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Chapter 12

Water Deficit Stress - Host Plant Nutrient Accumulations and Associations with Phytophagous Arthropods

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Additional information is available at the end of the chapter

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1. Introduction

When the availability of water is insufficient to maintain plant growth, photosynthesis, and transpiration, plants become water deficit stressed (Fan et al., 2006), a serious problem that reduces world crop production (Boyer, 1982; Vincent et al., 2005). While drought has profound direct detrimental effects against plants, including rendering otherwise arable regions less, or non-, arable, herbivorous arthropod populations and the injuries they cause can be affected by stress-related changes that occur in the plant. Moderate stress is known to heighten the nutritional value of some plants' tissues and juices, in some instances to reduce concentrations of plant defense compounds, and even to select against predators and parasitoids that otherwise help reduce pest populations to economically tolerable levels, each of which can contribute toward greater pest infestations. Sometimes the injury inflicted on water deficit stressed plants is intensified even if numbers of the pest haven't been affected, as in the instances of honeylocust spider mites, *Platytetranychus multidigituli* (Ewing), on honeylocust trees, *Gleditsia triacanthos* L. (Smitley & Peterson, 1996), and greenbug and flea beetle, *Aphtona euphorbiae* Schrank, on several different crop species (Popov et al., 2006). When the stress associated with water deficit is more severe, however, host plant suitability for utilization by arthropods declines (Mattson & Haack, 1987; Showler, 2012) because of insufficient availability of water for the pest, and from senescence and drying of the plant's tissues. As plants desiccate further, they eventually die and concerns about arthropod pest damage to that crop become moot unless the pests move from unsuitable dead plant material to vulnerable, living crops.

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Although severe water deficit stress that causes plant mortality usually renders plants useless to herbivores, chronic lower level or pulsed water deficit stress can enhance the nutritional value of plants to arthropods, resulting in selection preference, heightened populations, intensified injury to crops, and even outbreaks that affect production on area-wide scales. Twospotted spider mite, *Tetranychus urticae* Koch, populations, for example, increase on drought stressed soybeans, *Glycine max* (L.) Merrill (Klubertanz et al., 1990) and populations of the Russian wheat aphid, *Diuraphis noxia* (Morvilko), increased in nonirrigated wheat, *Triticum aestivum* L., fields as compared with fields that received irrigation (Archer et al., 1995). The cabbage aphid, *Brevicoryne brassicae* L., infested water deficit stressed rape, *Brassica napus* L., more heavily than nonstressed plants (Burgess et al., 1994; Popov et al., 2006), and greenbug, *Schizaphis graminum* (Rondani), densities were higher and more injurious to wheat stressed by drought (Dorschner et al., 1986). Water deficit stressed host plants are also known to favor the xerophilic maize leaf weevil, *Tanymecus dilaticollis* Gyllenhall (Popov et al., 2006); scolytid bark beetles infesting trees (Lorio et al., 1995); flea beetles on corn, *Zea mays* L. (Bailey, 2000); and the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), on tall fescue, *Festuca arundinacea* Schreb. (Bultman & Bell, 2003). Under circumstances where water deficit is beneficial to arthropod pests, population growth generally results in further damage to crops that have already been injured or stunted by water deficit stress itself.

Water deficit stress in plants can affect the amounts and composition of volatile compounds, and the concentrations of several kinds of nutrients beneficial to arthropod pests. Its associations with free amino acids and carbohydrates are chiefly described in this chapter because those two kinds of nutrients have been researched to an appreciable extent, permitting some conclusions to be drawn about arthropod host plant selection and levels of infestation.

2. Water deficit, host plant nutrient accumulation, and associations with phytophagous arthropods

Water deficit stress alters plant metabolism and biochemistry (Hsiao, 1973; Beck et al., 2007), and consequent changes to plant physiological processes have been reported as being factors affecting herbivorous arthropod host plant preferences, growth, and development (Mattson & Haack, 1987; Showler, 2012). Although soil dries in association with drought, evapotranspiration rates in affected plants are often maintained (Jordan & Ritchie, 1971) by elevated accumulations of free amino acids, especially proline, and other organic solutes (Janagouar et al., 1983). Osmotic stress in plants involves several interlinked molecular pathways that transmit signals and produce stress-responsive metabolites (Ingram & Bartels, 1996; Zhu, 2002), and gene transcripts associated with signaling can be up- or down-regulated minutes after stress induction (Seki et al., 2001; Showler et al., 2007). Water deficit stressed plants often have diminished osmotic potential (Labanauskas et al., 1981; Golan-Goldhirsch et al., 1989; Bussis & Heineke, 1998), heightened oxidative stress (Becana et al., 1998; Knight & Knight, 2001), and accumulations of osmolytes such as antioxidants, amino acids, carbohydrates, and inorganic ions, altering the attractiveness and nutritional value of the plant (Jones, 1991; Showler & Castro, 2010a). Reduced leaf water content relative to dry

