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PURPOSE

The purpose of *USGA Turfgrass and Environmental Research Online* is to effectively communicate the results of research projects funded under USGA's Turfgrass and Environmental Research Program to all who can benefit from such knowledge. Since 1983, the USGA has funded more than 290 projects at a cost of $25 million. The private, non-profit research program provides funding opportunities to university faculty interested in working on environmental and turf management problems affecting golf courses. The outstanding playing conditions of today's golf courses are a direct result of ***using science to benefit golf***.

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Physiological and Biochemical Responses of Resistant and Susceptible Buffalograsses to Chinch Bug Feeding

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SUMMARY

Researchers at the University of Nebraska have been investigating the physiological and biochemical responses of resistant and susceptible buffalograss to chinch bug feeding. Their findings include:

- The effects of western chinch bug feeding on the physiological responses of resistant ('Prestige') and susceptible ('378') buffalograsses was documented through measurements of carbon exchange rate, light and carbon assimilation (A-Ci) curves, chlorophyll fluorescence, and nonstructural carbohydrates. These studies suggest that compensatory photosynthesis takes place in 'Prestige', but not in '378'. Results from this research demonstrate that short- and long-term changes in photosynthetic compensation could be used to differentiate resistant and susceptible genotypes.
- Research also characterized protein changes in resistant and susceptible turfgrasses challenged by chinch bugs and explored the value of these changes as protein-mediated markers to screen for insect-resistant turfgrasses. These studies documented the loss of catalase activity in susceptible buffalograsses in response to chinch bug feeding, while resistant buffalograsses showed an increase in peroxidase activity. These findings suggest that an initial plant defense response to chinch bug feeding may be to elevate levels of specific oxidative enzymes, such as peroxidase, to help detoxify peroxides that accumulate in response to plant stress.
- Knowledge gained from this research will benefit golf course superintendents, sod producers, and other turfgrass managers by furnishing turfgrasses with improved resistance to chinch bugs.

Buffalograss has received considerable attention as an alternative turfgrass species because of its low maintenance requirements and excellent drought tolerance. Although few arthropods are injurious to buffalograss, the western chinch bug, *Blissus occiduus* Barber, has emerged as an important insect pest of this warm-season grass (1). Researchers at the University of Nebraska evaluated selected buffalograsses for resistance to the western chinch bug. Of the 90 buffalograss genotypes evaluated through greenhouse and field studies, four were categorized as highly resistant and 22 as moderately resistant (11, 13). Of the resistant buffalograsses studied, 'Prestige' exhibited the highest level of resistance even though it often became heavily infested with chinch bugs. Subsequent choice and no-choice studies characterized 'Prestige' as tolerant (14).

From an ecological perspective, plant tolerance to insect feeding has several advantages as a pest management tool. Unlike other management approaches, tolerance raises economic/aesthetic injury levels decreasing the likelihood of early pest management intervention and does not place selection pressure on pest populations. In spite of its advantages, the use of tolerance for pest management is limited primarily because the underlying mechanisms of the tolerance remain unclear.

The western chinch bug, *Blissus occiduus*, has emerged as an important insect pest of buffalograss.

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When developing insect-resistant turfgrasses, a thorough understanding of the underlying mechanisms is important for formulating optimal strategies for identifying and exploiting new sources of resistance. While considerable progress has been made in identifying germplasm resistant to insect pests, progress towards characterization of the physiological and biochemical mechanisms conferring the resistance has been limited. The USGA is currently funding this project focused on deciphering the role of oxidative enzymes and other proteins in the defense response of buffalograss to the western chinch bug and documenting the impact of chinch bug feeding on the plant physiology of resistant and susceptible buffalograsses.

Photosynthetic Responses

Understanding how chinch bug feeding affects the plant's physiology (e.g., carbon exchange rates and changes in non-structural carbohydrates) may help explain the physiological and biochemical mechanisms underlying plant tolerance. Gas exchange processes, such as photosynthesis, rapidly respond to external factors, so knowing how insect feeding alters gas exchange provides an immediate indication of plant stress. While a number of studies (20, 21, 22, 27) have assessed the impact of defoliating insects on carbon exchange rates, relatively few (12, 17, 24) have focused on sap-feeding insects and the possible role of changes in carbon exchange processes as a mechanism for plant tolerance to insect injury.

Plants experience different types of stress including alterations in chlorophyll content and photosynthetic activity in response to insect feeding. We documented the impact of western chinch bug feeding on the physiological responses of resistant (‘Prestige’) and susceptible ('378') buffalograsses through measurements of carbon exchange rate, light and carbon assimilation (A-Ci) curves, chlorophyll fluorescence, and non-structural carbohydrates.

Carbon exchange rates, and light and carbon assimilation curves were recorded at 5, 10, and 20 days after the introduction of chinch bugs onto resistant and susceptible buffalograsses using a portable photosynthetic system. Chlorophyll a kinetic transients were also measured at the same time intervals using a modulated chlorophyll fluorometer. Non-structural carbohydrate concentrations were quantified by determining the reducing sugar concentrations as glucose equivalents present in the plant material. The specific glucose equivalents were quantified by measuring the absorbency of Cu_2O at 600 nm by using a spectrophotometer.

