Ecophysiological Responses of Giant Reed (Arundo donax) to Herbivory

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The effect of invasive species might be lessened if herbivores reduced transpiration and growth rates; however, simply removing photosynthetic material might not ensure that the transpiration rate of active leaf tissue decreases. We assessed whether biological control has an injurious effect on the target plant species, giant reed (\textit{Arundo donax}), by quantifying leaf photosynthetic and transpiration responses to two herbivores: an armored scale, \textit{Rhizaspidiotus donacis}, and a stem-galling wasp, \textit{Tetramesa romana}. Herbivory by a sap-feeding scale and a stem-galling wasp both separately and together, reduces the rates of leaf level physiological processes in \textit{A. donax}. The effect of the wasp increases with density and reduces photosynthesis by reducing the carboxylation rate of ribulose-1,5-bisphosphate carboxylase oxygenase, which controls CO\textsubscript{2} fixation in photosynthesis. The scale insect reduces photosynthesis by decreasing the maximum rate of electron transport, which determines how much light energy can be captured in photosynthesis. The effect of the armored scale takes approximately 5 mo after infestation, which coincides with generation time. When both insects are present at the same time, the effect of their herbivory appears additive after time for the scale to reproduce. We conclude that a combination of two herbivores can have a stronger physiological effect than one type of herbivore, likely because of their different effects on leaf function.

\textbf{Nomenclature:} Arundo scale, \textit{Rhizaspidiotus donacis} Leonardi; Arundo wasp, \textit{Tetramesa romana} Walker; Giant reed, \textit{Arundo donax} L.

\textbf{Key words:} Biological control, leaf physiology, photosynthesis, \textit{Rhizaspidiotus donacis}, \textit{Tetramesa romana}, Transpiration, Water resources effect.

Giant reed (\textit{Arundo donax} L.) has been present in parts of the southwestern United States since at least the early 19th century (Dudley 2000; Hoshovsky 1988). Currently, it is found throughout the southern half of the continental United States, from California to Maryland, as well as on the Hawaiian archipelago (Bell 1997). Because of its rapid growth rate (Dudley 2000; Perdue 1958) and ready ability to resprout (Else 1996), \textit{A. donax} is capable of forming dense, monotypic stands within a relatively short time (Bell 1997; Coffman 2007; Perdue 1958; Rieger and Kreager 1989), thus reducing the biodiversity of the riparian zone.

Losses in the abundance and richness of the aerial invertebrate communities have been positively correlated with \textit{A. donax} coverage (Herrera and Dudley 2003). Mechanisms for this reduction in the biodiversity of communities in riparian zones that have been invaded by \textit{A. donax} are not yet clearly understood. It has been suggested that \textit{A. donax} tissue is not easily digested by generalist herbivores (Miles et al. 1993a, 1993b; Spencer et al. 2005). As a result of the reduced biodiversity of the arthropod community in riparian areas dominated by \textit{A. donax}, there is less likelihood that generalist herbivores will have a significant effect on the growth and spread of \textit{A. donax}. Mature \textit{A. donax} has a mean carbon to nitrogen (C : N) ratio of 22 : 1, which is considered too high to be favorable to generalist herbivores (Spencer et al. 2007). Young shoots might be the most favorable to many herbivores, but the rapid growth rate of this species presents only a small window of palatability.

One of the foremost methods for managing \textit{A. donax} is likely to be biological control (Goolsby and Moran 2009; Moran and Goolsby 2009). However, Peterson et al. (2005) note that assessment of the efficacy of biological control agents, in terms of having an injurious effect on the target plant species, is an important aspect in the decision-making process for managing invasive species and that evaluation of the change in plant physiology in response to herbivory is an effective tool in determining the potential value of introducing additional species to a given ecosystem. Although removal of photosynthetic material

DOI: 10.1614/IPSM-D-10-00007.1

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Interpretive Summary

The results of our greenhouse study clearly demonstrate that the stem-galling wasp *T. romana* is effective at negatively affecting leaf scale physiological processes of *A. donax* when present in high densities. However, low densities of wasps had no effect on leaf physiology. This study also shows that the armored scale *R. donacis* is effective at reducing the rates of $A$ and $E_i$ given enough time. The time necessary to see a physiological effect by the scale more or less matched the time necessary for females to reproduce, suggesting a connection between that stage of life history and peak demand for resources. Moreover, these two insect herbivores seem to affect *A. donax* leaf physiology differentially because *T. romana* appears to reduce the carboxylation capacity of Rubisco, whereas *R. donacis* measurably lowers the rate of electron transport. Incorporating the time necessary for the effect of the scale to be seen, then, the combination of two herbivores can have a stronger physiological effect than one type of herbivore, likely because of their different effects on leaf function.

