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Plant responses to insect herbivore damage are modulated by phosphorus nutrition

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Abstract

Interactions between plants and their herbivores are often multidimensional, complicating interpretation of herbivore-impact studies. A previous study, directed toward understanding variation in incidences of flower bud abscission among cotton plants attacked by *Lygus* plant bugs, revealed an unanticipated correlation between levels of phosphorus nutrition and the propensity of plants to abscise developing flower buds. Here, we further investigate the relationship between phosphorus nutrition and cotton [*Gossypium hirsutum* Tod. (Malvaceae)] plant responses to herbivory by tarnished plant bugs, *Lygus hesperus* Knight (Hemiptera: Miridae). Complementary experimental approaches and survey data both suggest that levels of phosphorus nutrition falling within the normal range of variation can influence the manner by which plants respond to herbivory. In particular, higher levels of phosphorus nutrition resulted in elevated bud abscission rates when buds were damaged. Interestingly, increased levels of abscission under high-phosphorus regimes did not translate into a decrease in overall cotton lint yield, suggesting that the 'phosphorus effect' may ultimately reflect how environmentally contingent differences in the allocation of vegetative vs. reproductive investments can provide parallel pathways to equal yields.

Introduction

The responses of plants to insect herbivory can be variable and context dependent, resulting in patterns that are hard to predict or even to understand, and complicating the interpretation of herbivore-impact studies (Baldwin & Preston, 1999). Plant responses to insect damage range from the production of toxic secondary chemicals (Wink, 1988) to cellular suicide or selective abscission of damaged parts (Marquis, 1992) to the release of volatiles that recruit predators and parasitoids of the offending herbivores (Turlings & Wäckers, 2004). Complicating matters further are variations in environmental circumstance that can vary the expression and intensity of defenses (Julkunen-Tiitto et al., 1993; Sivola & Ahlholm, 1993). Determining whether a plant is resistant to, tolerant of, or susceptible to herbivory is therefore not a straightforward affair.

An ecologically pertinent (and economically relevant) example of the non-linear relationship between herbivory and plant responses involves the relationship between plant bugs in the genus *Lygus* (Hemiptera: Miridae) and commercially grown cotton [*Gossypium* spp. (Malvaceae)] in North America. The species *Lygus hesperus* Knight feeds on virtually all parts of the cotton plant (Wheeler, 2001; Rosenheim et al., 2004), but its primary economic importance stems from the extensive damage it causes to the developing flower buds, or 'squares', which, if left unmolested, develop into the fruits that harbor the valuable cotton lint (Leigh et al., 1988; Leigh & Goodell, 1996). Abscission of buds by plants in response to *L. hesperus* feeding damage is common and can result in severe yield declines when *L. hesperus* densities are high (Ellsworth, 2000; Ellsworth & Barkley, 2001, 2003). However, when herbivory is not so extreme, cotton may be able to compensate by producing additional buds after early-season bud loss because of *Lygus* feeding damage (Gutierrez et al., 1977; Wilson et al., 2003). The definitive relationship between *Lygus* herbivory and end of season reproductive success for plants is therefore unknown. Empirical and theoretical attempts to more fully explain the relationship between cotton and *Lygus* have produced a range of results, variously describing an herbivore-sensitive system

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(Scott et al., 1986), an herbivore-insensitive system (Wilson et al., 2003), or, more frequently, ambiguity and/or context dependence (Falcon et al., 1971; Sevacherian & Stern, 1972; Gutierrez et al., 1977; Kerby & Buxton, 1981; Kerby & Hake, 1996; Musser et al., 2009). Ambiguity is particularly troublesome from an applied perspective because the result can be a bet-hedging strategy of pesticide over-application.