biomass in water deficit stressed plants, in combination with the increased quantities of nutritional metabolites (White, 1984; Dubey, 1999; Ramanulu et al., 1999; Garg et al., 2001), may contribute toward the increased nutritional value of plants per unit of surface area consumed by arthropods. It is likely that arthropods can perceive cues about host plant suitability from emission of plant volatile compounds, or semiochemicals.

Chemical cues from plants play a major, perhaps decisive, role in host plant selection and utilization by herbivorous arthropods (Schur & Holdaway, 1970; Fenemore, 1980; Waladde, 1983; Burton & Schuster, 1981; Ramaswamy, 1988; Salama et al., 1984; Udayagiri & Mason, 1995). Water deficit stress in plants alters plant metabolism which can affect quantities and combinations of volatile compounds (Apelbaum & Yang, 1981; Hansen & Hitz, 1982; Zhang & Kirkham, 1990). Apple trees, *Malus domestica* Borkh., for instance, emit 29 volatile compounds, some of them in elevated amounts during water deficit stress (Ebel et al., 1995). Many phytophagous arthropods appear to respond to certain blends of volatiles (Miller & Strickler, 1984) that signal the host plant's nutritional value (Mattson & Haack, 1987; Bernays & Chapman, 1994; Showler, 2012). Increased production of volatiles (*e.g.*, ethylene, acetaldehyde, and ethanol) resulting from plant stress (Kimmerer & Kozlowski, 1982) can be attractive to some herbivorous arthropods and repellent to others (Chrominsky et al., 1982; Dunn et al., 1986; Haack & Slansky, 1987; Bernays & Chapman, 1994). Ethylene, for example, attracts the boll weevil, *Anthonomus grandis grandis* Boheman (Hedin et al., 1976), and, in many host plants it can increase susceptibility to the Egyptian cotton leafworm, *Spodoptera littoralis* Boisd. (Stotz et al., 2000), but ethylene deters the fall armyworm from corn (Harfouche et al., 2006) and the olive moth, *Prays oleae* Bern, from olive trees (Ramos et al., 2008). Forest outbreaks of many species of scolytid bark beetles (Hodger & Lorio, 1975; Wright et al., 1979; Vité et al., 1986; Ormeño et al., 2007; Branco et al., 2010) and the western spruce budworm, *Choristoneura occidentalis* Freeman, are related to amounts and kinds of host plant volatiles emitted during conditions of drought (Cates & Redak, 1988).

Once the phytophagous arthropod has found or selected the host plant, contact chemoreceptors on many are important in the acceptance or rejection of a host plant based on the presence or absence of stimulant (*e.g.*, sugars, amino acids, vitamins) or deterrent chemicals, and moisture (Dethier, 1980; Schoonhoven, 1981; Städler, 1984; Otter, 1992; Krokos et al., 2002). Free amino acids, for example, elicit electrophysiological responses from the sensillae of lepidopteran larvae (Städler, 1984; Blaney & Simmonds, 1988). Many free essential amino acids (essential for insect growth and development) accumulate in plant tissues during water deficit stress in crop plants that range from cotton to sugarcane, *Saccharum* species, to pine trees, *Pinus* species (Mattson & Haack, 1987; Showler, 2012). Amino acids were even found to be more important determinants of corn susceptibility to neonate fall armyworms than toxins or other biochemical factors (Hedin et al., 1990). Resistance against the sugarcane aphid, *Melanaphis sacchari* (Zehnter), and the yellow sugarcane aphid, *Sipha flava* (Forbes), involved absence of some free essential amino acids in resistant sugarcane varieties (Akbar et al., 2010). Free amino acids are more available for use by herbivorous arthropods because insects absorb nitrogen through the gut mostly as free amino acids or small peptides (Brodbeck & Strong, 1987). Hence, enhanced foliar nutritional value as a result of water deficit is known to be an important determinant of