The objective of this study was to quantify the effect of an armored scale, *Rhizaspispidius donacis* Leonardi, and a stem-galling wasp, *Tetramesra romana* Walker, currently being considered as potential biological control agents on $A$ and $E_i$ of *A. donax* in the United States. These insects are commonly found on *A. donax* in the native range, predominately in the Mediterranean region (Goolsby and Moran 2009; Goolsby et al. 2009a). *Rhizaspispidius donacis* feeds on phloem and congregates at the base of leaf sheaths and at nodes along the stem, whereas *T. romana* forms a gall within the shoot meristem, generally near the apex, that is likely to acts as a sink for photosynthates. The effect of the armored scale was investigated at two different times after infestation and population build up, whereas the effect of the wasps was examined at two different densities. A final experiment examined the effect of these herbivores used in combination on $A$ and $E_i$.

Our secondary objective was to understand the mechanisms behind any affects on *A. donax* (Ni et al. 2008; Schroder et al. 2005) by measuring $g_s$ and intercellular CO$_2$ concentration ($C_{i}$) and through the examination of photosynthesis CO$_2$ ($A$/$C_{i}$) response curves. The shapes of these curves reveal potential decreases in carboxylation capacity or electron transport rate (Lambers et al. 1998; Larcher 2003), basic component(s) of the photosynthetic machinery in this C3 plant.

Materials and Methods

This study was conducted as a series of greenhouse experiments set up in an arthropod biological control containment facility located within Moore Air Base, operated by USDA-APHIS (Animal and Plant Health Inspection Service) in Hidalgo County, TX (26°23’39”N, 98°20’7”W), where the wasp, *T. romana*, and the scale, *R. donacis* were confined to separate greenhouses. Within each of these two greenhouses, pots containing shoots of *A. donax* were allocated to separate cages for this experiment. All pots were filled with a fertilized, uniform potting soil$^1$ and were watered twice daily. Furthermore, both greenhouses were supplemented with high-pressure sodium lighting$^2$ to provide 12 hr day of light when day length was short. Because of the mobility of *T. romana*, two identical cages, one each for the control and herbivory treatments, were established and lined with mesh$^3$ that prevented individual wasps from either entering or leaving the cages. By contrast, mobility was not a concern for *R. donacis*, so rhizomes for each of the treatments were established in large pots that were not segregated by treatment within the greenhouse. With climate control, the greenhouse with *T. romana* was kept at temperatures between 22 and 33 C, and the *R. donacis* greenhouse between 18 and 35 C.

Herbivory Trials. There were two trials for *R. donacis* one long-term (24 wk) and one short-term (14 wk). The long-
term trial held seven control shoots and seven treatment shoots with an exposure level of approximately 500 to 700 first-instar crawlers released onto each shoot, and the trial was conducted from February 26 to August 16, 2007. The short-term trial consisted of three control shoots and three treatment shoots, with an exposure level of at least 500 first-instar crawlers released onto each shoot, and the trial was run from November 24, 2007, to March 3, 2008 (Goolsby et al. 2009b). *Rhizaspidiotus donacis* females do not produce offspring until ar least 120 d when they are removed from the plant artificially, and the next generation is not found on the plant until over 160 d, when females are allowed to remain on the shoots (Moran and Goolsby 2010). Before the second trial was completed, one of the control shoots was broken during handling and was therefore not used. Leaf gas exchange survey data and CO$_2$ response curves were collected, and the parameters of interest were primarily $A_i, E_i, g_s$, and $C_i$. Further details on sampling gas exchange methodology and instrumentation are provided below.

Two experiments were conducted using *T. romana*: an initial low-herbivore density experiment followed by a high-herbivore density experiment. Within the greenhouse containing *T. romana*, during the low-density treatment experiment, two identical cages, one per treatment, housed six potted plants each (1 shoot plant$^{-1}$). The control and treatment cages experienced similar environmental conditions. Three 6-wk low-density trials were run from May to June, June to August, and October to November 2007, consisting of 12 shoots of *A. donax* per trial, each at least 1 m tall, that were grown from rhizomes of a standardized weight in a uniform mixture of potting soil. The shoots were paired by size, each pair being randomly divided between the two treatments, using height as a proxy for biomass (Spencer et al. 2006).