Not only has the relationship between *Lygus* and yield proven to be ambiguous, but the relationship between *Lygus* and flower bud abscission (i.e., the short-term expression of damage) remains unclear. Farmers and consultants have noted a disconnect between bug densities and bud shed; a previous study suggested that this variation was not because of variable insect behavior, but rather because of variable plant behavior (Rosenheim et al., 2006). In particular, the study showed an unexpected correlation between bud shed and P-nutrition: elevated phosphate (PO_4) levels in petiole samples were strongly correlated with a propensity for upland cotton (*Gossypium hirsutum* Tod.) to abscise buds. There was both a 'main effect' of phosphorus nutrition (i.e., higher levels of PO_4 were associated with greater rates of abscission, regardless of *Lygus* densities), as well as an interaction between phosphate and *Lygus* (i.e., PO_4 appeared to 'sensitize' the plant to *Lygus* herbivory). These findings were unexpected, as no previous literature suggests a role for phosphorus in cotton bud abscission. Cotton is not typically fertilized with phosphorus (Weir et al., 1996), but may experience elevated levels when planted after vegetables that routinely receive P fertilization (R Hutmacher, pers. comm.; Crozier et al., 2004). High levels of soil phosphorus are also known to increase both vegetative production and yield, up to a point (Crozier et al., 2004; but see Booker et al., 2007); though, how this relationship may interact with herbivore pressure is unknown.

Studies in other plant systems provide implicit corroboration for phosphorus as an abscission-inducing agent. Phosphorus used as a buffer in a standard growth medium was unexpectedly found to accelerate abscission of leaves and fruit of olive explants (Banno et al., 1993), a relationship confirmed by a number of later studies (Burnik-Tiefengraber et al., 1994; Yamada & Martin, 1994; Goren et al., 1998; Burns et al., 2008). Phosphorus has since been implicated in leaf and fruit abscission of a broad range of plant species, including apples, plums, cherries, oaks, poplars, grapes, and a variety of citrus (Banno et al., 1993; Goren et al., 1998).

To follow up on the unexpected relationship found by Rosenheim et al. (2006) between phosphorus, *L. hesperus*, and cotton bud abscission, we paired experimental studies with an analysis of data collected by agricultural consultants working in California cotton fields. Our focus was on determining whether the correlation between petiole-P and abscission in response to herbivory reflected a direct, causal link. We also attempted to provide further insight into the broader role of phosphorus in the life history and compensatory ability of plants.

Materials and methods

Experiment I

Our first experiment was designed to simulate the interaction between phosphorus nutrition, cotton, and *L. hesperus* under controlled conditions. In a greenhouse on the University of California, Davis campus (CA, USA), we planted insecticide-free seed of upland cotton, *G. hirsutum* (Acala cv. Phytogen 725) in 140 10-cm-tall ×10-cm-diameter pots filled with coarse sand. Pots were held in plastic drip trays, two pots in each tray, and were surface irrigated each morning with enough water to soak the sand and partially fill the drip tray. Once seeds had germinated and cotyledon leaves had unfurled, seedlings were thinned to two per pot and a nutrient fertilization regime was initiated. Trays were randomly assigned to one of two fertilization treatments ('low P' and 'high P'), and treatments were applied every other day (100 ml per pot). Phosphate treatments were established using aliquots of phosphoric acid (low P = 50 p.p.m., high P = 90 p.p.m.) in a modified phosphorus-free Hoagland solution (Hoagland & Snyder, 1933). A pilot experiment performed to test the efficacy of phosphorus treatments on manipulation of plant phosphorus demonstrated that these treatments resulted in plant petiole phosphate concentrations relevant to those found in cotton sampled from commercial fields in California.