neonate lepidopteran performance (Mattson, 1980; English-Loeb et al., 1997; Showler, 2001, 2012; Showler & Moran, 2003; Moran & Showler, 2005; Chen et al., 2008). In terms of water deficit stress, the mealybug *Phenacoccus herreni* Cox & Williams develops and reproduces better on drought stressed than on well watered cassava, *Manihot esculenta* Crantz, in response to greater concentrations and more nutritious combinations of free amino acids (Calatayud et al., 2002). The eldana borer, *Eldana saccharina* Walker, a stalkborer of sugarcane in Africa, prefers water deficit stressed host plants (Moyal, 1995), and the European corn borer, *Ostrinia nubilalis* (Hübner), inflicts up to twice the injury to water deficit stressed corn than to corn under conventional irrigation (Godfrey et al., 1991). Correlations were reported between elevated free amino acid concentrations in phloem sap of water deficit stressed wheat, *Triticum aestivum* L., and barley, *Hordeum vulgare* L., and population increases by the bird oat-cherry aphid (Weibull, 1987) and the cabbage aphid on *Brassica* spp. (Cole, 1997). Similarly, bark beetle outbreaks during times of drought are associated with greater concentrations of amino acids (and soluble sugars) in host plant phloem that likely contribute toward improved scolytid performance (Mattson & Haack, 1987).

In addition to elevated levels of free essential amino acids, free proline, a nonessential amino acid that accumulates in most water deficit-afflicted plants, is a feeding stimulant for many phytophagous arthropods (Mattson & Haack, 1987; Städler, 1984). Dadd (1985) reported that a number of amino acids, particularly glycine, alanine, serine, methionine, histidine, proline, and γ-aminobutyric acid, were phagostimulants to a number of insect species. Amino acids that elicited the greatest response as feeding stimulants to southwestern corn borer larvae were determined to be arginine, histidine, lysine, methionine, phenylanaline, valine (essentials), alanine, glycine, and serine (nonessentials) (Hedin et al., 1990), but not proline.

Water deficit stress has also been associated with increased concentrations of carbohydrates (which have important roles in osmotic adjustment) in many plants (Schubert et al., 1995; Kameli & Lösel, 1996; Massacci et al., 1996; Mohammadkhani & Heidari, 2008). Corn plants with elevated soluble carbohydrate concentrations were preferred by the European corn borer for oviposition (Derridj & Fiala, 1983; Derridj et al., 1986), and styloconic sensilla of larvae and adults of three noctuid species were highly responsive to sugars, especially sucrose and fructose (Blaney & Simmonds, 1988). These two sugars are known to be important feeding stimulants for both life stages (Frings & Frings, 1956; Blom, 1978), and fructose, glucose, maltose, and sucrose have been identified as phagostimulants for other insects (Bernays, 1985). Electrophysiological recordings revealed that the maxillary sensilla styloconica of fifth instar African armyworm, *Spodoptera exempta* (Walker), and the lepidopteran stalkborers *E. saccharina*, *Maruca testulalis* (Geyer), and *Chilo partellus* (Swinhoe), were stimulated by 13 different carbohydrates (Otter, 1992). In an experiment involving fall armyworm larval feeding, sucrose elicited ≥5-fold more feeding response than fructose or glucose (Hedin et al., 1990). Carbohydrates are well known as sources of energy for arthropods, and they are therefore highly important as nutrients (Nation, 2002). Studies on larval rice stem borers, for instance, showed that fructose, glucose, and sucrose are highly nutritious as compared with other carbohydrates based on their growth and development (Ishii et al., 1959; Ishii, 1971). Also, eastern spruce budworm, *Choristoneura fumiferana* Clemens, outbreaks often follow

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droughts (Mattson & Haack, 1987) because water deficit stressed trees accumulate sugar and sugar alcohols (Price, 2002).