Buffalograss	Days after Infestation	Mean Carbon Exchange Rates: Control	Mean Carbon Exchange Rates: Infested	% Reduction
		.........(μmol $CO_2 m^{-2} s^{-1}$).............		
Prestige	5	12.4 a	18.2 a	
378	5	18.7 a	16.5 a	11.7
Prestige	10	12.7 a	13.2 a	
378	10	11.4 a	9.1 a	20.2
Prestige	20	10.9 a	9.2 a	15.6
378	20	14.7 a	5.0 b	66.0

Means in the same row followed by the same letter are not significantly different ($P < 0.05$).

Table 1. Carbon exchange rates of resistant (‘Prestige’) and susceptible (‘378’) buffalograsses at 5, 10, and 20 days after chinch bug infestation

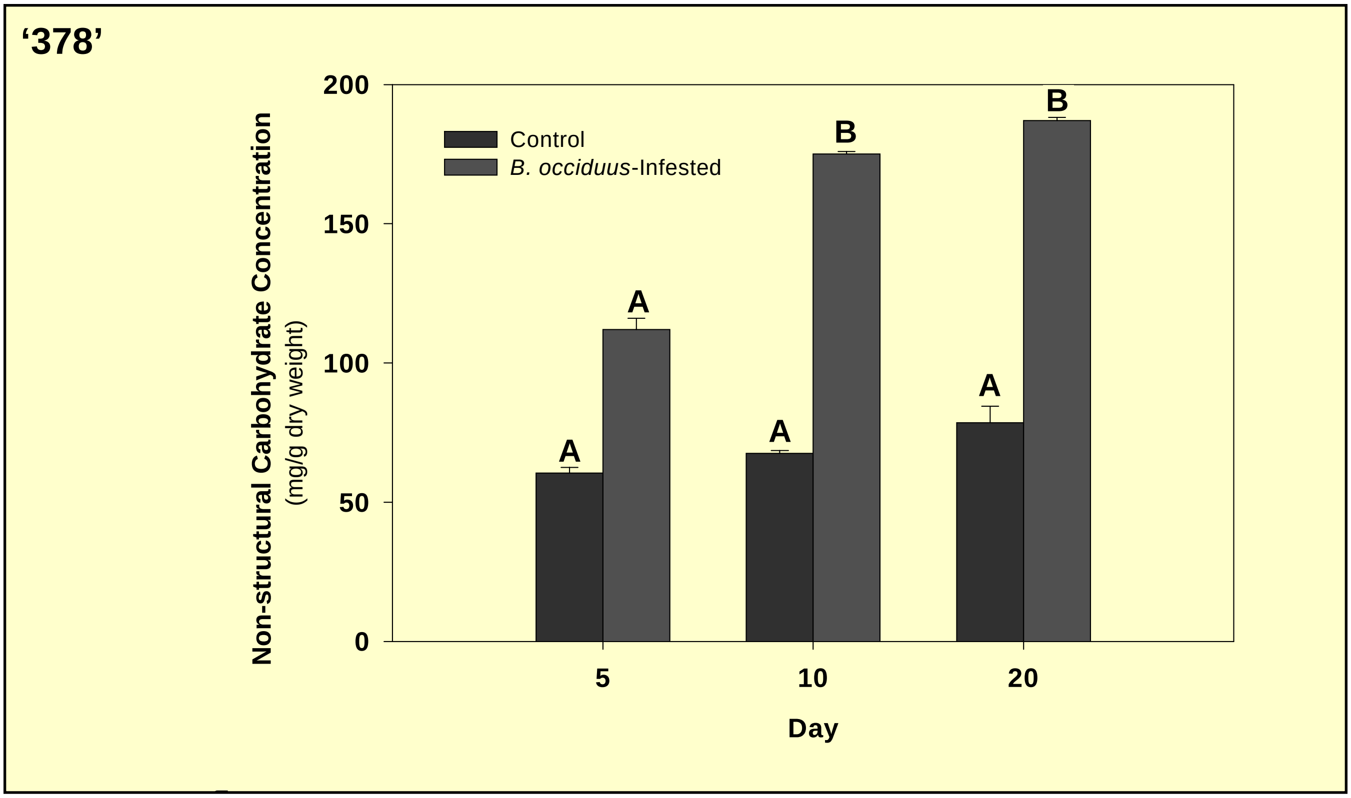

Figure 1. Non-structural carbohydrate concentrations of chinch bug-infested and non-infested susceptible buffalograss ('378') at 5, 10, and 20 days after chinch bug removal. Bars with the same letter are not significantly different ($P < 0.05$).

Results

No significant differences in carbon exchange rates were observed between infested and control plants for the susceptible buffalograss 378 at 5 and 10 days after chinch bug introduction. However, significant differences between infested and control '378' plants were detected at 20 days after chinch bug introduction (Table 1). Carbon exchange rates were similar between infested and control 'Prestige' plants at 5, 10, and 20 days after chinch bug introduction, suggesting that resistant plants can allocate energy for recovery from chinch bug injury. Susceptible plants appear unable to maintain compensatory photosynthesis and suffer substantially more tissue damage from feeding.