Cotton plants were thinned a second time at the 4–5 node stage to one plant per pot. At the 6–8 node stage, plants were enclosed in Super-Aire fiber mesh sleeves (Maryland Plants and Supplies, Baltimore, MD, USA). When all plants had reached the 8–9 node stage and had begun to produce buds, two adult female *L. hesperus* collected from alfalfa fields in El Macero, CA, were added to one bagged plant from each tray to establish a '+herbivory' treatment; the second plant in each tray was maintained without herbivores ('–herbivory' treatment). Plants were watered and fertilized as before for 10 days after *L. hesperus* introduction. After 10 days of exposure to *L. hesperus*, sleeves were removed and bugs were noted as being alive or dead. Developing buds were scored as 'abscised' or 'not abscised' and were dissected to determine the percentage of developing anther sacs that had been damaged by *L. hesperus* [damage is easily measured; individual anther sacs turn from white (undamaged) to black (damaged) shortly after *L. hesperus* feeding occurs]. Height and the numbers of fruiting, vegetative, and total nodes were measured for each plant, and a random subset of petioles from plants in each treatment was sent to the University of California Agriculture and Natural Resources Analytical Laboratory (Davis) for 2% acetic acid analysis of extractable phosphate and nitrogen. Data were analyzed using two-way analysis of variance (ANOVA). Data collected as percentages were √x-transformed to approximate a normal distribution.

Experiment II

A second experiment was also performed, designed to directly assess how phosphorus mediates cotton plant responses to damage to developing buds, i.e., removing variation caused by differences in *L. hesperus* feeding from the experiment. For this experiment, 200 cotton plants were grown under high and low phosphorus nutrition as in the first experiment, but plants were not enclosed in bags and were not subjected to *L. hesperus* herbivory. The first, second, and third buds to develop on each plant were damaged by puncturing the apical half of each bud, where the developing male structures are found, with a 0.1-mm-diameter minuten insect pin (Fine Science Tools, Foster City, CA, USA) once buds reached 5 mm in size. Buds of one plant in each tray were punctured three times, and buds of the second plant were punctured six times. Dissections of punctured buds revealed that each puncture resulted in damage to 1–2 anther sacs. Punctured buds were checked each day until they abscised or they reached 15 mm in size, at which point the latter group was scored as ‘not abscised.’ The fourth bud to develop on each plant was left unpunctured but also monitored and scored for abscission. Data were analyzed using two-way ANOVA. In contrast to experiment I, where there was variation in both the number of buds per plant and the number of buds damaged (by *L. hesperus*), in experiment II just three buds were damaged per plant (by the investigators). Results for bud abscission in experiment II were therefore expressed as number of buds abscised (out of three), allowing for a direct, empirical assessment of the influence of phosphorus fertilization on abscission of damaged buds.

Survey data

We paired our experimental data with a survey dataset, i.e., records of various kinds collected from cooperating farmers, agronomy consultants, and pest management consultants working in cotton fields [both upland cotton (*G. hirsutum*) and Pima cotton (*Gossypium barbadense* L.)] in California’s San Joaquin Valley. For many fields, data covered several years, spanning plantings of both cotton and other crops. Data categories included:

1. *L. hesperus* densities; weekly counts of *L. hesperus* densities, reported as means from multiple sweeps with an insect net in several locations in a single field on a single day (usually three sweeps in each of four locations per field). These data were available for 426 fields of upland cotton [some fields were planted with cotton multiple years (1–6 years), bringing the total number of data points to 869] and 321 fields of Pima cotton (total from 1–9 years: 626). Data collection usually began in late May or early June and ended in August.
2. Bud (‘square’) retention; weekly scores of retention of the first position buds on the top five fruiting branches on field-grown cotton (256 upland fields, 135 Pima fields).
3. Cotton phosphorus levels; phosphate (PO_4-P), in parts per million (p.p.m.), measured from petiole samples (25 upland fields, 41 Pima fields).
4. Cotton yield; end of year cotton lint yield, measured in kg ha^{-1}. We also calculated a ‘deviation from expected,’ determined using historical yields from each field and growing season so that we could correct for variation in soil quality, climate, and management practices that influence yields. Both metrics were available for most of the fields and years for which *L. hesperus* sweeps were collected.
5. Rotational histories of the fields; cotton in California is not routinely fertilized with phosphorus, so field to field variation in phosphate levels may be dependent on the rotational history of the field. The previous 1–10 years of crop-planting histories were recorded for focal fields (776 upland fields, 488 Pima fields). Crops from the previous year were grouped into categories based on their standard phosphorus fertilization regimes as reported by the University of California Agriculture and Natural Resources catalog (low-P crops: alfalfa, barley, maize, cotton, hay, oats, wheat; high-P crops: bean, beet, broccoli, cabbage, carrots, garlic, lettuce, melon, onions, potato, tomato, and turnip).