3. Water is a nutrient, too

Water deficit affects both the availability of water, which is a nutrient itself, to herbivores as well as the nutritional quality of dietary biochemical components that accumulate as osmoprotectants or for other purposes. When herbivorous arthropods are unable to have access to sufficient amounts of wager, their populations can decline. For example, aphid populations are reduced under conditions of continued and severe host plant water deficit (Showler, 2012). Black bean aphid, *Aphis fabae* Scopali, survivorship was diminished on continuously drought stressed sugar beet, *Beta vulgaris* L., leaves (Kennedy & Booth, 1959), and reproduction and survival were negatively affected for the mustard aphid, *Lipaphis erysimi* (Kalt.) on radish, *Raphanus sativus* L. (Sidhu & Kaur, 1976); the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), on alfalfa, *Medicago sativa* L. (McMurtry, 1962); the greenbug on sorghum, *Sorghum bicolor* (L.) Moench (Michels & Undersander, 1986); the potato aphid, *Macrosiphum euphorbiae* (Thomas), on potato, *Solanum tuberosum* L. (Nguyen et al., 2007); the bird oat-cherry aphid, *Rhopalosiphum padi* (L.), on tall fescue (Bultman & Bell, 2003); and the eastern spruce gall adelgid, *Adelges abietis* (L.), on Norway spruce, *Picea abies* (L.) Karst. (Bjőrkman, 2000). The most likely cause of the host plants' unsuitability for aphids under such conditions is low turgor which reduces the ability of aphids to feed (Levitt, 1951; Wearing & Van Emden, 1967). Turgor facilitates aphid ingestion by forcing fluids out of the plant and through the aphids' stylet lumens (Kennedy & Mittler, 1953; Maltais, 1962; Auclair, 1963: Magyarosy & Mittler, 1987; Douglas & Van Emden, 2007); turgor loss reduces or curtails feeding by aphids despite their cybarial pump. This has been reported to occur for the black bean aphid on different plant hosts (Kennedy et al., 1958); the cotton aphid, *Aphis gossypii* Glover on cotton, *Gossypium hirsutum* L. (Komazaki, 1982); the greenbug on wheat (Sumner et al., 1983); and the pea aphid, *Acyrthosiphon pisum* Harris, on alfalfa (Girousse & Bournoville, 1994). Also, greater concentrations of host plant osmolytes and other biochemicals associated with drought stress increase sap viscosity which resists flow through the stylets (Douglas & Van Emden, 2007), impeding ingestion despite the enriched nutritional quality of the sap (Kennedy et al., 1958).

The greater nutritional quality of water deficit stressed plants can be offset by the condition that causes it: insufficient water. When provided with dried, ground material from water-deficit stressed tomato plants, *Lycopersicon esculentum* Mill., incorporated into a nonnutritive diet, beet armyworm, *Spodoptera exigua* (Hübner), larval growth decreased (English-Loeb et al., 1997). Cecropia moth, *Hyalophora cecropia* L., larvae reared on water deficit stressed wild cherry, *Prunus serotina* Ehrh., leaves grew more slowly than those fed on well-watered plants, but they, and beet armyworm larvae on water deficit stressed cotton leaves, consumed greater quantities of leaf tissue in order to gain access to more water, and possibly in order to supplement body water with water derived from respiration (Scriber, 1977; Showler & Moran, 2003). Under field conditions, fall armyworm; soybean looper, *Pseudoplusia inclu-*

dens (Walker); and beet armyworm larval survivorships increased and development was hastened in soybeans that were irrigated compared with dryland-grown soybeans (Huffman & Mueller, 1983). These observations suggest that soft-bodied lepidopteran larvae that live on plant surfaces exposed to the desiccating effects of direct sunlight and ambient air (unlike lepidopteran stalkboring larvae that live in moist plant interiors) are especially vulnerable to the desiccating effects of insufficient water supply.

4. Some non-nutrient-related associations of water deficit with phytophagous arthropods

Host plant selection among insects also involves visual and physical factors such as leaf shape, color, and size (Ramaswamy, 1988; Renwick & Radke, 1988; Renwick & Chew, 1994; Showler & Castro, 2010b), and both constitutive and inducible plant chemical defenses can vary in response to water deficit stress (Lombardero et al., 2000), but visual and physical cues, and defensive compounds are not considered as being nutritional for the purposes of this chapter (although defensive compounds might loosely be considered as being types of nutrients, they mostly repel, interfere with feeding, or act as toxins). Concentrations of several classes of defensive secondary compounds tend to increase in plant tissues in response to moderate drought, including terpenoids (some of which are attractants (Mattson & Haack, 1987) and alkaloids (Gershenson, 1984; Hoffmann et al., 1984; Sharpe et al., 1985; Lorio, 1986; Mattson & Haack, 1987; Showler, 2012), but intensified drought stress can lead to reductions of these compounds (Mattson and Haack, 1987). Drought can also influence predator and parasitoid guilds that affect phytophagous arthropod populations (Showler, 2012), but plant stress is not directly involved. Other mechanisms that might also contribute toward plant vulnerability to herbivorous arthropods under conditions of water deficit stress have been suggested (Mattson & Haack, 1987), including acoustical cues, detoxification of foods by drought stressed insects, and drought-induced genetic changes in arthropods, but they have not been well substantiated.