Approximately 20 to 25 adult female *T. romana* were released into the treatment cage at the start of each low-density trial. This level is considered well below the minimum release rate that is the goal of the biological control program. Because the generation time of *T. romana* is approximately 4 wk (~25 d as larvae, 7 d as pupae) (Moran and Goolsby 2009), leaf gas exchange survey data, as well as CO$_2$ response curves were collected as near to 4 wk from the onset of each trial as possible, using the methodology and instrumentation described below. During the final low-density trial, two shoots from the control group were broken at the main stem before gas exchange measurements could be conducted and were therefore excluded from the study.

The high-density experiment was conducted as part of a single long-term trial that maintained a *T. romana*–only treatment as described by Goolsby and Moran (2009). Roughly one-third of the *T. romana* greenhouse was blocked off with the same fine black mesh used in cage construction, and this space was further divided to separate treatment and control sections. Seven potted plants of *A. donax* were added to each section. *Tetramesa romana* were released in high density into the treatment section, with an initial minimum of 60 wasps. Seven wasps per shoot per week were added, including additional wasps for shoots that appeared in the course of the trial. This treatment was considered high density because it approximates the level of the intended future mass releases of *T. romana* at established sites of *A. donax*.

In addition to the high-density *T. romana*–only trial, a simultaneous trial added another treatment—combined herbivory by *R. donacis* in addition to the high densities of *T. romana*. This trial consisted of seven additional pots, each starting out with a single shoot, and was also located within the same *T. romana* treatment section of the greenhouse. These pots were not separated from the wasp-only high-density treatment because of the negligible mobility of *R. donacis*, even in the first-instar crawling stage. At least 500 first-instar *R. donacis* crawlers were released on the internodes of each of these shoots at the onset of the trial. Leaf gas exchange survey data and CO$_2$ response curves were recorded after 10 and 26 wk of exposure to herbivory on all 21 plants, enough time for at least two generations of *T. romana* and one generation of *R. donacis*, respectively. Details about how plants responded to herbivory (e.g., changes in stem or leaf length, numbers of galls, etc.) over the course of this and the other experiments are reported in Goolsby et al. (2009b).

**Leaf Gas Exchange Methodology.** All leaf gas exchange data were collected using a LI-6400 open-pathway system with a 6400-02B LED light source and 6400-01 CO$_2$ injector. Using the automated cooling system, leaf and block temperatures were maintained near ambient. For each shoot, only the second fully expanded leaf was used for measurements to control for the effect of leaf age (Hikosaka 2005). Sampled shoots within treatment cages were preferentially selected above galls and, when present, clusters of *R. donacis*, but sampled leaves did not have insects on them or any localized herbivory damage from either *T. romana* or *R. donacis*. All measurements were conducted between 10:30 A.M. and 2:30 P.M. central standard time with a photosynthetic photon flux density (PPFD) fixed at 1,500 μmol m$^{-2}$ s$^{-1}$ and a CO$_2$ concentration at 370 μmol mol$^{-1}$. Leaves were given a minimum of 5 min to adjust to the conditions in the cuvette. Leaf gas exchange measurements were repeated on at least two, and usually three, consecutive days to obtain an average value per shoot. Calculations of the physiological parameters $A_i, E_i, g_s$, and $C_i$ were as described by vonCaemmerer and Farquhar (1981) and adjusted for sampled leaf area.

To understand through what mechanism the two herbivores, separately and in combination, affected leaf-
level physiology, we examined the shapes of $A/C_i$ response curves for any changes in the ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco)–limited carboxylation capacity or electron transport rate (Lambers et al. 1998). These measurements were taken from one leaf for each plant in each treatment. $A/C_i$ response curves were generated at intervals of 50 μmol mol$^{-1}$ from 50 to 400 μmol mol$^{-1}$ and intervals of 100 μmol mol$^{-1}$ from 400 to 800 μmol mol$^{-1}$. Parameter values to model the maximum carboxylation rate of Rubisco ($V_{\text{cmax}}$) and the maximum rate of electron transport ($J_{\text{max}}$) were taken from Sharkey et al. (2007). The activation energy ($E_a$) of A. donax was assumed to be 60 kJ mol$^{-1}$, a value expected for a C3 plant from a warm environment (Sage 2002).