Statistical analyses of these data were simple but robust. To account for lags between *L. hesperus* damage and any consequent abscission, *L. hesperus* counts averaged over each 2-week period were regressed against bud retention percentages over the 2-week period immediately subsequent. The residuals from this regression were then used to perform a second simple regression against measurements of petiole phosphorus. This rubric assesses the relationship between petiole phosphate concentrations and deviation from a ‘normal’ relationship between *L. hesperus* and bud retention. These calculations were performed for each 2-week period across the growing period.

Results

Experiment I

Plants in the 'high-P' treatment had higher post-experiment levels of petiole PO_4-P than plants in the 'low' treatment (Table 1; low P: mean ± SE = 1 450.0 ± 75.9 p.p.m.; high P = 2 083.9 ± 70.3 p.p.m.; ANOVA: $F_{1,138} = 20.7$, P<0.0001), demonstrating that establishment of treatment differences was successful. These values also reflect representative petiole phosphate values measured in California agricultural cotton (1 982.3 ± 566.4 p.p.m.; range from fields in database: 750–3 035 p.p.m.). There was no significant difference between treatments in post-experiment petiole nitrogen or potassium (ANOVA: N: $F_{1,138} = 1.2$, P = 0.29; K: $F_{1,138} = 3.5$, P = 0.074).

Phosphorus treatments influenced the growth and reproductive investment of experimental cotton plants (Table 1). Compared with plants in the 'low-P' treatment, 'high-P' treatment plants were taller (high P = 27.42 ± 0.53 cm, low P = 24.04 ± 0.55 cm; ANOVA: $F_{1,138} = 19.4$, P<0.0001), had significantly more fruiting nodes (high P = 4.68 ± 0.17, low P = 3.99 ± 0.18; ANOVA: $F_{1,138} = 8.6$, P = 0.004), had significantly fewer vegetative nodes (high P = 1.36 ± 0.14, low P = 2.01 ± 0.14; ANOVA: $F_{1,138} = 10.4$, P = 0.002), and had significantly more total bud positions (high P = 6.30 ± 0.30, low P = 4.69 ± 0.31; ANOVA: $F_{1,138} = 15.0$, P<0.0001).

There was no difference in the total percentage bud abscission between treatments when *L. hesperus* were present (high P = 20.0 ± 4.2%, low P = 20.7 ± 4.4%; ANOVA: $F_{1,138} = 0.01$, P = 0.91), and the percentage of anther sacs damaged by *Lygus* was significantly higher in 'low-P' treatments (low P = 83.4 ± 5.4%; high P = 68.8 ± 4.7%; ANOVA: $F_{1,138} = 4.2$, P = 0.045). Among those buds that actually sustained *L. hesperus* feeding damage, significantly more *Lygus*-damaged buds abscised in the 'high-P' treatment (46 of 55 buds, or 83.6%) than in the 'low-P' treatment (27 of 41, or 65.9%; two-tailed $\chi^2 = 4.08$, d.f. = 1, P = 0.044). Among buds with 20% or greater damage to anther sacs, the correlation with phosphorus treatment was even more pronounced, with 32 of 33 (97%) of damaged buds abscising in the 'high-P' treatment compared to just 27 of 39 (69%) of damaged buds abscising in the 'low-P' treatment (two-tailed $\chi^2 = 9.30$, d.f. = 1, P = 0.0023). We note that these last results, although indirectly supportive of our hypothesis, are comparative and not experimental; the design of experiment I did not explicitly vary both phosphorus concentrations and damage to a set number of individual buds (but see experiment II).