5. Multiple effects of water deficit: case study on sugarcane and the Mexican rice borer

The Mexican rice borer, *Eoreuma loftini* (Dyar), and its association with sugarcane is arguably one of the most illustrative examples of how an economically important phytophagous arthropod is affected by limited availability of water. The crambid moth is indigenous to western Mexico (Morrill, 1925; Van Zwaluwenberg, 1926) where it is a major pest of sugarcane, but it had spread by the mid 1970s to Veracruz, San Luis Potosi, and Tamaulipas in eastern Mexico (Johnson, 1984). First detected in the United States in the Lower Rio Grande Valley of Texas in 1980 (Johnson, 1981, 1984; Johnson & Van Leerdam, 1981), the pest dispersed into rice producing areas of east Texas (Browning et al., 1989; Reay-Jones et al., 2008), and in

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2008 it moved into Louisiana (Hummel et al., 2008, 2010). Because the Mexican rice borer was recently determined to prefer corn over other crop plants (Showler et al., 2011), its assumed range might be considerably underestimated (Showler & Reagan, 2012).

Eggs are mostly deposited in clusters within folds of dry sugarcane leaves, although eggs are also laid in folded green living tissue if available (Showler & Castro, 2010b). Van Leerdam et al. (1986) found 96% of the pest's eggs on the basal 80 cm of sugarcane plants where most dry leaf tissue is located. The Mexican rice borer is not so much stress-oriented as it is nutritionally-oriented in that it prefers to lay eggs on dry foliage of plants stressed by limited water and of plants growing in enriched soil (Showler & Castro, 2010a; Showler & Reagan, 2012). Water deficit stress in sugarcane plants, however, unlike over-fertilized plants, offers increased quantities of dry, folded leaf tissue per plant, contributing to the crop's vulnerability (Reay-Jones et al., 2005; Showler & Castro, 2010b). In a greenhouse no-choice cage experiment using sugarcane plants from which all dry leaf tissue was excised and removed from the cages, or placed at the bottom of the cages like a mulch, and intact (dry leaf tissue remained on the plants) sugarcane plants (controls), numbers of eggs and the degree of larval infestation was distinctly greater on the controls (Figs. 1 & 2; Showler & Castro, 2010b).

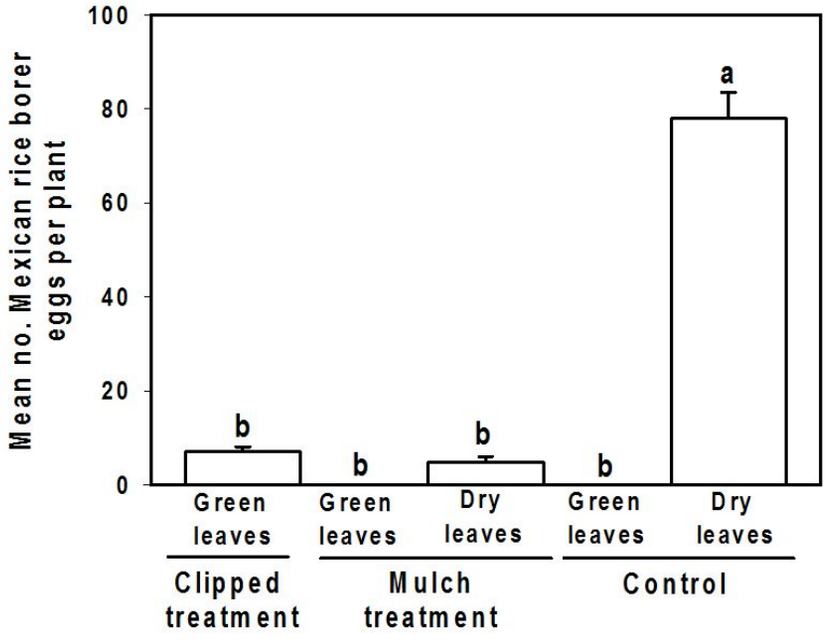


Figure 1. Mean (± SE) numbers of Mexican rice borer eggs on green and dry leaf tissue per sugarcane plant; ANOVA, Tukeys HSD ($P < 0.05$), $n = 7$ replicates per assay (Showler & Castro, 2010b).