Significant differences in the yield of photochemical efficiency of photosystem II and the photosynthetic electron transport ratio were detected between infested and control '378' plants, whereas no significant differences in these two fluorescence parameters were observed between control and infested 'Prestige' plants. Additionally, chinch bug feeding had no significant effect on the quenching coefficients and other fluorescence parameters [minimal fluorescence (F_o), maximal fluorescence (F_m), and steady-state (F_s) and maximal steady-state fluorescence (F_{ms})] measured.

Chinch bug-infested '378' and 'Prestige' plants consistently had similar or higher levels of non-structural carbohydrates compared with their respective control plants (Figures 1 and 2). These results suggest that buffalograss plants respond to chinch bug feeding in the long-term by maintaining a greater proportion of photosynthate as non-structural carbohydrates. The susceptible buffalograss '378' is unable to maintain adequate photosynthetic rates under chinch bug pressure eventually leading to extensive plant damage.

In contrast, the resistant 'Prestige' plants apparently compensate for chinch bug injury through enhanced photosynthesis, and, as a result, sustain less injury. Chlorophyll fluorescence measurements support this hypothesis. However,

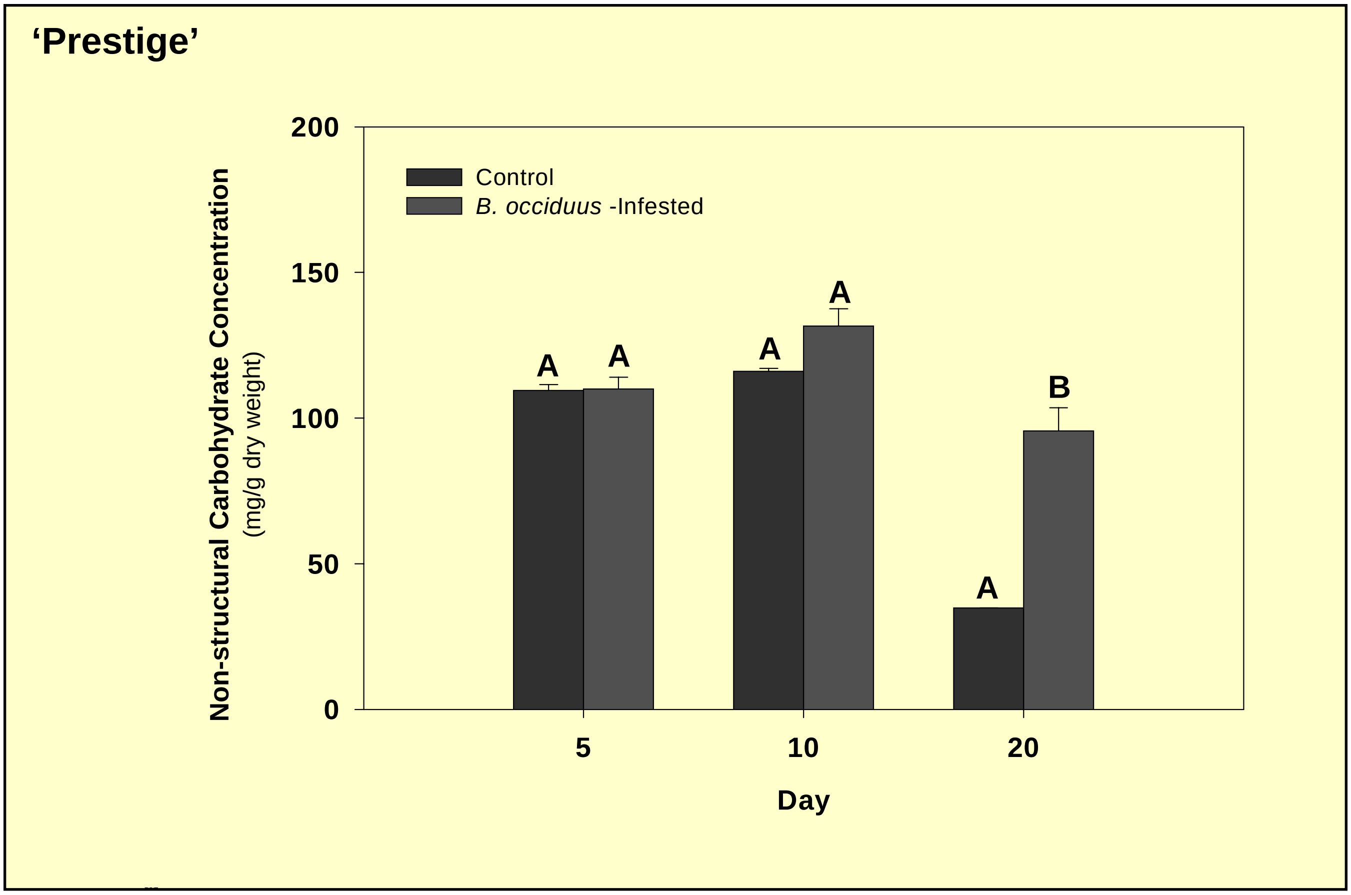

Figure 2. Non-structural carbohydrate concentrations of chinch bug-infested and non-infested resistant buffalograss ('Prestige') at 5, 10, and 20 days after chinch bug removal. Bars with the same letter are not significantly different ($P < 0.05$).

the mechanisms controlling global enhancement of non-structural carbohydrates in response to chinch bug feeding are not known. Our chlorophyll fluorescence data show significant reductions in the efficiency of the photochemical reactions of susceptible plants after exposure to chinch bugs. Reductions in the photochemical quantum yield and the electron transport rate were observed after prolonged chinch bug feeding, and corresponded with a 66% reduction in photosynthetic capacity of injured '378' plants (Table 1). These results strongly support photosynthetic compensatory mechanisms as an underlying source of chinch bug resistance in buffalograss.