Analysis. SPSS 14.0 was used to analyze the data in which experimental units, individual potted plants, were assigned to cages by initial plant height. Data were screened for outliers and checked for normality, then one-tailed Student’s $t$ tests were used at a significance level of $\alpha = 0.05$ to compare $A_l$, $E_l$, $g_s$, and $C_i$ between treatments. When the Levene’s test for equality of variances failed ($P < 0.05$), data were compared assuming unequal variances. One-tailed tests were deemed appropriate on the basis of the hypothesis that, in all cases, physiological processes will be reduced because of the method of herbivory by each of the two insects (Larson 1998; Meyer and Whitlow 1992; Peterson 2001; Peterson et al. 2005; Raghu and Dhileepan 2005; Raghu et al. 2006), and doing so enabled us to minimize Type II errors. Separate Student’s $t$ tests were conducted for the R. donacis experiment (pooled for both trials because of low sample size), the low- and high-density T. romana trials, and the combined R. donacis/T. romana trials. Additionally, component slopes of the $A/C_i$ response curves corresponding to Rubisco-limited carboxylation capacity or electron transport rate were compared to elucidate the mechanistic differences between the way different insects elicit responses in A. donax (Macedo et al. 2005; Peterson et al. 2005).

Results and Discussion

*Rhizaspidiotus donacis* Trials. *Rhizaspidiotus donacis* effectively reduced leaf gas exchange rates in A. donax despite only minor effects on growth at the whole-plant level (Goolsby et al. 2009b). Mean $E_l$ was 40% lower in leaves of plants with R. donacis than in control plants after several months of exposure to the herbivore (Table 1). Furthermore, mean $g_s$ was 46% lower in plants subject to herbivory. These strong reductions in water use were expected because of the nature of the method of feeding by R. donacis. As plants lose sap to scale herbivory, leaves are more likely to wilt or distort (Gullan and Cranston 1994). Because scale insects feed directly on nutrients in fluids...
Table 2. The efficacy of two insect herbivores, separately and in combination, in reducing the carboxylation rate of ribulose-1,5-bisphosphate carboxylate oxygenase ($V_{cmax}$) and the rate of electron transport ($J_{max}$). Mean and percent difference (% Diff.) shown.

<table>
<thead>
<tr>
<th>Agent</th>
<th>Control</th>
<th>Treatment</th>
<th>% Diff.</th>
<th>Control</th>
<th>Treatment</th>
<th>% Diff.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rhizaspidiotus donacis</em></td>
<td>59.9</td>
<td>49.1</td>
<td>-18.0</td>
<td>78.7</td>
<td>30.9</td>
<td>-60.7</td>
</tr>
<tr>
<td><em>Tetramesa romana</em></td>
<td>63.3</td>
<td>67.7</td>
<td>7.0</td>
<td>90.7</td>
<td>97.0</td>
<td>6.9</td>
</tr>
<tr>
<td><em>T. romanal R. donacis</em></td>
<td>38.7</td>
<td>12.6</td>
<td>-67.5</td>
<td>48.5</td>
<td>24.5</td>
<td>-49.4</td>
</tr>
</tbody>
</table>

from the phloem, they can act as a sink for photosynthates that would otherwise be directed toward plant growth, maintenance, or storage (Risebrow and Dixon 1987).

We found only weak evidence of a reduction in $A_l$ (Table 1). Mean $A_l$ in leaves of plants with *R. donacis* was 32% lower than mean $A_l$ in control leaves (Table 1); however, this reduction in treated plants was not significant ($t = 1.719$, $df = 17$, $P = 0.052$). This is likely a result of the large variance between leaves in the same treatment, given the low sample size of seven per treatment. The standard error was 15.5 and 16.2% for the control and scale treatments, respectively. Meyer and Whitlow (1992) also reported no effect of a phloem-feeding insect on rates of photosynthesis ($A_l$ in goldenrod, *Solidago altissima* L., normalized by leaf weight. The aphid used in Meyer and Whitlow's study actually had no measurable effect on *A. donax* leaves exposed to herbivory was limited to 12 d.

Because *R. donacis* had not yet reproduced at the time of the measurement in the short-term trial (Moran and Goolsby 2009), we investigated whether this problem affected our results. When those short-term data were excluded from the analysis, $A_l$ differed between treatments ($t = 2.279$, $df = 12$, $P < 0.025$). Leaf responses to herbivory by *R. donacis* were apparently sensitive to time of exposure, which is consistent with other studies (Schaffer and Mason 1990). *Rhizaspidiotus donacis* might not be capable of slowing physiological processes until after they reproduce, which occurred between the 14- and 24-wk trials (Moran and Goolsby 2010). It has already been shown elsewhere that, as scale insects reach sexual maturity or some other significant stage in their life history, their demand for resources increases (Boggs 1992).