Early instars feed on living leaf tissue, under fresh leaf sheaths, and some tunnel into the leaf midrib; later instars bore into the main stalk (Wilson, 2011). Injury from stalk tunneling results in deadheart, decreased sugar production, and stunting or lodging of stalks sometimes so severe that harvest becomes unfeasible (Johnson, 1985; Legaspi et al., 1997; Hummel et al., 2008). Tunnels within host plant stalks are packed with frass, blocking entry of predators and parasi-

toids (Hummel et al., 2008). Pupation occurs within the stalk after mature larvae make emergence holes protected with a thin window of outer plant tissue (Hummel et al., 2008). In the Lower Rio Grande Valley, a life cycle takes 30–45 days, and there are 4–6 overlapping generations per year (Johnson, 1985; Legaspi et al., 1997). Tunneling damage and the insect's prevalence has made it the key sugarcane pest of south Texas, displacing the sugarcane borer, *Diatraea saccharalis* (F.) (Van Leerdam et al., 1984; Legaspi et al., 1997).

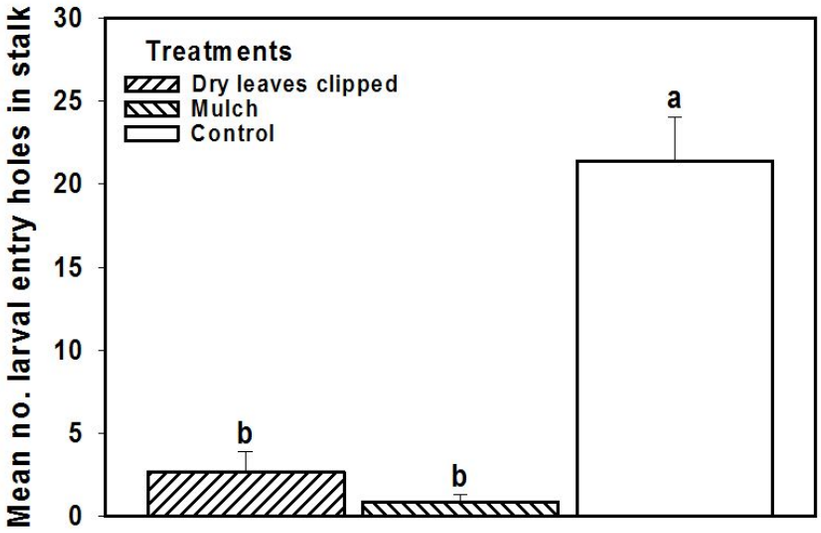


Figure 2. Mean (± SE) numbers of Mexican rice borer larval entry holes per sugarcane stalk; ANOVA, Tukeys HSD ($P < 0.05$), $n = 7$ replicates per assay (Showler & Castro, 2010b).

Approximately 20% of sugarcane internodes are injured by Mexican rice borers in south Texas, and larval entry holes also provide portals for red rot, resulting in additional loss of sugar (Van Zwaluwenberg, 1926; Osborn & Phillips, 1946; Johnson, 1985). On some varieties of sugarcane, up to 50% bored internodes have been reported (Johnson, 1981); Mexican rice borer injury results in losses of US$575 per hectare of sugarcane (Meagher et al., 1994) and US$10–20 million annually (Legaspi et al., 1997, 1999). Projected economic consequences of Mexican rice borer infestation of Louisiana includes US$220 million in sugarcane and US$45 million in rice (Reay-Jones et al., 2008). In corn, stalk boring and secondary infection by stalk rot pathogens can cause shattering, lodging, and complete collapse of stalks (Showler et al., 2011) such that by season's end >50% of stalks of susceptible varieties are destroyed (Showler, unpublished data).