The lack of chinch bug feeding effects on other fluorescence parameters (F_o, F_m, F_s, and F_{ms}) suggests that reductions in the photosynthetic capacity of infested plants is not directly related to the blockage of electron flow through the photosystem II complex. Based on the F_o and quenching coefficients, the possibility of size reductions of the quinone pool in infested plants, which would result in accumulation of active oxygen species and disrupt thylakoid membranes resulting in chlorophyll content reductions and chlorosis, can also be discounted (2).

The remaining question is, "What is causing disruption of the overall photochemical quantum yield and photosynthetic rate?" Chinch bug injury might be involved with either a modification in the photosystem II structure (e.g., detachment of the antennal chlorophyll complex from the photosystem) or with CO_2 fixation (10). Our non-structural carbohydrate data revealed an increased concentration of this reducing sugar in infested '378' plants after a few days of chinch bug feeding. This suggests the photosynthetic reductions observed in successive sampling dates may be related to end product inhibition resulting from phloem-loading and -unloading dynamics (16). It also supports the hypothesis that overall photochemical quantum yield and electron transport rates are more involved with CO_2 fixation inhibition.

A second study was conducted to investigate the ability of resistant (‘Prestige’) and susceptible (‘378’) buffalograsses to recover from chinch bug feeding. Carbon exchange rates of the resistant and susceptible buffalograsses were recorded at 3, 24, 48, and 72 hours after chinch bug removal using a portable photosynthetic system. Three types of carbon exchange measurements were performed: carbon exchange measurement (constant light and CO_2), light curves (constant CO_2 and light intensities ranging from 0 to 2,000 mol photons $m^{-2}s^{-1}$), and carbon assimilation (A-Ci) curves (constant light intensity and CO_2 concentrations ranging from 0 to 1,000 mol CO_2 mol^{-1}).

Significant differences in carbon exchange rates were detected between infested and control ‘378’ and ‘Prestige’ plants at all four evaluation times. Three hours after chinch bug removal, ‘378’ and ‘Prestige’ both exhibited carbon exchange rate reductions in response to chinch bug feeding (Table 2). Reductions in carbon exchange rates differed among the resistant and susceptible buffalograsses. At three hours after chinch bug removal, the tolerant buffalograss ‘Prestige’ showed an 11.3% reduction in activity compared to its uninfested control, whereas the chinch bug-susceptible ‘378’ exhibited a 35.5% reduction in activity when compared to its respective control. Infested ‘378’ plants continued to exhibit significant reductions in carbon exchange rates at 24, 48, and 72 hours after chinch bug removal.

Infested ‘Prestige’ plants, on the other hand, exhibited carbon exchange rates similar to their uninfested controls. In all cases, ‘378 plants’ had at least a three-fold increase in percent carbon exchange rate reduction when compared to their control plants. These results suggest the presence of compensatory photosynthesis in ‘Prestige’, but not in ‘378’.

Light response curves were accessed to provide information on the relationship between carbon exchange rates and light intensities, specifically, the photochemical efficiency of the buffalograss plants (4, 25). Light curves at 3 hours after chinch bug removal demonstrated that chinch bug feeding reduces assimilation rates at light intensities of 150 µmol photons $m^{-2}s^{-1}$ (Figure 3). Chinch bug feeding reduced carbon exchange rates for both ‘378’ and ‘Prestige’.

Buffalograss	Hours after Removal	Mean Carbon Exchange Rates Control	 Infested	% Reduction
		..........(µmol $CO_2m^{-2}s^{-1}$)..............		
Prestige	3	24.0 a	21.3 a	11.3
378	3	22.6 a	14.6 b	35.5
Prestige	24	24.6 a	23.0 a	0.07
378	24	23.1 a	17.7 b	23.4
Prestige	48	23.2 a	22.8 a	0.02
378	48	22.9 a	17.4 b	24.0
Prestige	72	22.6 a	21.1 a	0.07
378	72	21.4 a	16.8 b	21.0

Means in the same row followed by the same letter are not significantly different ($P < 0.05$).