The $A_l / C_i$ response curve yields further evidence for the negative effects of 24 wk of herbivory by *R. donacis* on leaf scale physiological processes. The maximum rate of electron transport, $J_{max}$, is drastically reduced by *R. donacis* (Table 2; Figure 1), so the presence of this herbivore clearly reduced the ability to capture energy for photosynthesis when CO$_2$ availability is unlimited. The carboxylation rate, $V_{cmax}$, was also lower in the attacked plants, but the effect was smaller than for $J_{max}$. *Rhizaspidiotus donacis* may act as a sink for photosynthates that prevents *A. donax* from growing new roots that could increase nutrient uptake (Li et al. 2006). Because $J_{max}$ is controlled by the supply of nitrogen-rich Rubisco enzyme (vonCaemmerer and Farquhar 1981), a reduction in $J_{max}$ could indicate that less nitrogen is being allocated to Rubisco (Hikosaka 2004; Hikosaka and Terashima 1996).

**Tetramesa romana Trials.** Herbivory by low densities of the galling wasp *T. romana* did not reduce the rates of either of the basic physiological processes of $A_l$ or $E_l$ in leaves of *A. donax* (Table 1). Parameters $C_i$ and $g_s$ were reduced by 9 and 26%, respectively (Table 1). The decrease in $C_i$ without a significant reduction of $A_l$ could be due to some compensation on the part of *A. donax* if leaves are able to more effectively utilize the available CO$_2$ in the intercellular airspaces. This situation would only plausibly arise if stomata are closed more in leaves of plants with galls, which the reduction in $g_s$ suggests. It was unexpected, though, that such a strong reduction in $g_s$ would not lead to a similar reduction in $E_l$. It might be the case that changes occurred below the detectable limit, especially because $g_s$ is largely derived from $E_l$. Leaf temperature and atmospheric pressure also factor into the...
calculation of $g_c$, so these variables were also compared between treatments, but no differences were found (data not shown). Although this is likely an indication that the $E_t$ data have large enough variances to preclude statistical differentiation between treatments, it is possibly an indication that leaves of galled shoots are susceptible to increased water loss through parts of the leaf other than the stomata. Nonetheless, the ability of $A. donax$ to balance the fundamental physiological processes of $A_i$ and $E_t$ does not seem to be perturbed by herbivory by $T. romana$ at low density. Additionally, the $A/C_i$ response curves for the low-density treatment of $T. romana$ demonstrate that there is little effect on $A. donax$ physiology. Neither $V_{cmax}$ nor $J_{max}$ were much different in the plants experiencing herbivory (Table 2; Figure 2).

By contrast, when $T. romana$ was present in high density, the response of $A. donax$ to herbivory was quite distinct. Parameters $A_i$, $E_i$, and $g_c$ were all lower in shoots that experienced herbivory, whereas $C_i$ was not different between the two treatments (Table 1). In the high-density treatment, $A_i$, $E_i$, and $g_c$ were 19, 27, and 32% lower, respectively, compared with the same parameters in control plants. The observation that both $A_i$ and $E_i$ are markedly lower in galled shoots in the high-density treatment, in contrast with the low-density experiment, clearly indicates that the effect of herbivory on $A. donax$ by $T. romana$ is density dependent. This phenomenon has been documented for galls by cynipid wasps on leaves (Bagatto et al. 1996; Dorchin et al. 2006), but to our knowledge, this is the first study to have documented this type of relationship for stem-galling wasps. Moreover, high densities of $T. romana$ suppress leaf and stem lengths and stimulate side shoot production (Goolsby et al. 2009b).

**Combination Trials.** After 10 wk of exposure to both $R. donacis$ and high-density $T. romana$, $A_i$, $E_i$, $C_i$, and $g_c$ were not significantly different between the two treatments (Table 1). These results are in contrast with the experiment of herbivory by $T. romana$ alone at high density. In this case, clear differences in these physiological parameters were evident within 10 wk (Table 1). Because these trials occurred simultaneously and within the same enclosure space, both the $T. romana$ high-density trials (with and without $R. donacis$) experienced similar levels of herbivory, having about the same number of galls per plant (Goolsby et al. 2009b). This suggests that leaves of $A. donax$ exhibit a compensatory response when the shoot experiences multiple forms of herbivory. Another plausible explanation is that adult $T. romana$ avoided shoots with $R. donacis$ present to reduce interspecific competition and that, as time passed, there was a cumulative effect on leaf physiology that led to the difference between these treatments in leaf physiology after 10 wk.