A connection between irrigation practices and severity of Mexican rice borer infestation was first suggested by Meagher et al. (1993), and later studies indicated that drought stressed sugarcane is preferred for oviposition because there is more dry leaf tissue and the nutritional value, at least in terms of a number of important free amino acids, is enhanced (Tables 1 & 2) (Muquing & Ru-Kai, 1998; Reay-Jones et al., 2005, 2007; Showler & Castro, 2010a). Although severe water deficit stress of sugarcane reduces sugar production, some cultivars under moder-

ate stress accumulate sugars (Hemaprabha et al., 2004), and Mexican rice borer preference among species of host plants (Showler et al., 2011) has been associated with concentrations of fructose (Showler, unpublished data). Differences in oviposition preference were not observed on excised dry leaf tissue regardless of whether the sugarcane plant from which it originated was water deficit stressed or well watered; hence, the expression of sugarcane vulnerability or resistance appears to require the pest's ability to detect nutrients in living leaf tissue (Showler & Castro, 2010b). Although a sugarcane cultivar with some degree of resistance to the Mexican rice borer was still better protected than a susceptible variety under drought conditions, water deficit increased injury to the crop by ≈2.5-fold in each (Reay-Jones et al., 2005). Reay-Jones et al. (2003) also reported that high soil salinity, a stress factor that also heightens free amino acid accumulations in plants (Labanauskas et al., 1981; Cusido et al., 1987), increases Mexican rice borer infestations in sugarcane. Further, relatively high concentrations of organic matter incorporated into soil of the Lower Rio Grande Valley (and conventionally fertilized with nitrogen) resulted in 18% more stalk production per sugarcane stool but this effect was offset by substantial increases in Mexican rice borer infestation, causing stalk weight, length, and percentage brix reductions relative to sugarcane fertilized with conventional nitrogen fertilizer or chicken litter (Showler, unpublished data). The composted soil was associated with greater accumulations of free amino acids and fructose (Showler, unpublished data). These associations reveal that the pest is not responding simply to water deficit, but instead to nutritional enhancement of the plant whether moderated by stress or by other factors.

		Treatment[b]			
Measurement	F, P[a]	L97-128 W	CP70-321 W	L97-128 D	CP70-321 D
Water potential	1,177.41, <0.0001	9.2 ± 0.5b	10.3 ± 0.36b	30.0 ± 0.2a	30.0 ± 0.2a
No. dry leaves	25.16, <0.0001	2.0 ± 1.0b	3.8 ± 0.8b	9.5 ± 0.8a	10.3 ± 0.4a
No. egg clusters	7.26, 0.0025	0.3 ± 0.3b	0.5 ± 0.3b	2.7 ± 0.6a	2.0 ± 0.4a
No. eggs	6.93, 0.0038	4.7 ± 4.7b	5.0 ± 3.2b	48.0 ± 13.7a	29.3 ± 8.5a
No. entry holes	20.33, <0.0001	5.8 ± 0.5b	4.8 ± 0.5b	10.2 ± 1.2a	10.8 ± 1.2a
No. exit holes	12.28, 0.0003	1.7 ± 0.4b	1.5 ± 0.2b	4.7 ± 0.7a	5.0 ± 0.7a

[a] One-way ANOVA, randomized complete block design, df = 3,15.

[b] W, well watered; D, drought stressed.

Table 1. Mean (± SE) water potential (bar), and numbers of dry leaves, Mexican rice borer egg clusters, total eggs, entry holes, and exit holes per stalk of two sugarcane varieties maintained under well watered or drought stressed greenhouse conditions (Showler & Castro, 2010a)

Free amino acids[a]	*F*, *P*	L97-128 W	CP70-321 W	L97-128 D	CP70-321 D
Alanine	3.55, 0.0480	7323 ± 1858ab	3478 ± 1124b	15078 ± 1847a	7857 ± 2167ab
Arginine	6.45, 0.0075	1358 ±347a	462 ± 129b	1272 ± 188a	855 ± 132ab
Aspartic acid	1.34, 0.308	2533 ± 257	2443 ± 157	1996 ± 187	2118 ± 289
Glutamic acid	13.07, 0.0004	6 ± 6ab	149 ± 69ab	29 ± 13bc	860 ± 206a
Glycine	5.36, 0.0142	484 ± 144b	441 ± 81b	1161 ± 87a	653 ± 105ab
Histidine	11.47, 0.0008	424 ± 103b	938 ± 199b	1618 ± 172a	1995 ± 211a
Isoleucine	16.68, 0.0001	703 ± 173c	1263 ± 145b	1916 ± 332a	2858 ± 215a
Leucine	17.75, 0.0001	731 ± 150b	946 ± 127b	1939 ± 285a	2639 ± 285a
Lysine	6.15, 0.0090	708 ± 91a	328 ± 87b	639 ± 92a	514 ± 68ab
Methionine	16.18, 0.0002	384 ± 57b	228 ± 76b	1224 ± 226a	1241 ± 250a
Phenylalanine	19.73, 0.0001	239 ± 59b	229 ± 23b	523 ± 84a	1008 ± 123a
Proline	16.89, 0.0001	421 ± 70b	497 ± 128b	1674 ± 520a	4062 ± 903a
Serine	5.51, 0.0130	3612 ± 809b	4290 ± 892ab	6875 ± 737ab	8875 ± 1125a
Threonine	9.01, 0.0021	1464 ± 251b	2568 ± 484ab	2863 ± 353a	3887 ± 306a
Tyrosine	32.51, <0.0001	209 ± 24c	138 ± 7c	318 ± 31b	515 ± 58a
Valine	12.63, 0.0005	1826 ± 391b	3188 ± 470a	3871 ± 490a	5584 ± 351a
Free essential amino acids	11.02, 0.0009	7841 ± 1248b	10153 ± 1686b	15365 ± 1678a	20585 ± 1474a
Total FAAs	6.92, 0.0059	22432 ± 4034b	21592 ± 3865b	42498 ± 4143a	45528 ± 4159a