Table 2. Carbon exchange rates of resistant (‘Prestige’) and susceptible (‘378’) buffalograsses at 3, 24, 48, and 72 hours after chinch bug removal

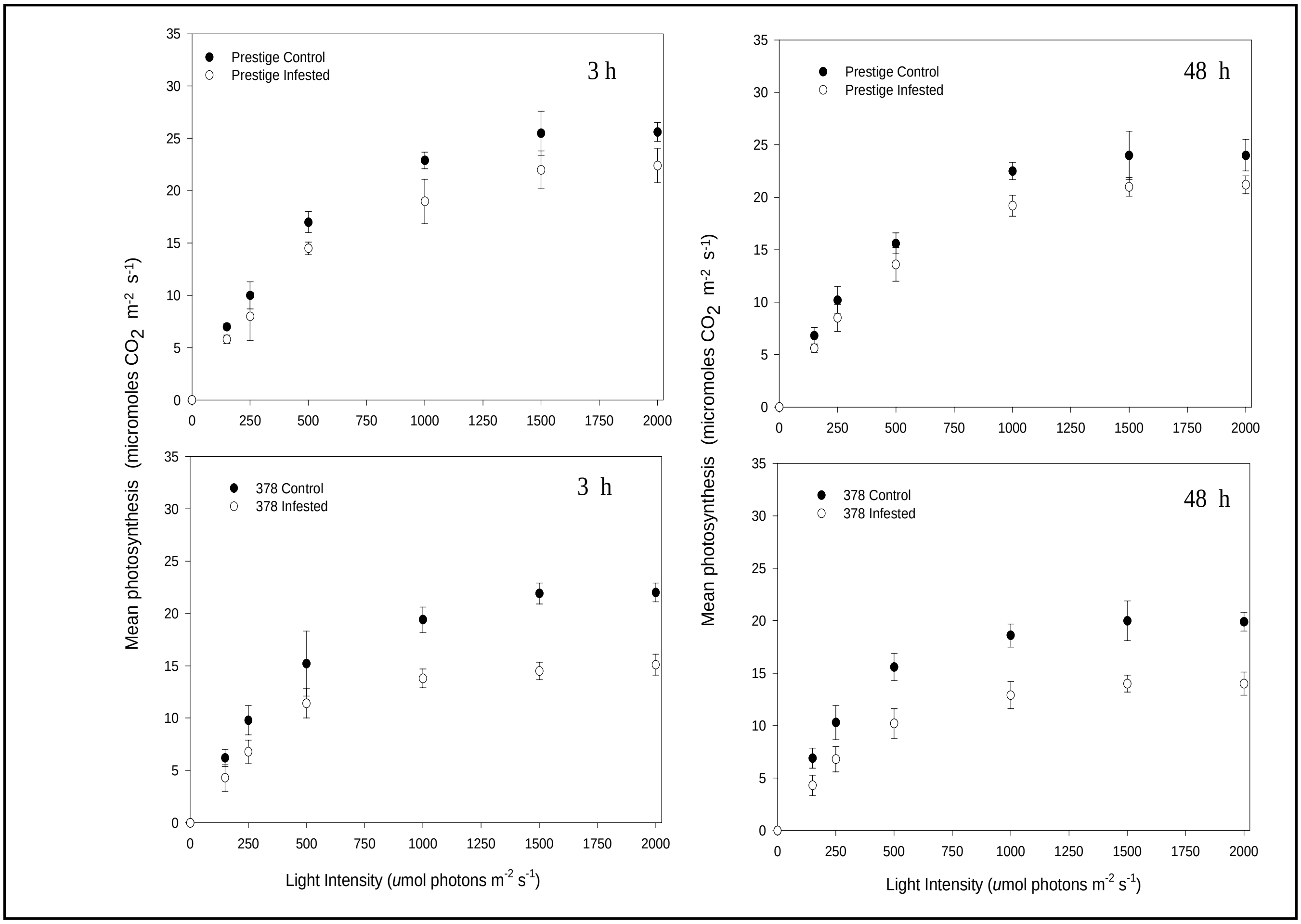

Figure 3. Relationships between different light intensities and carbon exchange rates (light curves) of buffalograsses. Carbon exchange rates were measured at 3 and 48 hours after chinch bug infestation.

However, the greatest differences in mean carbon exchange rates at the various light intensities were observed for ‘378’. Carbon exchange rates of chinch bug-infested ‘378’ plants did not exceed 15 µmol CO_2 $m^{-2}s^{-1}$ compared with 22 µmol CO_2 $m^{-2}s^{-1}$ for the control plants. Carbon exchange rates were similar for infested and control ‘Prestige’ plants at both 3 and 48 hours after chinch bug removal at the different light intensities evaluated.

At 48 hours after chinch bug removal, the greatest differences in mean carbon exchange rates at the various light intensities were observed for ‘378’ (Figure 3). These differences in carbon exchange rates between infested and control buffalograsses indicate less efficient photochemical processes in chinch bug-infested ‘378’ plants. The similarities in carbon exchange rates between infested and uninfested ‘Prestige’ plants suggest that chinch bug feeding has minimal influence on the photochemical efficiency of these resistant plants.