Experiment II

Experiment II allowed for direct assessment of the question: how does variation in phosphorus nutrition influence the abscission of a predetermined number of damaged buds? In the 3-puncture treatment (three buds, punctured 3× each), 'high-P' plants were significantly more likely to abscise damaged buds than 'low-P' plants (2.85 ± 0.05 vs. 2.27 ± 0.11 abscised buds per plant; two-way ANOVA: $F_{1,92} = 22.9$, P<0.0001). The same was true in the 6-puncture treatment ('high P' = 2.88 ± 0.06 vs. 'low P' = 2.51 ± 0.09 abscised buds per plant; two-way ANOVA: $F_{1,95} = 11.2$, P = 0.0012). Non-punctured fourth buds were retained on 100% of plants in both nutrient treatments.

Survey data

Although the focus of previous work and of the experimental sections of our study were on upland cotton (*G. hirsutum*), the dataset contained too few upland cotton fields (n = 2) that had both measurements of bud retention and petiole phosphate. Instead, we analyzed the relationship between PO_4-P and retention in Pima cotton (*G. barbadense*) fields (n = 41). For two consecutive mid-season periods, higher levels of petiole phosphate in Pima cotton were significantly associated with higher than expected levels of 'top-5' bud abscission after standardizing for *L. hesperus* herbivory pressure (1–15 July: $F_{1,38} = 34.3$, $r^2 = 0.47$, P<0.0001; 16–30 July: $F_{1,39} = 10.1$, $r^2 = 0.21$, P = 0.0029). Early- and late-season periods did not show significant patterns (Table 2). Despite the relationship between phosphate content and mid-season abscission in response to herbivory, there was no significant correlation between petiole phosphate and the degree to which final crop yield deviated from historical average yield for that field ($r^2<0.01$, P = 0.83; n = 32).

Table 1 Differences in mean (± SE) plant production measures between phosphorus treatments in Experiment I. All comparisons except for 'total nodes' were significantly different (see text for tests and P-values)

Treatment	n	Post-experimental petiole PO_4-P (p.p.m.)	Plant height (cm)	Total no. nodes	No. vegetative branches	No. fruiting branches	No. buds
Low P	35	1450.0 ± 75.9	24.04 ± 0.55	9.40 ± 0.14	2.01 ± 0.14	3.99 ± 0.18	4.69 ± 0.31
High P	35	2083.9 ± 70.3	27.42 ± 0.53	9.53 ± 0.13	1.36 ± 0.14	4.68 ± 0.17	6.30 ± 0.30

Table 2 Bivariate linear regression of petiole phosphate measurements from Pima cotton with residuals taken from regressions between *Lygus hesperus* sweep samples over a 2-week period and retention measurements the week before

Dates of *L. hesperus* sweep samples	Dates of top-5 retention measurements	n	r^2	P	Effect of higher P on bud retention
June 1–15	June 16–30	25	0.05	0.27	Negative
June 16–30	July 1–15	40	0.47	<0.0001	Negative
July 1–15	July 16–31	41	0.21	0.0029	Negative
July 16–31	August 1–15	16	0.02	0.44	Positive
August 1–15	August 16–31	16	0.03	0.51	Positive

Upland cotton planted in fields 1 year after a traditionally high-P fertilized crop had significantly higher levels of current-year petiole phosphate than cotton grown in fields after a low-P crop (mean for fields with high vs. low-P crops = 2 144.7 ± 89.7 vs. 1 823.21 ± 67.3 p.p.m.; t-test: t = 3.1, d.f. = 20.6, P = 0.0087). The same was true for Pima cotton (mean for fields with high vs. low-P crops = 2 513.4 ± 187.0 vs. 1 889.8 ± 78.8 p.p.m.; t-test: t = 3.8, d.f. = 12.1, P = 0.0037). Figure 1 shows mean PO_4 levels in cotton grown in fields 1 year after a variety of crops.