Apparently, compensation, if any, only lasts for a limited time. Twenty-six weeks after the two herbivores were released onto $A. donax$, very strong differences between the treatments were evident. Parameters $A_i$ and $E_i$ were 67 and 42% lower in leaves of attacked shoots than in leaves of shoots without herbivores, respectively (Table 1). Conversely, $C_i$ was greater in the herbivory treatment by approximately 25%, suggesting reduced carbon assimilation; but $g_c$ was not different between treatments (Table 1). Such strong reductions in $A_i$ support earlier explanations from the effect of second-generation $R. donacis$. This observation suggests that the photosynthetic machinery in the leaves subjected to prolonged herbivory by both insects is less capable of utilizing available carbon (Meyer and Whitlow 1992).

The $A/C_i$ response of $A. donax$ after 26 wk of exposure to the two herbivores also points to a large cumulative effect of both insects, each likely acting in a different capacity. For example, the combination of the two insects demonstrated a similar reduction in $J_{max}$ as $R. donacis$ alone, suggesting that $R. donacis$ negatively affects the process of electron transport (Table 2; Figure 3). Conversely, the much greater reduction in $V_{cmax}$ with the additional presence of high densities of $T. romana$ suggests that the carboxylation capacity of Rubisco was reduced largely as a result of the presence of a large number of galls (Table 2; Figure 3). Plants are already known to reduce both $V_{cmax}$ and $J_{max}$ in the presence of herbivores (Schroder et al. 2005), so this outcome is expected. The presence of two herbivores in large numbers might also induce the production of plant secondary metabolites in $A. donax$. This could act as a further sink for energy gained from photosynthesis (Karban and Myers 1989), although this question was not explicitly addressed in this work. However, this study is only the second to document that

![Image](45x546 to 294x725)

Figure 2. CO$_2$ response of leaves of *Arundo donax* to herbivory from low densities of the stem-galling wasp *Tetranea romana*. Mean values ± standard error are given. Photosynthetic photon flux density was 1,500 μmol m$^{-2}$ s$^{-1}$.
two insect herbivores differentially affect the physiology of their host species (Peterson et al. 2005). Because neither of these two insects consume leaves, understanding the effects on leaf physiology is particularly valuable (Karban 1997).

Little research has been done on the combined herbivory by two or more phytophagous insects from different feeding guilds. We have shown that effects are not always directly additive (cf. Meyer and Whitlow 1992). It is well known that plants respond differently to these various forms of herbivory (Gavloski and Lamb 2000; Trumble et al. 1993). Our study suggests that the stem-galling wasp forms of herbivory (Gavloski and Lamb 2000; Trumble et al. 1993). Our study suggests that the stem-galling wasp reduced A. donax capacity to optimize carbon gain and water loss, but that the addition of a sap-feeding insect might stimulate temporary compensatory responses in the plant. It appears to take a comparatively long time for sap-feeding scale insects to affect leaf physiological processes, but once realized, we found additive responses between these insects from different feeding guilds on characteristics of leaf gas exchange. Arundo donax might compensate for scale insects by using stored carbon resources to produce young tissue (Boose and Holt 1999; Decruyenaere and Holt 2001), the vigor of individual plants declining only once these resources become exhausted. Further research is needed to determine whether these types of damage are sufficient to control this weed in the field.

**Sources of Materials**

1. Potting soil, Sunshine Mix #1, Sungrow Horticulture, Bellevue, WA.
2. High-pressure sodium lighting, GE Multi-Vapor 400 watt, General Electric Co., Cleveland, OH.
3. Mesh, sheer black silk, Los Dos Rios Fabric Store, McAllen, TX.
4. 6400-02B LED lights, 6400-01 CO₂ injector, Li-Cor Inc., Lincoln, NE.
5. SPSS software 14.0, IBM Company, Chicago, IL.

Acknowledgments

Funding for this project was provided by the Rio Grande Basin Initiative via the U.S. Department of Agriculture (USDA) CSREES Program, the USDA—Agricultural Research Service via the Arundo Biological Control Program, and the U.S. Department of Homeland Security via the Science and Technology Directorate. We are grateful to USDA-APHIS for use of the quarantine facility and temporary lodging. Technical assistance was provided by Ann Vacek, Kira Zhaurova, Sarah Snively, Ilia Billman, and Crystal Salinas.

**Literature Cited**


Received January 21, 2010, and approved June 1, 2010.