A-Ci curves provided information on Rubisco activity and ribulose 1, 5-bisphosphate regeneration in the dark reaction (Calvin cycle) (6). At both 24 and 72 hours after chinch bug removal, A-Ci curves were similar between infested and control ‘Prestige plants’ (Figure 4), indicating that chinch bug feeding did not alter fixation over these time intervals. Infested ‘378’ plants had lower levels of photosynthetic activity at each CO_2 concentration when compared with their uninfested controls. These reductions are consistent with photosynthetic reductions resulting from limitations in fixation. Given the absence of signficant injury effects on chlorophyll fluorescence and lack of changes in non-structural carbo-

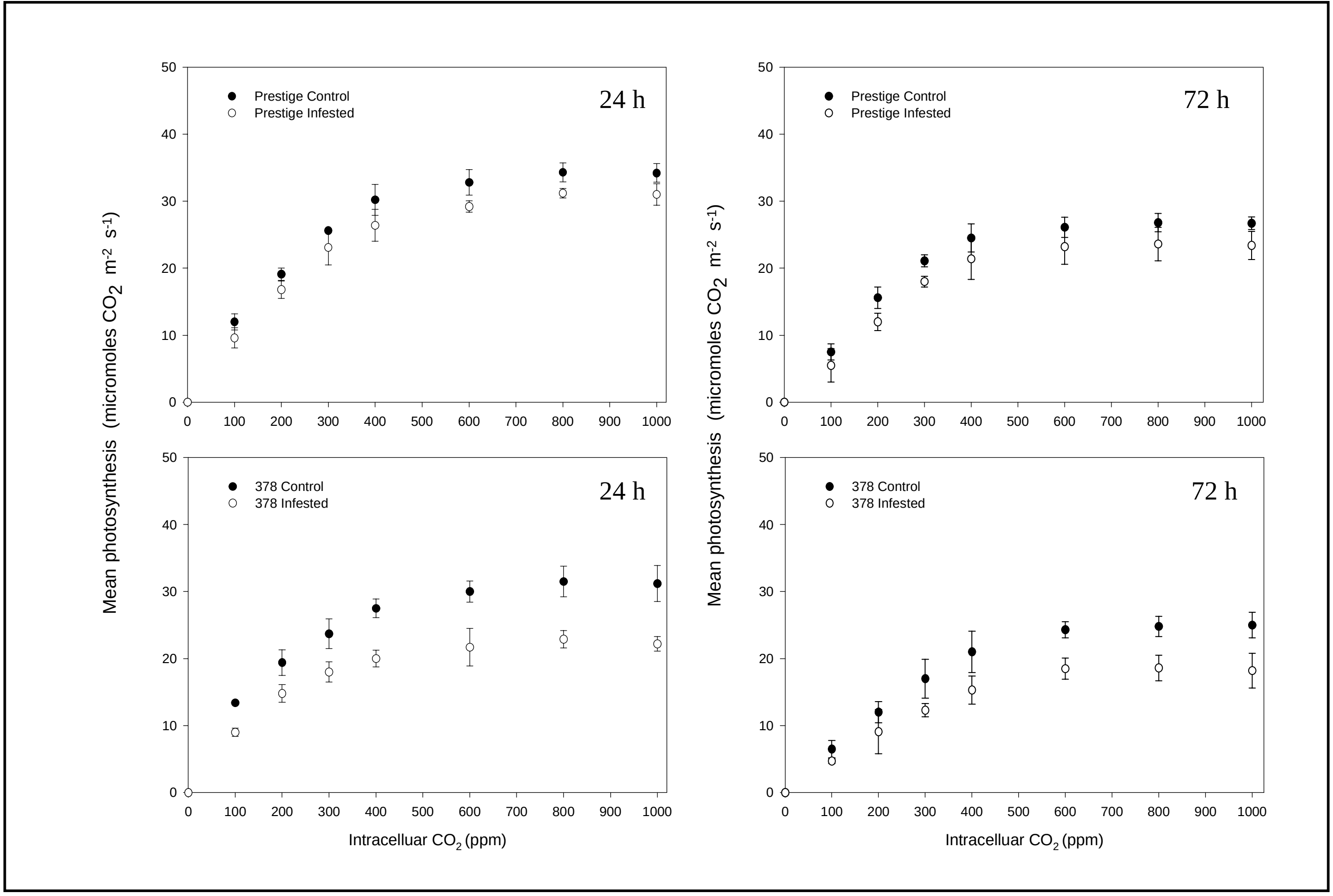

Figure 4. Relationships between intercellular CO_2 concentrations and carbon exchange rates (A-Ci curves) of buffalograsses. Carbon exchange rates were measured at 24 and 72 hours after chinch bug infestation.

hydrates with injury, these A-Ci curve results support the hypothesis that photosynthetic reductions are associated with end-product inhibition.

Our research provides the first investigation of the physiological responses of buffalograss to chinch bug feeding and demonstrate that short- and long-term changes in photosynthetic compensation can be used to differentiate resistant and susceptible genotypes. Future studies will focus on evaluating the activity levels of key enzymes involved in either synthesis or degradation of both sucrose and starch and on elucidating differences in plant responses associated with chinch bug injury.

Oxidative Enzyme Responses

A second component of our research investigated oxidative enzyme responses in resistant and susceptible buffalograsses challenged by chinch bug feeding. Plants contain several stress-related proteins, several of which are dramatically elevated or repressed under stressful conditions. Modifications in plant protein profiles and alterations in plant oxidative enzyme levels have been reported to be among a plant's first response to insect feeding (3, 7, 8, 9, 15, 18, 23, 26). However the biochemical and physiological function of these oxidative enzymes and their role in the plant's defense response remains unclear. Several researchers have speculated that oxidative enzymes may play a direct role in the plant's response to insect attack by conferring resistance through adversely affecting the development or behavior of the insect, strengthening cell walls through lignification, and/or enabling the plant to detoxify intermediate compounds produced in response to plant wounding (5, 8, 15).