Means within each row followed by different letters are significantly different ($P < 0.05$).

[a] Cystine was detectable but not found in the samples.

[b] One-way ANOVA, randomized complete block design, df = 3, 12.

[c] W, well watered; D, drought stressed

Table 2. Mean (± SE) picomoles of free amino acid per µl of sugarcane leaf juice in two varieties, L97-128 and CP70-321, that were well watered or drought stressed (Showler & Castro, 2010a)

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In addition to water deficit stress associations with Mexican rice borer preferences for physical (*i.e.*, dry, curled leaf tissue) and nutritional factors (*i.e.*, amino acids and possibly sugar accumulations), water availability has a strong influence on abundances of a voracious predator, the red imported fire ant, *Solenopsis invicta* Buren, which has already been shown to be an efficient predator of the stalk boring moth, *D. saccharalis*, in Louisiana (Showler, 2012; Showler & Reagan, 2012). Originally from wet habitats of South America, the red imported fire ant entered the United States in 1929 and it spread throughout much of the wet southern states (Lofgren, 1986). To provide another example of the predator's effectiveness against insect pests, red imported fire ant foraging activity accounts for 58% of boll weevil mortality along the relatively wet coastal cotton-growing region of Texas (Sturm & Sterling, 1990), and red imported fire ant predation on immature boll weevils averaged 84% compared with 0.14% and 6.9% mortality caused by parasitism and desiccation, respectively (Fillman & Sterling, 1983). In the drier subtropics of south Texas, however, even in cotton with rank weed growth commonly associated with thriving red imported fire ant populations in wetter regions (Showler et al., 1989; Showler & Reagan, 1991), few or no red imported fire ants were found and boll weevil infestations were not affected by predation (Showler & Greenberg, 2003). While sugarcane in relatively dry regions, such as south Texas, is not protected by red imported fire ants, it is possible that the predator's greater abundance in the more moist sugarcane growing conditions of Louisiana will suppress Mexican rice borer populations (Showler & Reagan, 2012) despite its cryptic larval behavior.

6. Conclusion

Water deficit might initially appear to affect herbivorous arthropod populations because of a single factor, but the associations of the Mexican rice borer with water indicate a more complex relationship that can involve physical, biochemical, and ecological factors. Levels of Mexican rice borer infestation are likely influenced by low water availability in at least three ways, only one of which is directly related to the nutritional status of the crop. Drought changes many environmental conditions relative to arthropods, such as soil condition, leaf size and color, lignification of plant cell walls, secondary protective compounds, and natural enemy activity, but accumulations of nutrients, particularly free amino acids and carbohydrates, unlike the other drought-related conditions, directly result from water deficit stress to the plant. This plant stress response to water deficit influences levels of pest infestations by causing the plant emit volatile semiochemicals and by enhancing the nutritional quality of the plant. Water deficit can also make it difficult for some plant sucking insects (*e.g.*, aphids) to attain water and nutrients, and soft-bodied lepidopteran larvae living on surfaces of water deficit stressed plants ingest insufficient amounts of water to sustain themselves against desiccation despite compensating by consuming greater quantities of plant tissue. While non-nutritional factors are often important under conditions of water deficit, the nutritional status of the plant to herbivorous arthropods is directly modulated by water deficit stress, and host plant nutritional quality is arguably the most fundamental component of plant-herbivore interactions.

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