To further explore the relationship between phosphorus nutrition and yield, we performed paired comparisons of cotton yield within the same field over different years. Such paired tests control for variation stemming from between-field differences. Previous-year crop assignments (low P or high P; see description in methods) were used as working proxies for current-year phosphorus content among fields in our database. Previous-year phosphorus assignments did not significantly predict differences in yield (t-test: t = 0.38, d.f. = 68, P = 0.70; n = 69).

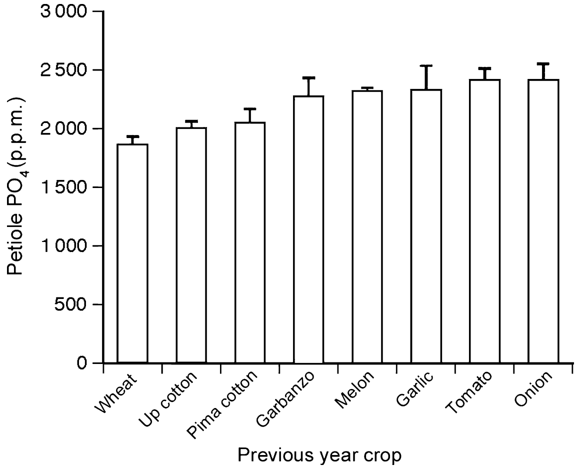

Figure 1 Relationship between crops planted in fields in the year immediately previous to upland cotton (*Gossypium hirsutum*) and the mean (+ SE) PO_4-P content of current-year cotton petioles. Wheat, upland cotton, and Pima cotton are traditionally fertilized with low levels of P or none at all. Garbanzo beans, melons, garlic, tomatoes, and onions usually have considerably higher P fertilization regimes (University of California Agriculture and Natural Resources Catalog).

Discussion

Taken together, our experimental results and analyses of farmer- and consultant-collected data suggest two conclusions: (1) higher levels of available phosphorus increase the frequency of cotton bud abscission in response to damage during pre-flowering stages of cotton plant growth, but (2) corresponding effects on cotton yield are probably minimal or non-existent, likely owing to the ability of the plant to compensate for early-season bud loss. We discuss each of these in turn.

First, high levels of phosphorus increased the likelihood that damaged buds would abscise. Experiment I demonstrated this effect indirectly (more damaged buds abscised in the high-P treatment than in the low-P treatment), but differences in *L. hesperus* feeding intensities and plant growth between the two treatments served to mask this result when treatments were compared. In the second experiment, we simplified the experimental design to allow for direct assessment of the relationship between damage to buds and subsequent abscission under different phosphorus treatments. Here, high-phosphorus plants abscised significantly more damaged buds than low-phosphorus plants. Finally, the dataset from commercial growers also showed that cotton with higher levels of petiole PO_4-P had lower levels of bud retention during the early and midseason weeks of the growing season. Together, these results support the pattern resolved by Rosenheim et al. (2006), indicating a relationship between high-phosphorus plants and greater than expected rates of bud abscission when *L. hesperus* are present.

Abscission of buds is not a passive response, but rather an active physiological process initiated by the plant. *Lygus hesperus* do not forcefully remove buds; their feeding damages anther sacs and other tissues. Abscission itself results from the formation of an abscission layer by the plant at the base of the bud, which is followed soon after by bud abscission (Shackel et al., 2005). It is also important to note that artificial damage as simulated in experiment II generates a different impact on the plant than does natural *L. hesperus* herbivory: in our experiment, damage is more dramatically mechanical (given that the minuten pin is larger than a *L. hesperus* stylet) and less enzymatic (*L. hesperus* inject a cocktail of enzymes into the plant when they feed). Nevertheless, plants responded with abscission to both varieties of injury, and both pointed to a role for phosphorus in mediating the response.