Our research also characterized protein changes in chinch bug-challenged resistant and

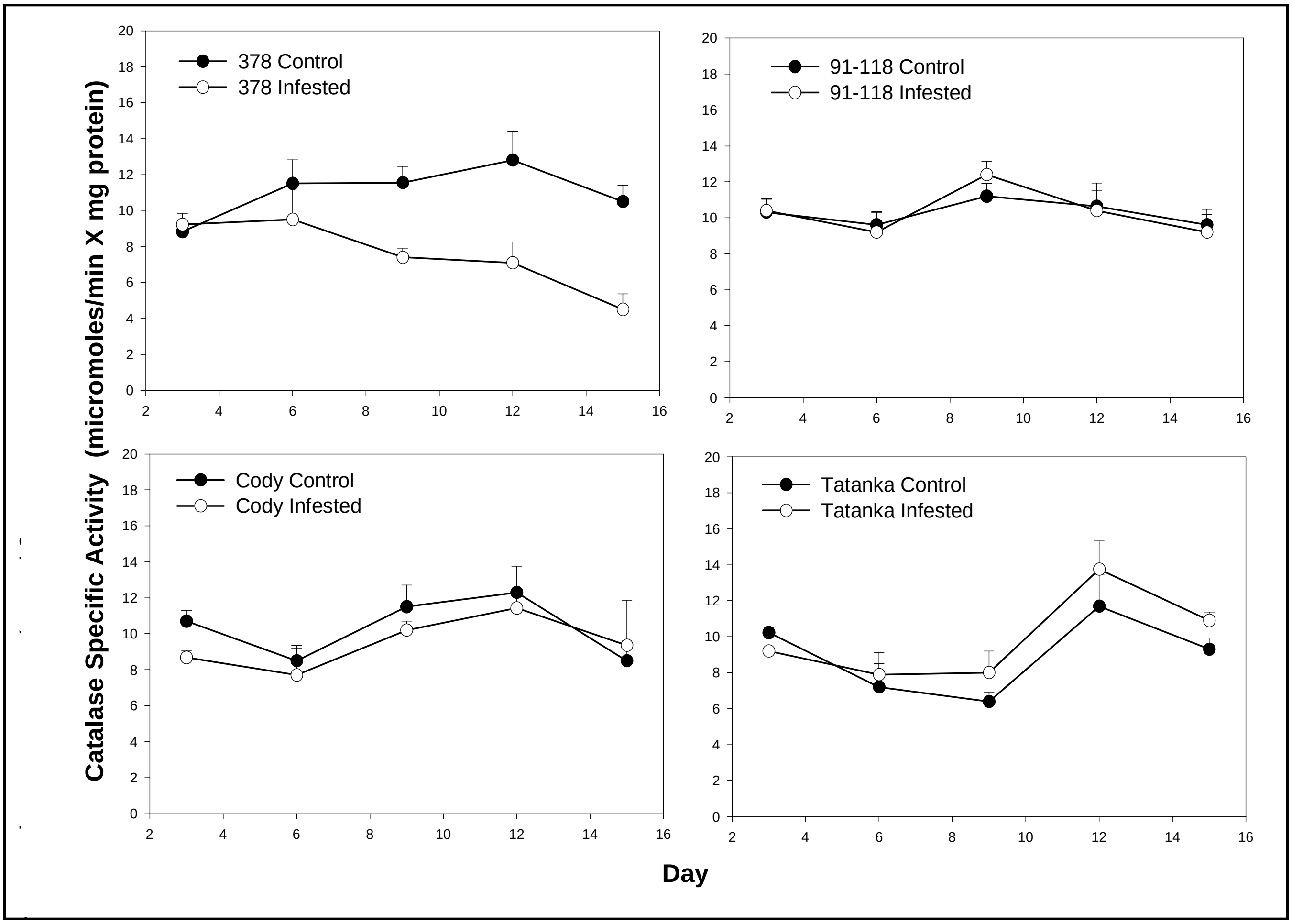

Figure 5. Catalase specific activity (µmol/min x mg protein) of buffalograsses

susceptible turfgrasses and explored the utility of these changes as protein-mediated markers for screening insect-resistant turfgrasses. The effect of chinch bug feeding on plant protein content and enzyme (peroxidase, polyphenol oxidase, and catalase) activities were examined using a spectrophotometer. Four buffalograsses, three resistant cultivars (‘Prestige’, ‘Cody’, and ‘Tatanka’) and the susceptible cultivar ‘378’ (13) were selected for protein analyses. Buffalograss samples consisting of the crown, leaf blades, and lower leaf sheaths were collected for protein analyses at 3, 6, 9, 12, and 15 days after chinch bug introduction.

Changes in catalase and peroxidase activity were observed in both resistant and susceptible buffalograsses in response to chinch bug feeding. Susceptible plants had lower levels of catalase activity when compared to their uninfested controls (Figure 5). In contrast, catalase activities of resistant plants were similar between infested and control buffalograsses throughout the study. Resistant plants had higher levels of peroxidase activity when compared to their controls, while peroxidase activity for control and infested susceptible plants remained at similar levels or were slightly lower for infested plants (Figure 6). These findings suggest that chinch bug feeding results in a reduction of catalase activity in susceptible buffalograsses, while resistant buffalograsses are able to tolerate chinch bug feeding by increasing their peroxidase activity. There were no differences in polyphenol oxidase between control and infested plants for any of the buffalograsses evaluated.

