have been perplexing but intriguing. For example, Boiteau and Singh[36] reported that the non-vector insect *Leptinotarsa decemlineata* (Say) preferred virus infected potato leaves, but its fecundity and longevity on infected leaves were lower than on healthy leaves. Similarly, Kunkel[33] reported that insects collected on aster yellows-infected plants survived on healthy plants but did not reproduce. Maramorosch[34] and Purcell[37] have reported on the expansion of host plant range in *Dalbulus maidis* after feeding on aster plants infected with the aster yellows mycoplasmalike organism, a plant pathogen not transmitted by the leafhopper. A possible explanation for the complexity of the interactions between plant pathogens and non-vector insects may be that while pathogens may not have cytopathological effects on, nor survive in non-vector insects, changes in the non-vector insect may result from changes induced in the diseased host plant. In most studies to date it has not been possible to unambiguously demonstrate and differentiate between direct and indirect effects of pathogens. In contast, as CSS can not be detected in the non-vector *P. maidis*[65], any effect of feeding on infected plants can be ascribed on pathogen induced changes in the chemistry of the plant, i.e. an indirect effect.

Our results suggest that feeding on CSS-infected plants has a beneficial effect for the non-vector in terms of increased fecundity. To assess whether these results could be related to changes in plant chemistry, we analyzed the phloem of healthy and CSS-infected corn plants for amino acid and pH levels. Phloem analysis should provide insights into causal mechanisms for the observed changes in insects. This is the first study in which phloem amino acid and pH levels of healthy and diseased plants of any kind are compared.

Of thirty seven amino acids detected in the phloem of healthy and diseased corn plants, tryptophan, considered to be essential for insects[66] was detected at significantly higher levels in CSS-infected plants, while glycine, also considered an essential amino acid, was detected at higher levels in healthy plants. Not much is known about the nutritional requirements of leafhoppers and planthoppers[67,68]. However, the reduced fecundity of non-vector insects on healthy corn plants could be due to the presence of amino acids that inhibit oviposition. Koyama and Mitsuhashi[69] determined that arginine, glutamic acid, tyrosine, and valine acted as oviposition inhibitors in the planthopper *Laodelphax striatellus* Fallén. Of these amino acids, arginine and glutamic acid were detected at significantly higher concentration in healthy corn plants. Therefore, it is possible that the lower fecundity of non-vector insects in healthy plants was due to a long term effect after having been exposed (for 15 days as immatures) to increased levels of amino acids that may act as oviposition inhibitors. The lack of significant differences in *D. maidis* fecundity suggests that these insects have a different nutritional requirement when compared to the non-vector insect.

The lower weight of the non-vector insect after feeding for 15 days on CSS-infected corn plants could be due to a lower nutritional quality of the CSS-infected plants (which is supported by the phloem amino acid analysis) and to a possible reduction in feeding due to the decrease in pH as the disease progressed (table 4). Some studies suggest that pH changes can be detected by insects[70,71], with consequent alterations in their behavior. For example, the tobacco whitefly (*Bemisia tabaci*) differentiates between pH differences of 0.25 (ref. 70); the highest pH difference between healthy and diseased corn plants in our experiment was 0.49 (on the third sampling date). Similarly, the potato aphid (*Macrosiphum euphorbiae* [Thomas]) was shown to prefer slightly acidic diets over neutral or weakly alkaline ones[71]. The low pH measured on the last date in CSS-infected corn plants is unusually low for phloem exudate, when compared to that of other species[72]. This increased phloem

acidity is in agreement with results in which CSS was grown in artificial media[73,74]. Liao and Chen[73] found that media in which CSS is growing becomes acidic, requiring the addition of a buffer. Unlike other mollicutes, CSS apparently lacks mechanisms with which to buffer acidic environments under natural conditions[74].

Malogolowkin-Cohen and Rodrigues-Pereira[75] have shown that in some *Drosophila* interactions with another mollicute, the male-lethal spiroplasma, infection can reduce the age at which females are receptive to mating, while Ebbert[76] has shown that infection improves early reproduction. The lack of detection of CSS in *P. maidis* using DNA probes[65] after different periods of exposure to CSS-infected plants suggests that CSS does not improve early reproduction nor reduces the age for female receptivity to mating.

Madden and Nault[29] and Madden et al.[30] have also reported no significant differences in survival or fecundity in *D. maidis* due to CSS-infection, although the effect of the pathogen varied with the *Dalbulus* species studied. For example, survival and fecundity in *D. gelbus* and *D. elimatus* were reduced due to CSS infection while infection with another mollicute transmitted by *D. maidis*, the maize bushy stunt mycoplasmalike organism, reduced survival and fecundity in *D. maidis* but not in *D. elimatus*[30]. It can be argued that competition for a nutrient source (i.e., the phloem) works in two different ways when the plant is infected with CSS.

For congeners of *D. maidis*, feeding on CSS-infected plants can reduce fecundity and longevity; therefore, we can speculate that transmission of CSS by *D. maidis* serves as a strategy to exclude possible competitors by plant chemistry manipulation via the pathogen (indirect effects). This strategy does not work against *P. maidis*, an insect that feeds on the phloem and uses corn as one of its many host plants.

Our results indicate that even though an insect might not transmit a specific pathogen, feeding on the infected plant could have important consequences on its biology and thus significant implications to its ecology. This is particularly noteworthy given that for many plants, especially agricultural plants, the proportion of non-vector species associated with the crop far exceeds that of vector species. Yet the effects on co-inhibiting non-vector herbivores, induced by vectors, may be dramatic. Thus, the role of plant pathogens in the biology and ecology of non-vector insects should receive more attention.

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