Interestingly, our study does not suggest a role for phosphorus in promoting abscission of undamaged buds, and this finding may shed further light on the underlying physiological relationship between P and abscission. In experiment II, non-damaged fourth developing buds were uniformly retained on all plants, providing a stark contrast to the 76–96% abscission among damaged first to third developing buds. This result is contrary to the suggestion from Rosenheim et al. (2006) that phosphorus is a general abscission agent in cotton and at first glance, appears to contradict the studies by Banno et al. (1993), Burnik-Tiefengraber et al. (1994), and Goren et al. (1998), in which insect herbivory was not required for abscission. However, what unites the current study with previous work is that all identify phosphorus as a mediator of abscission. Banno et al. (1993), Goren et al. (1998), and others are concerned with the role of phosphorus as a fruit loosening agent during the period in which fruit abscission is beneficial to the plant: when fruits are ripe and ready to drop. Likewise, our study identifies phosphorus as a mediator of abscission under conditions wherein fruit shed may be similarly beneficial: fruit quality has been compromised via herbivore damage, and abscission of damaged fruits will allow investment in new growth.

Our second key result is that the relatively higher rates of *L. hesperus*-related bud abscission found in high-phosphorus cotton fields did not translate into a consequent reduction in eventual lint yield. Plants with elevated levels of phosphorus exhibited higher early-season bud shed in response to *L. hesperus* damage, but those same plants also appeared to compensate for nearly all of this loss, maintaining nearly normal yields. Plants with high levels of phosphorus in experimental plantings grew larger and more productively (Table 1), and phosphorus was not associated with an economically relevant effect on yield, despite its association with abscission. Furthermore, cotton grown in fields 1 year after a high-phosphorus crop did not have significantly lower deviations from expected lint yield than cotton grown 1 year after a low-phosphorus crop.

Compensatory growth in response to damage from insect herbivory in cotton has been well described (reviewed in Wilson et al., 2003), and nutrient availability has been implicated as an important mediator (Hicks & Turkington, 2000); though, a particular role for phosphorus nutrition is generally undescribed. One exception involves cultivars of cowpea with high phosphorus requirements that tend to have higher rates of both abscission and overall yield when supplied with sufficient phosphorus fertilization (Okelana & Adedipe, 1981). One parsimonious hypothesis is that a surplus of phosphorus aids the plant in efficiently allocating photoassimilates to locations most in need. Higher levels of phosphorus allow cotton to grow faster and produce more buds, such that when herbivory occurs, abscission of damaged buds is more efficient and less costly to the plant's reproductive fitness (plants with more phosphorus have less to lose by aborting damaged buds). Cotton photosynthetic rates are known to increase following fruit or flower abscission (Holman & Oosterhuis, 1999; Wells, 2001) and fruit loss can delay senescence, allowing more time for later-produced fruits to mature (Zhao et al., 2005). We stress that these data do not suggest that P-levels have no effect on yield in cotton; manipulations of soil phosphorus have shown a linear relationship to yield that levels off as leaf P approaches 2 000 p.p.m. (Crozier et al., 2003, 2004). As most fields in our dataset fall close to or above that 2 000 p.p.m. cutoff point, the most parsimonious explanation for there being no yield effect is that adequate phosphorus exists in most California cotton fields for maximum yield to be achieved.

Another interesting result stemming from our compilation of agricultural data is the relationship between rotational history and variation in cotton phosphorus levels. Our classifications of 'low-P' and 'high-P' crops grown in fields the year immediately previous to a cotton crop significantly predicted variation in cotton petiole phosphate. Rotational history then might affect both bud abscission in response to *L. hesperus* herbivory and the ability of plants to compensate for damage. From an applied perspective then, our results imply that management decisions might place a higher premium on environmental contingency; if growers can be armed with a greater understanding of crop responses, they can tailor their management practices to their particular circumstances.

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