Among the enzymes examined, no differences in isozyme profiles for peroxidase and polyphenol oxidase were detected between control and infested ‘378’, ‘Prestige’, ‘Cody’, or ‘Tatanka’ plants. Gels stained for catalase identified differences in the isozyme profiles of infested

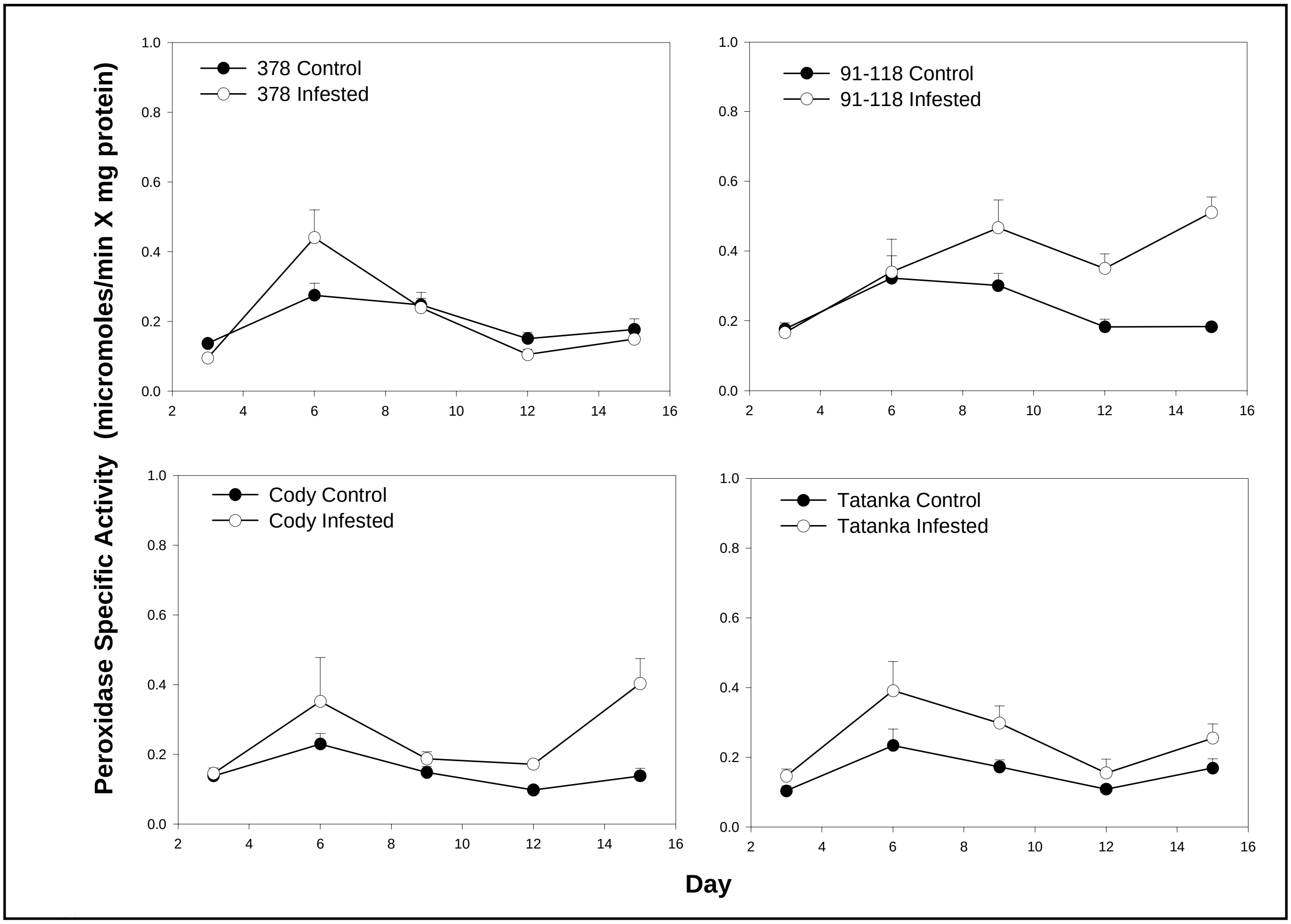

Figure 6. Peroxidase specific activity (µmol/min x mg protein) of buffalograsses

and uninfested '378' plants. However, infested and control 'Prestige', 'Cody', and 'Tatanka' plants had similar isozyme profiles. No differences in protein profiles were observed between chinch bug-infested '378', 'Prestige', 'Cody', or 'Tatanka' plants and their respective uninfested controls.

Our research offers a new perspective on plant resistance to insects and provides a model for studying insect-plant interactions. The identification of protein-mediated markers for insect resistance provides a novel approach for screening insect-resistant turfgrasses. Ultimately, these molecular markers will provide a set of tools for screening other buffalograsses for resistance to chinch bugs and furnish a starting point for characterizing additional protein-mediated markers specific to insect resistance.

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